Winter habitat use of harbour seals *(Phoca vitulina)* fitted with Fastloc™GPS/GSM tags in two tidal bays in France

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ABSTRACT

Winter movements and habitat use of harbour seals *(Phoca vitulina)* were investigated in two tidal bays in France, at the southern limit of their species range in the Northeast Atlantic. We fitted 15 seals with Fastloc™GPS/GSM tags in the Baie du Mont-Saint-Michel *(BMSM)* and the Baie des Veys (*BDV*). Tags relayed 20.6±7.1 GPS locations per seal-day, 81% of all dives performed by the seals and 87% of haulouts, during an average tracking duration of 108±56 days. One seal travelled 380 km away from the *BMSM* but the other seals remained stationary, with 95% and 55% of at-sea locations ≤ 5 km from the haulout sites in *BMSM* and *BDV* respectively. Home range sizes were 137 and 161 km² in *BMSM* and *BDV*, and core areas' sizes, 35 and 22 km² respectively. The seals remained very coastally in both sites with 93% and 71% of at-sea locations located in the intertidal zone of *BMSM* and *BDV* respectively. Accordingly, dives were shallow with 63% and 61% of dive maximum depths <4 m and 94% and 88% <10 m (in *BMSM* and *BDV* respectively). Preferred foraging areas were located in tidal channels in *BMSM*, sometimes in the vicinity of rocks or mussel farms. In *BDV* one seal made foraging trips 10-15 km offshore but all other seals repeatedly used coastal areas, often foraging around mussel farms, shipwrecks or intertidal rocks in tidal currents. We suggest that the importance of the tides combined with local features of the topography allow seals to predict prey availability, driving their foraging strategies towards a number of specific coastal areas. These results further illustrate the behavioural plasticity of the species according to habitat and environmental conditions. Fastloc™ GPS/GSM telemetry is particularly well adapted for the study of seals' habitat use at a fine geographical and temporal scale, as long as they occasionally come close to shore within GSM coverage.

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INTRODUCTION

Harbour seals *(Phoca vitulina)* are generally considered as shallow-water foragers, moving relatively short distances from their haulout sites to their foraging grounds, compared to other pinniped species. Their foraging trips are generally within 50 or 70 km of their departure haulout site (Thompson 1993, Thompson *et al.* 1996, Thompson *et al.* 1998, Tollit *et al.* 1998, Gjertz *et al.* 2001, Lowry *et al.* 2001), but dispersal and seasonal movements may extend over several hundreds of km (Pitcher and McAllister 1981, Brown *et al.* 1983, Bjørge *et al.* 2002b, Lesage *et al.* 2004). Most frequent dive depths on foraging grounds vary between regions, but can extend to 200 m (*e.g.* Bjørge *et al.* 1995, Gjertz *et al.* 2001, Kraft *et al.* 2002, Hastings *et al.* 2004) while individual dives have been reported down to 500 m (Kolb and Norris 1982, Hastings *et al.* 2004). It has been suggested that harbour seals' optimal dive depths and foraging areas will be influenced by local bathymetric conditions, distance to haulout areas and prey availability (Thompson 1993, Tollit *et al.* 1998, Frost *et al.* 2001).

We investigated harbour seal movements and habitat use in *Baie des Veys and Baie du Mont Saint-Michel,* two tidal bays along the north-western French coast, at the southern limit of the species range in the Northeast Atlantic. About 40 and 60 seals respectively are counted on haulout sites during the peak summer season at these sites; annual pup production is about 10 individuals in each bay, and seal numbers have increased over the last decade (Elder, 2006). Local habitat available to the seals is shallow and strongly influenced by the tidal cycle. We aimed at investigating the behavioural plasticity of harbour seals in this habitat, as well as at providing local managers with useful information for the conservation of this protected species. Harbour seals are protected in France and listed in the Appendix II (species of Community interest) of the 'Habitat' Directive (92/43/EEC) which urges EU member states to set up a 'Natura 2000' network of protected areas to allow for the recovery or maintenance of the species. In France, this Natura 2000 network only includes terrestrial areas or areas lying within the tidal range, but extension to offshore areas is under progress. Intertidal areas of the 2 study sites where the seals haul out are already protected (all haulout sites included in Natura 2000 and high tide haulout sites in *BDV* also included in the National Nature Reserve of *Domaine de Beauguillot*), but the pattern of marine habitat use by the seals remains unknown and this study was also aimed at mapping this habitat use.

In order to document the foraging behaviour and habitat use by harbour seals at sea, telemetry studies have been conducted based either on VHF or Argos technologies, or occasionally combined with ultrasonic telemetry (Bjørge *et al.* 1995). At-sea locations of the seals can be obtained from triangulation of VHF transmissions (Suryan and Harvey, 1998; Thompson *et al.* 1998, Bjørge *et al.* 2002a) or by satellite telemetry usually combined with behavioural data (Gjertz *et al.* 2001, Lowry *et al.* 2001, Hastings *et al.* 2004, Smith *et al.* 2006). On marine mammals however, Argos locations are relatively sparse and their accuracy ranges from 150 to 5,000 m (68 percentile error), the latter being the most common (Vincent *et al.* 2002). In this paper, we present a new technology that combines more frequent and accurate locations (Fastloc™ GPS) with Global System for Mobile Communication (GSM), allowing more data to be transmitted than by satellite. Because harbour seals frequently return to coastal areas within the GSM coverage corridor, we expect that this innovative technology would be suitable for the study of this species. The aim here is to document the harbour seals' strategies of habitat use in these two tidal estuarine bays.

MATERIALS AND METHODS

Study area and seals capture

The study was conducted in the *Baie du Mont-Saint-Michel (BMSM)* and the *Baie des Veys (BDV)*, in Brittany and Normandy, France (Fig. 1), outside the breeding and moulting seasons. The *BMSM* is a large sandy estuarine bay (Fig. 1), 500 km^2 wide, characterized by a very high tidal range (14 m). Within 70 km of the bay the water depth is less than 50 m. The Baie des Veys is much smaller (30 km^2), also charac-

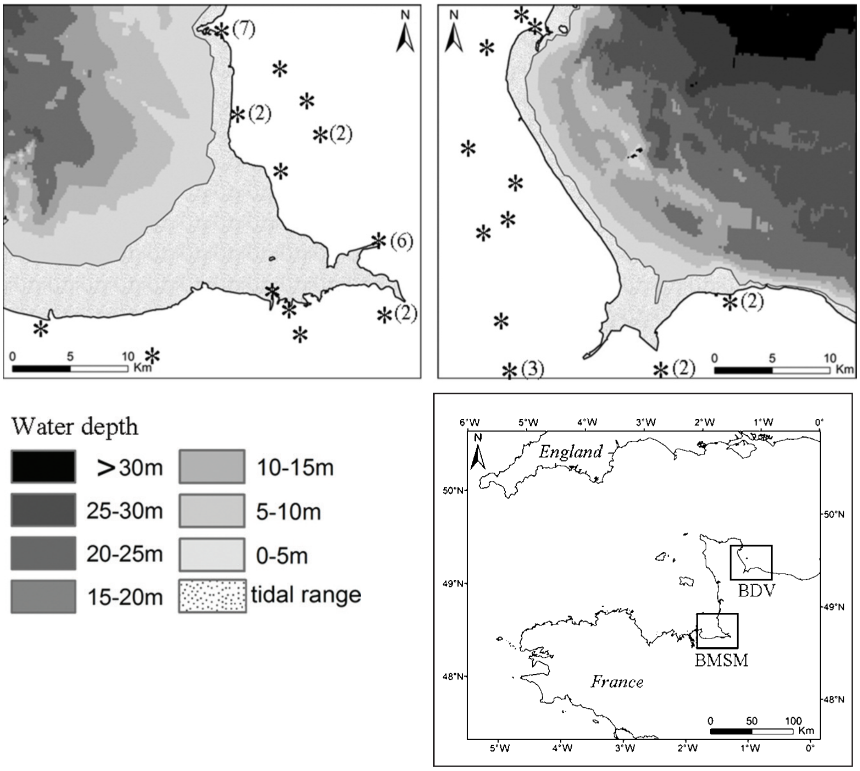

Fig. 1.
Location of the two study sites in western France: the Baie du Mont-Saint-Michel (BMSM, top left corner) and Baie des Veys (BDV, top right corner). Bathymetry is indicated (intertidal area and classes of 5 m depth below this tidal range), as well as the location of GSM relay towers (asterisks) in the vicinity of the study areas (when more than one antenna is present at a short distance, the total number of antennas is indicated in brackets). Bathymetry data provided by Ifremer (France), location of GSM relay towers by www.cartoradio.fr (update 10 February 2009).

terized by a sandy seabed and a tidal amplitude of about 9 m. Within 50 km of the bay the water depth is less than 50 m. Both bays are used for oyster or mussel farms, fisheries, navigation and recreational human activities. GSM coverage[1] is better in the *BMSM* than in the *BDV*, mostly because a GSM relay tower is located on the *Mont Saint-Michel* itself, a small peninsula 90 m high located in the bay. In *BDV* the relay towers are located further from the shore inland (Fig. 1).

