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Coastal habitat use by ringed seals *Pusa hispida* following a regional sea-ice collapse: importance of glacial refugia in a changing Arctic

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ABSTRACT: Declines in Arctic sea ice are predicted to have large consequences for Arctic marine mammals. To study the consequences of a sudden collapse in sea ice in 2006 within Svalbard (Norway), 38 ringed seals *Pusa hispida* were equipped with Satellite Relay Data Loggers in the period 2010–2012; the behaviour of these seals was then compared with data collected during deployments of similar equipment on 22 ringed seals in 2002–2003, prior to the sea-ice collapse. In the present study, statistical models were used to investigate whether the altered sea-ice regime modified movement patterns or foraging behaviour in coastal areas. All seals in these areas concentrated their time close to tidal glacier fronts. However, seasonally resident individuals (immature seals) spent less time close to glacier fronts when in the fjords, than year-round coastal residents (mature seals), likely due to competitive exclusion of the younger animals in these key feeding and resting habitats. Movements and space use became restricted in winter due to formation of land-fast ice. This spatial restriction was delayed and less extreme in 2010–2012, consistent with the late formation and limited extent of land-fast ice in this period. Ringed seals in 2010–2012 also made longer dives, surface intervals between dives were shorter, and increased proportions of the dives were spent descending, with decreased proportions of time at the bottom of dives compared to 2002–2003, indicating increased foraging effort. Further sea-ice deterioration and retreat of glacier fronts are predicted for Svalbard, which are likely to increase intraspecific competition and affect ringed seal distribution, reproductive success and abundance.

KEY WORDS: Arctic · Behaviour · Climate change · Marine mammal · Svalbard

INTRODUCTION

Climate change is already impacting flora and fauna across the globe and is expected to cause a myriad of additional changes in ecosystem structure and function over the coming decades (IPCC 2014). These changes are especially severe in the Arctic, where surface temperatures have warmed by more than 3 times the global average over the past few decades (Comiso & Hall 2014). Endemic Arctic marine mammals are facing many challenges in a warming Arctic including invasion by temperate species, increased disease transmission and food web changes induced by warmer water temperatures, ocean circulation patterns and acidification (Moore & Huntington 2008, Kovacs et al. 2011, Gilg et al. 2012). One of the largest threats to endemic Arctic marine life is the decline in the prevalence of sea ice (Laidre et al. 2008, 2015, Kovacs et al. 2011).

Sea ice is an important habitat for most endemic Arctic marine mammals; for example sea ice is used as a pupping and nursing platform for seals, a transport corridor for bears and it provides predator and storm protection for ice-associated whales. Many

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members of this mammalian guild also forage on ice-associated lower trophic prey (Kovacs et al. 2009, Laidre et al. 2015). Declines in sea ice are expected to have large consequences for the distribution, abundance and long-term survival of many Arctic marine mammals (Laidre et al. 2008, 2015, Moore & Huntington 2008, Kovacs et al. 2011). Summer sea-ice extent in the Arctic is currently declining by 11.5% per decade and the Arctic is expected to be sea-ice free in the summer by as early as the late 2030s (Wang & Overland 2009, Comiso & Hall 2014). However, little hard data exist at present that quantify the impacts of sea-ice losses. The variance inherent in Arctic marine systems along with the present lack of data make foreseeing the consequences of continued sea-ice loss difficult (Post et al. 2013).

Ringed seals *Pusa hispida* are a keystone circumpolar Arctic endemic species. They are the primary prey item for polar bears *Ursus maritimus* and are also an important food resource for humans in coastal communities (Derocher et al. 2002, Iversen et al. 2013). Ringed seals are an abundant species in the Arctic, making them an important consumer in Arctic food webs. Like most endemic Arctic marine mammals, ringed seals are sea-ice obligate. They maintain breathing holes in thick sea ice, facilitating their wide distribution (McLaren 1958, Laidre et al. 2008). Snow lairs dug above these breathing holes are used for pupping, nursing and resting (Smith & Stirling 1975, Lydersen & Gjertz 1986). Sea ice is also used as a moulting platform during the spring and summer and as a resting platform throughout the year. Ringed seals also often forage in association with sea ice (Reeves 1998, Labansen et al. 2007). Body condition and growth of ringed seals are related to sea-ice conditions on broad, regional scales (Harwood et al. 2012). Most fattening and growth takes place in the late summer and autumn when ringed seals forage heavily to regain weight lost during spring reproductive activities and subsequent early summer moulting (Ryg et al. 1990).

Svalbard is a Norwegian High Arctic archipelago located between 74° and 81°N and 10° and 35°E (Fig. 1). The West Spitsbergen Current (WSC), which is a branch of the North Atlantic Current, transports Atlantic Water along the west coast of Svalbard. Consequently, the west side of Svalbard is influenced by Atlantic Water to a greater extent than the east side of Svalbard, which is more exposed to Arctic Water masses (Ingvaldsen & Loeng 2009). Air and water temperatures in the Svalbard region have been increasing over recent decades. For example, the temperature of the WSC increased by 0.06°C yr^{-1} from 1997 to 2010 and Arctic Water masses in the Northern Barents Sea have also increased in temperature since the early 2000s (Beszczynska-Möller et al. 2012, Lind & Ingvaldsen 2012). Sea-ice conditions in Svalbard changed dramatically in 2006. The summer sea-ice extent shifted northward from a position over the continental shelf to locations where the summer ice edge is now over the deep Arctic Ocean Basin at the time of the ice minima and the amount of land-fast ice forming in the fjords during winter/spring, especially in western Spitsbergen, decreased sharply. This altered sea-ice regime has prevailed in the years since 2006.

Svalbard ringed seals have 2 different movement strategies during their late summer/autumn foraging period: some make offshore foraging trips to the northern ice edge while others remain in the fjords of the archipelago (Freitas et al. 2008a). Changes in movement and diving parameters for ringed seals that use the offshore trip strategy (before and after the collapse in sea-ice conditions) are reported in Hamilton et al. (2015). Herein, the movement, diving behaviour and habitat preferences of ringed seals in coastal areas are compared before and after the regional sea-ice collapse and contrasted with offshore movement patterns in these time periods.

MATERIALS AND METHODS

Capture and instrumentation

A total of 60 ringed seals were captured and equipped with Satellite Relay Data Loggers (SRDLs) (Sea Mammal Research Unit, University of St Andrews) at several locations in Svalbard, Norway, in 2 study periods, i.e. before and after the major collapse in sea ice described above (Fig. 1, Table 1). A total of 22 seals were captured in 2002 and 2003 (11 from 19 July to 21 July 2002 and 11 from 19 July to 24 July 2003) when sea-ice conditions were historically 'normal'. The general behaviour of these animals has been published previously (Freitas et al. 2008a), but herein the behaviour patterns of these seals are compared to those of individuals following the regional collapse of sea ice that occurred in 2006. This was achieved by instrumenting 38 additional ringed seals in 2010 to 2012 (9 from 25 July to 3 August 2010, 11 from 20 July to 3 August 2011 and 18 from 29 July to 26 August 2012) (Table 1). All of the seals were captured using drift nets set from shore. Immediately after capture they were placed in individual restraint nets in which body mass was measured (Salter spring

