Haul-out behaviour of Arctic ringed seals (*Pusa hispida*): Inter-annual patterns and impacts of current environmental change

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Abstract Hauling out onto a solid substrate is an integral part of most pinnipeds' activity budgets. Ringed seals (*Pusa hispida*) are an Arctic species that hauls out on sea ice routinely throughout the year. In 2006, a sudden change in the sea-ice regime occurred in Svalbard (Norway). Among other changes, the amount of land-fast ice declined sharply. This study examined the intra- and inter-annual haul-out behaviour of sixty ringed seals equipped with satellite-relay data loggers before (2002-2003 (n=22)) and after (2010-2012 (n=38)) the sea-ice decline occurred. In total, ringed seals hauled out 5% to 20% of the time (between August-May) with a mean haul-out duration of 3.3 h. The mean interval between haul-out events was 36 h, with a seasonal pattern that peaked in October (max 81 d). Haul-out probability was influenced by wind speed, temperature and solar hour to varying extents seasonally. After the sea-ice decline, intervals between haul-out events were significantly longer, and from December-March seals had shorter haul-out durations and hauled out a smaller proportion of the time. Haul-out probabilities in the winter and spring were more heavily influenced by weather conditions in 2010-2012 compared to 2002-2003, especially on the west coast where sea-ice declines have been greatest. These changes are likely due to ringed seals hauling out less often in snow lairs due to inadequate snow and ice conditions. Ringed seal haul-out behaviour will likely continue to be impacted negatively by ongoing environmental change, with concomitant impacts on their activity/energy budget and polar bears' hunting behaviour.

Keywords Climate change, Energetics, Rest, Sea ice trends, Svalbard

Introduction

Hauling out onto a solid substrate (e.g. land or ice) is a vital part of the annual activity budget for pinnipeds. Pinnipeds haul out for a variety of reasons, including for birthing and nursing of pups, moulting (i.e. annual replacement of the hair and upper layers of skin), resting and to seek protection from aquatic predators (Feltz & Fay 1966; Kovacs & Lavigne 1986, 1992; Boily 1995). When not hauled out pinnipeds' spend their time in the water - foraging, travelling and resting at the surface, on the bottom or within the water column (Lydersen 1991; Thompson et al. 1991; McConnell et al. 1999; Harkonen et al. 2008; Mitani et al. 2010). Some pinnipeds, such as northern elephant seals (*Mirounga angustirostris*), Ross seals (*Ommatophoca rossii*) and Caspian seals (*Pusa caspica*), can be aquatic for months without hauling out while others, such as walruses (*Odobenus rosmarus*) and harbour seals (*Phoca vitulina*), haul out daily or at least every few days throughout the year (Le Boeuf et al. 2000; Blix & Nordøy 2007; Hamilton et al. 2014, 2015a; Dmitrieva et al. 2016).

Arctic ringed seals (*Pusa hispida*) are an ice-obligate seal with a circumpolar distribution (Reeves 1998). They make and maintain breathing holes in ice-covered areas in the winter and spring, above which they dig out snow lairs that are used by adult females for birthing and nursing of pups, and by all age classes of both sexes for resting (McLaren 1958; Smith & Stirling 1975; Lydersen & Gjertz 1986). Land-fast ice or nearshore, high density pack ice is the preferred breeding habitat for ringed seals because of its stability and seasonal duration (Kingsley et al. 1985; Hammill & Smith 1989; Simpkins et al. 2003; Frost et al. 2004; Bengston et al. 2005; Chambellant et al. 2012), but in some areas this species does use drifting pack ice for breeding (Finley et al. 1983; Reeves 1998; Wiig et al. 1999). Sea ice of both types is also used as a moulting platform in the late spring and early summer and, when available, as a haul-out platform throughout the year (Reeves 1998). Ringed seals in Arctic areas that currently have the largest declines in sea ice are experiencing decreases in reproduction, pup survival, recruitment and body condition and increased stress levels and foraging effort (Ferguson et al. 2005, 2017; Hamilton et al. 2015b, 2016).

Ringed seals are the primary prey of polar bears (*Ursus maritimus*) throughout the Arctic (Derocher et al. 2002; Thiemann et al. 2008; Iversen et al. 2013). Although polar bear kills of ringed seals have been documented in open water (Furnell & Oolooyuk 1980), the primary hunting methods used by polar bears are stalking hauled out seals on sea ice or still-hunting at breathing holes (Stirling 1974). Predation success is linked to ringed seal's seasonal cycles; spring-time reproduction is a key period of vulnerability, but any haul-out behaviour (including concentrated periods such as occurs during moulting) increases ringed seals' accessibility to bears (Pilfold 2015).

Svalbard is a Norwegian High Arctic archipelago (74-81°N, 10-35°E) situated between the Barents Sea, the Greenland Sea and the Arctic Ocean Basin. The West Spitsbergen Current (WSC), a branch of the North Atlantic Current, transports Atlantic Water northward along the west coast of Svalbard along the continental shelf break. The east side of Svalbard is influenced predominantly by Arctic Water masses, with the East Spitsbergen Current (ESC) transporting Arctic Water around the southern tip of Svalbard, northward along the western coast of Svalbard as a coastal current. Water mass exchange occurs periodically across the polar front that exists between the WSC and ESC, mainly driven by wind, and results in intrusions of Atlantic Water into the fjords on the west coast of Svalbard. The magnitude of water mass exchange varies both intra- and inter-annually (Svendsen et al 2002; Cottier et al. 2005; Tverberg et al. 2014). This results in the west coast of Svalbard being more heavily influenced by Atlantic Water than the east coast; correspondingly, air temperatures are also warmer on the west coast (Przybylak et al. 2014).

Svalbard has had the largest increase in air temperatures in the Eurasian Arctic and the largest decline in the seasonal duration of sea-ice cover within the circumpolar Arctic (Nordli et al. 2014; Laidre et al. 2015). These ongoing environmental changes have had a multitude of impacts on Svalbard's wildlife (Descamps et al. 2017). In 2006, there was a sudden change in the sea-ice conditions in coastal areas in Svalbard. Amongst other changes, there was a large decrease in the amount of land-fast ice that formed in the fjords, especially on the west coast of Svalbard, with land-fast ice failing to form in many of the fjords in the last decade (Muckenhuber et al. 2016). Changes in land-fast ice cover are primarily due to an increase in the temperature of the WSC and increased frequencies of intrusions of Atlantic Water into fjords along the west coast (Cottier et al. 2007; Beszczynska-Möller et al. 2012).

Ringed seals in Svalbard have two post-moulting movement strategies; they either undertake offshore excursions in the late-summer and autumn to the marginal ice zone located in the northern Barents Sea or southern Arctic Ocean, or they remain coastal, mainly in association with tidal glacier fronts (Freitas et al. 2008a; Hamilton 2015b, 2016). Ringed seals performing offshore trips are primarily sub-adults but only a portion of the sub-adults travel offshore. The remainder of the sub-adults and most of the large, older seals display the coastal strategy (Hamilton et al. 2015b). Seals performing both movement strategies have been impacted by the decline in sea-ice conditions, with effects including increased foraging effort (Hamilton et al. 2015b, 2016).

Most studies of Arctic ringed seal haul-out behaviour to date have been conducted in association with survey efforts conducted during the annual moulting period when seals spend a lot of time on the ice. They have thus had short seasonal time frames (i.e. spring and early summer) (e.g. Burns & Harbo 1972; Finley 1979; Carlens et al. 2006; Chambellant et al. 2012). Some few studies have reported haul-out behaviour over near-annual time frames, based on biotelemetry data, documenting the overall proportion of time spent hauled out, average haul-out durations and whether there was a circadian or annual pattern in these indices (Heide-Jørgensen et al. 1992; Teilmann et al. 1999; Born et al. 2002; Kelly et al.

2010; Martinez-Bakker et al. 2013). The purpose of the present study is to provide a more in-depth analysis of the haul-out behaviour of ringed seals, including how intervals between haul-out events, haul-out duration, proportion of time hauled out and haul-out probability are affected by biological (including movement strategies of the individuals), temporal (season and solar hour) and physical environmental variables throughout the tagging period (August-May). Potential effects of the major change in sea-ice conditions that took place in Svalbard (2006-onward) are addressed by comparing haul-out behaviour before and after the regional sea-ice collapse.

Materials and methods

Capture and instrumentation

A total of 60 ringed seals were captured with monofilament drift-nets set from shore both before (2002-2003; n=22; 11 from 19 to 21 July 2002 and 11 from 19 to 24 July 2003) and after (2010-2012; n=38; 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) a collapse in sea-ice conditions took place (2006) in Svalbard, Norway (Tables 1-2). Seals were captured in 2002-2003 on the east coast of Svalbard while in 2010-2012 seals were captured on both the east (n=17) and west coasts (n=41; see Hamilton et al. 2016 for further details). Immediately after capture the seals were placed in individual restraining nets and body mass was measured (Salter spring scales, precision ± 0.5 kg) and sex was determined. Various models of Satellite Relay Data Loggers (SRDLs, Sea Mammal Research Unit, University of St Andrews, St Andrews, Scotland) were glued to the hair on their back mid-dorsally using quick-setting epoxy (see Freitas et al. 2008a and Hamilton et al. 2016 for further details). Some of the tagged ringed seals (n=19; 9 in 2002-2003, 10 in 2010-2012) took offshore trips in the late-summer and autumn (i.e. offshore seals) before they returned to the coast and remained in coastal areas until data transmission ceased (i.e. seasonally-resident seals). The remainder of the tagged ringed seals (n=41) stayed coastal throughout the period of data transmission (i.e. year-round resident seals). Four and two of the seals tagged on the east coast in 2002-2003 and 2010-2012, respectively, travelled to the west coast during the time of data transmission. The general movement patterns and aquatic behaviour of these seals have been published in Hamilton et al. (2015b, 2016) and the haul-out behaviour of a subset of east coast animals was explored previously in relation to polar bear spatial patterns (Hamilton et al. 2017).

Data acquisition

SMRU SRDLs are equipped with a wet-dry switch; the tag has to be dry for 10 min for a haul-out event to begin and a haul-out event ends when the tag is wet for 40 s. The SRDLs record and transmit start and end times for individuals haul-out events as well as summary information for 6 h intervals (% time hauled out, diving or resting (wet) at the surface). Haul-out events are given consecutive numbers by the SRDL, which makes it possible to identify gaps in the haul-out record (i.e. haul-out events that were not transmitted). For example, a sequence of 5,6,7,8 indicates that all haul-out events in that time period were transmitted while a sequence of 5,6,8 indicates that one haul-out event was not transmitted. Missing haul-out events were added to the data records when this was possible by using a combination of the summary information, location quality and diving data (Tables 1-2).

ARGOS positions (CLS 2016) were pre-filtered using the speed-distance-angle filter (SDA) in the argosfilter package in R (Freitas et al. 2008b; R Core Team 2016), with additional obviously erroneous locations (i.e. 789 positions far inland – 0.5% of the locations) being removed manually using ArcMap10 (ESRI, Redlands CA). Subsequently, tracks were filtered using the continuous-time correlated random walk model in the CRAWL package in R with a stopping model to account for time spent hauled out (Johnson et al. 2008). The haul-out locations for the ringed seals were extracted from the CRAWL models. All statistical analyses were completed in R version 3.3.1 (R Core Team 2016).

Weather data for the haul-out probability models (see below) were extracted from the Norwegian Meteorological Institute's atmospheric and wave archive for Norwegian and surrounding areas (NORA10; Reistad et al. 2011; Haakenstad et al. 2012). The spatial resolution of this archive is 11 km, with an hourly temporal resolution. Temperature (°C), wind speed (m s^{-1}), precipitation (mm h^{-1}), air pressure (hPa), air pressure change over the past 3 and 12 h (hPa) and cloud cover (%) were collated for the study period(s). Wind chill (T_{wc}; °C) was calculated as,

$$(1)\ T_{wc} = 13.12 + 0.6215 * T_a - 11.37 * V^{0.16} + 0.3965 * T_a * V^{0.16}$$

$$(2)\ T_{wc} = T_a + \left(\frac{-1.59 + 0.1345 * T_a}{5}\right) * V^{0.16}$$

where T_a and V stand for ambient temperature (°C) and wind speed (km h^{-1}), respectively. (1) was used when $T_a \leq 0$°C and $V \geq 5$ km h^{-1} and (2) was used when $T_a \leq 0$°C and $V < 5$ km h^{-1} (Environment Canada, http://climate.weather.gc.ca).

Individual haul-out patterns

A principal component analysis (PCA) was conducted on the average, standard deviation and maximum value of haul-out duration, interval between haul-out events and proportion of time spent hauled out for each individual (by movement strategy) to identify whether there was individual variation in haul-out patterns. The PCA identifies the axes of maximum variance in the data and which of the variables were responsible for this variation (Zuur et al. 2007). A fuzzy k-means cluster, using the Manhattan distance matrix in the cluster package, was conducted to determine the probability of each individual (according to location for the animals that moved offshore) belonging to a cluster (Maechler et al. 2016). A fuzzy k-means cluster differs from a traditional k-means cluster, in that it calculates the probability of a point belonging to each cluster rather than only reporting the cluster to which a point has the highest probability of belonging.