Five and 3 harbour seals were captured in *BMSM* in January-March 2006 and October 2007 respectively, and 7 seals in *BDV* in October 2007. They were 9 males and 6 females, ranging from 45 - 96 kg. Seals were captured using individual hoop nets, at low tide, and chemically immobilized using Zoletil (Virbac, France). They were measured (length and girth), weighed, and flipper tagged. The GPS phone tags were glued to the fur using quick-setting epoxy glue.

Fastloc™ GPS/GSM tags and data analysis

Fastloc™ GPS/GSM tags[2] were developed by Sea Mammal Research Unit (University of St-Andrews, UK). Based on a previous generation of GSM tags for marine telemetry (McConnell *et al.* 2004), they include a Fastloc™ GPS (Wildtrack Telemetry Systems Limited), a wet-dry, pressure and temperature sensors, and a Siemens MC55/56 GSM modem. The accuracy of the Fastloc GPS is ±55 m (95 percentile error) when 5 or more satellites are used to locate the tag[3]. This GPS/GSM tag stores data (up to 6 months) until it next comes within GSM coverage, whereupon data are relayed ashore. GPS locations are attempted every 20 min, but the attempt is delayed if the seal is underwater and reduced if the seal is hauled-out. These locations were filtered following McConnell *et al.* (1992). Data transmitted include GPS pseudo-range data, start and end date/time of haulouts (starting when the sensor is dry for more than 10 min and end-

1) *www.cartoradio.fr (location of GSM Relay Towers updated on 10 February 2009).*
2) *http://www.smru.st-andrews.ac.uk/protected/downloads/GPS_Phone_Tag22.pdf*
3) *Wildtrack Telemetry Systems Limited (http://www.wildtracker.com/fastloc.htm)*

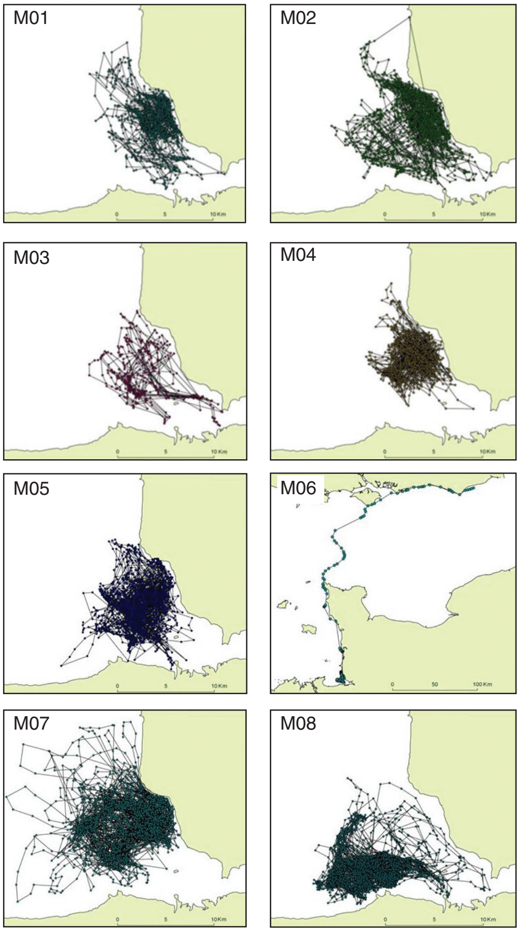

Fig. 2. *Individual tracking maps of seals fitted with GPS/GSM tags in the Baie du Mont-Saint-Michel in 2006 (seals M01 to M05) and 2007 (seals M06 to M08).*

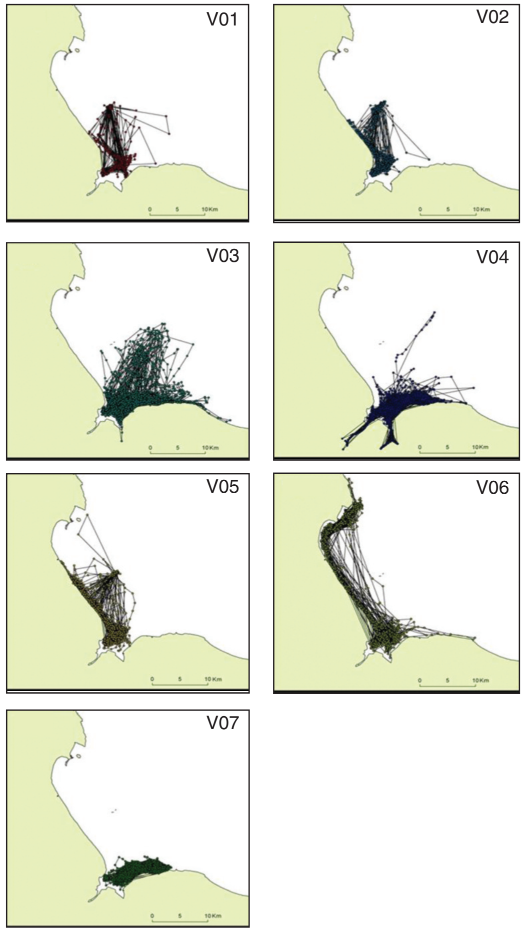

Fig. 3. Individual tracking maps of seals fitted with GPS/GSM tags in the Baie des Veys in 2007.

ing when it is wet for 40s), maximum depth, duration and 10 depth points of individual dives. A depth threshold of 1.5 m was chosen for the detection of dives, with the exception of the first two (M01 and M02) seals for which this threshold was set at 6 m. GPS locations were classified as 'haulout locations' when obtained while the seal was hauled-out, and 'at-sea locations' the rest of the time (tag in 'wet' mode). Summary records comprised the activity budget over 2-hour periods (%hauled-out, %diving and % at surface, and total number of dives performed by the seal). Individual dives were also associated with a TAD value (Time Allocation at Depth, Fedak *et al.* 2001) which summarizes the dive shape, indicating if the seal spent more time in a particular depth bin during its dive. Spatial analyses were performed on ArcGIS 9.2 (ESRI™) using the Spatial Analyst extension (ESRI™) and the Hawth's Analysis Tools for ArcGIS (Beyer, 2004). Global space use was calculated from Minimum Convex Polygons (MCPs), individual and overall (site-based) home ranges were estimated from the 95% fixed kernel polygons and "core areas" from the 50% fixed kernel polygons. Land areas were excluded from all polygons. All mean values are given ± SD. Statistical analyses were performed with Xlstats (Addinsoft).

Table 1. Summary of tracking durations, transmissions of Fastloc™ GPS locations, diving and haulout data for all seals in BMSM and BDV. * Locations were filtered following McConnell *et al.* (1992). **Diving data from seals M01 and M02 were not taken into account for calculation of the number of dives transmitted per day, due to the higher dive threshold set for these two first animals (6 m instead of 1.5 m).