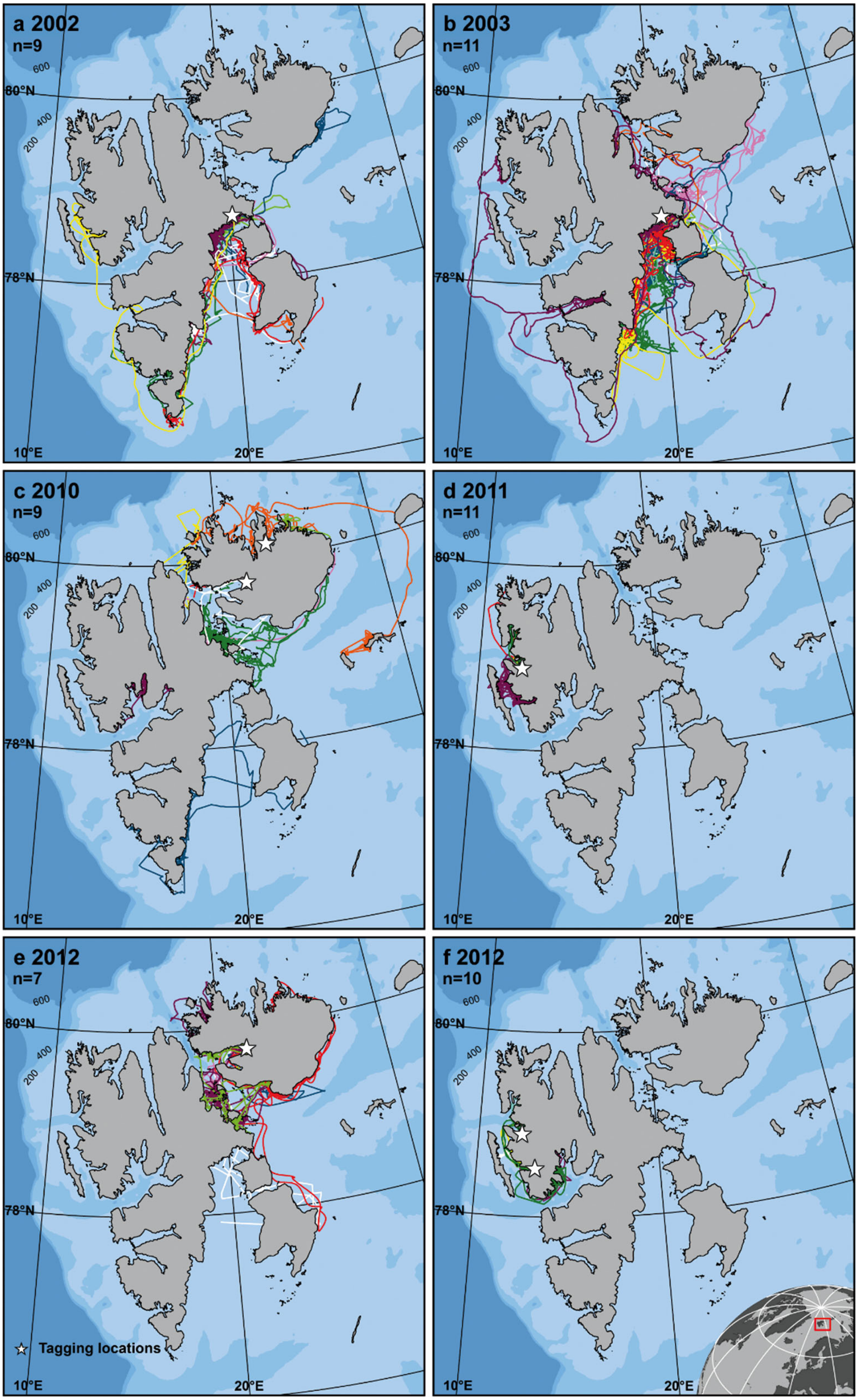

Fig. 1. Maps of the coastal tracks from the 57 ringed seals equipped with Satellite Relay Data Loggers (SRDLs) in (a,b) 2002–2003 and (c–f) 2010–2012 in Svalbard, Norway. ☆: tagging locations for each year

Table 1. Summary information for 57 ringed seals equipped with Satellite Relay Data Loggers (SRDLs) in 2002–2003 and 2010–2012 in Svalbard, Norway, showing tagging and dive statistics from coastal areas. For 19 of these seals that took offshore trips, only the time period after they returned to the coast is included

		All seals	2002	2003	2010	2011	2012	2012
Number of seals		57	9	11	9	11	7	10
Tagging location			East	East	East	West	East	West
Sex ratio	F:M	33:24	5:4	8:3	6:3	6:5	5:2	3:7
Mass at capture	Mean ± SD	57 ± 20	44 ± 16	52 ± 17	46 ± 11	75 ± 16	44 ± 11	76 ± 17
	Range	28–103	28–72	28–89	34–62	55–100	34–62	60–103
Tracking duration (total, days)		8544	883	1619	1269	1656	1493	1652
Tracking duration (per seal, days)	Mean ± SD	150 ± 66	98 ± 40	147 ± 64	141 ± 57	151 ± 32	213 ± 74	165 ± 81
	Range	3–282	55–170	37–260	11–217	92–204	117–282	3–257
Number of locations (total)		138 221	7365	24 310	13 403	35 191	17 461	40 491
Number of locations (per seal)	Mean ± SD	2425 ± 1993	818 ± 668	2210 ± 1065	1489 ± 1897	3199 ± 1427	2494 ± 1375	4049 ± 3023
	Range	47–8510	153–1808	241–4076	85–6171	1156–5400	215–4512	47–8510
Number of dives (total)		132 550	12 437	45 457	21 203	38 408	6765	8280
Number of dives (per seal)	Mean ± SD	2325 ± 2216	1381 ± 1240	4132 ± 1844	2356 ± 3328	3492 ± 1816	966 ± 698	828 ± 1057
	Range	3–10 902	241–3127	685–6942	111–10 902	901–6782	36–2034	3–3632
Dive duration (min)	Mean ± SD	4.0 ± 2.8	2.5 ± 2.2	3.5 ± 2.7	4.4 ± 2.3	4.6 ± 2.9	4.5 ± 3.0	5.1 ± 2.9
	Max	45.5	34.3	45.5	39.3	39.3	39.3	21.2
Surface duration (min)	Mean ± SD	1.2 ± 1.4	1.4 ± 1.8	1.5 ± 1.8	0.9 ± 0.9	1.1 ± 1.1	0.8 ± 0.8	1.1 ± 1.1
	Max	15.7	10	11.6	9.1	9.3	9.1	15.7
Max dive depth (m)	Mean ± SD	34 ± 30	33 ± 32	37 ± 31	36 ± 31	29 ± 27	35 ± 28	35 ± 27
	Max	302	270	302	279	171	153	163

scales; precision ±0.5 kg) and sex was determined. Overall slightly more females were caught than males, although in some years the sex ratio was almost equal or dominated by males (Table 1). Various models of SRDLs (see below) were glued to the hair on the back mid-dorsally using quick-setting epoxy. The weight of the SRDLs represented on average 1.1% of the seals' body mass (range: 0.4 to 2.0%). All animal-handling protocols were approved by the Governor of Svalbard and the Norwegian Research Council.

Data acquisition

SRDLs collect information on the seals' behaviour including dive depth and duration, percentage of time hauled out and various parameters describing dive profiles. Data were transmitted via the Argos satellite system, which in addition also computes a location for the seals (see Fedak et al. 2002, CLS 2015 for details). The SRDLs used in 2002–2003 were equipped with temperature sensors (see Lydersen et al. 2004) while those used in 2010–2012 were equipped with conductivity-temperature-depth (CTD) sensors to measure oceanographic data (for details, see Fig. A1 in the Appendix and SMRU Instrumentation, www.smru.st-andrews.ac.uk/Instrumentation/).

Of the 60 seals, 41 remained inshore throughout their data records. The remaining 19 took offshore trips; 3 of these seals (2 captured in 2002 and 1 captured in 2012) ceased transmitting while offshore (Hamilton et al. 2015). Coastal data from the other 16 animals, once they returned from their offshore trips, are included in the analyses below. Thus, the analyses herein include data from 57 seals. Data from year-round resident seals were compared to data from seasonally resident seals of similar body mass to test for potential differences in behaviour (strategy effect). If no difference was found for a particular parameter, the seals were merged and treated as one group for that particular analysis. All seals in 2002–2003 were tagged on the east coast of Spitsbergen (Fig. 1). In 2010– 2012, seals were tagged on both the east coast and the west coast in order to see if their behaviour differed according to the oceanographic conditions they experienced (Atlantic vs. Arctic Water masses). Also, the sea-ice decline has been much more severe on the west coast of Svalbard than the east coast. The seals tagged on the west coast in

2010–2012 were generally larger than those tagged on the east coast in either tagging period (Fig. 1, Table 1), which created a need to include a tagging group factor variable with 3 levels in the analyses: seals tagged in 2002 and 2003 on the east coast, 2010–2012 on the east coast and 2010–2012 on the west coast.

Data exploration took place as recommended in Zuur et al. (2010). Generalized additive mixed effect models (GAMMs) were used when data exploration showed the relationships between the variables to be non-linear. Generalized linear mixed effect models (GLMMs) were used when linear relationships were found. All data analyses were completed in R version 3.0.3 (R Core Team 2014) and all results are presented as mean ± 95% CI unless otherwise specified. All maps were made using ArcMap10 (ESRI).

The Argos locations for each seal were first filtered using the speed-distance-angle (SDA) filter in the argosfilter package using the default settings (Freitas et al. 2008b) and in addition by manually removing obviously erroneous locations (i.e. locations far inland) using ArcMap10. Subsequently, they were filtered using the CRAWL package with a stopping model to account for time periods spent hauled out (Johnson et al. 2008). Hourly locations and all dive locations were extracted from the CRAWL model.

Bathymetry data at 500 m resolution were retrieved from the International Bathymetric Chart of the Arctic Ocean (IBCAO) version 3.0 (Jakobsson et al. 2012). Shapefiles of the Svalbard coastline and tidal glacier fronts were obtained from the Norwegian Polar Institute (www.npolar.no).