Haul-out indices

The daily haul-out proportion was calculated from the summary records. All four daily summary records had to be transmitted for a given day to be included in these analyses. Fifty-eight of the seals were included in the daily haul-out proportion analyses; seal M89-12 only transmitted three summary records and seal M44-12 never transmitted all four daily summary records (i.e. only 6% of the haul-out events were transmitted by this SRDL; Table 2).

The mean interval between haul-out events (h), haul-out proportion (%) and haul-out duration (h) for each month were bootstrapped from individual seal means using the boot package and 10 000 replicates (Canty & Ripley 2016). These three types of data were also analysed using generalized additive mixed effect models (GAMMs) using the mgcv and gamm4 packages and linear mixed-effect models (LMEs) using the lme4 package, using the Gaussian family and an identity link (Wood 2006; Bates et al. 2015; Wood & Scheipl 2016). Separate models were run for the offshore and coastal seals. Interval between haul-out events and haul-out duration were log-transformed to meet model assumptions. Tag year and individual id were added as nested random effects in all models. Tag year was also added as a VarIdent variance structure to account for heterogeneity in the residuals in the offshore haul-out proportion model (i.e. when the mgcv package was used, Zuur et al. 2009). A linear mixed-effect model was used for the offshore haul-out duration model as data exploration and AICc indicated that none of the predictor variables had non-linear relationships. Possible predictor variables included: study period; movement strategy (i.e. seasonally-resident or year-round resident – only coastal models); coast (i.e. east or west coast - only coastal models); day of year (a running number with July 20, the earliest tagging date, being 1); sex;

body mass; preceding haul-out duration (only interval between haul-out events and haul-out duration models) and; interval between haul-out events (only haul-out duration models). AICc was used for model selection and to evaluate whether a predictor variable should be included in the model linearly or as a smooth term (Burnham & Anderson 2002). Model validation took place as recommended by Zuur et al. (2009).

Haul-out probability

The data transmission period for each seal was divided into half-hour intervals to explore how the probability of hauling out was affected by environmental and physical covariates. An interval was assigned the value 1 if the seal was hauled out for the majority of the time and 0 was assigned if this was not the case. GAMMs were used to analyse haul-out probability using the mgcv package (Wood 2006). The binomial family was used to assess residual variance and the response variable was included using a logistic link (Wood 2006). Fifty-nine seals were included in the haul-out probability analysis. Seal M44-12 only transmitted 6% of the haul-out events (Table 2) so it was removed from this analysis.

The haul-out probability analyses were done separately for the offshore and coastal seals in each study period. Possible predictor variables included: wind chill (°C); temperature (°C); wind speed (m s^{-1}); solar hour; air pressure (hPa); change in air pressure over the last 3 and 12 h (hPa); cloud cover (%); light (categorical variable where 0 = dark, 1 = nautical dawn, 2 = nautical dusk and 3 = light); precipitation (both as a continuous (mm h^{-1}) and as a categorical variable with 0 = no precipitation and 1 = precipitation > 0); coast (only coastal models); movement strategy (only coastal models) and; body mass (kg). All continuous variables were standardized. Variables that were highly correlated (i.e. wind chill is correlated with temperature and wind speed; movement strategy and mass are confounded) were not included simultaneously in the same model. Wind chill, temperature, wind speed, solar hour and air pressure were included using a cubic regression spline to assess if non-linear relationships existed between these variables and the response variable. The variable was included linearly if a non-linear relationship was not found. Solar hour was included as a cyclic cubic regression spline to ensure circularity of the variable (Wood 2006). A k of 4 was used for the smooth curves to achieve model convergence. Seal id and tagging year were included as nested random effects and seal id was also included as a grouping factor in an autoregressive model of order 1 (corAR1) structure to account for temporal autocorrelation (Zuur et al. 2009).

For the offshore seal models, backwards model selection using p-values took place. As p values in GAMM models are approximate (Wood 2006), variables and smooth terms with $p < 0.2$ were included in the final model. To see if the factors affecting haul-out probability of the offshore seals changed between the two study periods, the model from the first period was used to predict the haul-out probability of the seals in the second period. The predicted values and their respective 95% confidence intervals were then compared to the haul-out probability values from the second period.

For the coastal seal models, a further aim of the haul-out probability analyses was to assess if the predictors important for haul-out probability varied over the tagging period. Therefore, the same model was run for each period and season (summer = July to August, autumn = September to November, winter = December to February, spring = March to May). The variables included in the models were: temperature (°C); wind speed ($m\ s^{-1}$); solar hour; air pressure (hPa); light; movement strategy and; coast. Interactions between coast and temperature, coast and wind speed and movement strategy and solar hour were included. Air pressure was included as a cubic regression spline and solar hour was included as a cyclic cubic regression spline. Precipitation ($mm\ h^{-1}$) and cloud cover (%) were not included in the seasonal models because data exploration showed they did not impact haul-out probability;

similarly temperature and wind speed were found to better explain variations in haul-out probability than wind chill (°C) and movement strategy had a larger impact on haul-out probability than body mass. Tagging year was not included as a random effect in the coastal models as it increased the difficulty of model convergence. Models that did converge indicated that the variance associated with tagging year (when it was included as a random effect) was very low (i.e. $<1 \times 10^{-4}$). Model estimates and smooth values were compared between the periods and seasons to assess how the influence of the predictor variables on haul-out probability varied intra-annually, and before and after the change in the sea-ice conditions.

All models were investigated for model fit. Because residuals from binary models are difficult to interpret, the raw data, fitted values, normalized and deviance residuals were grouped by day and seal id to verify model fit (Zuur et al. 2009). The fitted values and residuals were plotted against each other and the normalized residuals were plotted against each predictor variable included and excluded from the final models. To verify that k used in the smooth terms was high enough, a GAM was run on the deviance residuals using an increased value of k to ensure that no pattern remained (Wood 2017). A quantile-quantile plot was constructed to verify linearity of the random effects. Spatial variograms were constructed from the normalized residuals to assess potential spatial correlation.

Results

In total, 6,376 haul-out events were obtained for the ringed seals (2,181 in 2003-2004 and 4,195 in 2010-2012 – 485 from offshore areas and 5,891 from coastal areas; Fig. 1). This represents 89% of the overall number of haul-out events documented in the summary records. For 77% of the seals ≥ 80% of their haul-out events were transmitted (Tables 1, 2). Percentage of haul-out events transmitted was similar between years, except for 2012, when only two of eight seals tagged on the east coast of Svalbard transmitted ≥ 80% of their haul-out events; the other six individuals transmitted 7% to 79% (mean 62% of their haul-out events). For the 46 seals for which records are quite complete, 104 ± 80 (mean ± SD) haul-out events were recorded per individual (range 2-422). Offshore trips took place from 22 July to 18 November and all seals were coastal from 19 November to 29 May.

Individual haul-out patterns

The first two PCA axes explained 81.1% of the variation in the data. Two clusters were chosen based on the NbClust package and by plotting the number of clusters versus the within group sum of squares and validated using the internal validation and stability measure validation functions in the clValid package (Brock et al. 2008; Charrad et al. 2014). Individuals belonging to cluster one were characterized by hauling out for more time each day, having shorter intervals between haul-out events and longer haul-out durations while individuals belonging to cluster two were characterized by hauling out for less time each day, having longer intervals between haul-out events and having shorter haul-out durations (Fig. 2). Not all individuals had a high probability of belonging to one of the two groups; 27 of the 72 individual - movement strategy combinations (38%) did not have a probability of membership ≥ 70% for either of the two groups.

Haul-out proportion

The ringed seals spent an average of 11% (95% CI = 9% to 12%, *n* = 58) of their time hauled out during the tagging period. The proportion of time spent hauled out decreased through the autumn and increased again in the spring (Fig. 3). There was a lot of individual variation in the time animals spent hauled out. The maximum amount of time spent hauled out for an individual was 28% of the total time (seal M34-02), while the minimum was 2% (seal F58-03; Fig. 3).

Offshore seals spent an average of 13% (95% CI = 10% to 17%, *n* = 19) of their time hauled out. Time spent hauled out varied between the two periods, with offshore seals in 2002-2003 spending more time hauled out than offshore seals in 2010-2012 in August and October and shorter amounts of the time in September (Tables 3, Fig. 4, Online Resource 1). Overall, offshore seals in 2002-2003 and 2010-2012 spent 16% (95% CI = 11% to 21%, *n* = 9) and 10% (95% CI = 5% to 15%, *n* = 10), respectively, of their time hauled out.

Coastal seals spent an average of 9% (95% CI = 8% to 11%, *n* = 55) of their time hauled out during the tagging period. Coastal seals on the east coast in 2002-2003 spent a larger proportion of the time hauled out than their counterparts in 2010-2012 (Table 3, Online Resource 1). Coastal seals on the west coast in 2010-2012 spent greater proportions of the time hauled out in August to October and shorter proportions of the time hauled out from December to March compared to seals on the east coast in either of the periods (Table 3, Fig. 4, Online Resource 1). Seasonally-resident seals spent less time hauled out than year-round resident seals when in coastal areas (Table 3, Online Resource 1). Overall, seals in 2002-2003 on the east coast spent 10% (95% CI = 7% to 13%, *n* = 19) and on the west coast spent 11% (95% CI = 3% to 19%, *n* = 3) of their time hauled out. Seals in 2010-2012 on the east coast spent 6% (95% CI = 5% to 8%, *n* = 14) and on the west coast spent 12% (95% CI = 10% to 14%, *n* = 22) of their time hauled out.

Offshore seals hauled out for a greater proportion of time than coastal seals in 2002-2003 and 2010-2012 during the seasonal time frame when seals take offshore trips (Linear mixed effect models - 2002-2003: $t = 5.70$, $p < 0.001$; 2010-2012 east coast: $t = 5.63$, $p < 0.001$; 2010-2012 west coast: $t = 2.50$, $p = 0.014$).

Haul-out duration

The mean haul-out duration for ringed seals was 3.3 h (95% CI = 3.0 h to 3.6 h, n = 60) in total during the tagging period; there was no seasonal variation (i.e. between August and May) in this haul-out parameter (Fig. 3). The three longest haul-out events were 39.4 h (seal F40-12 while on an offshore trip), 32.0 h (seal M59-03, year-round resident) and 30.1 h (seal F57-02 while on an offshore trip).

Offshore seals had a mean haul-out duration of 5.5 h (95% CI = 4.5 h to 6.5 h, n = 19). Mean haul-out duration did not vary between the two study periods (Table 3, Online Resource 1). Coastal seals had a mean haul-out duration of 3.0 h (95% CI = 2.7 h to 3.2 h, n = 56). Mean haul-out duration did not vary overall between the two periods, but seals in 2010-2012 had longer haul-out durations than seals in 2002-2003 from September to November and shorter haul-out durations from December to March (Table 3, Fig. 4, Online Resource 1). Seasonally-resident seals had slightly longer haul-out durations than year-round resident seals (Table 3). Offshore seals had longer haul-out durations than coastal seals in both periods during the seasonal time frame when seals take offshore trips (Linear mixed effect models - 2002-2003: $t = 5.10$, $p < 0.001$; 2010-2012: $t = 4.02$, $p < 0.001$).

Interval between haul-out events

The mean interval between haul-outs events for ringed seals during the tagging period was 36 h (95% CI = 28 h to 44 h, n = 60). The mean interval between haul-out events varied on a seasonal basis (i.e. between August and May), reaching a peak in October (Fig. 3). The three longest intervals between haul-out events were 81 d (seal M36-10 did not haul out between 14 August 2010 and 3 November 2010 - while on an offshore trip), 61 d (seal F57-02 did not haul out between 25 August 2002 and 25 October 2002 - while on an offshore trip) and 53 d (seal F40-10 did not haul out between 7 September 2010 and 30 October 2010 -

while on an offshore trip). Seven of the ten longest intervals between haul-out events (i.e. 33 d to 81 d) were performed by ringed seals during offshore trips (Fig. 3). These 10 longest intervals were evenly split between seals tagged in the two study periods.

Offshore ringed seals had a mean interval between haul-out events of 36 h (95% CI = 25 h to 48 h, *n* = 19). The interval between haul-out events did not vary between the two periods but did increase with day of the year (Table 3, Online Resource 1). Coastal seals had a mean interval between haul-out events of 39 h during the tagging period (95% CI = 31 h to 47 h, *n* = 56). Seals in 2010-2012 had longer intervals between their haul-out events than seals in 2002-2003, and seasonally-resident seals had longer intervals between haul-out events than year-round residents (Table 3, Online Resource 1). The interval between haul-out events had a seasonal pattern (i.e. between August and May) for the coastal seals, peaking in November-December (Fig. 4). Offshore seals had shorter intervals between haul-out events than coastal seals in 2010-2012 (Linear mixed effect model, $t = 3.17$, $p = 0.002$) but similar intervals between haul-out events compared to coastal seals in 2002-2003 during the seasonal time frame when seals take offshore trips (Linear mixed effect model, $t = 0.15$, $p = 0.882$).

Haul-out probability

Different predictor variables affected the haul-out probabilities of offshore seals in the two periods (Table 4). In 2002-2003, increased wind speeds decreased haul-out probability and seals were less likely to haul out in daylight than darkness. Seals also had a larger haul-out probability when air pressure was high in this early period (Fig. 5, Table 4). In 2010-2012, increased temperature decreased haul-out probability and seals preferred to haul out in the afternoon (Fig. 5, Table 4). Fifty-six percent of the haul-out probability values in 2010-2012 were not in the 95% haul-out probability confidence intervals predicted using the 2002-2003 model, indicating that factors affecting haul-out probability changed between the two periods.