		BMSM (2006)	BMSM (2007)	BMSM (2006+2007)	BDV (2007)	ALL
N seals	5	3	(5+3)	7	15	
Total tracking duration (in days)	*mean ± S.D*	60 ± 28	106 ± 75	77 ± 51	143 ± 41	**108 ± 56**
GPS locations						
Percentage of tracking days	*range (individuals)*	91-100%	100%		87-100%	**87-100%**
with GPS data transmitted	*overall %*	97%	100%	98%	94%	**96%**
Percentage of rejected locations*	*range (individuals)*	0.4-3.8%	0.7-3.4%		0.8-3.6%	**0.4-3.8%**
	overall %	2.0%	2.3%	2.2%	2.5%	**2.3%**
Number of satellites used	*range (individuals)*	5-8	5-10		5-11	**5-11**
per GPS location estimate	*mean ± S.D*	6.2 ± 1.0	6.4 ± 1.1	6.3 ± 1.1	6.5 ± 1.1	**6.4 ± 1.1**
Mean number of filtered GPS	*range (individuals)*	17.8-36.7	11.7-24.9		8.6-22.8	**8.6-36.7**
ocations per seal and per day	*mean ± S.D*	26.1 ± 7.2	18.0 ± 6.5	23.1 ± 7.7	17.8 ± 5.4	**20.6 ± 7.1**
Percentage of GPS locations	*range (individuals)*	89-97%	83-89%		80-90%	**80-97%**
obtained when seals in the water	*overall %*	95%	87%	91%	87%	**89%**
**Diving data ** **						
Percentage of dives transmitted /	*range (individuals)*	40-100%	100%		38-100%	**40-100%**
all performed by seals	*overall %*	88%	100%	93%	66%	**81%**
Number of dives transmitted	*range (individuals)*	222-242	223-377		244-366	**222-377**
per tracking day	*mean ± S.D*	247 ± 5	299 ± 77	273 ± 56	310 ± 45	**293 ± 52**
Haulouts						
Percentage of tracking days	*range (individuals)*	31-100%	100%		57-100%	**31-100%**
with haulout data transmitted	*overall %*	83%	100%	89%	85%	**87%**

RESULTS

Data recorded and tag performances

The average tracking duration was 108±56 days, with a total of 606 and 994 seal-days in *BMSM* and *BDV* respectively (Table 1). Fastloc™ GPS locations were obtained during 96% of the tracking days (98% in *BMSM* and 94% in *BDV*), and only 2.3% of these locations were rejected using the filter of McConnell *et al.* (1992) with maximum swim speed set to 2 m/s. The mean number of satellites used for the GPS location estimate was always ≥5 (6.4±1.1 satellites). Overall, 20.6±7.1 'good' (filtered) GPS locations were obtained per seal-day (23.1±7.7 and 17.8±5.4 in *BMSM* and *BDV* respectively), and 89% of these were obtained while the seals were in the water (91% and 87% in *BMSM* and *BDV* respectively). Tags transmitted over 315,000 individual dives in total, *i.e.* a mean number of 293±52 dives per day and per seal. This represents 81% of all dives performed by the animals during their tracking time (Table 1). Eighty seven percent of the haulout events were also transmitted by the tags.

Table 2. Summary data on seals' tracking duration, movements, home ranges, dive depths and activity. Mean daily tracking distances were calculated assuming straight movements between successive GPS locations. * Seals M01 and M02 had a different dive threshold (-6 m instead of -1.5 m).

SEAL	Sex	Body weight (kg)	Start date	Total duration (days)	Maximum distance rom capture site (km)	Mean daily max. distance from capture site (km)	Mean daily tracking distance (km)	Maximum dive depth (m)		Percentage of tracking time spent:			Home range		
								max. record	mean ± S.D.	at surface (0-1.5m)	diving (<-1.5m)	hauled-out	MCP (km²)	95% Kernel density (km²)	50% Kernel density (km²)
M01	F	45	30/1/06	58	8	4	17	18	8.3 ± 2.2*	84% *	3% *	13%	105	77	15
M02	F	80	30/1/06	62	10	5	22	18	9.7 ± 3.1*	84% *	4% *	12%	154	102	19
M03	M	95	27/3/06	17	8	6	19	12	3.0 ± 1.6	54%	26%	20%	91	92	23
M04	M	96	28/3/06	68	7	3	14	12	3.9 ± 2.3	43%	36%	21%	75	58	15
M05	M	94	28/3/06	95	9	5	17	14	3.2 ± 4.1	41%	30%	29%	127	81	16
M06	M	80	26/10/07	23	380	50	32	92	17.6 ± 16.9	30%	53%	17%	16,000	358	19
M06 in BMSM						*7*	*15*	*13*	*5.8 ± 2.9*	*32%*	*48%*	*20%*			
M07	M	78	27/10/07	167	13	5	15	23	5.2 ± 3.6	35%	46%	19%	259	126	32
M08	F	63	28/10/07	129	7	5	12	16	3.1 ± 2.6	61%	20%	18%	161	94	19
V01	M	76	24/10/07	140	16	10	15	31	6.3 ± 6.1	32%	48%	20%	149	55	8
V02	M	76	24/10/07	93	14	12	20	25	5.3 ± 3.9	41%	43%	16%	111	60	6
V03	M	66	24/10/07	123	22	13	28	30	6.0 ± 6.5	43%	38%	19%	286	152	26
V04	F	74	24/10/07	190	22	8	25	32	4.3 ± 4.7	48%	32%	20%	221	56	14
V05	M	75	24/10/07	101	25	13	27	26	3.9 ± 3.3	50%	32%	18%	170	75	19
V06	F	76	29/10/07	201	32	15	18	23	4.7 ± 3.8	46%	41%	13%	386	121	29
V07	F	48	29/10/07	148	12	9	18	16	3.7 ± 2.2	38%	47%	14%	43	44	16

Table 3. Mean number and duration of individual trips in BDV.

Seal			Mean duration (and S.D) of return trips from Baie des Veys to:						Mean number of trips outside Baie des Veys, per tracking day
			Baie des Veys	St- Marcouf islands	open sea	east coast	west coast	land channels	
V01	N trips		40	32	11	0	17	0	
	duration (hours):	mean ± S.D	46.3 ± 70.3	21.6 ± 13.4	1.9 ± 2.7	-	-	1.9 ± 2.6	0.43
		range	6.0 - 422.4	1.6 - 55.0	0.1 - 9.7	-		0.2 - 9.2	-
V02	N trips		35	35	0	0	31	0	0.71
	duration(hours):	mean ± S.D	17.6 ± 16.3	26.1 ± 30.4	-	-	2.0 ± 2.4	-	-
		range	2.0 - 99.6	2.0 - 133.6	-	-	0.4 - 9.5	-	-
V03	N trips		91	0	59	73	0	1	1.09
	duration (hours):	mean ± S.D	18.9 ± 19.5	-	6.7 ± 3.1	6.1 ± 6.9	-	0.5	-
		range	0.5 - 104.5	-	0.5 - 12.5	0.4 - 34.5	-	0.5	-
V04	N trips		218	0	1	147	0	88	1.24
	duration (hours):	mean ± S.D	11.1 ± 18.9	-	9.9	7.2 ± 5.6	-	3.3 ± 2.0	-
		range	0.1 - 154.5	-	9.9	0.4 - 37.5	-	0.5 - 13.0	-
V05	N trips		61	32	0	0	69	0	1.00
	duration (hours):	mean ± S.D	15.0 ± 13.3	18.4 ± 14.6	-	-	6.7 ± 8.2	-	-
		range	2.2 - 98.5	1.1 - 58.4	-	-	0.5 - 36.0	-	-
V06	N trips		48	0	6	0	41	0	0.23
	duration (hours):	mean ± S.D	43.6 ± 85.1	-	4.0 ± 4.4	-	44.0 ± 70.0	-	-
		range	1.4 - 551.0	-	0.4 - 12.0	-	0.5 - 426.0	-	-
V07	N trips		116	0	0	117	0	0	0.79
	duration (hours):	mean ± S.D	8.6 ± 8.2	-	-	-	11.7 ± 5.4	-	-
		range	0.3 - 60.5	-	-	-	0.5 - 34.9	-	-