Activity pattern

The SRDLs produce summary tables that provide the percentage of time a seal spent hauled out, diving and swimming at the surface in consecutive 6-h intervals (i.e. 4 per day; see SRDL overview, www.smru.st-andrews.ac.uk/Instrumentation/Downloads/), in addition to data on duration and depth of dives and duration of periods spent at the surface. A GAMM was used to model the percentage of time hauled out daily using the mgcv package (Wood 2006). The identity link was used for the response variable and the Gaussian family was used to assess residual variance (Zuur et al. 2009). Variables included in the model were days since 19 July (i.e. the earliest tagging date), tagging group (i.e. 2002–2003 east coast, 2010–2012 east coast and 2010–2012 west coast), time period (2002–2003 and 2010–2012), body mass and sex. Time period and tagging group were not included in the same model because they are not independent. Days since 19 July was included as a cubic regression spline with a k of 10. Separate smooth terms were created for each factor level of tagging group and time period. Seal ID was included as a random effect and as a grouping variable in the corAR1 temporal autocorrelation term (Pinheiro & Bates 2000). Model selection took place via Bayesian information criterion values (BIC) (Burnham & Anderson 2002). For model validation the deviance and normalized residuals were plotted against the fitted values as well as against each term included and excluded from the selected model. A quantile-quantile plot was used to investigate the linearity of the random effect and normality of the residuals and the deviance residuals were applied to the smooth terms with an increased k to ensure that no pattern remained (see Zuur et al. 2009, Wood 2014 for details).

Distances between consecutive hourly locations were used to estimate distance travelled per day. A linear mixed effects model with an identity link and Gaussian family was used to analyse the daily distance travelled. The response variable was log transformed to meet model assumptions. Explanatory variables included month, time period, tagging group, sex and body mass. Seal ID was included as a random effect. BIC was used for model selection. For model validation quantile-quantile plots were constructed to investigate linearity of the residuals and of the random effect. Residuals were plotted against the fitted values and also against variables included or excluded from the selected model.

Home range analysis

The dynamic Brownian bridge movement model was used to calculate 50% and 95% home ranges for each seal on a monthly basis as well as for the entire tracking period (Kranstauber et al. 2012). For monthly home ranges the seal had to transmit data for at least 20 d in a particular month to be included. The inputs were hourly locations for each seal and a grid size of 2.5 × 2.5 km, location error of 1 km, a window size of 47 and margin of 11 were used in these analyses (see Kranstauber et al. 2012 for details).

A linear mixed effects model and a linear model were used to analyse the size of the 50% and 95% home ranges by month and for the entire tracking duration, respectively. The identity link was used for the response variable and the Gaussian family was used to assess residual variance. The response variable was log transformed to meet model assumptions (Zuur et al. 2009). Possible predictor variables were month (in monthly models), number of days of transmitted data (in the entire tracking duration models), tagging group, time period, body mass and sex. Seal ID was included as a random effect and as a grouping factor in the corAR1 temporal autocorrelation term in the linear mixed effect models. Model selection and validation were conducted in the same manner as for the daily distance model.

Habitat characteristics

The proportion of time a seal spent within 5 km of a tidal glacier front, and the number of unique tidal glacier fronts visited, were calculated for each month and for the entire tracking duration of each seal. A 5 km radius was used in order to account for Argos location errors and the lack of precision in the actual current positions of the glacier fronts, which are in the majority of cases retreating. Proportion of time within 5 km of a tidal glacier front for the entire tracking duration was analysed using a linear model with the identity link and Gaussian family, as preliminary analyses using month in linear mixed effects models revealed no seasonal pattern. A GLMM with the Poisson family and a log link was used to analyse the number of unique tidal glacier fronts visited per month. Explanatory variables included tagging group, time period, strategy (for proportion of time within 5 km of a tidal glacier front), month (for number of unique tidal glacier fronts visited), sex and body mass. Seal ID was included as a random effect in the linear mixed effect model. Model selection and validation took place in a manner similar to the daily distance travelled model.

Time spent in area (TSA) was calculated for 2.5 × 2.5 km grid cells with the trip statistical package (Sumner 2013) using hourly interpolated locations for each seal and month. Distance to the nearest tidal glacier front, distance to the nearest coastline and mean bathymetry were extracted for each TSA grid cell.

A GAMM was used to model the response of the TSA values to environmental variables using the mgcv package (Wood 2006). The identity link and Gaussian family were used in the GAMM model. The TSA values were log transformed to meet model assumptions. Variables included were distance to the nearest tidal glacier front, distance to the nearest coastline, month, bathymetry, tagging group, time period, strategy, sex and body mass. Distance to the nearest tidal glacier front and distance to the nearest coastline were highly correlated and therefore were not included in the same model. Month and distance to the nearest tidal glacier front were modelled by cubic regression splines with separate smooth curves created for each factor level of tagging group, time period and strategy. Seal ID was included as a random variable. Model selection and validation took place in the same manner used for the percentage of time hauled out model.

Dive variables

Dive variables investigated included dive duration, surface duration, maximum dive depth, bottom time percentage, percentage of dive time spent in descent, percentage of dive time spent in ascent, temperature at maximum dive depth and surface temperature (temperature at 5 m depth). The surface temperature and temperature at the maximum dive depth were extracted from CTD profiles collected by the seals themselves. Bottom time percentage is the percentage of the total dive time that seals spent at depths ≥80 % of the maximum dive depth. Percentage of dive time spent in descent and ascent are the proportions of total dive time that the seals spent going and returning from 80 % of the maximum dive depth, respectively

Linear mixed effect models were run for each dive variable using the identity link and the Gaussian family. The response variable was transformed as necessary to fulfil model assumptions. Main predictor variables were tagging group, time period, month, strategy (for bottom time, and ascent and descent percentages), body mass and sex. Seal ID was included as a random effect and as a grouping variable in the corAR1 temporal autocorrelation term. Model selection and validation took place in a manner similar to the distance travelled daily model.

RESULTS

Three of the 60 tags stopped sending data without having spent significant amounts of time in coastal areas. Of the remaining 57 ringed seals analysed in this study, 41 were classified as year-round residents and 16 were classified as seasonally resident. The seals tagged on the west coast in 2010–2012 were heavier (76 ± 16 kg, mean ± SD) than seals tagged on the east coast in either time period (2010–2012: 45 ± 10 kg, $t = 5.862$, $p < 0.001$; 2002–2003: 48 ± 17 kg, $t =$

6.136, $p < 0.001$). There was no difference in body mass between the seals tagged on the east coast in the 2 time periods ($t = 0.610$, $p = 0.544$). In total the 57 seals transmitted data for 8544 tracking days from coastal areas (150 ± 66 d per seal, Table 1), excluding the days spent on offshore trips for the seasonally resident seals. A total of 138 221 locations (2425 ± 1993 locations per seal) and 132 550 dives (2325 ± 2216 dives per seal) were transmitted in these tracking records (Table 1).

Activity patterns

Time spent hauled out per day decreased from the autumn to the winter and then increased again during the spring (Fig. 2, the best model contained day of the year, Table 2). Year-round resident seals hauled out a larger proportion of time than seasonally resident seals in September, which was the time of the year when most seasonally resident seals returned to the coast following their offshore trips. These 2 groups of seals hauled out for similar proportions of the time during the remainder of the year.

The seals travelled the greatest distances in the late summer. The distance travelled daily decreased through the autumn and into the winter. The seals were subsequently quite sedentary until the following spring for all groups of seals (Fig. 2). The best model fit included a 3-way interaction between tagging group, month and sex (Table 2). Male seals tagged in 2010–2012 on the west coast travelled greater distances daily from December to February compared with the other groups of seals (Fig. 2).

Home range

Large seals had smaller 50 % home ranges (i.e. core areas) than smaller seals when home range was calculated for the entire tracking duration (Fig. 3a, the best model contained body mass, Table 2). The heavier seals tagged on the west coast in 2010–2012 had smaller 95 % home ranges than the lighter seals tagged in 2002–2003 or 2010–2012 on the east coast when calculated for the entire tracking duration (Fig. 3b). The seals tagged in 2002–2003 and 2010–2012 on the east coast had 95 % home ranges of similar size (Fig. 3b, the best model contained tagging group, Table 2).

The size of 50 % monthly home ranges decreased throughout the tracking period (Fig. 3c, the best model contained month, Table 2). The size of the 95 % monthly home range also decreased in a similar manner, but showed differences according to tagging group (Fig. 3d, the best model contained month and tagging group, Table 2). The seals tagged in 2010–2012 on the west coast had smaller 95 % monthly home ranges compared to the other 2 groups of seals. The seals tagged in 2010–2012 on the east coast had slightly smaller 95 % home ranges than seals tagged on the east coast in 2002–2003 (Fig. 3d).

