Vol. 675: 153–164, 2021
https://doi.org/10.3354/meps13822

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 30

Seasonal habitat use of a lagoon by ringed seals *Pusa hispida* in Svalbard, Norway

Jade Vacquié-Garcia[1,2], Christian Lydersen[1], Espen Lydersen[3], Guttorm N. Christensen[4], Christophe Guinet[2], Kit M. Kovacs[1,*]

[1]Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway
[2]Centre d'Etudes Biologiques de Chize (CEBC), UMR 7372 CNRS–Universite de La Rochelle, 79360 Villiers-en-Bois, France
[3]Department of Natural Sciences and Environmental Health, University of Southeast Norway, 3800 Bø, Midt-Telemark, Norway
[4]Akvaplan-niva, Fram Centre, 9296 Tromsø, Norway

ABSTRACT: Climate change is impacting ice-affiliated marine mammal habitats throughout the Arctic, with sea ice declines reducing traditional haul-out and breeding habitats, putting a premium on alternative useable areas. In the Arctic, ice forms early in the season and is retained late into the spring in coastal lagoons, but little information is available regarding how this nature type is used by marine mammals. This study documents use of a lagoon by 20 ringed seals tracked for an average of 188 d via satellite-linked GPS tags. Overall, tagged seals spent 8.9 ± 0.4 % (±SD) of their time per day inside the lagoon, with strong summer and autumn peaks that dropped off in winter and ceased in spring. Inside the lagoon, seals spent significantly larger proportions of their time hauled out and less time diving in comparison to when they were outside the lagoon. Additionally, the seals dove deeper (19 vs. 7 m) and for longer periods (4 vs. 2.5 min) when outside the lagoon, indicating that most feeding took place out in the fjord. However, residency periods in the lagoon of up to 43 d as well as more intense diving than would be expected for transport to and from haul-out areas within the lagoon suggest that ringed seals also feed in the lagoon. Regular opportunistic sightings of ringed seals in lagoons around Svalbard, Norway, together with the quantitative behavioural documentation of lagoon use in the present study, suggest that lagoons may serve as refugia areas, which might become increasingly important as climate change continues to alter Arctic marine ecosystems.

KEY WORDS: Climate change · Foraging · Habitat use · Haul-out behaviour · Ice-associated seals · Refugia

1. INTRODUCTION

Lagoons are shallow, coastal bodies of water separated from the ocean by a barrier, but connected at least intermittently to the ocean by one or more restricted inlets (Kjerfve 1994). Lagoons are among the most productive ecosystems on the planet and are assumed to be of significant importance for biodiversity (de Wit 2011). Most of the time, lagoons are subject to tidal mixing, where seawater mixes with freshwater from their land-based catchments (Garrido et al. 2011). Because of their physical characteristics, especially their shallowness, lagoons are highly sensitive to changes in precipitation, runoff from glaciers, evaporation and wind (de Wit 2011). They experience high fluctuations of salinity and temperature, which can present stressful conditions for many marine species. However, lagoons often comprise a mosaic landscape containing many different ecotones (i.e. areas of transition between 2 habitat types) (de Wit 2011). Their high productivity, as well as the relatively calm conditions associated with lagoons, are advantageous for many species that can deal with dynamic environments (de Wit

*Corresponding author: kit.kovacs@npolar.no

Publisher: Inter-Research · www.int-res.com

2011, Garrido et al. 2011). Some invertebrate and fish species spawn in the open sea where salinities are constant, but juvenile life stages migrate into lagoons where they benefit from the calm conditions and plentiful food resources (Kathiresan & Bingham 2001, Heck et al. 2003, Kennish & Paerl 2010). This rich diversity of lower trophic animals is thought to make lagoons favourable foraging environments for marine predators, such as birds and marine mammals (Paiva et al. 2008).

Arctic lagoons represent an important nature type (a classification system for ecosystem and landscape levels of ecodiversity; see Halvorsen et al. 2020), particularly in this time of rapid climate change. Sea ice has declined markedly during the last few decades, which threatens ice-associated species including all Arctic endemic marine mammals (Meredith et al. 2019). However, due to their brackish nature and low wave action, lagoons generally freeze up earlier and retain ice longer than adjacent ocean areas, making them potentially useful environments for ice-associated seals. In addition, several important Arctic fish species such as polar cod *Boreogadus saida* and Arctic charr *Salvelinus alpinus* are known to be found in lagoons (Johnson 1980, Craig 1984, Haug & Myhre 2016), making these areas potential foraging sites as well.