Individual movements and home ranges

Seven seals out of 8 captured in the *BMSM* remained in the bay during their tracking (Fig. 2). One adult male (M06) left the bay and crossed the English Channel within 27 hours, then moving eastwards along the south coast of England until the GPS stopped 2 days later. This seal travelled at least 380 km from its capture site, while all the others remained within a maximum distance of 7-13 km (Table 2). M06 was resighted in *BMSM* in the following spring thanks to photo-identification (G. Gautier, *unpublished data*). Resighting data was also available from previous photographs of this seal in the *BMSM*, observed during summers before the telemetry study. Home ranges were variable among individuals: 95% fixed kernel densities varied from 58 to 126 km² (358 km² for M06 with all locations outside the bay included), and core areas (50% fixed kernel densities) varied from 15 to 23 km². These home range sizes were not significantly correlated to the number of locations obtained (Pearson, p=0.668 and p=0.780, R^2=0.016 and R^2=0.007 for 95% and 50% kernel densities respectively). The high number of GPS locations allowed us to estimate the minimum distance covered by the seals during their movements at a fine scale, by summing the distances between successive locations (mean daily tracking distance, Table 2): seals moved 12-22 km/ day on average in *BMSM*, excepting M06 which travelled further (115 km/day across the English Channel, and 62 km/day along the English coast). There was no significant correlation between the mean number of GPS locations and the mean daily tracking distance, including or excluding M06 (Pearson, p=0.553 and p=0.074, R^2=0.062 and R^2=0.504 respectively).

All seals captured in *BDV* moved out of the bay, which is much smaller than the *BMSM* (Fig. 3). Three of them moved to the *Saint-Marcouf islands* (about 12 km north of the *BDV*); they made 32 to 35 return trips to this small archipelago during their tracking time, and these trips' duration were 18.4±14.6 to 26.1±13.4 hours on average (Table 3). All seals frequently moved along the east or west mainland coast from the bay, one seal spent a significant proportion of its time in the inland channels (V04) and only one made frequent trips further offshore, up to 15 km north of the east coast (Fig. 3). All these trips were shorter than those to the *Saint-Marcouf islands* (2 to 12 hours on average), with the exception of the long trips of seal V06 along the west coast, up to 37 km away from the *BDV*, that lasted 44.0±70.0 hours on average (Table 2). The maximum distance travelled from the capture site varied among individuals (12-32 km; Table 2), but was not correlated with tracking duration (Pearson, p=0.308, R^2=0.205). Seals in the *BDV* moved a minimum distance of 15-28 km per day on average (Table 2), with no significant correlation with the mean daily number of GPS locations (Pearson, p=0.81, R^2=0.488). Individual home ranges varied from 44 to 152 km² (95% fixed kernel densities) and core home ranges varied from 6 to 29 km² (Table 2).

Terrestrial and marine habitat use

Overall, seals spent 18% of their tracking time hauled-out, 43% in the water 'at surface' and 38% diving (Table 2, M01 and M02 not taken into account for the calculation of the diving time due to the different dive threshold used for these 2 individuals). Seals hauled-out during 69 to 95% of the tracking days in *BMSM*, and 64 to 96% of the days from *BDV* (81% on average). The percentage of time spent hauled-out during the whole tracking duration varied from 12 - 29% among seals in *BMSM*, and from 13 - 20% in *BDV* (Table 2). There was no significant difference between sites (Mann-Whitney, p=0.694). In *BMSM*, all seals hauled-out in the bay along tidal channels emerging at falling or low tide (Fig. 4). In *BDV*, all seals hauled-out in the bay, either on high-tide or low-tide haulout sites; 2 seals also hauled-out in the *Saint-Marcouf islands* and 2 others hauled-out in the inland channels. These alternative haulout sites only represented 4.2% of all haulout events recorded however, all others occurring in the *BDV*.

The maximum dive depth recorded was 92 m, however only one seal (M06) dived deeper than 32 meters (while crossing the English Channel). Overall, 94% and 88% of the seals' dives did not exceed 10 m and 63% and 61% did not exceed 4 m, in *BMSM* and *BDV* respectively (Table 4). Maximum dive depths were shallow and mainly corresponded to the local depth of water: 83% and 67% of all dives were located in the intertidal area of *BMSM* and *BDV* respectively. Only 1% and 13% respectively occurred in areas of water depths greater than 5 m over the flats (which means a maximum water depth of about 19 m in *BMSM* and 14 m in *BDV*, at highest tides). 94% of dive durations were ≤5 minutes and 77% ≤3 minutes. We analyzed the proportion of V-shaped (0.4<TAD<0.6) and U-shaped (TAD>0.8) dives in the different areas visited by the seals. In the tidal range of *BMSM*, we obtained 31% of V-shape dives and 29% of U-shaped dives. These proportions were significantly different from the 14% of V-shaped and 60% of U-shaped dives recorded outside this tidal range (Z test, $p<0.0001$ for both V- and U-shaped dives; data from M06 away from the *BMSM* excluded). For *BDV* seals, we distinguished dives performed in the *BDV* itself ('bay'), those in the tidal range outside the bay ('tidal', including islands) and those further offshore ('offshore'). Seals spent 41%, 47% and 12% of their time in these 3 areas respectively. The proportion of V-shaped dives was 37% in the bay, 30% in the 'tidal areas' and 14% 'offshore'. All these proportions were significantly different between areas (Z test, $p<0.0001$ in all cases). The proportion of U-shaped dives was 24% in the bay, 27% in the 'tidal areas' and 51% 'at sea'. Again these proportions were significantly different between areas (Z test, $p<0.0001$ in all cases).

In *BMSM*, the 95% fixed kernel density home range was 146 km² for all locations and 137 km² for at-sea locations only. The core area (50% fixed kernel home range) was 40 and 35 km² respectively. The core area of the tracked seals coincided with tidal channels where they hauled-out at low tide, along the northern coast of the bay and in the southwest of the bay (Fig. 4). The general home range was also extended to the seaward end of the main channel. Apart from areas containing mussel farms and a rock shelf in the south-western part of the bay, habitat use was generally over a sandy seabed. Ninety five percent of all at-sea locations were within 5 km of the haulout locations (Table 4). In *BDV*, the 95% fixed kernel density home range was 184 km² for all locations and 161 km² for at-sea locations only. The core area (50% fixed kernel home range) was 25 and 22 km² respectively. The core areas of the tracked seals were located in the *BDV*, where seals hauled-out most regularly, and the *Saint-Marcouf islands*, where 3 seals made regular trips and occasionally hauled-out (Fig. 4). The general home range was extended along the mainland coast west and east of the *BDV,* as well as the open sea between the coast and islands, and the offshore waters 10 to 15 km north of the *BDV*. Fifty five percent of at-sea locations were ≤5 km from the haulout sites (Table 4). When moving eastwards or westwards from the *BDV*, the seals remained coastally and swam between the beach and the mussel farms at high tide, and just offshore of the farms at low tide. Most locations further offshore corresponded to seals travelling to the *Saint-Marcouf islands*, while some narrow concentrations of GPS locations coincided with the location of a shipwreck. Only one seal (V03) made regular trips at sea away from the coast. In the *Saint-Marcouf islands*, the 3 seals concentrated diving activity in localised hot spots (Fig. 5). Only seal V02 hauled-out regularly on the islands during its trips there; seal V05 hauled-out only twice whilst seal V01 never hauled-out in the islands, despite its 33 trips there (Table 3). The high use close to the main island, in the northeast corner of the map, is close to the main haulout site used by V05. Other highly used areas correspond to intertidal rocks surrounded by strong tidal currents (Fig. 5).

DISCUSSION

This study constitutes the first telemetry study on wild harbour seals in France. The Fastloc™ GPS/GSM tag technology provided the necessary accuracy and frequency of data for the scale of movements shown by the tagged seals.

Fastloc™ GPS/GSM tags performance
Tags transmitted data for 108±56 days on average, which is close to the tracking duration of harbour seals obtained from satellite-linked transmitters (Lowry *et al.* 2001, Smith *et al.* 2006). Tracking duration was however twice as long in 2007 as in 2006, after the first deployment of Fastloc™ GPS/GSM tag prototypes (132±52 and 60±28 days respectively).