Habitat characteristics

All of the ringed seals spent a lot of their time close to tidal glacier fronts in coastal areas, but the actual proportion of time varied according to strategy and

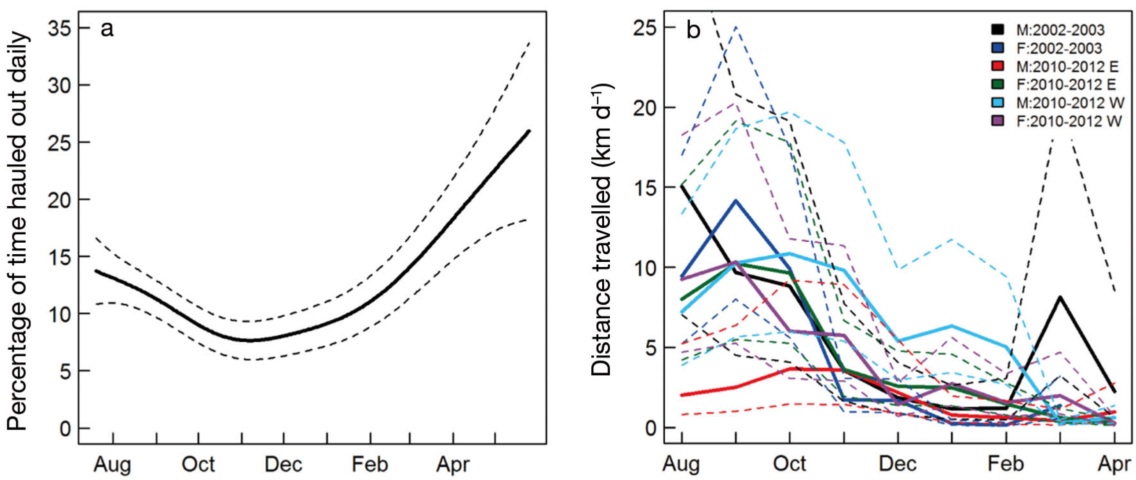

Fig. 2. (a) Generalized additive mixed effect model (GAMM) smooth curve showing the percentage of time seals spent hauled out daily (mean ± 95 % CI) by month and (b) distance travelled for 57 ringed seals equipped with Satellite Relay Data Loggers in 2002–2003 and 2010–2012 in Svalbard, Norway, from coastal areas

Table 2. Bayesian Information Criterion (BIC) tables showing the BIC value, change in BIC (ΔBIC) and BIC weight (BIC_w) for the top 3 models for each habitat, activity and dive variable for 57 ringed seals equipped with Satellite Relay Data Loggers (SRDLs) in 2002–2003 and 2010–2012 in Svalbard, Norway. The BIC-selected model is shown in bold type. As per Burnham & Anderson (2002), if the change in BIC was <2 then the simplest model was selected

Variable	Model	BIC	ΔBIC	BIC_w
Dive duration (min)	**~TimePd×Month**	**304 222**	**0**	**1.00**
	~TimePd×Month+Sex	304 237	15	0.00
	~TagLoc×Month	304 327	105	0.00
Surface duration (min)	**~TimePd×Month**	**363 772**	**0**	**1.00**
	~TimePd×Month+Sex	363 787	15	0.00
	~TagLoc×Month	363 787	16	0.00
Max depth (m)	**~TagLoc×Month**	**1 178 105**	**0**	**0.92**
	~TagLoc×Month+Sex	1 178 110	5	0.08
	~TimePd×Month	1 178 292	187	0.00
Max depth temperature (°C)	**~TagLoc×Month**	**281 011**	**0**	**1.00**
	~TagLoc×Month+Sex	281 023	13	0.00
	~TimePd×Month	281 685	675	0.00
Surface temperature (°C)	**~TagLoc×Month**	**200 540**	**0**	**1.00**
	~TagLoc×Month+Sex	200 553	13	0.00
	~TimePd×Month	200 922	282	0.00
Bottom time (%)	**~TimePd×Month**	**–30 341**	**0**	**0.50**
	~TimePd×Month+Strategy	–30 341	0	0.50
	~TimePd×Month+Sex	–30 329	12	0.00
% dive in descent	~TagLoc×Month+Sex	1 099 775	0	0.69
	~TagLoc×Month	**1 099 777**	**2**	**0.25**
	~TagLoc×Month+Strategy	1 099 780	5	0.06
% dive in ascent	**~TagLoc×Month**	**1 124 285**	**0**	**0.87**
	~TagLoc×Month+Strategy	1 124 289	4	0.12
	~TagLoc×Month+Sex	1 124 293	8	0.02
% time hauled out	**~s(DayofYear)**	**42 592**	**0**	**0.68**
	~s(DayofYear)+Strategy	42 593	1	0.28
	~s(DayofYear)+Mass	42 598	6	0.02
Distance travelled (km d^{-1})	**~TagLoc×Month×Sex**	**31 898**	**0**	**1.00**
	~TagLoc×Month×Sex+Mass	31 914	16	0.00
	~TagLoc×Month	31 970	72	0.00
50% home range (km^2) (tracking duration)	**~Mass**	**161**	**0**	**0.32**
	~Mass+TimePd	162	1	0.19
	~TagLoc	162	1	0.19
95% home range (km^2) (tracking duration)	**~TagLoc**	**169**	**0**	**0.40**
	~TagLoc+Mass	171	2	0.17
	~TagLoc×Mass	173	4	0.08
50% home range (km^2) (monthly)	**~Month**	**634**	**0**	**0.82**
	~Month+TimePd	639	5	0.07
	~Month+TagLoc	640	6	0.05
95% home range (km^2) (monthly)	**~Month+TagLoc**	**709**	**0**	**0.70**
	~Month+TimePd	711	2	0.27
	~Month+TagLoc+Sex	716	7	0.02
Time spent in area (TSA)	**~s(DistGlac,by=TagLoc×Strategy)+ s(month,by=TagLoc)+Bath**	**71 720**	**0**	**0.98**
	~s(DistGlac,by=TagLoc×Strategy)+ s(month,by=TagLoc)+Bath+Sex	71 729	9	0.01
	~s(DistGlac,by=TagLoc×Strategy)+ s(month,by=TagLoc)+Bath+Mass	71 730	10	0.01
% time within 5 km of glacier front	**~TagLoc+Strategy**	**5**	**0**	**0.91**
	~TagLoc×Strategy	10	5	0.07
	~TagLoc+Strategy×Sex	13	8	0.02
Number of glacier fronts	**~Month**	**1214**	**0**	**0.72**
	~Month+Mass	1218	4	0.07
	~Month+TimePd	1218	4	0.07

tagging group (Fig. 4). Of the 57 tagged seals, 50 spent over 50% of their time close to glaciers and 9 seals (out of 21) tagged on the west coast in 2010–2012 spent 100% of their tracking period in close proximity to these environmental features. The year-round resident seals spent 31% (±14%) more time within 5 km of a glacier front than the seasonally resident seals (Fig. 4) and the seals tagged in 2010–2012 on the west coast spent 31% (±14%) more time within 5 km of a tidal glacier front than then seals tagged in 2002–2003 and 2010–2012 on the east coast (Fig. 4). The 2 groups of seals tagged on the east coast spent similar amounts of time close to tidal glacier fronts (Fig. 4, the best model contained tagging group and strategy, Table 2). The number of tidal glacier fronts seals visited per month decreased from an average of 6 in August to 2 in April (the best model contained month, Table 2). Three seals were within 5 km of over 15 tidal glacier fronts in either August, September or October. The maximum number of glacier fronts seals visited in April was 5.

For the seals tagged in 2002–2003 and 2010–2012 on the east coast, year-round resident seals had higher TSA values directly in front of tidal glacier fronts within a distance of ~5 km while the seasonally resident seals had higher TSA values further away (Fig. 5a,b). The 2 strategy groups behaved similarly for the seals tagged in 2010–2012 on the west coast. However, only one of these 21 seals was resident on a seasonal basis (Fig. 5c). The seals tagged in 2010–2012 on the west coast had higher TSA values close to the tidal glacier fronts than the other 2 groups of seals (Fig. 5).