Weather conditions in the areas occupied by the offshore seals differed between the two periods. Seals in 2010-2012 were exposed to slightly higher wind speeds, less precipitation and less cloud cover than seals in 2002-2003.

The coastal haul-out probability models showed that the factors affecting haul-out probability varied seasonally (i.e. between August and May), between the two periods, movement strategies and the east and west coasts (Figs. 6, 7, Table 5). Weather conditions also differed between the periods and the two coasts. The west coast of Svalbard was generally warmer, had lower air pressure and more precipitation than the east coast in both periods. There was no clear pattern in wind speed or cloud cover.

Increasing temperatures resulted in increasing haul-out probability in the autumn on the east coast and in the winter on both coasts in 2002-2003 and in summer on the east coast and in autumn, winter and spring on the west coast in in 2010-2012. Conversely, increasing temperature negatively affected haul-out probability in summer on the west coast in both periods, as well as in autumn on the east coast in 2010-2012. Increasing wind speed generally had a negative impact on haul-out probability, with significant reductions in the probability of hauling out in summer and autumn on both coasts in 2002-2003, in autumn and winter in 2010-2012 on both coasts, as well as in spring on the west coast in 2010-2012 (Table 5). Weather covariates had a stronger impact on haul-out probabilities in the winter and spring in 2010-2012, especially on the west coast, compared to 2002-2003 (Table 5). The response of haul-out probability to air pressure varied seasonally and between the different periods, but air pressure generally had little effect; or alternatively, ringed seals preferred to haul out under intermediate or high values of air pressure (Fig. 6).

The response of haul-out probability to solar hour varied seasonally (i.e. between August and May), as well as between the periods and with movement strategy (Fig. 7). A diel pattern was slight or absent during the midnight sun (summer) and polar night (winter) periods. Seasonally-resident seals had a slight diel pattern in the winter in 2010-2012 (Fig. 7). A slight diel pattern was also present in the autumn, with seals preferring to haul out in the late-afternoon and at night (Fig. 7). A stronger diel pattern was present in the spring, although its shape varied between the two study periods and with movement strategy. Seasonally-resident seals in 2002-2003 and year-round resident seals in 2010-2012 had the highest haul-out probabilities during the afternoon, while year-round resident seals in 2002-2003 and seasonally-resident seals in 2010-2012 had the highest haul-out probabilities during the night (Fig. 7).

Seals tagged on the west coast had a higher haul-out probability than seals on the east coast during the summer for both periods and during the autumn and spring in 2010-2012 (Table 5). The effect of movement strategy was not consistent, but seasonally-resident seals generally had a lower haul-out probability than year-round resident seals in the summer and winter in 2002-2003 and in autumn in 2010-2012 (Table 5).

Discussion

The haul-out behaviour of ringed seals in Svalbard varied seasonally and decadally, as well as between the east coast and west coast and according to the movement strategy of individuals. In July and August, ringed seals had short intervals between haul-out events and spent a lot of time hauled out. These haul-out patterns are at least in part associated with moulting, which occurs in the summer; this process is more energetically efficient if seals are hauled out of the water (Feltz & Fay 1966; Boily 1995). During the autumn (September-November), intervals between haul-out events are longer and daily haul-out proportion decreased in Svalbard, consistent with studies conducted in other areas (Heide-Jørgensen et al. 1992; Born et al. 2002; Kelly et al. 2010). The post-moulting period is the primary foraging time for ringed seals. It is during this period that adults regain mass lost during the breeding and moulting periods earlier in the year. It is also an important period of mass gain for sub-adults who have also gone through moult and additionally have energy requirements for growth (Young & Ferguson 2013). For Svalbard ringed seals, the proportion of time hauled out reached maximum values in March and April during the tagging period, with mean haul-out durations also reaching maximum values at this time. Pupping in Svalbard occurs in late March and April (Lydersen 1998), but only two of the ten seals transmitting haul-out data in March were adult females, so pupping is unlikely the sole reason for the increase observed in this study. Other possible reasons for increased time spent hauled out include increased time on the sea ice constructing snow lairs and underwater competition/exclusion by breeding males resulting in young animals spending more time on the ice surface.

Generally speaking, ringed seals in Svalbard hauled out for similar amounts of time and had similar mean haul-out durations compared to ringed seals in other areas (Teilmann et al. 1999; Born et al. 2002; Kelly et al. 2010). However, there is some variation between studies that is likely a result of small sample sizes and high levels of variation in this behaviour, similar to the current study. For example, ringed seals in Svalbard hauled out for a greater proportion of the time compared to four seals tagged in NW Greenland in 1996 (from August-December), but had similar amounts of time hauled out compared to 15 seals tagged in the same area in 1997 and 1999 (Teilmann et al. 1999; Born et al. 2002).

Ringed seals in Svalbard followed similar seasonal patterns in proportion of time spent hauled out to those exhibited in other regions as well, with late-spring/early summer peaks in proportion of time spent hauling out, associated with breeding and moulting (Heide-Jørgensen et al. 1992; Born et al. 2002; Kelly et al. 2010). The spring increase in percentage of time hauled out in the Beaufort and Chukchi Seas occurs a bit later than in Svalbard (April as opposed to March; see Kelly et al. 2010). Ringed seals generally spend the maximum of time hauled out (up to 60% of the time) and reach their greatest densities on the ice in late-May and June, after the end of the data transmission period in the current study (Finley 1979; Smith & Hammill 1981; Kelly & Quakenbush 1990; Born et al. 2002; Bengston et al. 2005; Moulton et al. 2005; Carlens et al. 2006).

The present study did not find differences in haul-out duration between the sexes, likely due to the small number of seals transmitting data in the spring, when males and females are most likely to diverge in their haul-out behaviours. Other studies have found that in the spring and early summer, adult females have longer haul-out durations and haul out for a greater proportion of the time than adult males or sub-adults, likely due to maternal care demands (Kelly & Quakenbush 1990; Carlens et al. 2006).

Haul-out behaviour patterns associated with age are somewhat confounded with movement strategies of the different age classes of ringed seals. Juveniles in many areas of the Arctic, including Svalbard, tend to migrate to offshore areas containing drifting sea ice on a seasonal basis and hence experience different ice conditions and meteorological conditions compared to most of the adults (Kelly et al. 2010; Crawford et al. 2012; Harwood et al. 2015; Hamilton et al. 2015b, 2016).

Seals that took offshore trips in this study had similar haul-out durations and intervals between haul-out events between the two study periods, but seals in 2002-2003 hauled out for greater proportions of the time than seals in 2010-2012 in August and October and smaller proportions of the time in September. The observed difference in the proportion of the time spent hauled out was not due to a lack of suitable haul-out platforms in the second period, as seals in both periods travelled to the marginal ice zone (located in the northern Barents Sea in 2002-2003 and over the Arctic Ocean Basin in 2010-2012). Rather, the differences are likely due to the increased foraging effort documented for the offshore seals in the second study period (Hamilton et al. 2015b).

Overall, coastal ringed seals in 2010-2012 had longer intervals between haul-out events and longer haul-out durations than coastal seals in 2002-2003 from September to November. Ringed seals on the east coast also hauled out less in 2010-2012 compared to 2002-2003 in September to October. These changes may arise from a few, non-mutually exclusive reasons. Declines in sea-ice between the two periods likely decreased the number of suitable resting platforms available to ringed seals, particularly in coastal areas on the west side of Svalbard. This may have resulted in an increase in the intervals between haul-out events, which seals compensated for by hauling out for longer time periods. Coastal seals did increase foraging effort after the change in sea-ice conditions (Hamilton et al. 2016), which concomitantly results in increased intervals between resting events. Ringed seals on the west coast hauled out for greater proportions of the time than ringed seals on the east coast from August to October in both periods. Possible explanations for this include lower predation pressure due to fewer polar bears on the west coast than the east coast and the relative availability of food on the two coasts. The ringed seals had higher body masses on the west coast in the most recent study period, likely due to reproductive failure during the spring breeding season (see Hamilton et al. 2016), decreasing the amount of mass they need to recover during the autumn foraging period. The more in-depth analysis of haul-out behaviour done in this study found differences in daily haul-out proportions between the study periods that were not found in Hamilton et al. (2016).

After the sea-ice collapse in 2006, land-fast ice now forms later in the year or fails to form at all in the fjords on the west coast of Svalbard (Muckenhuber et al. 2016). This limits the amount of time for snow to accumulate to sufficient depths for snow lair formation (minimum and average depth of 32 and > 60 cm, respectively; Smith & Stirling 1975; Lydersen & Gjertz 1986; Hammill & Smith 1989; Furgal et al. 1996). Thus, it is not surprising that during the winter months (December to March), coastal ringed seals in 2010-

2012 had longer intervals between haul-out events and shorter haul-out durations than coastal seals in 2002-2003 and that the seals hauled out less on the west coast than on the east coast in both periods. Weather effects also had stronger impacts on haul-out probability following the sea ice collapse during the winter and spring, especially on the west coast. Ringed seals in 2010-2012 are almost certainly more exposed when they do haul out, without shelter from snow lairs, especially on the west coast where sea-ice changes have been most drastic.

The seasonally-resident seals in this study were primarily sub-adults (Hamilton et al. 2015b), and these younger animals are likely restricted to sub-optimal habitats in the outer regions of the land-fast ice habitat when they share areas with adult animals (Smith 1973a; Furgal et al. 2002; Krafft et al. 2007; Hamilton et al. 2016). Adult females occupy the innermost parts of a fjord while adult males occupy both the inner (likely successful breeding males) and outermost parts (likely those not able to maintain inner-fjord territories) of a fjord (Krafft et al. 2007). The innermost parts of fjords with tidal glacier fronts are prime ringed seal habitat in Svalbard, as calved pieces of glacier ice frozen into the annual land-fast ice tend to accumulate snow to sufficient depths for the formation of snow lairs. The sea ice is also most stable and has the longest period before break-up in spring or summer in these areas (Lydersen & Gjertz 1986; Lydersen et al. 1990; Lydersen & Ryg 1991; Smith & Lydersen 1991; Lydersen et al. 2014). This difference in habitat could explain why seasonally-resident seals hauled out less than year-round resident seals during the tagging period.

Year-round resident ringed seals in the present study lacked a clear diel pattern in their haul-out probability during times of year when light regimes were constant (i.e. the midnight sun and polar night periods), similar to other studies of ringed seals and other Arctic animals (i.e. harbour seals, Svalbard reindeer (*Rangifer tarandus platyrhynchus*), Svalbard rock ptarmigan (*Lagopus mutus hyperboreus*) and walruses) (Reierth & Stokkan 1998; Born et al. 2002; van Oort et al. 2005; Hamilton et al. 2014, 2015a). Both seasonally-resident and year-round resident seals in the present study had a higher haul-out probability in the late afternoon and evening in the months when a light-dark cycle was present. A tendency to haul-out during the evening has also been found for both pups, sub-adults and adults in the subnivean period in early spring (Kelly & Quakenbush 1990; Lydersen & Hammill 1993; Kelly et al. 2010). This diel tendency is likely related to: conditions in their under-ice environment; behaviour of their prey; or behaviour of their primary predator (or a combination thereof). Ringed seals often feed sympagically on ice-associated fish and invertebrates (Reeves 1998; Labansen et al. 2007). Sympagic prey may be easier for ringed seals to find when light is present in the morning or early afternoon.

The changes in the diel pattern of haul-out probability between the two periods in the spring might be related to changes in ringed seals' prey base. Following the shift in the sea-ice conditions in Svalbard, changes in the stable isotope composition in ringed seal whiskers, an increase in foraging effort and a change in foraging behaviour have all indicated that changes have occurred in the marine food web of the region (Hamilton et al. 2016; Lowther et al. 2017). An alternative reason why ringed seals may have changed their diel haul-out pattern is related to the deterioration of sea-ice and snow conditions. Changes in the exposure to environmental conditions, due to less time being spent in snow lairs, and a decreased length of time nursing pups due to higher pup mortality rates may have altered the diel pattern of haul-out probability.

Similar to many studies of pinniped haul-out behaviour, the ringed seals in this study were affected by environmental conditions. For example, increasing wind speeds decreased haul-out probability (Smith 1973b; Finley 1979; Smith & Hammill 1981; Carlens et al. 2006). The probability of hauling out also generally increased with increasing air temperature, similar to the findings of other studies (Moulton et al. 2002; Carlens et al. 2006), though it is worth noting that some studies have found no clear trend between haul-out behaviour and air temperature (Finley 1979; Smith & Hammill 1981; Moulton et al. 2002). In the current study, some inconsistencies were displayed in this relationship both within and between study periods. One potential explanation for the mixed responses observed is the avoidance of unusually warm conditions. Watts (1992) found that seals haul out less frequently when they begin to gain net heat from the environment. This has been suggested for ringed seals by Burns & Harbo (1972; 7°C to 15°C), Finley (1979; 5°C to 9°C) and Moulton et al. (2002; >7°C), as well as for other Arctic pinnipeds including walruses and harp seals (*Pagophilus groenlandicus*; Fay & Ray 1968; Moulton et al. 2000). The maximum temperature recorded for offshore seals in 2010-2012 was 6.2°C and for coastal seals, the maximum temperature ranged from 5°C to 9.8°C for the time periods that had a negative relationship with temperature. Another potential reason for ringed seals decreasing the probability of hauling out with increasing temperature might be the avoidance of high wind speeds. Increases in air temperature were sometimes associated with increases in wind speed (e.g. for offshore seals in 2010-2012). Hamilton et al. (2014) also found that harbour seals in Svalbard had a lower haul-out probability when air temperature increased, and suggested that this was likely due to high air temperatures being related to low pressure systems and concomitant high wind speeds.