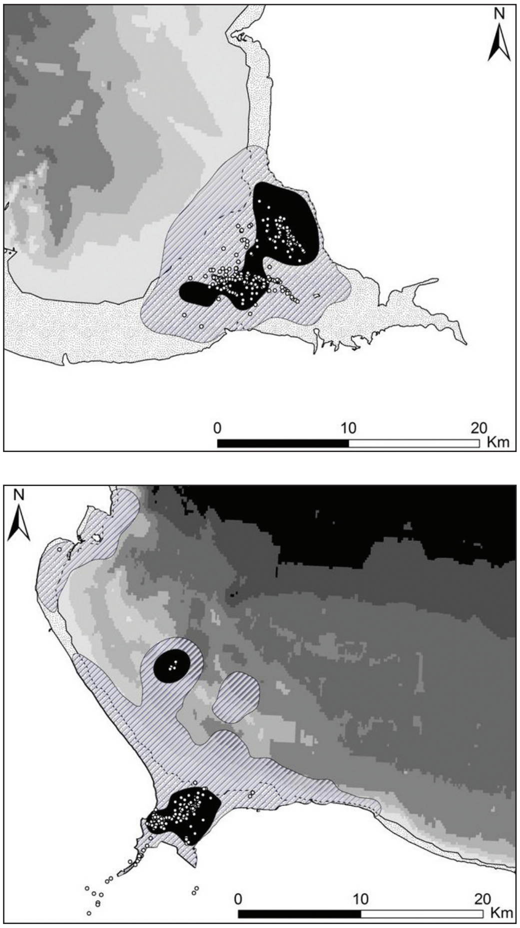

Fig. 4. Habitat use and home ranges of harbour seals tracked in BMSM (top) and BDV (below). Haulout locations (white dots) are shown as well as 95% fixed kernel densities (dashed lines area) and 50% fixed kernel densities (black areas) of at-seal locations from the tracked seals. See Fig. 1 for the legend of bathymetry.

Fastloc™ GPS locations were obtained on 96% of the tracking days, and only 2.3% of these were rejected by the filtering algorithm (McConnell *et al.* 1992). This is far better than for Argos locations: Frost *et al.* (2001) rejected 36% of the Argos locations obtained while tracking harbour seals in Prince William Sound (Alaska), while we rejected 21% of the Argos locations while tracking grey seals at the same latitude of this study sites (Vincent *et al.* 2005). The total number of filtered GPS locations obtained was high, averaging 20.6±7.1 locations per seal-day. Again, this far exceeds the number of Argos locations reported in the literature (*i.e.* 2 to 4.5 locations per harbour seal-day reported by Lowry *et al.* 2001, and Smith *et al.* 2006, 6.6 locations per grey seal-day reported in Vincent *et al.* 2005). Eighty nine percent of these locations were obtained while the seals were in the water, demonstrating the value of the Fastloc™ GPS system in marine mammal tracking. In addition to their high number, the accuracy of the locations is also greatly enhanced compared to the Argos system. This accuracy was not tested in the present study but the number of satellites used for the estimation of GPS location was always ≥5 (the minimum number of satellites required for the expected accuracy of ±55 m, Wildtrack Telemetry Systems Limited), and seal locations obtained in the land channels during this study suggest that this accuracy falls within the channels' width (35 to 70 m). The accuracy of the Fastloc GPS™ combined with the high amount of data transmission allowed by the GSM communication constitute a unique opportunity to get up to one precise location per seal per hour, over several months of tracking. In addition to locations, tags transmitted 87% of all haulout events, and 81% of all dives performed by the seals. For each individual dive, 10 depth points and the TAD index were provided in addition to duration and maximum depth. The amount and degree of detail of diving data transmitted by these tags far exceed those obtained from Satellite-Linked Depth Recorders (SLDR, *i.e.* Frost *et al.* 2001, Hastings *et al.* 2004) and approaches the quality of datasets obtained from Time Depth Recorders (TDRs), though not as detailed at the individual dive scale (*e.g.* Lesage *et al.* 1999, Baechler *et al.* 2002). We observed a longer delay between successive data transmissions in *BDV* than in *BMSM*, which can probably be explained by the greater distance between the seals' haulout sites and the GSM relay towers in *BDV* than in *BMSM* (cf. Fig. 1). The Fastloc™ GPS/GSM telemetry system seems particularly well adapted for the study of seals' habitat use at a fine geographical and temporal scale, as long as they occasionally come within GSM coverage.

Harbour seals habitat use

We tracked harbour seals during winter, outside the breeding and moulting period. Seals spent

Table 4. Summary data of harbour seals' habitat use and diving behaviour in BMSM and BDV.

		BMSM	BDV
% at-sea locations within 5 km of main haulout sites		95%	55%
% at-sea locations in tidal range		93%	71%
Home ranges (all seals) estimated	MCP (km²)	305	539
from ALL locations	95% Kernel (km²)	146	184
	50% kernel (km²)	40	25
Home ranges (all seals) estimated	MCP (km²)	303	537
from AT SEA locations	95% Kernel (km²)	137	161
	50% kernel (km²)	35	22
% of time spent hauled-out by the seals		19%	17%
% of dives occurring in tidal range		83%	67%
% of dives occurring above sea-floor below 5m over the flats		1%	13%
% maximum dive depth <4m		63%	61%
% maximum dive depth <10m		94%	88%

82% of their time in the water (81% in *BMSM* and 83% in *BDV* on average), which is similar to the proportion of winter time spent in the water reported by Kraft *et al.* (2002), and slightly higher than the 68-75% reported by Frost *et al.* (2001) and Hastings *et al.* (2004). It is not possible to compare the proportion of time spent diving between our study and the literature, because the dive threshold we used was lower than those usually applied. Most authors do not consider dives shallower than 4 m in their analyses, mainly due to the resolution of the instruments (Bowen *et al.* 1999, Frost *et al.* 2001, Gjertz *et al.* 2001, Baechler *et al.* 2002, Hastings *et al.* 2004). However, Lesage *et al.* (1999) set this threshold at 2 m and reported that 54% of the harbour seals' dives in the St. Lawrence estuary were shallower than 4 m, and that 40% of the feeding events monitored from stomach temperature were recorded in these shallow dives. In our study the threshold was set at 1.5 m and we obtained 62% of dives shallower than 4 m (63% in *BMSM*, 61% in *BDV*). This result is not surprising given that seals spent most of their time in intertidal habitat (93% in *BMSM* and 71% in *BDV*), even if the tidal amplitude is high in these two areas (14 and 9 m respectively).

Interpreting the behaviour of the seals from such shallow dives in shallow waters is challenging. Most if not all studies reported that harbour seals, like many other pinnipeds, make U-shaped dives to the sea floor when they forage (Bjørge *et al.* 1995, Tollit *et al.* 1998, Lesage *et al.* 1999, Baechler *et al.* 2002), even if several authors suggested that other dives (like V-shaped dives) might also correspond, less frequently, to foraging (Lesage *et al.* 1999). We assume a large proportion of dives were close to the sea bed in our study, given the shallow depths available in the study areas and dive depths recorded accordingly. It would be necessary however to model the tide height at given dive times according to precise locations to have an accurate estimation of the proportion of dives to the seafloor. In *BMSM*, we obtained more U-shaped dives in the deepest part of the bay, outside the tidal range (60% of U-shaped dives against 14% in the intertidal area), but these dives only represented 17% of all dives recorded. In *BDV*, this percentage of U-shaped dives was also much higher offshore (51%) than in the intertidal area (24 to 27%), and they represented 29% of all dives recorded. It seems clear that seals probably do not only forage in these "deepest" areas (not exceeding 10 or 15 m over the flats here). In *BMSM*, the majority