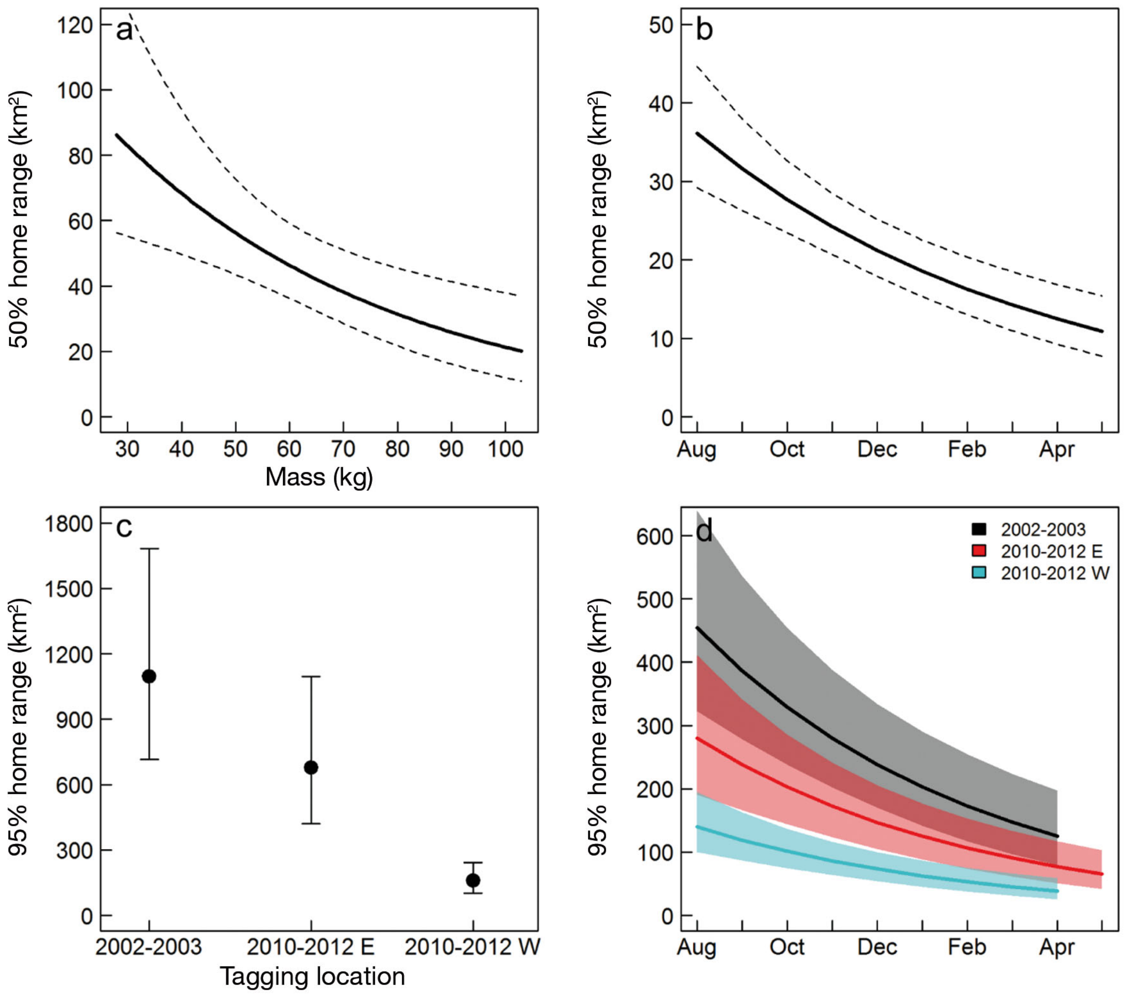

Fig. 3. (a) 50 % home range (mean ± 95 % CI) versus seal body mass and (b) by month for 57 ringed seals equipped with Satellite Relay Data Loggers in 2002–2003 and 2010–2012 in Svalbard, Norway, from coastal areas; (c) 95 % home ranges for seals captured in 2002–2003, 2010–2012 on the east coast and 2010–2012 on the west coast, and (d) by month for these 3 groups of seals

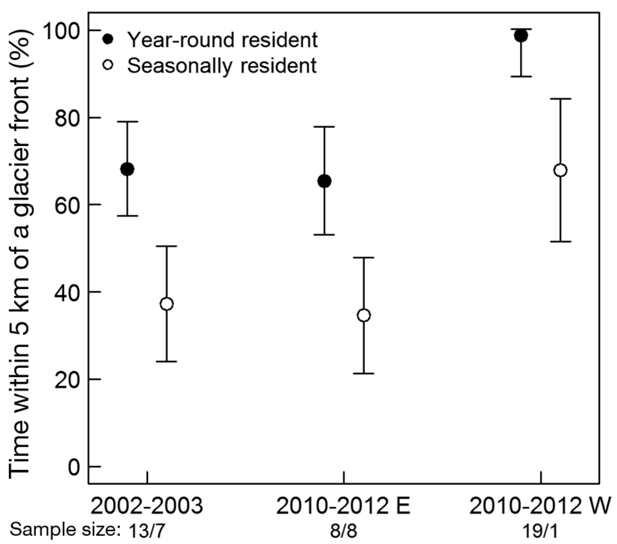

Fig. 4. Proportion of time spent within 5 km of a glacier front (mean ± 95 % CI) for 57 seasonally resident and year-round resident ringed seals equipped with Satellite Relay Data Loggers in Svalbard, Norway, from coastal areas, in 2002–2003, 2010–2012 on the east coast and 2010–2012 on the west coast. Sample size is shown below the *x*-axis according to their residency states

Month had only a negligible effect on TSA values in summer and autumn for all 3 groups of seals (Fig. 6) but TSA values for the seals tagged in 2002–2003 did increase in December and January; this increase was less pronounced for the 2 groups of seals tagged in 2010–2012 (Fig. 6). Bathymetry also influenced TSA values; the seals had higher TSA values in areas shallower than 50 m than in deeper areas (see Table 2 for model selection results).

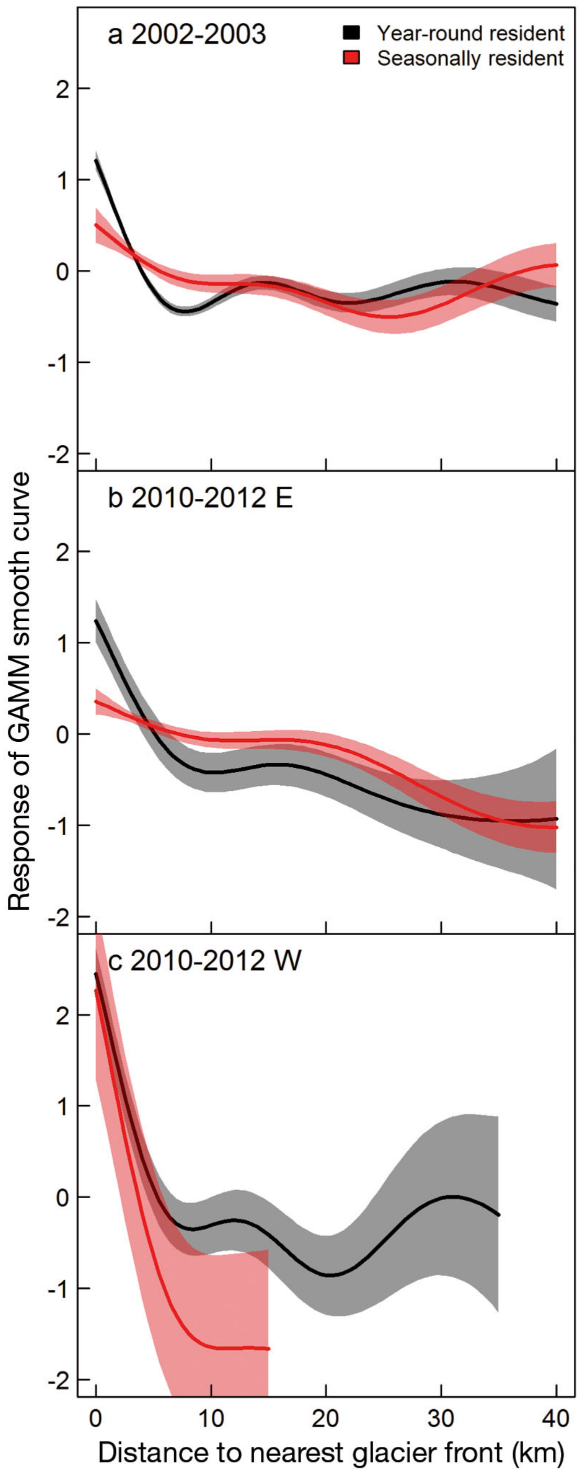

Fig. 5. GAMM smooth curves (mean ± 95% CI) showing the response of time spent in area (TSA) to distance to the nearest glacier front for year-round resident and seasonally resident ringed seals equipped with Satellite Relay Data Loggers in (a) 2002–2003, (b) 2010–2012 on the east coast and (c) 2010–2012 on the west in Svalbard, Norway, from coastal areas. Note that only 1 seal in 2010–2012 on the west coast was seasonally resident

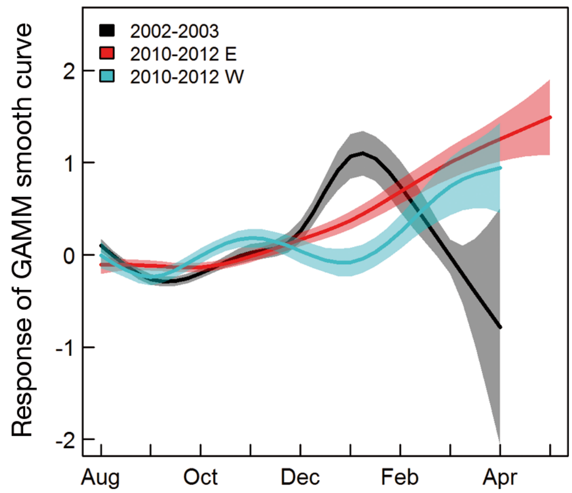

Fig. 6. GAMM smooth curves (mean ± 95% CI) showing the response of time spent in area (TSA) to month for 57 ringed seals equipped with Satellite Relay Data Loggers in 2002–2003, 2010–2012 on the east coast and 2010–2012 on the west coast in Svalbard, Norway, from coastal areas

Dive behaviour

The maximum recorded dive duration and depth in coastal areas were 45.5 min and 302 m, respectively. 95% of transmitted dives were <10 min and <100 m maximum depth and 50% of dives were <4 min and had maximum depths <25 m (Fig. A1 in the Appendix). Transmitted surface durations were <3.5 min for 95% of dives and <1 min for 60% of all dives (Fig. A1).