The changes in haul-out patterns documented here will likely affect polar bear predation on ringed seals, as the traditional hunting methods of polar bears rely on ringed seals hauling out on sea ice (Stirling 1974). The change in sea-ice conditions in Svalbard has impacted the amount of sea ice available for haul-out in the summer and autumn months, particularly on the west side of the archipelago, which has been suggested as the reason for marked changes in coastal polar bear movement patterns in summer. Polar bears are spending much more time on land targeting terrestrial prey during the summer months following the sea-ice collapse (Hamilton et al. 2017).

This study has documented the overall seasonal patterns in ringed seal haul-out behaviour in Svalbard. It also explored how haul-out patterns are changing in relation to the ongoing climate-change driven changes. A primary breeding requirement for ringed seals is having a stable sea-ice platform with sufficient snow cover during the birthing and nursing periods, as snow lairs provide pups with both thermal and predator protection (Smith & Stirling 1975; Lydersen & Gjertz 1986). Years with low snow depths, particularly less than 32 cm, are linked to low pup survival and recruitment (Lydersen & Smith 1989; Ferguson et al. 2005, Iacozza & Ferguson 2014). Ringed seal haul-out behaviour will likely continue to be negatively impacted by the ongoing environmental changes occurring in the Arctic, with impacts on their activity budgets and breeding success, which will have wider implications for Arctic marine and terrestrial food webs.

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Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All procedures performed were approved by the Norwegian Animal Research Authority and the Governor of Svalbard.

References

Bates D, Mächler M, Bolker B, Walker SC (2015) Fitting linear mixed-effect models using lme4. J Stat Softw 67. doi:10.18637/jss.v067.i01

Bengston JL, Hiruki-Raring LM, Simpkins MA, Boveng PL (2005) Ringed and bearded seal densities in the eastern Chukchi Sea, 1999-2000. Polar Biol 28:833-845 doi:10.1007/s00300-005-0009-1

Beszczynska-Möller A, Fahrbach E, Schauer U, Hansen E (2012) Variability in Atlantic water temperature and transport at the entrance to the Arctic Ocean, 1997-2010. ICES J Mar Sci 69:852-863. doi:10.1093/icesjms/fss056

Blix AS, Nordøy ES (2007) Ross seal (*Ommatophoca rossii*) annual distribution, diving behaviour, breeding and moulting, off Queen Maud Land, Antarctica. Polar Biol 30:1449-1458. doi:10.1007/s00300-007-0306-y

Boily P (1995) Theoretical heat flux in water and habitat selection of phocid seals and beluga whales during the annual molt. J Theor Biol 172: 235-244. doi:10.1006/jtbi.1995.0020

Born EW, Teilmann J, Riget F (2002) Haul-out activity of ringed seals (*Phoca hispida*) determined from satellite telemetry. Mar Mamm Sci 18:167-181. doi:10.1111/j.1748-7692.2002.tb01026.x

Brock G, Pihur V, Datta S, Datta S (2008) clValid: An R package for cluster validation. J Stat Softw 25. doi:10.18637/jss.v025.i04

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY

Burns JJ, Harbo Jr SJ (1972) An aerial census of ringed seals, northern coast of Alaska. Arctic 25:279-290. doi:10.14430/arctic2972

Canty A, Ripley B (2016) boot: Bootstrap R (S-Plus) functions. R package version 1.3-18

Carlens H, Lydersen C, Krafft BA, Kovacs KM (2006) Spring haul-out behaviour of ringed seals (*Pusa hispida*) in Kongsfjorden, Norway. Mar Mamm Sci 22:379-393. doi:10.1111/j.1748-7692.2006.00034.x

Chambellant M, Lunn NJ, Ferguson SH (2012) Temporal variation in distribution and density of ice-obligated seals in western Hudson Bay, Canada. Polar Biol 35:1105-1117. doi:10.1007/s00300-012-1159-6

Charrad M, Ghazzali N, Boiteau V, Niknafs A (2014) NbClust: An R package for determining the relevant number of clusters in a data set. J Stat Softw 61. doi:10.18637/jss.v061.i06

Collecte Localisation Satellites (CLS) (2016) Argos user's manual. www.argos-system.org/manual/. Accessed 15 March 2017

Cottier F, Tverberg V, Inall M, Svendsen H, Nilsen F, Griffiths C (2005) Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. J Geophys Res 110:C12005. doi:10.1029/2004JC002757

Cottier FR, Nilsen F, Inall ME, Gerland S, Tverberg V, Svendsen H (2007) Wintertime warming of an Arctic shelf in response to large-scale atmosphere circulation. Geophys Res Lett 34:L10607. doi:10.1029/2007GL029948

Crawford JA, Frost KJ, Quakenbush LT, Whiting A (2012) Different habitat use strategies by subadult and adult ringed seals (*Phoca hispida*) in the Bering and Chukchi seas. Polar Biol 35:241-255. doi:10.1007/s00300-011-1067-1

Derocher AE, Wiig Ø, Andersen M (2002) Diet composition of polar bears in Svalbard and the western Barents Sea. Polar Biol 25:448-452. doi:10.1007/s00300-002-0364-0

Descamps S, Aars J, Fuglei E, Kovacs KM, Lydersen C, Pavlova O, Pedersen AØ, Ravolainen V, Strøm H (2017) Climate change impacts on wildlife in a High Arctic archipelago – Svalbard, Norway. Glob Change Biol 23:490-502. doi:10.1111/gcb.13381

Dmitrieva L, Jüssi M, Jüssi I, Kasymbekov Y, Verevkin M, Baimukanov M, Wilson S, Goodman SJ (2016) Individual variation in seasonal movements and foraging strategies of a land-locked, ice-breeding pinniped. Mar Ecol Prog Ser 554:241-256. doi:10.3354/meps11804

Fay FH, Ray C (1968) Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from thermoregulatory behavior. Zoologica (NY) 53:1-18

Feltz ET, Fay FH (1966) Thermal requirements *in vitro* of epidermal cells from seals. Cryobiology 3:261-264. doi:10.1016/S0011-2240(66)80020-2

Ferguson SH, Stirling I, McLoughlin P (2005) Climate change and ringed seal (*Phoca hispida*) recruitment in Western Hudson Bay. Mar Mamm Sci 21:121-135 doi:10.1111/j.1748-7692.2005.tb01212.x

Ferguson SH, Young BG, Yurkowski DJ, Anderson R, Willing C, Nielsen O (2017) Demographic, ecological, and physiological responses of ringed seals to an abrupt decline in sea ice availability. PeerJ 5:e2957 doi:10.7717/peerj.2957

Finley KJ (1979) Haul-out behaviour and densities of ringed seals (*Phoca hispida*) in the Barrow Strait area, N.W.T. Can J Zool 57:1985-1997. doi:10.1139/z79-263

Finley KJ, Miller GW, Davis RA, Koski WR (1983) A distinctive large breeding population of ringed seals (*Phoca hispida*) inhabiting the Baffin Bay pack ice. Arctic 36:162-173. doi:10.14430/arctic2259

Freitas C, Kovacs KM, Ims RA, Fedak MA, Lydersen C (2008a) Ringed seal post-moulting movement tactics and habitat selection. Oecologia 155:193-204. doi:10.1007/s00442-007-0894-9

Freitas C, Lydersen C, Fedak M, Kovacs KM (2008b) A simple new algorithm to filter marine mammal Argos locations. Mar Mamm Sci 24:315-325. doi:10.1111/j.1748-7692.2007.00180.x

Frost KJ, Lowry LF, Pendleton G, Nute HR (2004) Factors affecting the observed densities of ringed seals, *Phoca hispida,* in the Alaskan Beaufort Sea, 1996-99. Arctic 57:115-128. doi:10.14430/arctic489

Furgal CM, Innes S, Kovacs KM (1996) Characteristics of ringed seal, *Phoca hispida*, subnivean structures and breeding habitat and their effects on predation. Can J Zool 74:858-874. doi:10.1139/z96-100

Furgal CM, Innes S, Kovacs KM (2002) Inuit spring hunting techniques and local knowledge of the ringed seal in Arctic Bay (Ikpiarjuk), Nunavut. Polar Res 21:1-16. doi:10.3402/polar.v21i1.6470

Furnell DJ, Oolooyuk D (1980) Polar bear predation on ringed seals in ice-free water. Can Field Nat 94:88-89

Haakenstad H, Reistad M, Haugen JE, Breivik Ø (2012) Update of the NORA10 hindcast archive for 2011 and a study of polar low cases with the WRF model. Rep no. 17/2012. Norwegian Meteorological Institute, Oslo

Hamilton CD, Lydersen C, Ims RA, Kovacs KM (2014) Haul-out behaviour of the world’s northernmost population of harbour seals (*Phoca vitulina*) throughout the year. PLoS ONE 9:e86055. doi:10.1371/journal.pone.0086055

Hamilton CD, Kovacs KM, Lydersen C (2015a) Year-round haul-out behaviour of male walruses *Odobenus rosmarus* in the Northern Barents Sea. Mar Ecol Prog Ser 519:251-263. doi:10.3354/meps11089

Hamilton CD, Lydersen C, Ims RA, Kovacs KM (2015b) Predictions replaced by facts: a keystone species’ behavioural responses to declining Arctic sea ice. Biol Lett 11:20150803. doi:10.1098/rsbl.2015.0803

Hamilton CD, Lydersen C, Ims RA, Kovacs KM (2016) Coastal habitat use by ringed seals *Pusa hispida* following a regional sea-ice collapse: importance of glacial refugia in a changing Arctic. Mar Ecol Prog Ser 545:261-277. doi:10.3354/meps11598

Hamilton CD, Kovacs KM, Ims RA, Aars J, Lydersen C (2017) An Arctic predator-prey system in flux: climate change impacts on coastal space use by polar bears and ringed seals. J Anim Ecol 86:1054-1064. doi:10.1111/1365-2656.12685

Hammill MO, Smith TG (1989) Factors affecting the distribution and abundance of ringed seal structures in Barrow Strait, Northwest Territories. Can J Zool 67:2212-2219. doi:10.1139/z89-312

Harkonen T, Jüssi M, Jüssi I, Verevkin M, Dmitrieva L, Helle E, Sagitov R, Harding KC (2008) Seasonal activity budget of adult Baltic ringed seals. PLoS ONE 3:e2006. doi:10.1371/journal.pone.0002006

Harwood LA, Smith TG, Auld JC, Melling H, Yurkowski DJ (2015) Seasonal movements and diving of ringed seals, *Pusa hispida*, in the Western Canadian Arctic, 1999-2001 and 2010-11. Arctic 68:193-209. doi:10.14430/arctic4479

Heide-Jørgensen MP, Stewart BS, Leatherwood S (1992) Satellite tracking of ringed seals *Phoca hispida* off northwest Greenland. Ecography 15:56-61. doi:10.1111/j.1600-0587.1992.tb00008.x

Iacozza J, Ferguson SH (2014) Spatial-temporal variability of snow over sea ice in western Hudson Bay, with reference to ringed seal pup survival. Polar Biol 37:817-832. doi:10.1007/s00300-014-1484-z

Iversen M, Aars J, Haug T, Alsos IG, Lydersen C, Bachmann L, Kovacs KM (2013) The diet of polar bears (*Ursus maritimus*) from Svalbard, Norway, inferred from scat analysis. Polar Biol 36:561-571. doi:10.1007/s00300-012-1284-2

Johnson DS, London JM, Lea MA, Durban JW (2008) Continuous-time correlated random walk model for animal telemetry data. Ecology 89:1208−1215. doi:10.1890/07-1032.1

Kelly BP, Quakenbush LT (1990) Spatiotemporal use of lairs by ringed seals (*Phoca hispida*). Can J Zool 68:2503-2512. doi:10.1139/z90-350

Kelly BP, Badajos OH, Kunnasranta M, Moran JR, Martinez-Bakker M, Wartzok D, Boveng P (2010) Seasonal home ranges and fidelity to breeding sites among ringed seals. Polar Biol 33:1095-1109. doi:10.1007/s00300-010-0796-x

Kingsley MCS, Stirling I, Calvert W (1985) The distribution and abundance of seals in the Canadian High Arctic, 1980-82. Can J Fish Aquat Sci 42:1189-1210. doi:10.1139/f85-147

Kovacs KM, Lavigne DM (1986) Maternal investment and neonatal growth in phocid seals. J Anim Ecol 55:1035-1051. doi:10.2307/4432

Kovacs KM, Lavigne DM (1992) Maternal investment in otariid seals and walruses. Can J Zool 70:1953-1964. doi:10.1139/z92-265

Krafft BA, Kovacs KM, Lydersen C (2007) Distribution of sex and age groups of ringed seals *Pusa hispida* in the fast-ice breeding habitat of Kongsfjorden, Svalbard. Mar Ecol Prog Ser 335:199-206. doi:10.3354/meps335199

Labansen AL, Lydersen C, Haug T, Kovacs KM (2007) Spring diet of ringed seals (*Phoca hispida*) from northwestern Spitsbergen, Norway. ICES J Mar Sci 64:1246-1256. doi:10.1093/icesjms/fsm090