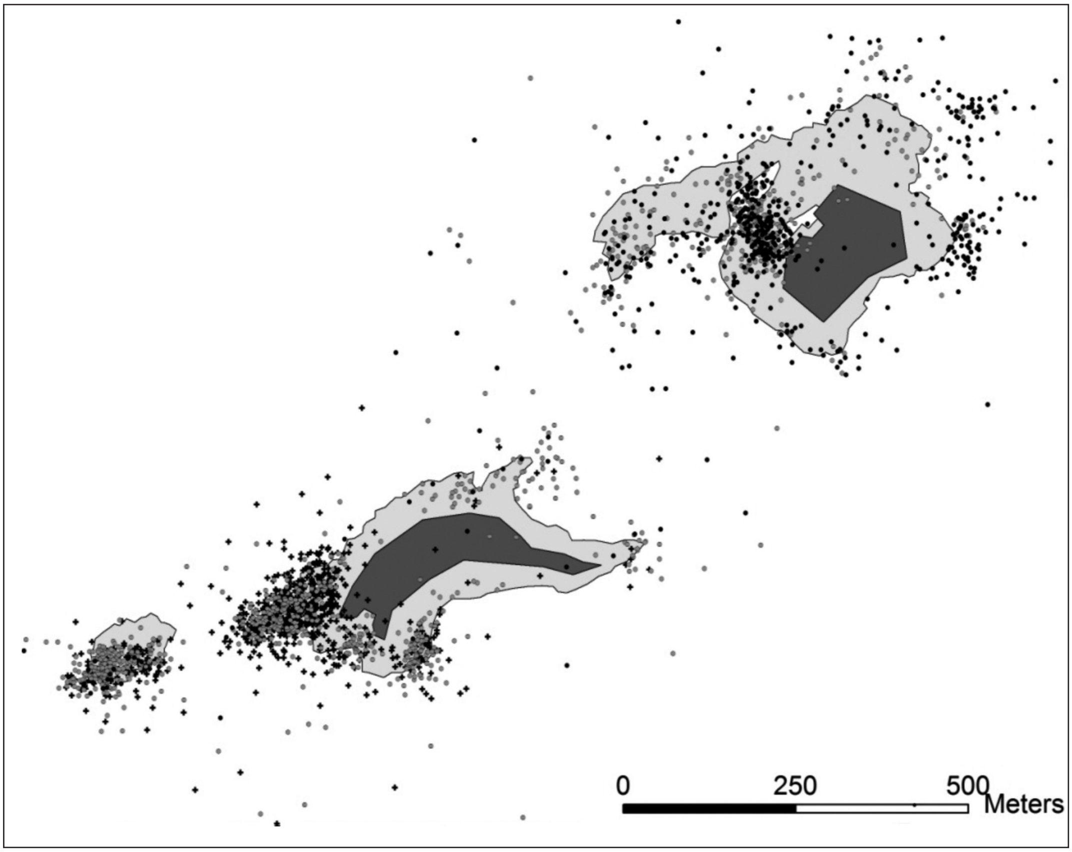

Fig. 5. *At-sea locations of seals V01 (black crosses), V02 (light grey dots) and V05 (black dots) around the Saint-Marcouf islands, north of BDV. The intertidal (rocky) area is indicated (in light grey), as well as the land (in dark grey).*

of dives were located in the middle of the bay, along the tidal channels along which seals haul out at low tide. Although harbour seals' diet in *BMSM* is not documented yet, potential prey including mullets (*Mugilidae*) (the most abundant fish species in the bay), gobies (*Gobiidae*) or sea bass, *Dicentrarchus labrax*, are reported in *BMSM* (Lafaille *et al.* 1998). Mullet movements in particular are known to be strongly dependent upon the tidal state (Almeida 1996), and they use salt marshes as trophic areas at high tides in the *BMSM* (Lafaille *et al.* 2002). Hot-spots of seals' diving activity were observed along the north side of the bay (while they did not haul out so close to the shore), at the exiting part of the main tidal channel and close to mussel farms and a small rocky point in the south-western part of the bay (Fig. 4). We suggest that these represent the preferred foraging areas of the seals in *BMSM*, but we do not exclude feeding activity outside these spots, elsewhere in the bay (possibly in the close vicinity of haulout sites). Mussel farms may act as artificial reefs in sandy habitats and provide suitable habitats for fish communities (*e.g.* Powers *et al.* 2007), although increased fish productivity around these structures was not always demonstrated (Clynick *et al.* 2008). Apart from these areas, it was difficult to describe the seals' marine habitat at a fine scale due to the moving nature of the tidal channels (their location within the bay changes on every spring tide and is not documented accurately enough for comparison with the seal locations). In *BDV* and *BMSM* as well, deeper U-shaped dives were observed outside the tidal range, where seals spent less tracking time than in the intertidal area. One seal made repeated trips at sea (88 trips in 123 days), up to 15 km away from its haulout site, but all other seals made frequent trips to one or a few intertidal areas located along the mainland's or islands' coast, 3 to 15 km from the main haulout in most cases (up to 35 km for one seal). These routine movements were very frequent (30 to 150 trips per seal to the same area for an average tracking duration of 143±41 days in *BDV*). These areas were repeatedly used by the same individual seals away from their haulout sites, and probably constitute their preferred foraging areas. Trip durations from the *BDV* were usually 2 to 12 hours, except trips to the *Saint Marcouf islands* which lasted on average close to 24 hours (Table 3).

Foraging trip duration and distance between haulout sites and foraging area are usually correlated (Thompson *et al.* 1998), and the results obtained here show that harbour seals in *BDV* make relatively short trips "at sea" (sometimes only moving along the coast) for foraging, in terms of distance and duration. Previous studies reported harbour seals moving up to 70 km away from their haulout site for foraging (Thompson and Miller 1990, Thompson *et al.* 1996, Tollit *et al.* 1998, Thompson *et al.* 1998, Gjertz *et al.* 2001); however shorter distances of 5-10 km have been reported for harbour seal winter foraging trips, in Prince Williams Sound (Alaska) or the Moray Firth (Scotland) (Lowry *et al.* 2001 and Thompson 1993, respectively). Tollit *et al.* (1998) assumed that all locations within 2 km from haulout sites were associated with haulout behaviour. In our study, 95% and 55% of at-sea locations were ≤ 5 km from the haulout sites in *BMSM* and *BDV* respectively. Feeding close to haulout sites cannot be excluded due to the high proportion of time spent in the water in the close vicinity of these locations, as well as direct observation of seals capturing prey in tidal channels close to haulout sites (J.-F. Elder pers. comm.). This however could represent opportunistic feeding as opposed to the foraging areas visited on a regular basis by the seals during return trips away from their main haulout area. Detection of actual prey capture from specific sensors (*e.g.* Bjørge *et al.* 1995, Austin *et al.* 2006) is now needed to better document the relationship between diving and location data records and the seals' behaviour in this habitat.

Seals travelled on average 16 km/day in *BMSM* and 22 km/day in *BDV* (Table 2). Even if these distances are minimum estimations (assuming straight movements between two successive GPS locations), the high rate of locations obtained reduces any under estimation. The Minimum Convex Polygons (MCP) sizes we obtained from seal locations were rather small, with the exception of seal M06 that moved away from the *BMSM* during the study. Although the GPS stopped soon after the seal left the bay, we may consider this as a seasonal movement and not as a foraging trip. Photo-identification data for this seal suggests movements across the Channel repeated over several years (photo ID of this seal in the *BMSM* only during summers prior to this study). Such seasonal movements (before and after breeding and moulting especially) have already been reported in a number of studies (*e.g.* Thompson *et al.* 1996, Lowry *et al.* 2001). This seal excluded, the average size of MCPs was 139 km² in *BMSM* and 195 km² in *BDV*, which is much smaller than those reported by Lowry *et al.* (2001) in Prince William Sound (Alaska). Minimum Convex Polygons give a good overview of how far locations were dispersed but might not, however, constitute the best parameter for inter-study comparison, due to the relationship between the number of locations and the size of the MCP obtained (Bjørge *et al.* 2002a). Fixed kernel densities are therefore used to define the general home ranges (95% fixed kernel densities) and "core areas" (50% fixed kernel densities) of the seals. We made calculations from all locations and at-sea locations only. Home range and core area sizes were underestimated by 6-12.5% when haulout locations were excluded, which is probably due to the reduced number of locations kept in the analysis. In *BMSM* where haulout locations were rather dispersed in the tidal range of the bay and overlaying at-sea locations, we would suggest keeping all locations in the home range's size calculation, when assessing the seals' habitat use in the bay. In *BDV*, haulout locations were more concentrated in 2 areas within the *Baie des Veys*, 4.2% of individual haulouts were located on an alternative site and seals made regular trips distant from these haulout areas. In this case, it could be more sensible to map the known haulout locations and assess home range sizes from at-sea locations. Whatever the location data kept for analysis, it is important to assess how this choice affects the size of home ranges. Home ranges estimated from at-sea locations were 137 km² wide in *BMSM* and 161 km² wide in *BDV*, while core areas were 35 km² and 22 km² wide respectively. These results are slightly lower than those reported by Smith *et al.* (2006), who calculated 95% and 50% kernel densities from satellite tracking of harbour seals in *Lac des Loups Marins* (Quebec) and obtained a median surface of 368 and 38 km² respectively. Bjørge *et al.* (2002a) reported smaller home ranges and core areas (10.4 and 1.2 km² respectively) in harbour seal along the coasts of Norway, but they were pups. The small home ranges estimated in this study might be related to prey availability in these two highly productive tidal bays, with at least 100 fish species known to be present in the intertidal area of *BMSM* for instance (Lafaille *et al.* 2000, Lefeuvre *et al.* 2000).