Seals tagged in the 2 time periods dove to similar depths and spent similar proportions of the dive ascending (Fig. 7, Table 2). However, ringed seals tagged in 2010–2012 generally had dives of longer duration with shorter surface intervals between dives than seals tagged in 2002–2003 (Fig. 8, Table 2). The seals tagged in 2010–2012 also spent less time at the bottom of their dives and more time descending than seals tagged in 2002–2003 (Figs. 7 & 8, Table 2).

The seals tagged on the east and west coasts in 2010–2012 had similar increases in dive duration and decreases in surface duration and bottom time compared to seals tagged in 2002–2003 (Table 2). The increase in percentage of time descending was more pronounced for seals tagged on the west coast than those on the east coast in 2010–2012 (Fig. 7b, Table 2).

Seals tagged on the west coast in 2010–2012 experienced warmer water temperatures both at the surface (from September to January) and at maximum dive depth (from July to January) compared to the seals tagged on the east coast during either tagging

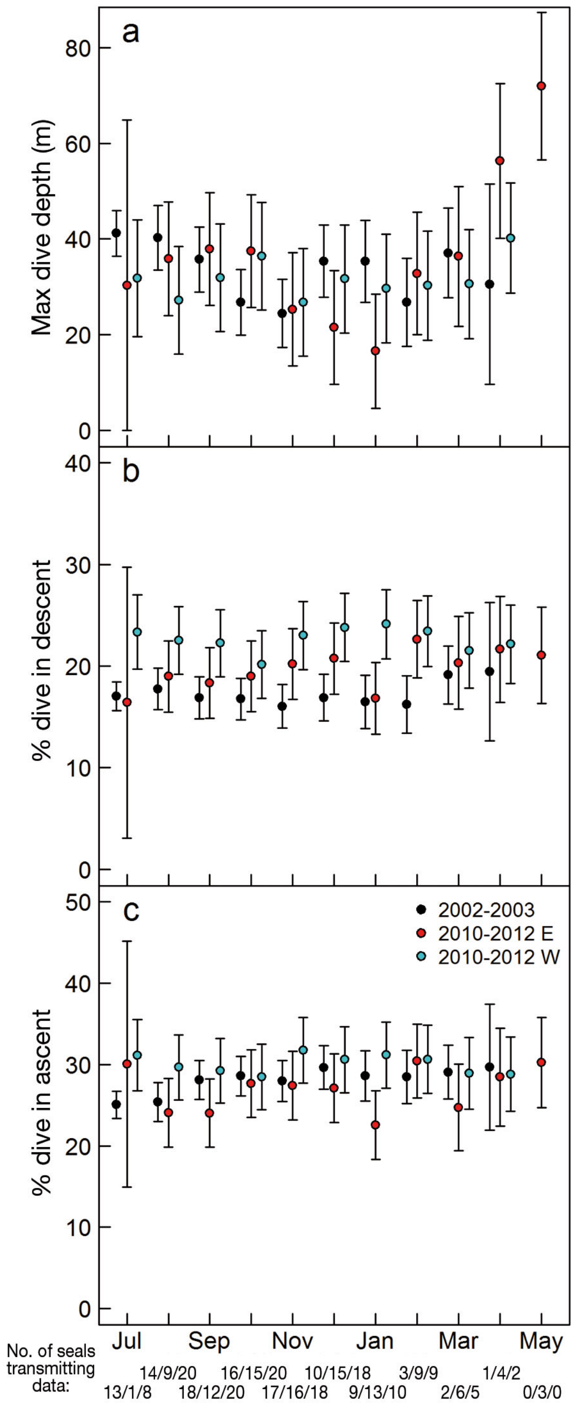

Fig. 7. Results of the BIC-selected model showing (a) maximum dive depth (mean ± 95% CI), (b) percentage of dive in descent and (c) percentage of dive in ascent for the 57 ringed seals equipped with Satellite Relay Data Loggers in 2002–2003, 2010–2012 on the east coast and 2010–2012 on the west coast in Svalbard, Norway, from coastal areas. The number of seals transmitting data in each month is shown below the *x*-axis with the number of seals in 2002–2003, 2010–2012 on the east coast and 2010–2012 on the west coast before, between and after the slashes, respectively

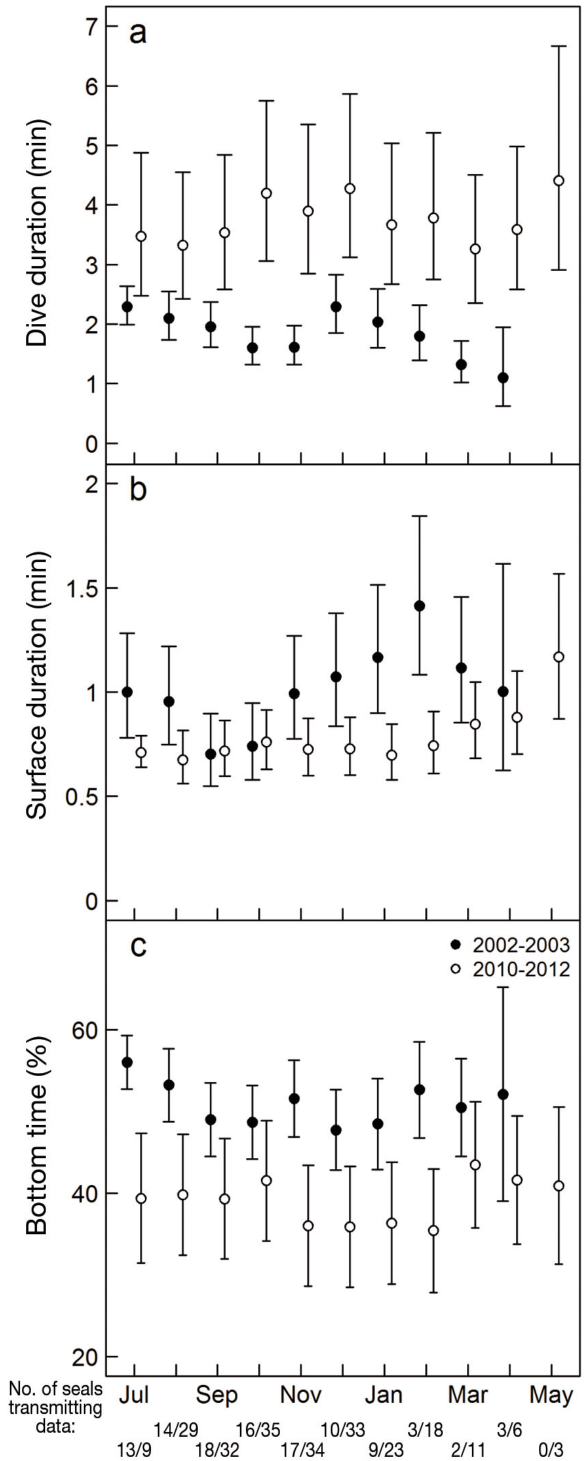

Fig. 8. Results of the BIC-selected model showing (a) dive duration (mean ± 95% CI), (b) surface duration and (c) bottom time by month for 57 ringed seals equipped with Satellite Relay Data Loggers in 2002–2003 and 2010–2012 in Svalbard, Norway, from coastal areas. The number of seals transmitting data in each month is shown below the *x*-axis with the number of seals in 2002–2003 and 2010–2012 before and after the slash, respectively