Laidre KL, Stern H, Kovacs KM, Lowry L, Moore SE, Regehr EV, Ferguson SH, Wiig Ø, Boveng P, Angliss RP, Born EW, Litovka D, Quakenbush L, Lydersen C, Vongraven D, Ugarte F (2015) Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conserv Biol 29:724-737. doi:10.1111/cobi.12474

Le Boeuf BJ, Crocker DE, Costa DP, Blackwell SB, Webb PB, Houser DS (2000) Foraging ecology of northern elephant seals. Ecol Monogr 70:353-382. doi:10.1890/0012-9615(2000)070[0353:FEONES]2.0.CO;2

Lowther AD, Fisk A, Kovacs KM, Lydersen C (2017) Interdecadal changes in the marine food web along the west Spitsbergen coast detected in the stable isotope composition of ringed seal (*Pusa hispida*) whiskers. Polar Biol 40:2027-2033. doi:10.1007/s00300-017-2122-3

Lydersen C (1991) Monitoring ringed seal (*Phoca hispida*) activity by means of acoustic telemetry. Can J Zool 69:1178-1182. doi:10.1139/z91-167

Lydersen C (1998) Status and biology of ringed seals (*Phoca hispida*) in Svalbard. NAMMCO 1:46-62. doi:10.7557/3.2980

Lydersen C, Gjertz I (1986) Studies of the ringed seal (*Phoca hispida* Schreber 1775) in its breeding habitat in Kongsfjorden, Svalbard. Polar Res 4:57−63. doi:10.3402/polar.v4i1.6920

Lydersen C, Smith TG (1989) Avian predation on ringed seal *Phoca hispida* pups. Polar Biol 9:489-490. doi:10.1007/BF00261031

Lydersen C, Jensen PM, Lydersen E (1990) A survey of the Van Mijen fiord, Svalbard, as habitat for ringed seals, *Phoca hispida*. Holarctic Ecol 13:130-133. doi:10.1111/j.1600-0587.1990.tb00598.x

Lydersen C, Ryg M (1991) Evaluating breeding habitat and populations of ringed seals *Phoca hispida* in Svalbard fjords. Polar Rec 27:223-228. doi:10.1017/S0032247400012614

Lydersen C, Hammill MO (1993) Diving in ringed seal (*Phoca hispida*) pups during the nursing period. Can J Zool 71:991-996. doi:10.1139/z93-131

Lydersen C, Assmy P, Falk-Petersen S, Kohler J, Kovacs KM, Reigstad M, Steen H, Strøm H, Sundfjord A, Varpe Ø, Walczowski W, Weslawski JM, Zajaczkowski W (2014) The importance of tidewater glaciers for marine mammals and seabirds in Svalbard, Norway. J Mar Syst 129:452-471. doi:10.1016/j.jmarsys.2013.09.006

Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K (2016) cluster: Cluster analysis basics and extensions. R package version 2.0.4. https://CRAN.R-project.org/package=cluster

Martinez-Bakker ME, Sell SK, Swanson BJ, Kelly BP, Tallmon DA (2013) Combined genetic and telemetry data reveal high rates of gene flow, migration, and long-distance dispersal potential in Arctic ringed seals (*Pusa hispida*). PLoS ONE 8: e77125. doi:10.1371/journal.pone.0077125

McConnell BJ, Fedak MA, Lovell P, Hammond PS (1999) Movements and foraging areas of grey seals in the North Sea. J Appl Ecol 36:573-590. doi:10.1046/j.1365-2664.1999.00429.x

McLaren IA (1958) The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. Bull Fish Res Board Can 118

Mitani Y, Andrews RD, Sato K, Kato A, Naito Y, Costa DP (2010) Three-dimensional resting behaviour of northern elephant seals: drifting like a falling leaf. Biol Lett 6:163-166. doi:10.1098/rsbl.2009.0719

Moulton VD, Miller EH, Ochoa-Acuña H (2000) Haulout behaviour of captive harp seals (*Pagophilus groenlandicus*): incidence, seasonality, and relationships to weather. Appl Anim Behav Sci 65:367-378. doi:10.1016/S0168-1591(99)00062-3

Moulton VD, Richardson WJ, McDonald TL, Elliott RE, Williams MT (2002) Factors influencing local abundance and haulout behaviour of ringed seals (*Phoca hispdia*) on landfast ice of the Alaskan Beaufort Sea. Can J Zool 80:1900-1917. doi:10.1139/z02-173

Moulton VD, Richardson WJ, Elliott RE, McDonald TL, Nations C, Williams MT (2005) Effects of an offshore oil development on local abundance and distribution of ringed seals (*Phoca hispida*) of the Alaskan Beaufort Sea. Mar Mamm Sci 21:217-242. doi:10.1111/j.1748-7692.2005.tb01225.x

Muckenhuber S, Nilsen F, Korosov A, Sandven S (2016) Sea ice cover in Isfjorden and Hornsund, Svalbard (2000-2014) from remote sensing data. Cryosphere 10:149-158. doi:10.5194/tc-10-149-2016

Nordli Ø, Przybylak R, Ogilvie AEJ, Isaksen K (2014) Long-term temperature trends and variability on Spitsbergen: the extended Svalbard Airport temperature series, 1898-2012. Polar Res 33:21349. doi:10.3402/polar.v33.21349

Pilfold NW, Derocher AE, Stirling I, Richardson E (2015) Multi-temporal factors influence predation for polar bears in a changing climate. Oikos 124:1098-1107. doi:10.1111/oik.02000

Przybylak R, Araźny A, Nordli Ø, Finkelnburg R, Kejna M, Budzik T, Migała K, Sikora S, Puczko D, Rymer K, Rachlewicz G (2014) Spatial distribution of air temperature on Svalbard during 1 year with campaign measurements. Int J Climatol 34:3702-3719. doi:10.1002/joc.3937

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Reeves RR (1998) Distribution, abundance and biology of ringed seals (*Phoca hispida*): an overview. NAMMCO 1:9-45. doi:10.7557/3.2979

Reierth E, Stokkan KA (1998) Activity rhythm in High Arctic Svalbard ptarmigan (*Lagopus mutus hyperboreus*). Can J Zool 76:2031-2039. doi:10.1139/z98-173

Reistad M, Breivik Ø, Haakenstad H, Aarnes OJ, Furevik BR, Bidlot JR (2011) A high-resolution hindcast of wind and waves for the North Sea, the Norwegian Sea, and the Barents Sea. J Geophys Res 116:C05019. doi:10.1029/2010JC006402

Simpkins MA, Hiruki-Raring LM, Sheffield G, Grebmeier JM, Bengston JL (2003) Habitat selection by ice-associated pinnipeds near St. Lawrence Island, Alaska in March 2001. Polar Biol 26:577-586. doi:10.1007/s00300-003-0527-7

Smith TG (1973a) Population dynamics of the ringed seal in the Canadian Eastern Arctic. Bull Fish Res Board Can No 181

Smith TG (1973b) Censusing and estimating the size of ringed seal populations. Fish Res Board Can Tech Rep 427

Smith TG, Stirling I (1975) The breeding habitat of the ringed seal (*Phoca hispida)*. The birth lair and associated structures. Can J Zool 53:1297−1305. doi:10.1139/z75-155

Smith TG, Hammill MO (1981) Ecology of the ringed seal, *Phoca hispida*, in its fast ice breeding habitat. Can J Zool 59:966-981. doi:10.1139/z81-135

Smith TG, Lydersen C (1991) Availability of suitable land-fast ice and predation as factors limiting ringed seal populations, *Phoca hispida*, in Svalbard. Polar Res 10:585-594. doi:10.1111/j.1751-8369.1991.tb00676.x

Stirling I (1974) Midsummer observations on the behaviour of wild polar bears (*Ursus maritimus*). Can J Zool 52:1191-1198. doi:10.1139/z74-157

Svendsen H, Beszczynska-Møller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Ørbæk JB, Bischof K, Papucci C, Zajaczkowski M, Azzolini R, Bruland O, Wiencke C, Winther JG, Dallmann W (2002) The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. Polar Res 21:133-166. doi:10.3402/polar.v21i1.6479

Teilmann J, Born EW, Acquarone M (1999) Behaviour of ringed seals tagged with satellite transmitters in the North Water polynya during fast-ice formation. Can J Zool 77: 1934-1946. doi:10.1139/z99-163

Thiemann GW, Iverson SJ, Stirling I (2008) Polar bear diets and Arctic marine food webs: Insights from fatty acid analysis. Ecol Monogr 78:591-613. doi:10.1890/07-1050.1

Thompson D, Hammond PS, Nicholas KS, Fedak MA (1991) Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). J Zool 224:223-232. doi:10.1111/j.1469-7998.1991.tb04801.x

Tverberg V, Nøst OA, Lydersen C, Kovacs KM (2014) Winter sea ice melting in the Atlantic Water subduction area, Svalbard Norway. J Geophys Res 119:5645-5967. doi:10.1002/2014JC010013

van Oort BEH, Tyler NJC, Gerkema MP, Folkow L, Blix AS, Stokkan KA (2005) Circadian organization in reindeer. Nature 438:1095-1096. doi:10.1038/4381095a

Watts P (1992) Thermal constraints on hauling out by harbour seals (*Phoca vitulina*). Can J Zool 70:553-560. doi:10.1139/z92-083

Wiig Ø, Derocher AE, Belikov SE (1999) Ringed seal (*Phoca hispida*) breeding in the drifting pack ice of the Barents Sea. Mar Mamm Sci 15:595-598. doi:10.1111/j.1748-7692.1999.tb00828.x

Wood SN (2006) Generalized additive models: An introduction with R. Chapman & Hall/CRC, Boca Raton, FL

Wood SN (2017) choose.k in Package “mgcv” reference manual. https://cran.r-project.org/web/packages/mgcv/mgcv.pdf. Accessed 01 March 2017

Wood S, Scheipl F (2016) gamm4: Generalized additive mixed models using “mgcv” and “lme4.” R package version 0.2-4. https://CRAN.R-project.org/package=gamm4

Young BG, Ferguson SH (2013) Seasons of the ringed seal: pelagic open-water hyperphagy, benthic feeding over winter and spring fasting during molt. Wildl Res 40: 52-60. doi:10.1071/WR12168

Zuur AF, Ieno EN, Smith GM (2007) Analysing ecologial data. Springer, New York, NY

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY

Tables

Table 1 Haul-out data for the ringed seals (*Pusa hispida*) in Svalbard, Norway equipped with Satellite Relay Data Loggers in 2002-2003, including the duration of data transmission (d), whether the seal took an offshore trip, the number of haul-out events transmitted, the number of missing haul-out events added and the proportion of the haul-out record (%) obtained. The first letter in the seal ID indicates the sex, the numbers before the dash indicate the seal's body mass (kg) and the numbers after the dash indicate the tagging year

Seal ID	Tagging date	Duration of haul-out record (d)	Tagging latitude (°N)	Tagging longitude (°E)	Trip	Number of transmitted haul-out events	Total number of haul-out events	Number of missing haul-out events added	Complete haul-out record (%)
F31-02	21-07-2002	112	78.7	20.2	Y	150	152	1	99
F33-02	21-07-2002	40	78.7	20.2	Y	43	43	0	100
F36-02	21-07-2002	63	78.7	20.2	Y	55	56	0	98
F37-02	20-07-2002	164	78.7	20.2	Y	50	56	0	89
F57-02	19-07-2002	159	78.7	20.2	Y	38	41	1	95
F59-02	21-07-2002	71	78.7	20.2	Y	60	62	0	97
M28-02	20-07-2002	114	78.7	20.2	N	66	68	1	99
M34-02	19-07-2002	55	78.7	20.2	N	97	148	12	74
M50-02	19-07-2002	91	78.7	20.2	Y	54	58	1	95
M65-02	20-07-2002	155	78.7	20.2	N	97	101	2	98
M72-02	21-07-2002	43	78.7	20.2	N	106	152	9	76
F28-03	20-07-2003	151	78.7	20.2	N	111	111	0	100
F34-03	19-07-2003	130	78.7	20.2	Y	52	57	2	95
F37-03	22-07-2003	230	78.7	20.2	Y	78	79	0	99
F53-03	21-07-2003	182	78.7	20.2	N	200	215	2	94
F57-03	21-07-2003	39	78.7	20.2	N	49	59	1	85
F58-03	19-07-2003	103	78.7	20.2	N	44	44	0	100
F59-03	20-07-2003	99	78.7	20.2	N	61	63	1	98
F89-03	20-07-2003	107	78.7	20.2	N	81	83	1	99
M40-03	22-07-2003	245	78.7	20.2	N	154	161	6	99
M57-03	21-07-2003	170	78.7	20.2	N	194	210	9	97
M59-03	24-07-2003	154	78.7	20.2	N	274	309	18	95
MEAN		**122**				**96**	**106**		**95**
SD		**58**				**62**	**70**		**7**

Table 2 Haul-out data for the ringed seals (*Pusa hispida*) in Svalbard, Norway equipped with Satellite Relay Data Loggers in 2010-2012, including the duration of data transmission (d), whether the seal took an offshore trip, the number of haul-out events transmitted, the number of missing haul-out events added and the proportion of the haul-out record (%) obtained. The first letter in the seal ID indicates the sex, the numbers before the dash indicate the seal's body mass (kg) and the numbers after the dash indicate the tagging year