The high number of Fastloc™ GPS locations obtained together with their accuracy allowed us to document the harbour seals habitat use at a fine geographical scale. One example was given in Fig. 5, showing the concentration of at-sea locations around several intertidal rocks in the *Saint-Marcouf islands*, at the limit of the intertidal zone. These foraging areas, only 50 to 150 m wide, are known by local fishermen as they correspond to narrow points between the islands, crossed by strong currents changing direction depending on the tides. Mullet and garfish, Belone belone, are particularly abundant in these tidal currents between the islands (J.-F. Elder pers. comm.), and these represent two important prey species identified in the harbour seal diet in *BDV* (Spitz *et al.* 2010). It was already demonstrated that in such tidal environments, the interactions between topographical features, tidal currents and fish can influence the foraging behaviour of vertebrate predators, and seals in particular (Zamon 2001). We suggest that in our 2 study sites, the importance of the tides combined to local features of the topography (rock points, mussel farms, or sometimes shipwrecks) allow seals to predict prey availability, driving their foraging strategies towards a number of specific coastal areas. Individual seals may select different foraging areas depending on their previous experience (Tollit *et al.* 1998). Other detailed maps obtained in this study (not shown here) highlighted that seals in *BDV* or *BMSM* were diving along either side of mussel farms depending on tidal phases. This behaviour could be linked to the use of mussel farms as favourable habitats for fish assemblies, or rather linked to the proximity of the coastline. Juvenile plaice, *Pleuronectes platessa*, for instance were reported migrating high up the beaches during the flood tide (Burows *et al.* 1994, Beyst *et al.* 2002). Although plaice represents one of the main harbour seal prey species in *BDV* during summer (Spitz *et al.* 2010), further studies of diet composition in terms of prey species and length distribution are needed during winter.

Important geographical variations have been reported in harbour seal habitat use and foraging strategies, and were linked to the available marine habitat in the vicinity of haulout sites (Thompson *et al.* 1996, Hastings *et al.* 2004). In addition to the distance between haulout sites and foraging areas, regional variations were observed in bathymetry and sediment type of habitats used by the seals: harbour seals can forage in shallow estuarine bays or deep basins, 100 or 200 m deep (with maximum dive depths recorded up to 500 m), on rock, gravel, sand or mud habitats (*e.g.* Bjørge *et al.* 1995, Thompson *et al.* 1996, Eguchi and Harvey 2005). Harbour seals in the Wadden Sea foraged near their haulout site, over water depths of 1-3 m over the flats (with a tidal amplitude of 1.4-3.8 m; Ries *et al.* 1997); such short foraging trips and shallow dives were also observed in most of our study seals which probably constitute an extreme example of coastal and shallow habitat use in harbour seals. We suggest that this habitat use strategy is related to the low water depths available in the area as well as the prey abundance and the predictability of the interactions between shallow topographical features and tidal currents structuring harbour seal foraging tactics (Zamon 2003). It further illustrates the behavioural plasticity of the species according to habitats, which might be related to the trade off between energy expenditure during foraging trips and prey availability in terms of abundance, distribution and vulnerability (Tollit *et al.* 1998, Frost *et al.* 2001, Zamon *et al.* 2001, Eguchi and Harvey 2005).

Seasonal variations have also been reported in harbour seals foraging trips. Many authors reported that seals moved further offshore during winter than during the summer breeding and moulting season, when they spend more time ashore (Härkönen, 1987; Thompson *et al.* 1989; Frost *et al.* 2001, Gjertz *et al.* 2001). Thompson (1993) however reported foraging trips shorter in winter (5-10 km) than in the summer (20-40 km) in the Moray Firth (Scotland), and related this to seasonal prey availability. In *BMSM* and *BDV*, diet information was obtained in the summer (Spitz *et al.* 2010) while telemetry tracking was conducted during winter; it would be interesting to obtain complementary information on both aspects at all seasons to better understand the inter-annual variability of harbour seal foraging strategies in relation to habitat and prey availability in the area.

One objective of this study was, for regional managers, to identify the critical habitat of harbour seals living in the *BMSM* and *BDV*. Our results suggest that the present network of marine reserves already encompasses most of the habitat used by the seals in these two bays, with the exception of more offshore areas north of *BDV*, south and east of the *Saint-Marcouf islands.* These offshore areas are already incorporated into the areas proposed by the regional managers for the offshore extension of the Natura 2000 network in France. It is important to remember however that seasonal movements may occur and that habitat use over the whole annual cycle of the seals has to be taken into account in management plans which might go beyond local or regional scale.

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REFERENCES

Almeida, P.R. 1996. Estuarine movement patterns of adult thin-lipped grey mullet, *Liza ramada* (Risso) (Pisces, Mugilidae), observed by ultrasonic tracking. *J. Exp. Mar. Biol. Ecol.* 202:137-150.

Austin, D., Bowen, D.W., McMillan, J.I. and Boness, D.J. 2006. Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. *J. Anim. Ecol.* 75: 408-420.

Baechler, J., Beck, C.A. and Bowen, W.D. 2002. Dive shapes reveal temporal changes in the foraging behaviour of different age and sex classes of harbour seals *(Phoca vitulina)*. *Can. J. Zool.* 80:1569-1577.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools

Beyst, B., Vanaverbeke, J., Vincx, M. and Mees, J. 2002. Tidal and diurnal periodicity in macrocrustaceans and demersal fish of an exposed sandy beach, with special emphasis on juvenile plaice *Pleuronectes platessa. Mar. Ecol. Prog. Ser.* 225:263-274.

Bjørge, A., Thompson, D., Hammond, P., Fedak, M.A., Bryant, E., Aarefjord, H., Roen, R. and Olsen, M. 1995. Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway. In: Blix, A.S., Walloe, L., Ulltang, O. (eds.); *Whales, seals, fish and man.* Elsevier, Amsterdam, 211-223.

Bjørge, A., Bekkby, T., Bryant, E.B. 2002a. Summer home range and habitat selection of harbour seal *(Phoca vitulina*) pups. *Mar. Mamm. Sci.* 18(2):438-454.

Bjørge, A., Øien, N., Hartvedt, S., Bøthun, G. and Bekkby, T. 2002b. Dispersal and bycatch mortality in gray, Halichoerus grypus, and harbour, *Phoca vitulina*, seals tagged at the Norwegian coast. *Mar. Mamm. Sci.* 18:963-976.

Bowen, W.D., Boness, D.J. and Iverson, S.J. 1999. Diving behavior of lactating harbour seals and their pups during maternal foraging trips. *Can. J. Zool*. 77:978-988.

Brown, R.F. and Mate, B.R. 1983. Abundance, movements, and feeding habits of harbour seals, *Phoca vitulina*, at Netarts and Tillamook bays, *Oregon. Fish. Bull.* 81(2):291-301.

Burrows, M.T., Gibson, R.N., Robb, L. and Comely, C.A. 1994. Temporal patterns of movement in juvenile flatfishes and their predators: underwater television observations. *J. Exp. Mar. Biol. Ecol.* 177:251-268.