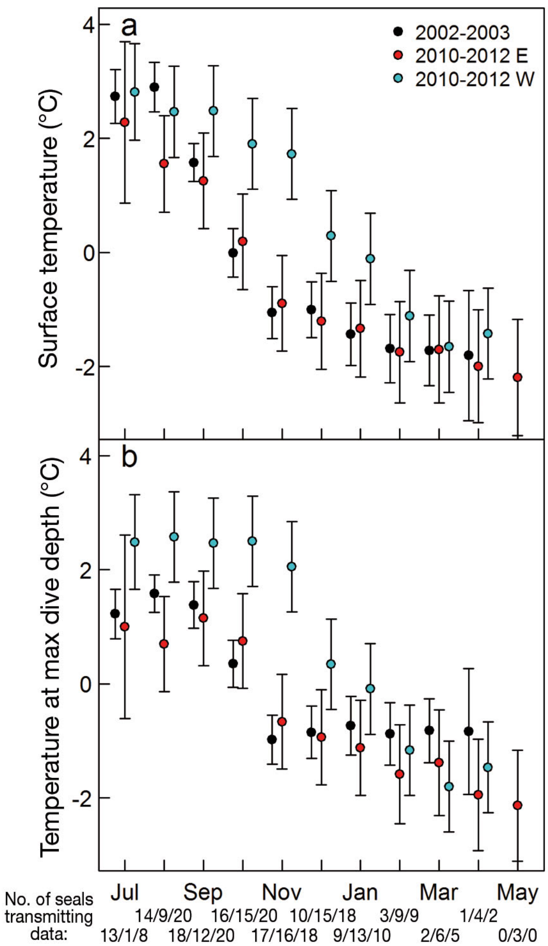

Fig. 9. Results of the BIC-selected model showing (a) surface temperature (mean ± 95% CI) and (b) temperature at the maximum dive depth for 57 ringed seals equipped with Satellite Relay Data Loggers in 2002–2003, 2010–2012 on the east coast and 2010–2012 on the west coast in Svalbard, Norway, from coastal areas. The number of seals transmitting data in each month is shown below the *x*-axis with the number of seals in 2002–2003, 2010–2012 on the east coast and 2010–2012 on the west coast before, between and after the slashes, respectively

period (Fig. 9, Table 2). Seals tagged on the east coast experienced similar water temperatures at the surface and maximum dive depth from July to April in the 2 study periods (Fig. 9, Table 2).

Dive duration, surface duration, maximum dive depth, bottom time percentage and percentage of dive in ascent and descent did not show any consistent changes seasonally (Figs. 7 & 8). Temperature at the surface and at maximum dive depth were highest in the late summer (i.e. July and August) and decreased throughout the fall and winter months, remaining cold through the end of the tracking period in spring (Fig. 9).

DISCUSSION

This study clearly demonstrated that areas close to tidal glacier fronts were the preferred habitat for ringed seals in Svalbard, Norway, throughout the year in coastal areas. The seals spent the majority of their time, and had the highest TSA values, in close proximity to tidal glacier fronts. Several individuals spent their entire tracking period in these areas. Glacier fronts are important feeding areas for many species of marine mammals and seabirds during summer (Lydersen et al. 2014). Large subsurface plumes of fresh meltwater are discharged from glaciers and rise towards the surface; as the meltwater rises it entraps seawater equivalent to tens to hundreds of times the original volume. Plankton carried with the seawater either becomes stunned or dies due to osmotic shock or escapes the freshwater by swimming to depth, becoming trapped along the bottom. This creates rich feeding opportunities for higher trophic level animals (Lydersen et al. 2014). Polar cod *Boreogadus saida* is a major component of the diet of different marine mammals inhabiting Svalbard fjords, including bearded seals *Erignathus barbatus* (Hjelset et al. 1999), white whales *Delphinapterus leucas* (Dahl et al. 2000) and ringed seals (Labansen et al. 2007). This small Arctic fish species is found associated with sea ice, in the water column beneath sea ice, in open water and near the bottom depending on age class (Hop & Gjøsæter 2013). It is likely that the fish concentrate in front of glaciers to take advantage of concentrated, stunned zooplankton. Krill are also frequently eaten by ringed seals at glacier fronts during the summer months (Weslawski et al. 1994).

Ringed seals require a snow pack of at least 45 cm depth for the construction of snow lairs on top of breathing holes in the sea ice, which are used for birthing and nursing of pups and for resting by all age and sex groups (Smith & Stirling 1975, Lydersen & Gjertz 1986). The snow lairs provide pups with thermal shelter and also some protection against predators. If ringed seals are unable to make snow lairs due to insufficient snow conditions they have to give birth directly on the sea ice, which dramatically increases pup mortality (Smith & Lydersen 1991). Average snow depths in Svalbard are generally not sufficient for lair formation; in this region, construction of lairs is dependent on calved pieces of glacier ice frozen into annual fast–ice, creating drifts on their leeward sides, where enough snow accumulates for the seals to dig out lairs (Lydersen & Gjertz 1986, Smith & Lydersen 1991).

Tidal glacier fronts are often found in the inner parts of fjords where there has traditionally been extensive fast-ice formation in Svalbard. Sexually mature ringed seals (i.e. most of the year-round residents in the present study) are often found close to tidal glacier fronts in the winter and spring as they prefer areas with stable ice conditions during the breeding period (Krafft et al. 2007) and these areas have a high density of calved pieces of glacier ice. Under normal Arctic conditions adult females have a network of snow lairs and breathing holes so that they can shift the location of their pup if one structure is attacked by a predator. Males maintain underwater territories ('maritories') that encompass the fast-ice areas of several females (Smith & Hammill 1981, Krafft et al. 2007, Kelly et al. 2010). Similar to other phocids, mating takes place toward the end of lactation (Reeves 1998).

The year-round resident seals (62 ± 20 kg, mean ± SD) were of larger mass than the seasonally resident seals (45 ± 15 kg) (Hamilton et al. 2015). The tagged seals in this study were captured live, so precise ages are not known because teeth were not available to determine age. However, morphological data collected from this population (Lydersen & Gjertz 1987) indicate that the year-round resident seals were the size of sexually mature animals while the seasonally resident seals were mainly sub-adults.

In the breeding period, sub-adult and non-breeding ringed seals tend to occupy the outer edges of the fast-ice habitat where ice conditions are less stable (Krafft et al. 2007). Seasonally resident ringed seals, which were smaller, younger animals, spent larger proportions of their time at greater distances from tidal glacier fronts than year-round resident seals. These younger ringed seals are likely competitively excluded from the prime breeding (and foraging) areas close to the tidal glacier fronts by the larger year-round resident seals upon their return to the Svalbard coast. This competitive exclusion likely begins before the fast-ice forms, as indicated by the seasonally resident seals hauling out a smaller proportion of the time than the year-round resident seals in September. Ringed seals in Svalbard rarely haul out on shore; the only haul-out substrate in September in most Svalbard fjords is therefore calved pieces of glacier ice that are concentrated in front of tidal glaciers, but are also found at lower densities at greater distances from the glacier fronts. Competitive exclusion likely also explains the larger 50% home ranges of smaller, compared to larger, animals. Because sub-adults are confined to suboptimal habitats they would need to use larger areas to fulfil their needs. Sub-adult ringed seals from the Chukchi Sea travel south to the ice edge in the Bering Sea during winter and spring where there are better foraging conditions and a decreased predation risk (Crawford et al. 2012). Similarly, seasonal movements are performed by many young ringed seals in Svalbard following the moult in summer, but in Svalbard they go north in search of ice edges (Freitas et al. 2008a, Hamilton et al. 2015). However, during the late fall they return to the coast and remain there through the winter, spring and early summer until moulting is completed.

The decrease in monthly home range size and daily distance travelled from August through to May found in this study is in accordance with results from tracking studies of ringed seals from other Arctic areas (Born et al. 2004, Kelly et al. 2010, Luque et al. 2014). The number of different tidal glacier fronts visited by seals concomitantly decreased from August through to May. The seasonal reduction in these parameters reflects the need for ringed seals to construct and maintain a network of breathing holes in the fast-ice habitat and to establish and defend territories (see above) which restricts their movement in the winter and spring compared to the autumn.

The late formation of land-fast sea ice in 2010–2012 compared to 2002–2003 resulted in significantly lower TSA values in December and January for the seals tagged in the more recent period. The low TSA values from February to April for the seals in 2002–2003 are most likely due to the decrease in the number of seals transmitting data during this late season period. Only 2 individuals transmitted data for all of February (F37-03 and M40-03); both of these seals were sub-adults. The seals tagged in 2010–2012 on the east coast had significantly higher TSA values from January to the end of the tagging period than the seals tagged in 2010–2012 on the west coast. The ringed seals tagged on the west coast were larger than those tagged on the east coast in 2010–2012 and thus the opposite pattern would be expected (see above). However, declines in fast-ice have been much more extreme on the west coast than the east coast of Svalbard, with the fast-ice in most fjords in the west side forming late or not at all in recent years. In the extreme years (i.e. when no fast-ice has formed or the ice formed too late to accumulate snow) pup rearing has failed (K. M. Kovacs & C. Lydersen unpubl. data) and it is likely impossible for ringed seals to establish territories or for the normal breeding system to function without ice. It is not known whether mating takes place or not in open water conditions.

The seals tagged in 2010–2012 on the west coast spent a larger proportion of time close to glacier fronts and also had smaller 95% home ranges compared with the other 2 groups of seals. The seals tagged in 2010–2012 on the west coast were larger than the other 2 groups of seals and were likely all sexually mature. As glacier fronts are profitable foraging areas (Lydersen et al. 2014), there are no obvious reasons for these ringed seals to leave the areas close to glacier fronts; many of them remained within 5 km of the glacier fronts throughout their tracking periods.