The physical environment in Svalbard, Norway, is characterized by a diverse array of landforms that reflect a long history of ice cover and active geological processes in combination with a High Arctic climate (Haug & Myhre 2016). Lagoons are one of these landforms; 127 lagoons have been identified along Svalbard's coastlines (Haug & Myhre 2016). Knowledge about species diversity in lagoons within Svalbard is scarce and fragmentary; however, all 3 resident phocid seals (ringed *Pusa hispida*, harbour *Phoca vitulina* and bearded *Erignathus barbatus*) have been opportunistically, but regularly, observed in lagoons (Haug & Myhre 2016, K. M. Kovacs & C. Lydersen pers. obs.). Using biotelemetry equipment, the present study quantitatively explored the use of lagoons by the most numerous of these seal species in Svalbard, the ringed seal, to document seasonal use and shed light on the potential importance of this habitat for this climate-change-sensitive species. Ringed seals are a very tightly ice-associated species that use sea ice for resting, moulting and breeding; they are also highly dependent on prey that associate with sea ice, most importantly polar cod, which dominates the diet of ringed seals in Svalbard (Labansen et al. 2007, Bengtsson et al. 2020). Given the declines in sea ice over the past 2 decades in Svalbard as well as the limited adaptability and resilience shown by ringed seals to date (e.g. Hamilton et al. 2019, Bengtsson et al. 2020), this species is becoming a conservation concern.

2. MATERIALS AND METHODS

2.1. Data logger deployments and data collection

Fieldwork was conducted in Charleslaguna in St Jonsfjorden, Svalbard, Norway. This coastal lagoon has a 90 m wide opening and a surface area of about 1 km^2 (Haug & Myhre 2016). The lagoon was created by the retreat of a glacier, the front of which is no longer in contact with the water. The shoreline of the lagoon is relatively flat, with large tidal mudflats in the inner reaches of the lagoon; the lagoon is surrounded by adjacent mountains with river valleys running between them (Haug & Myhre 2016). Several landward ponds are also present that drain into the lagoon (Haug & Myhre 2016). A total of 20 ringed seals were captured in this lagoon and equipped with GPS CTD satellite-relay data loggers (GPS-CTD-SRDL hereafter) (Sea Mammal Research Unit). Captures took place in July–August (2012: 5 seals; 2016: 5 seals; 2017: 10 seals) following the seals' annual moult, using monofilament nets set from shore. Immediately after capture, seals were placed in individual restraint nets, body mass was measured (Salter spring scales; precision: ±0.5 kg) and sex was determined. The GPS-CTD-SRDLs were then glued to the hair on the back mid-dorsally using quick setting epoxy. The animals were then released. All animal-handling protocols were approved by the Governor of Svalbard and the Norwegian Animal Research Authority.

GPS-CTD-SRDLs collect and transmit (via the Argos satellite system) locations, information on the seals' behaviour and CTD up-casts. Information on the seals' behaviour included (1) the percentage of time spent hauled out, at the surface and diving summarized for 6 h periods, as well as the mean dive depth and dive duration and the maximum dive depth and dive duration within each period (i.e. summary file) and (2) more detailed information for a random selection of haul-outs and dives including start and end times, but also the surface time, maximum depth and 4 time–depth points per dive (i.e. details file) (for details see Fedak et al. 2002). Dives were defined as starting when the wet–dry switch of the tags was wet and the depth was deeper than 1.5 m for 8 s and ending when the tag was dry or when the depth was shallower than 1.5 m. Haul-out periods were defined as starting when the tag was dry for

10 min and ending when it was wet for 4 s. Surface periods correspond to the remaining periods. CTD data were not used in this study because few CTD profiles were reported from the lagoon since only the deepest CTD profiles are selected for transmission. The tags were not duty-cycled, but rather set to report whenever the tags were exposed to the air; 100 000 transmissions over a period of 300 d fit within battery capacity.

2.2. Data processing

All data processing and analyses were done using the R statistical framework (R v.3.6.0; R Core Team 2019). Satellite-derived locations were first filtered to remove all repeated locations and then processed further using a speed filter to remove all unrealistic locations (McConnell et al. 1992). This was done using the R package 'argosfilter' (version 0.62; Freitas 2012); the swimming speed threshold was set at 2 m s^{-1} (Freitas et al. 2008).