Clynick, B.G., McKindsey, C.W. and Archambault, P. 2008. Distribution and productivity of fish and macroinvertebrates in mussel aquaculture sites in the Magdalen islands (Québec, Canada). *Aquaculture* 283:203-210.

Eguchi, T. and Harvey, J. 2005. Diving behavior of the Pacific harbour seal *(Phoca vitulina richardii)* in Monterey Bay, California. *Mar. Mamm. Sci.* 21:283-295.

Elder, J.-F. 2006. Le phoque veau marin *(Phoca vitulina*, Linné, 1758) en Baie des Veys (Manche, France). *Bull. Soc. Linn. Normandie* 119:113-120 (in French.)

Fedak, M.A., Lovell, P. and Grant, S.M. 2001. Two approaches to compressing and interpreting time-depth information as collected by time-depth recorders and satellite-linked data recorders. *Mar. Mamm. Sci*. 17:94-110.

Frost, K., Simpkins, M. and Lowry, L.F. 2001. Diving behavior of subadult and adult harbour seals in Prince William Sound, Alaska. *Mar. Mamm. Sci.* 17:813-834.

Gjertz, I., Lydersen, C. and Wiig, Ø. 2001. Distribution and diving of harbour seals *(Phoca vitulina)* in Svalbard. *Polar Biol*. 24:209-214.

Härkönen, T.J. 1987 . Influence of feeding on haul-out patterns and sizes of sub-populations in harbour seals. *Neth. J. Sea Res.* 21:331-339.

Hastings, K.K., Frost, K.J., Simpkins, M.A., Pendleton, G.W., Swain, U.G. and Small, R.J. 2004. Regional differences in diving behavior of harbour seals in the Gulf of Alaska. *Can. J. Zool*. 82:1755-1773.

Kolb, P.M. and Norris, K.S. 1982. A harbour seal, *Phoca vitulina richardsi*, taken from a sable fish trap. *Calif. Fish. Game* 68:123-124.

Krafft, B.A., Lydersen, C., Gjertz, I. and Kovacs, K.M. 2002. Diving behavior of sub-adult harbour seals *(Phoca vitulina)* at Prins Karls Forland, Svalbard. *Polar Biol.* 25:230-234.

Lafaille, P., Brosse, S., Feunteun, E., Baisez, A. and Lefeuvre, J.-C. 1998. Role of fish communities in particulate organic matter fluxes between salt marshes and coastal marine waters in the Mont Saint-Michel bay. *Hydrobiologia* 373/374:121-133.

Lafaille, P., Feunteun, E. and Lefeuvre, J.-C. 2000. Composition of fish communities in a European macrotidal salt marsh (the Mont Saint-Michel bay, France). *Estuar. Coast. Shelf Sci.* 51:429-438.

Lafaille, P., Feunteun, E., Lefebvre, C., radureau, A., Sagan, G. and Lefeuvre, J.-C. 2002. Can thin-lipped mullet directly exploit the primary and detritic production of European macortidal salt marshes? *Estuar. Coast. Shelf Sci.* 54:729-736.

Lefeuvre, J.-C., Bouchard, V., Feunteun, E., Grare, S., Lafaille, P. and Radureau, A. 2000. European salt marshes diversity and functioning : the case study of the Mont Saint-Michel bay, France. *Wetlands Ecol. Manage.* 8:147-161.

Lesage, V., M. Hammill, M.O. and Kovacs, K.M. 1999. Functional classification of harbour seal *(Phoca vitulina)* dives using depth profiles, swimming velocity, and an index of foraging success. *Can. J. Zool.* 77:74-87.

Lesage, V., Hammill, M.O. and Kovacs, K.M. 2004. Long-distance movements of harbour seals *(Phoca vitulina)* from a seasonally ice-covered area, the St. Lawrence River estuary, Canada. *Can. J. Zool*. 82:1070-1081.

Lowry, L., Frost, K., Ver Hoef, J.M. and DeLong, R.A. 2001. Movements of satellite-tagged subadult and adult harbour seals in Prince William Sound, Alaska. *Mar. Mamm. Sci*. 17: 835-861.

McConnell, B.J., Chambers, C. and Fedak, M.A. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the southern ocean. *Antarct. Sci.* 4:393-398.

McConnell, B.J., Beatoçn, R., Bryant, E., Hunter, C., Lovell, P. and Hall, A. 2004. Phoning home – a new GSM mobile phone telemetry system to collect mark-recapture data. *Mar. Mamm. Sci.* 20:274-283.

Pitcher, K.W. and McAllister, D.C. 1981. Movements and haulout behavior of radio-tagged harbour seals, *Phoca vitulina. Can. Field-Nat.* 95:292-297.

Powers, M.J., Peterson, C.H., Summerson, H.C. and Powers, S.P. 2007. Macroalgal growth on bivalve aquaculture netting enhances nursery habitat for mobile invertebrates and juvenile fishes. *Mar. Ecol. Prog.* Ser. 339:109-122.

Ries, E., Traut, I.M., Paffen, P. and Goedhart, P.W. 1997. Diving patterns of harbour seals *(Phoca vitulina)* in the Wadden Sea, the Netherlands and Germany, as indicated by VHF telemetry. *Can. J. Zool.* 75:2063-2068.

Smith, R., Cox, T.M. and Westgate, A.J. 2006. Movements of harbour seals *(Phoca vitulina mellonae)* in Lacs des Loups Marins, Quebec. *Mar. Mamm. Sci*. 22:480-485.

Spitz, J., Mariotti, L., Ridoux, V., Caillot, E. and Elder, J.-F. 2010. The diet of harbour seal *Phoca vitulina* at the southern limit of its European distribution (Normandy, France). *NAMMCO Sci. Publ.* 8:313-328.

Suryan, R.M. and Harvey, J.T. 1998. Tracking harbour seals *(Phoca vitulina richardsi)* to determine dive behaviour, foraging activity, and haul-out site use. *Mar. Mamm. Sci.* 14:361-372.

Thompson, P.M., Fedak, M.A., McConnell, B.J. and Nicholas, K.S. 1989. Seasonal and sex-related variation in the activity patterns of common seals *(Phoca vitulina)*. *J. Appl. Ecol.* 26:521-535.

Thompson, P.M. and Miller, D. 1990. Summer foraging activity and movements of radio-tagged common seals (*Phoca vitulina* L.) in the Moray Firth, Scotland. *J. Appl. Ecol.* 27:492-501.

Thompson, P.M. 1993. Harbour seal movement patterns. *Symp. Zool. Soc. Lond*. 66:225-239.

Thompson, P.M., McConnell, B.J., Tollit, D.J., Mackay, A., Hunter, C. and Racey, P.A. 1996. Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, N.E. Scotland. *J. Appl. Ecol.* 33:1572-1584.

Thompson, P.M., Mackay, A., Tollit, D.J., Enderby, S. and Hammond, P. 1998. The influence of body size and sex on the characteristics of harbour seal foraging trips. *Can. J. Zool.* 76:1044-1053.

Tollit, D.J., Black, A.D., Thompson, P.M., Mackay, A., Wilson, B., Van Parijs, S.M., Grellier, K. and Parlane, S. 1998. Variations in harbour seal *(Phoca vitulina)* diet and dive-depths in relation to foraging habitat. *J. Zool.* 244:209-222.

Vincent, C., McConnell B.J., Fedak M.A. and Ridoux V. 2002. Assessment of Argos location accuracy from satellite tags deployed on captive grey seals. *Mar. Mamm. Sci.* 18:156-166.

Vincent, C., Fedak M. A., McConnell B. J., Meynier, L., Saint-Jean, C. and Ridoux V. 2005. Status and conservation of the grey seal, *Halichoerus grypus,* in France. *Biol. Conserv.* 126:62-73.

Zamon, J. 2001. Seal predation on salmon and forage fish schools as a function of tidal currents in the San Juan Islands, Washington, USA. *Fish. Oceanogr.* 10:353-366.

Zamon, J. 2003. Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. *Mar. Ecol. Prog. Ser.* 261: 243-255.