The increased dive duration and decreased surface duration of dives in 2010–2012 compared to 2002–2003 indicate an increase in foraging effort following the sea-ice collapse. Foraging behaviour also changed as shown by the decreased bottom time and increased proportion of dive time spent in the descent phase of diving during 2010–2012 compared to 2002–2003. These changes may be due to several, non-mutually exclusive reasons: neritic feeding may have been replaced by more pelagic feeding; the number of predictable foraging patches may have decreased; or different prey species might have been targeted in the different time periods. For example, instead of seals diving repeatedly to a known prey resource, for example a school of polar cod close to the bottom, they might be spending more time searching in the pelagic water masses during the descent phase in the recent tagging period.

The increases in foraging effort and change in foraging behaviour were not likely due to size or age differences in the sampling periods or areas. Although the seals tagged in 2010–2012 on the west coast were heavier than the seals tagged on the east coast in that same period, the seals tagged in 2010–2012 on the east coast were in the same range of body masses as the seals tagged in this area in 2002–2003 and the observed changes in behaviour were recorded in both areas. There have been large changes in water temperature in the Barents Sea and the western fjords of Spitsbergen (Beszczynska-Möller et al. 2012, Lind & Ingvaldsen 2012, Pavlov et al. 2013). The whole system along the west coast of Svalbard is showing change, with an increasing number and abundance of boreal species that typically associate with Atlantic Water masses, such as Atlantic salmon *Salmo salar*, Atlantic cod *Gadus morhua*, Atlantic herring *Clupea harengus* and Atlantic mackerel *Scomber scombrus*, all of which now occur regularly in the fjords (Jensen et al. 2014, Berge et al. 2015, Fossheim et al. 2015). However, the similar temperatures at the surface and maximum dive depth for seals tagged in the 2 time periods on the east coast indicate that oceanographic conditions in these areas have not changed markedly. However, land-fast sea-ice extent, sea-ice thickness and the seasonal duration of land-fast ice have also declined on the east coast of Svalbard, and these changes are likely impacting Arctic biota, though not to the degree that has taken place in the western parts of the Archipelago (Norwegian Meteorological Institute, http://polarview.met.no/; Leu et al. 2011, Wassmann et al. 2011). But, the increase in foraging effort and changes in foraging behaviour for all of the coastal seals suggests that the changing conditions are impacting prey species composition, abundance and distribution across the Svalbard Archipelago and that these changes are negatively impacting ringed seals. A similar increase in foraging effort has also been documented for the ringed seals that took offshore trips after the summer sea-ice extent shifted from remaining over the continental shelf to a position over the deep Arctic Ocean Basin (Hamilton et al. 2015). Changes in $\delta^{13}C$ stable isotope ratios in ringed seal whiskers in Svalbard in 2013 compared to during the 1990s indicate that more pelagic, and less sympagic, foraging is taking place (A. D. Lowther pers. comm.). This reinforces the suggestion that the changes in diving behaviour documented in this study between the 2 time periods are due to changes in the prey species available to the ringed seals.

The ringed seals tagged on the west coast of Svalbard in July and August 2010–2012 were among the heaviest seals ever captured in Svalbard since research began on this population in the 1980s (Lydersen & Gjertz 1987, Krafft et al. 2006). Normally, pupping in ringed seals occurs in early April in Svalbard and nursing lasts for about 39 d (Hammill et al. 1991). During the nursing period females lose ~0.65 kg d^{-1} despite feeding extensively (Lydersen & Kovacs 1999). When female ringed seals are unable to construct snow lairs due to poor ice conditions or insufficient snow depths, very high levels of pup mortality occur (Lydersen & Smith 1989, Smith & Lydersen 1991). In these circumstances adult females will not deplete their blubber energy stores to the same degree as when they have to complete a normal lactation period. Females would thus enter the summer period with much larger blubber reserves. Male ringed seals also have increased energetic costs during the breeding period in connection with maintaining underwater territories when ice conditions are favourable for breeding. Thus, the lack of fast ice during the breeding period in recent years has likely also affected the spring energy budget of male ringed seals. The large body masses of ringed seals in summer in recent years is thus likely due in part to the poor breeding conditions, although increased food availability might also play a role.

Changes in ringed seal reproductive parameters, pup survival, recruitment and diet have been observed in western Hudson Bay, Canada, in recent decades, which have been linked to ongoing environmental changes (Ferguson et al. 2005, Stirling 2005, Chambellant et al. 2013). It is likely that other Arctic areas are also undergoing changes similar to those occurring in Svalbard, but lack of monitoring leaves them undetected.

The present study clearly demonstrates the importance of areas close to tidal glacier fronts as habitat for coastal ringed seals in Svalbard throughout the year. Tidal glacier front areas are spatially restricted compared to the vast northern ice edge, which is the alternative foraging hot-spot for ringed seals in Svalbard. This space limitation likely leads to high intraspecific competition in these areas, which could explain why mostly large individuals are caught in these areas during summer. Collected behavioural data indicate that, following the major change in sea-ice conditions, ringed seals in coastal areas display increased foraging effort and also a shift in foraging tactics, suggesting that changes in prey species abundance, composition or distribution have occurred at lower trophic levels all across Svalbard.

Sea-ice conditions are predicted to deteriorate further in the coming decades. Less land-fast ice cover and reduced likelihood of the ice being in place long enough for snow accumulation sufficient for construction of snow lairs will impact ringed seal pup production. Tidal glacier fronts in Svalbard are also currently in a negative mass balance (Kohler et al. 2007, Błaszczyk et al. 2009) and both the number of tidal glacier fronts and the length of their fronts have decreased over a 30 to 40 yr period (Błaszczyk et al. 2009). Tidal glacier fronts are the source of the ice pieces that accumulate snow in Svalbard on the land-fast ice, so these glacier changes will impact reproductive habitats as well as prime foraging habitats for ringed seals in Svalbard.

The other summer foraging strategy undertaken by Svalbard ringed seals is offshore foraging/migration trips to the marginal ice zone (Hamilton et al. 2015). The location of the marginal ice zone during summer has shifted from remaining over the productive continental shelf basin to the less productive deep Arctic Ocean basin. These ringed seals thus have to travel further to reach areas with their preferred sea-ice characteristics, and when in these areas travel greater distances per day, have less spatially concentrated foraging activity, spend less time resting on sea ice and have increased foraging effort (Hamilton et al. 2015). Thus, ringed seal foraging strategies have become more challenging; further negative consequences can be expected with continued environmental change that is accompanying global warming.

Surface temperatures in Svalbard are warming at the fastest rate in the Eurasian Arctic (Nordli et al. 2014) and the northern Barents Region is undergoing sea-ice losses at more than twice the rate of other Arctic areas (Laidre et al. 2015). Svalbard can be considered a 'canary in the coal mine' with regard to the effects of climate change, with changes occurring in this region expected to spread to other Arctic areas in the coming decades.

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Appendix. Ringed seal dive statistics for coastal areas in Svalbard, Norway

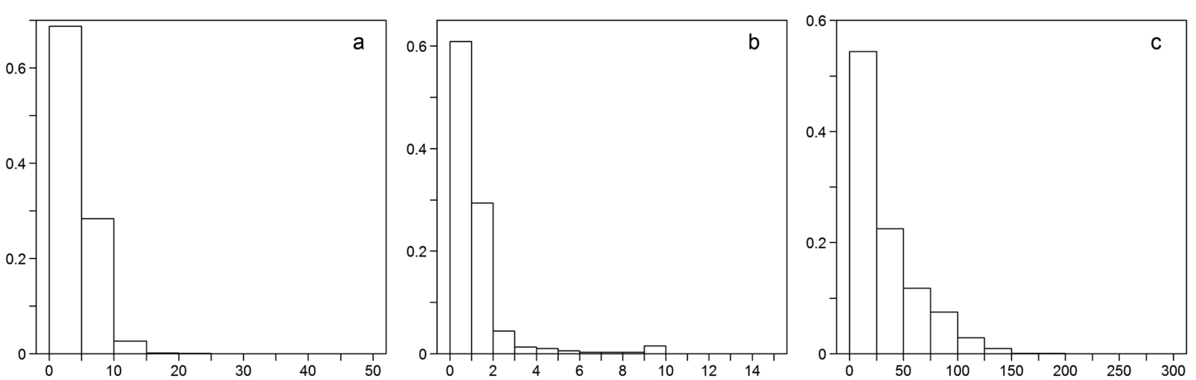

Fig. A1. Proportional distribution of (a) dive duration, (b) surface duration and (c) maximum dive depth for 57 ringed seals equipped with Satellite Relay Data Loggers (SRDLs) in 2002–2003 and 2010–2012 in Svalbard, Norway, while in coastal areas

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