Seal ID	Tagging date	Duration of haul-out record (d)	Tagging latitude (°N)	Tagging longitude (°E)	Trip	Number of transmitted haul-out events	Total number of haul-out events	Number of missing haul-out events added	Complete haul-out record (%)
F34-10	3-8-2010	146	79.8	21.7	Y	55	70	7	89
F40-10	25-7-2010	232	80.2	23.2	Y	91	110	8	90
F43-10	3-8-2010	99	79.8	21.7	N	30	39	4	87
F52a-10	2-8-2010	191	79.8	21.7	N	143	190	22	87
M34-10	2-8-2010	177	79.8	21.7	N	54	58	3	98
M36-10	26-7-2010	118	80.2	23.2	Y	12	12	0	100
F52b-10	3-8-2010	209	79.8	21.7	Y	65	83	1	80
F60-10	29-7-2010	192	80.2	23.1	Y	76	99	9	86
M62-10	1-8-2010	177	79.8	21.7	Y	50	119	5	46
F61-11	28-7-2011	139	78.9	12.4	N	102	108	4	98
F66-11	30-7-2011	169	78.9	12.4	N	222	344	15	69
F72-11	3-8-2011	46	78.9	12.4	N	88	190	5	49
F73-11	22-7-2011	86	78.9	12.4	N	131	178	11	80
F76-11	30-7-2011	75	78.9	12.4	N	107	136	18	92
F99-11	29-7-2011	196	78.9	12.4	N	110	111	1	100
M55-11	28-7-2011	112	78.9	12.4	N	124	184	7	71
M57-11	3-8-2011	132	78.9	12.4	N	126	158	4	82
M81-11	24-7-2011	143	78.9	12.4	N	105	178	9	64
M90-11	3-8-2011	148	78.9	12.4	Y	72	74	1	99
M100-11	20-7-2011	203	78.9	12.4	N	229	248	7	95
F34-12	5-8-2012	114	79.8	21.7	N	58	73	0	79
F35-12	30-7-2012	305	79.8	21.7	Y	120	181	8	71
F40-12	1-8-2012	176	79.8	21.7	Y	76	100	6	82
F56-12	6-8-2012	192	79.8	21.7	N	73	103	6	77
F62-12	6-8-2012	213	79.8	21.7	N	128	181	5	73
M38-12	5-8-2012	281	79.8	21.7	N	123	217	13	63
M44-12	29-7-2012	151	79.8	21.7	N	16	291	4	7
M46-12	1-8-2012	6	79.8	21.7	Y	2	2	0	100
F61a-12	15-8-2012	69	78.9	12.4	N	97	99	2	100
F61b-12	17-8-2012	257	78.9	12.4	N	163	169	4	99
F64-12	18-8-2012	179	78.9	12.4	N	81	85	0	95
M60a-12	25-8-2012	211	78.6	12.6	N	175	263	0	67
M60b-12	15-8-2012	258	78.9	12.4	N	422	422	0	100
M74-12	25-8-2012	108	78.6	12.6	N	23	23	0	100
M88-12	26-8-2012	177	78.6	12.6	N	224	242	4	94
M89-12	19-8-2012	6	78.9	12.4	N	3	3	0	100
M100-12	25-8-2012	190	78.6	12.6	N	78	78	0	100
M103-12	25-8-2012	179	78.6	12.6	N	147	148	1	100
MEAN		**160**				**105**	**141**		**83**
SD		**68**				**78**	**93**		**20**

Table 3 Results of the daily haul-out proportion (%), haul-out duration (h) and interval between haul-out events (h) models for the ringed seals (*Pusa hispida*) equipped with Satellite Relay Data Loggers in Svalbard, Norway, in 2002-2003 and 2010-2012, showing the estimate, SE, *t* and *p* values for the predictor variables. PrecHaulDur stands for duration of the preceding haul-out event (h) and TimeLastHaul stands for aquatic duration to the last haul-out event (h)

Model	**Variable**	**Estimate**	**SE**	***t***	***p***
Haul-out proportion (%)	Intercept	14.107	3.948	3.573	<0.001
(offshore)	2010-2012	-2.366	5.329	-0.444	0.657
Haul-out proportion (%)	Intercept	11.649	1.160	10.043	<0.001
(coastal)	Offshore	-5.444	1.461	-3.727	<0.001
	2002-2003:West	-11.382	23.175	-0.491	0.623
	2010-2012: East	-3.589	1.622	-2.213	0.027
	2010-2012:West	0.765	1.454	0.526	0.599
Haul-out duration (h)	Intercept	5.058	0.128	39.510	<0.001
(offshore)	PrecHaulDur	0.313	0.063	4.934	<0.001
	2010-2012	-0.032	0.198	-0.163	0.873
Haul-out duration (h)	Intercept	4.454	0.070	63.363	<0.001
(coastal)	TimeLastHaul	-0.051	0.017	-3.046	0.002
	Offshore	0.157	0.094	1.666	0.096
	2010-2012	0.026	0.081	0.316	0.752
Interval between haul-out events (h)	Intercept	5.524	0.228	24.204	<0.001
(offshore)	DayOfYear	0.309	0.127	2.424	0.016
	2010-2012	-0.026	0.352	-0.075	0.940
Interval between haul-out events (h)	Intercept	5.202	0.129	40.243	<0.001
(coastal)	2010-2012	0.383	0.150	2.550	0.011
	Offshore	0.462	0.177	2.611	0.009

Table 4 Results of the haul-out probability models run for ringed seals (*Pusa hispida*) equipped with Satellite Relay Data Loggers in Svalbard, Norway that took offshore trips in 2002-2003 and 2010-2012. The estimate, SE, *t* and *p* values are shown for the linear predictor variables and the estimated degrees of freedom (edf) and *p* value are shown for the predictor variables included in a smooth function in each model, as well as the variance of the random effects and the level of temporal autocorrelation (phi)

Variables	**Parameter**	**2002-2003**	**2010-2012**
Intercept	Estimate	-1.551	-2.475
	SE	0.225	0.431
Temperature (°C)	Estimate	na	-0.247
	SE	na	0.101
	t	na	-2.436
	p	na	**0.015**
Precipitation (mm h^{-1})	Estimate	na	-0.041
	SE	na	0.029
	t	na	-1.393
	p	na	0.164
Air pressure change (12 h)	Estimate	na	-0.102
	SE	na	0.072
	t	na	-1.417
	p	na	0.157
Wind speed (m s^{-1})	Estimate	-0.118	na
	SE	0.054	na
	t	-2.174	na
	p	**0.030**	na
Light_dawn	Estimate	-0.194	0.178
	SE	0.118	0.176
	t	-1.648	1.012
	p	0.099	0.312
Light_dusk	Estimate	-0.126	-0.094
	SE	0.116	0.179
	t	-1.082	-0.529
	p	0.279	0.597
Light_light	Estimate	-0.277	0.270
	SE	0.130	0.194
	t	-2.126	1.390
	p	**0.034**	0.165
Solar hour	edf	na	1.265
	p	na	0.179
Air pressure (hPa)	edf	3.671	na
	p	**<0.001**	na
Random effect SD	Tag year	0.001	0.519
	ID	0.500	0.536
Phi		0.913	0.898

Table 5 Results of the haul-out probability model run for each season for the coastal ringed seals (*Pusa hispida*) that were equipped with Satellite Relay Data Loggers in Svalbard, Norway, in 2002-2003 and 2010-2012. The estimate, SE, *t* and *p* values are shown for the linear predictor variables and the estimated degrees of freedom (edf) and *p* value are shown for the predictor variables included in a smooth function in each model, as well as the variance of the random effect and the level of temporal autocorrelation (phi)

Variable	**Parameter**	**2002-2003**				**2010-2012**			
		Summer	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**	**Spring**
Intercept	Estimate	-2.615	-2.612	-1.991	-1.634	-3.027	-2.859	-2.873	-2.775
	SE	0.434	0.240	0.129	0.354	0.350	0.161	0.205	0.276
Temperature (°C)	Estimate	-0.031	-0.063	0.220	0.001	0.315	-0.140	0.065	0.006
	SE	0.049	0.053	0.106	0.223	0.142	0.068	0.077	0.134
	t	-0.631	-1.174	2.070	0.006	2.224	-2.067	0.853	0.043
	p	0.528	0.241	0.038	0.995	0.026	0.039	0.394	0.966
Wind speed (m s^{-1})	Estimate	-0.154	-0.125	-0.079	0.342	-0.071	-0.222	-0.295	0.171
	SE	0.048	0.050	0.077	0.202	0.104	0.060	0.062	0.099
	t	-3.211	-2.490	-1.019	1.690	-0.680	-3.717	-4.783	1.719
	p	0.001	0.013	0.308	0.091	0.496	<0.001	<0.001	0.086
Light_Dawn	Estimate	ref	-0.089	0.013	-0.144	ref	-0.106	-0.029	0.163
	SE	ref	0.058	0.070	0.238	ref	0.041	0.056	0.147
	t	ref	-1.536	0.183	-0.605	ref	-2.608	-0.517	1.107
	p	ref	0.125	0.855	0.545	ref	0.009	0.605	0.268
Light_Dusk	Estimate	-0.051	0.002	-0.047	-0.338	0.135	-0.084	0.031	0.188
	SE	0.204	0.056	0.073	0.233	0.148	0.040	0.054	0.147
	t	-0.252	0.040	-0.638	-1.448	0.915	-2.097	0.576	1.277
	p	0.801	0.968	0.524	0.148	0.360	0.036	0.565	0.202
Light_Light	Estimate	0.062	-0.079	-0.398	-0.186	0.209	-0.187	-0.058	0.065
	SE	0.202	0.073	0.249	0.299	0.151	0.052	0.208	0.160
	t	0.309	-1.080	-1.599	-0.624	1.388	-3.607	-0.280	0.405
	p	0.757	0.280	0.110	0.533	0.165	<0.001	0.780	0.685
Coast_West	Estimate	1.907	0.527	0.091	na	0.774	0.536	0.276	1.182
	SE	0.476	0.349	0.510	na	0.367	0.185	0.246	0.277
	t	4.009	1.512	0.178	na	2.108	2.905	1.120	4.252
	p	<0.001	0.131	0.859	na	0.035	0.004	0.263	<0.001
Movement strategy_Offshore	Estimate	-1.256	-0.441	-0.768	1.075	-0.615	-0.732	-0.324	0.170
	SE	0.713	0.406	0.247	0.621	0.512	0.213	0.254	0.300
	t	-1.761	-1.088	-3.113	1.732	-1.201	-3.434	-1.279	0.566
	p	0.078	0.276	0.002	0.084	0.230	<0.001	0.201	0.571
Temperature (°C)*Coast_West	Estimate	-1.138	0.382	-0.081	na	-0.380	0.499	0.386	0.572
	SE	0.478	0.122	0.522	na	0.154	0.080	0.104	0.171
	t	-2.380	3.140	-0.155	na	-2.471	6.252	3.699	3.339
	p	0.017	0.002	0.877	na	0.014	<0.001	<0.001	<0.001
Wind speed (m s^{-1})*Coast_West	Estimate	-0.336	-0.642	-0.401	na	0.082	-0.038	0.072	-0.424
	SE	0.295	0.164	0.333	na	0.120	0.070	0.082	0.129
	t	-1.138	-3.921	-1.203	na	0.684	-0.537	0.874	-3.303
	p	0.255	<0.001	0.229	na	0.494	0.591	0.382	<0.001
Solar hour_coastal	edf	1.216	1.493	<0.001	1.789	1.263	1.945	1.264	1.881
	p	0.080	0.019	0.888	<0.001	0.060	<0.001	0.067	<0.001
Solar hour_offshore	edf	0.653	1.483	0.245	0.804	<0.001	0.922	1.407	1.659
	p	0.223	0.023	0.317	0.183	0.570	0.154	0.037	0.003
Air pressure (hPa)	edf	1.920	1.000	1.000	1.000	1.954	1.926	1.611	1.000
	p	<0.001	0.006	0.009	0.088	<0.001	0.003	0.299	0.972
Random effect	SD	1.355	0.728	<0.001	<0.001	0.728	0.380	0.492	<0.001
Temporal correlation	Phi	0.786	0.841	0.885	0.826	0.792	0.840	0.823	0.849

Figure Captions

Fig. 1 Haul-out locations for ringed seals (*Pusa hispida*) equipped with Satellite Relay Data Loggers in Svalbard, Norway, in 2002-2003 and 2010-2012 (by tagging location in 2012)

Fig. 2 PCA plot showing the results of a fuzzy cluster analysis for ringed seals (*Pusa hispida*) equipped with Satellite Relay Data Loggers in Svalbard, Norway, in 2002-2003 and 2010-2012. Each circle or triangle represents a seal – movement strategy combination belonging to group 1 (red circle) or group 2 (blue triangle). Darker red and blue colours indicate a higher probability of membership to groups 1 and 2, respectively. The arrows show the variables used in the PCA analysis

Fig. 3 a) The daily haul-out proportion (mean ± 95% CI; %), b) haul-out duration (mean ± 95% CI; h) and c) interval between haul-out events (mean ± 95% CI; d) for ringed seals (*Pusa hispida*) equipped with Satellite Relay Data Loggers in Svalbard, Norway, in 2002-2003 and 2010-2012. The values at the top and bottom (only haul-out proportion) of the plots indicate the maximum and minimum values of that index for each month. The values beneath the x-axis indicates the number of seals transmitting data in each month

Fig. 4 Response of generalized additive mixed effect models' smooth curves to day of year for a) daily haul-out proportion (%) for offshore ringed seals (*Pusa hispida*) in 2002-2003 (purple) and 2010-2012 (blue), b) daily haul-out proportion (%) for coastal ringed seals in 2002-2003 on the east coast (purple), 2010-2012 on the east coast (blue) and 2010-2012 on the west coast (green), [coastal seals in 2002-2003 on the west coast were not included due to a low number of haul outs in this category] c) haul-out duration (h) for coastal ringed seals in 2002-2003 (purple) and 2010-2012 (blue) and d) interval between haul-out events (h) for coastal seals equipped with Satellite Relay Data Loggers in Svalbard, Norway. The grey on the rug plots indicates values present in all groups and the navy on the rug plot in b) indicates values present on both coasts in 2010-2012

Fig. 5 Response of the haul-out probability generalized additive mixed effect model (GAMM) smooth curves to a) air pressure (hPa; 2002-2003) and b) solar hour (2010-2012) for ringed seals (*Pusa hispida*) equipped with Satellite Relay Data Loggers in Svalbard, Norway that undertook offshore migrations

Fig. 6 Response of haul-out probability generalized additive mixed effect model (GAMM) smooth curves to air pressure (hPa) for a) summer, b) autumn, c) winter and d) spring for coastal ringed seals (*Pusa hispida*) equipped with Satellite Relay Data Loggers in Svalbard, Norway in 2002-2003 and 2010-2012. The green on the rug plot indicates values present in both periods

Fig. 7 Response of haul-out probability generalized additive mixed effect model (GAMM) smooth curves to solar hour for a) summer, b) autumn, c) winter and d) spring for the year-round resident and seasonally-resident ringed seals (*Pusa hispida*; when in coastal areas) equipped with Satellite Relay Data Loggers in Svalbard, Norway in 2002-2003 and 2010-2012

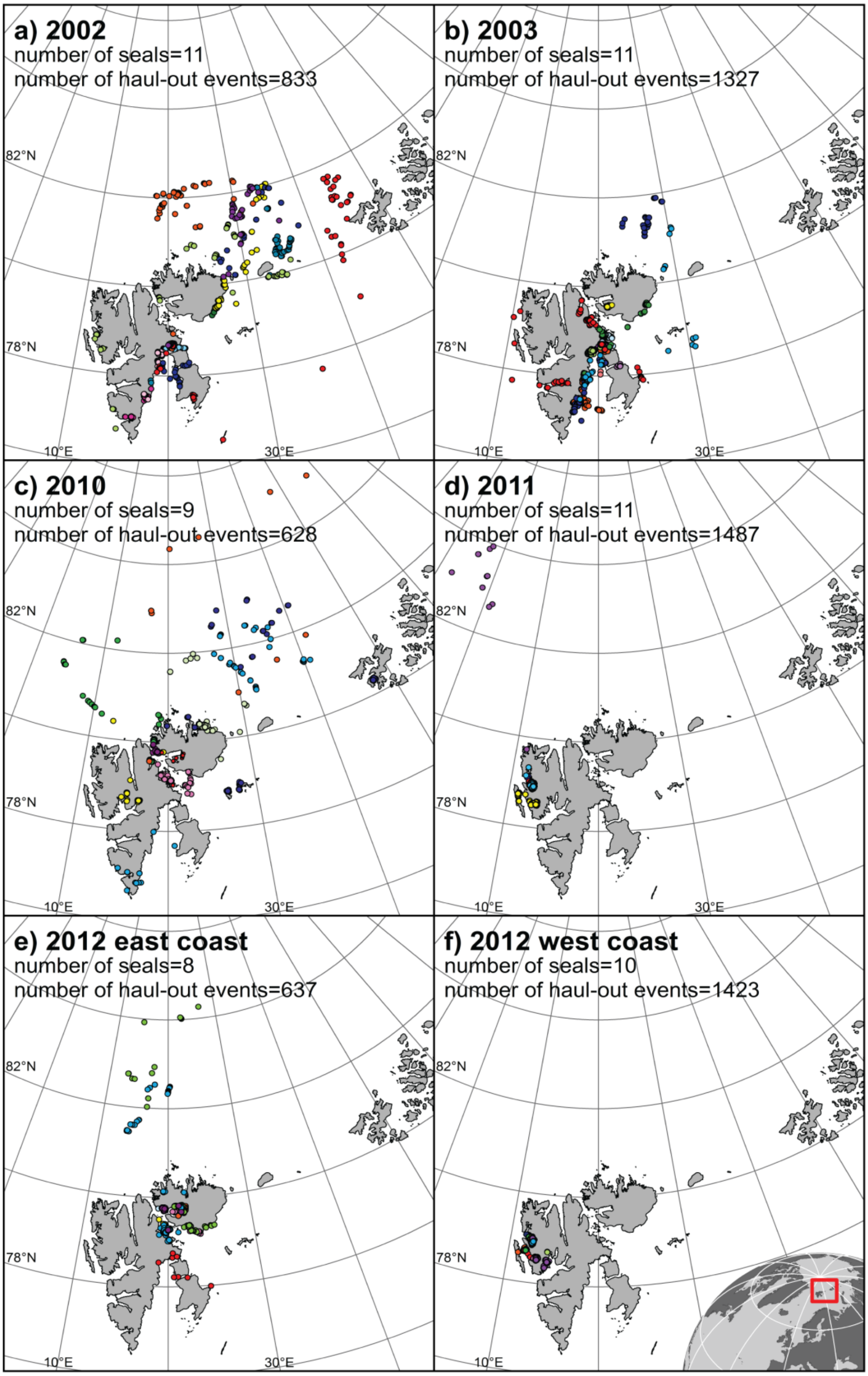
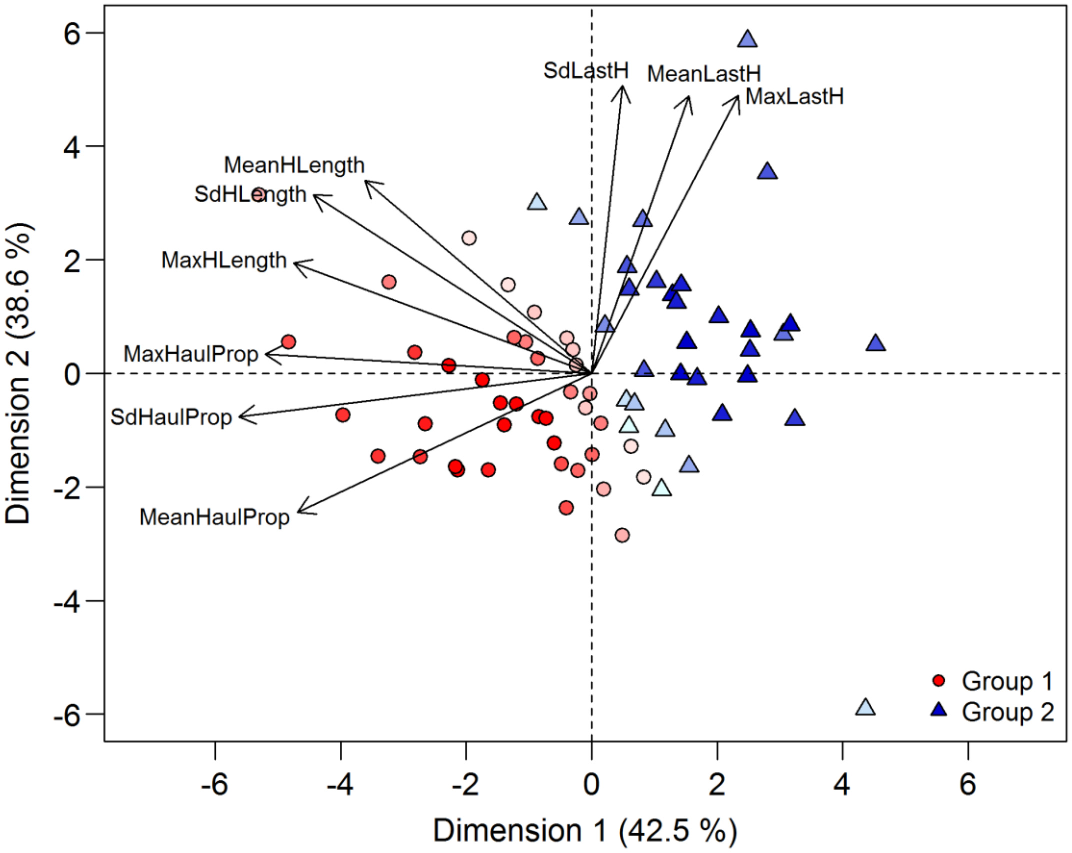

a) 2002
number of seals=11
number of haul-out events=833
b) 2003
number of seals=11
number of haul-out events=1327
c) 2010
number of seals=9
number of haul-out events=628
d) 2011
number of seals=11
number of haul-out events=1487
e) 2012 east coast
number of seals=8
number of haul-out events=637
f) 2012 west coast
number of seals=10
number of haul-out events=1423
82°N
78°N
10°E
30°E

Figure 1



SdLastH
MeanLastH
MaxLastH
MeanHLength
SdHLength
MaxHLength
MaxHaulProp
SdHaulProp
MeanHaulProp
● Group 1
▲ Group 2
6
4
2
0
-2
-4
-6
Dimension 2 (38.6 %)
-6
-4
-2
0
2
4
6
Dimension 1 (42.5 %)

Figure 2

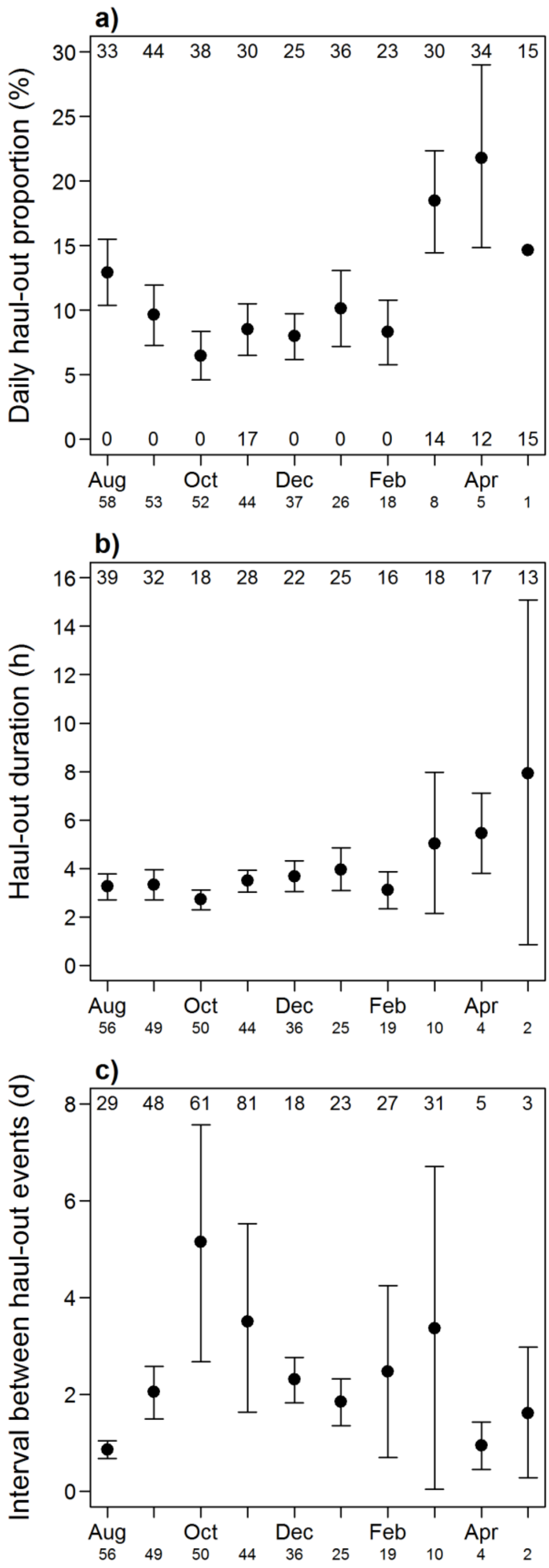
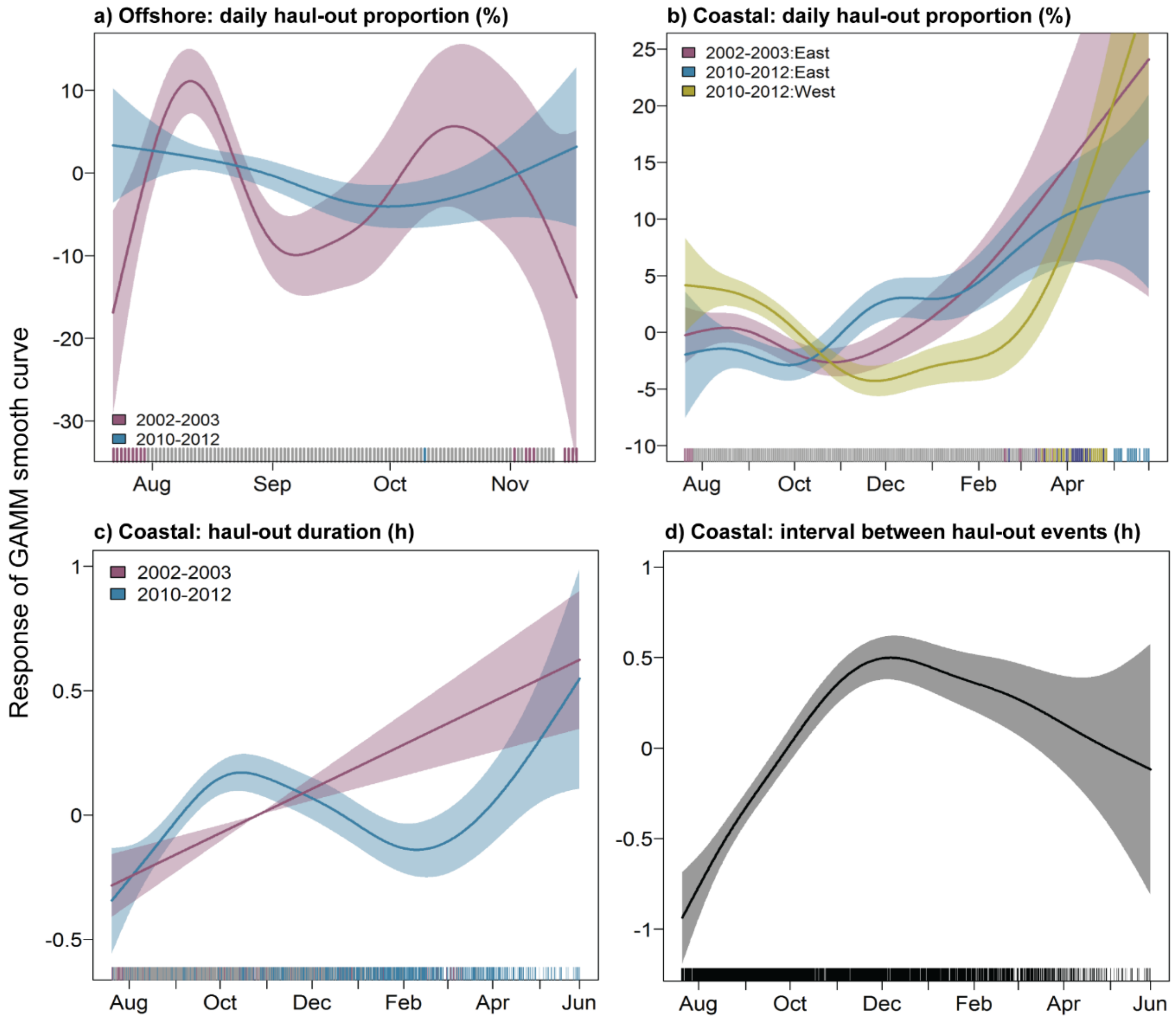

a)
Daily haul-out proportion (%)
0
5
10
15
20
25
30
33 44 38 30 25 36 23 30 34 15
0 0 0 17 0 0 0 14 12 15
Aug
Oct
Dec
Feb
Apr
58 53 52 44 37 26 18 8 5 1
b)
Haul-out duration (h)
0
2
4
6
8
10
12
14
16
39 32 18 28 22 25 16 18 17 13
Aug
Oct
Dec
Feb
Apr
56 49 50 44 36 25 19 10 4 2
c)
Interval between haul-out events (d)
0
2
4
6
8
29 48 61 81 18 23 27 31 5 3
Aug
Oct
Dec
Feb
Apr
56 49 50 44 36 25 19 10 4 2

Figure 3



a) Offshore: daily haul-out proportion (%)
10
0
-10
-20
-30
2002-2003
2010-2012
Aug
Sep
Oct
Nov
b) Coastal: daily haul-out proportion (%)
25
20
15
10
5
0
-5
-10
2002-2003:East
2010-2012:East
2010-2012:West
Aug
Oct
Dec
Feb
Apr
Response of GAMM smooth curve
c) Coastal: haul-out duration (h)
1
0.5
0
-0.5
2002-2003
2010-2012
Aug
Oct
Dec
Feb
Apr
Jun
d) Coastal: interval between haul-out events (h)
1
0.5
0
-0.5
-1
Aug
Oct
Dec
Feb
Apr
Jun

Figure 4

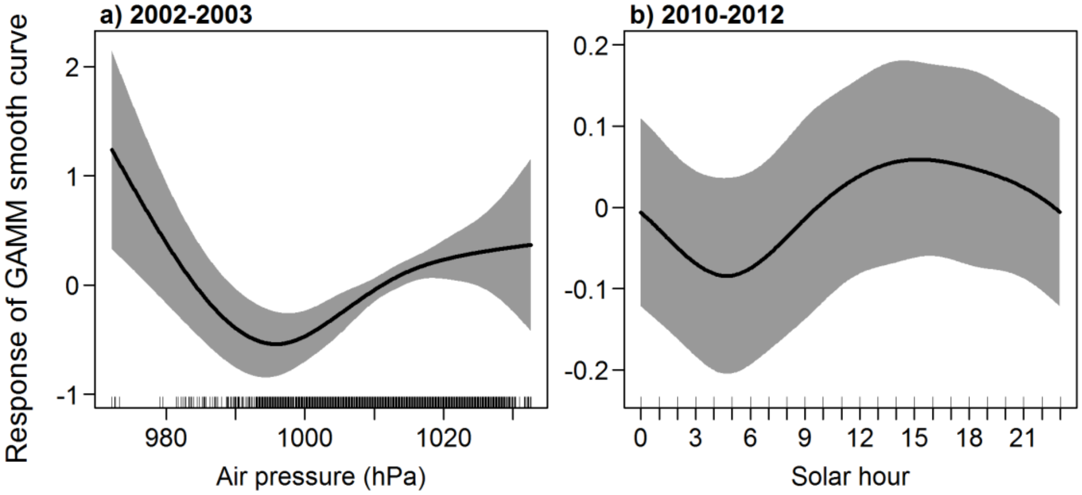

a) 2002-2003
b) 2010-2012
Response of GAMM smooth curve
2
1
0
-1
980
1000
1020
Air pressure (hPa)
0.2
0.1
0
-0.1
-0.2
0
3
6
9
12
15
18
21
Solar hour

Figure 5

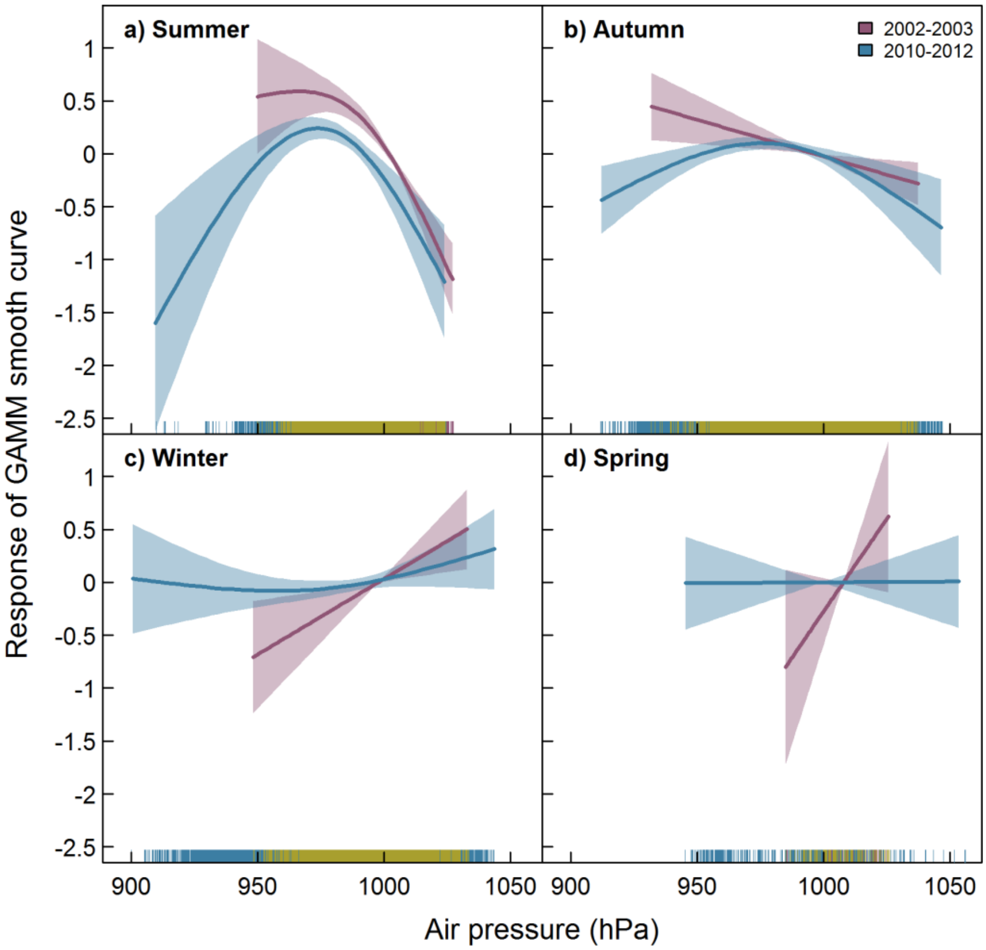

a) Summer
b) Autumn
c) Winter
d) Spring
2002-2003
2010-2012
Response of GAMM smooth curve
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
900
950
1000
1050
Air pressure (hPa)

Figure 6

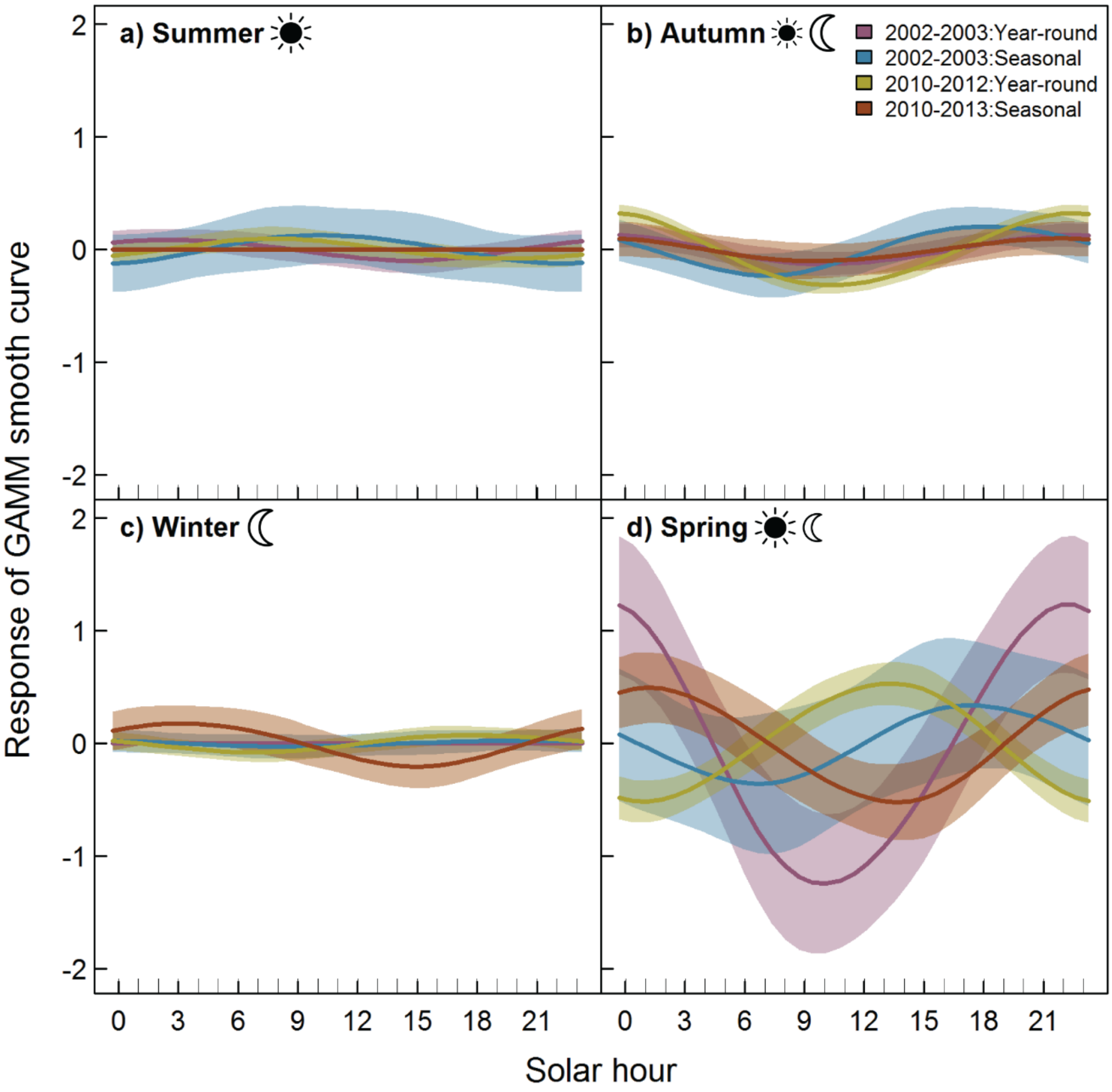

a) Summer
b) Autumn
c) Winter
d) Spring
2002-2003:Year-round
2002-2003:Seasonal
2010-2012:Year-round
2010-2013:Seasonal
Response of GAMM smooth curve
Solar hour
2
1
0
-1
-2
0
3
6
9
12
15
18
21

Figure 7