The presence of the seals inside the lagoon was investigated throughout the year in order to study potential seasonality of visits to the lagoon. Because location data were not reported frequently along the tracks (mean ± SE duration between consecutive locations = 2.59 ± 0.04 h with 96% of the locations occurring within 12 h of another point), filtered locations were interpolated, creating locations that were regularly spaced at 1 h intervals (corresponding to the median time interval between 2 locations) along all track-lines. Subsequently, all hourly interpolated locations occurring inside Charleslaguna were manually checked, and the proportion of locations identified as being inside the lagoon was calculated for each individual for each day.

The activity patterns of the seals inside versus outside the lagoon were compared throughout the year. Each 6 h period reported by the tags, with its corresponding percentage of time hauled out, at the surface and diving, was classified as 'in the lagoon' when all locations during the period were in the lagoon. Similarly, periods with all locations outside the lagoon were classified as 'outside the lagoon'. Only filtered locations (interpolated ones were not used for this classification to avoid classifying a period inside the lagoon when no actual raw locations were located there) were used and 6 h periods during which filtered locations occurred both inside and outside the lagoon were removed from these analyses, resulting in a conservative quantification of lagoon use.

Haul-out durations were compared inside and outside the lagoon throughout the year. Since haul-out events can be short and transmission rates are higher during haul-out than during non-haul-out activities, the 1 h interpolations were considered too coarse. Therefore, a second set of interpolations was conducted on the filtered locations, resulting in locations that were regularly spaced at 1 min intervals along the track-line. Haul-out periods were then identified from these 1 min interpolated locations using the start and end times for haul-out periods provided by the tags. Finally, each haul-out period was classified as an 'in the lagoon' haul-out period (when all 1 min interpolated locations of the haul-out occurred inside the lagoon) or an 'outside the lagoon' period (when all 1 min interpolated locations of the haul-out occurred outside the limits of the lagoon). The same process was conducted for dive durations inside and outside the lagoon throughout the year. However, in contrast to the transmitted haul-out periods (provided by the details file) that account for most (98%) of the actual haul-out periods provided by the summary file (i.e. compared with the percentage of haul-out time per 6 h period; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m675p153_supp.pdf), transmitted dives (from the details file) represented only a small fraction of the actual number of dives recorded by the tags (from the summary file) (Fig. S1). Thus, to compare seasonal diving behaviour inside versus outside the lagoon, we decided to use the mean dive duration and mean dive depth provided from the summaries for the 6 h periods.

2.3. Analysis and modelling approach

The seasonality of use of the lagoon, as well as the seasonality of activities inside and outside the lagoon, were investigated using generalized additive mixed models (GAMMs; 'gamm' function in the R package 'mgcv'; see Wood 2017), in which the linear predictor is given by a user-specified number of smooth functions for the covariates, plus a conventional parametric component. The proportions of 1 h interpolated locations identified as being inside the lagoon for each day (knot value, k, set at 5), as well as the percentage of time hauled out, at the surface and diving for each 6 h period (k set at 6), were examined in relation to the day of the year (the number of days since 1 July, i.e. the earliest tagging date irrespective of year), in separate models. Sex differences were investigated in both models, but this variable was not retained as no differences in either seasonality or activities were detected between males and females. For models investigating the percentage of time spent in the different activities for each 6 h period, 'location' (i.e. inside vs. outside the lagoon) was included as a 'by-variable' (i.e. day of the year smooth curves were made for each type of location). A quasibinomial error distribution and a logit link function were used in these models, and 'individual' was included as a random effect and as a grouping factor in the first order autoregressive (corAR1) structure to minimize the effects of the hierarchical structure of the data. Model selection and model validation were done using the confidence intervals of the corresponding smoothing curves, as recommended by Zuur et al. (2009).

The seasonality of haul-out durations as well as of the mean dive duration and mean dive depth per 6 h period — inside and outside the lagoon — were also investigated using GAMMs. The haul-out durations as well as the mean dive durations and mean dive depths for each 6 h period were examined in relation to the day of the year in separate models (*k* was set at 4) with 'location' (i.e. inside vs. outside the lagoon) included as a 'by-variable'. Haul-out duration was log transformed before modelling to meet model assumptions, and the models were fitted with a Gaussian family distribution. Individual was included as a random effect and as a grouping factor in the corAR1 structure to minimize the effects of the hierarchical structure of the data. Model selection and model validation were done as recommended by Zuur et al. (2009).

3. RESULTS

The data loggers deployed on the ringed seals provided data for periods ranging between 30 and 283 d, with an average (±SE) duration of 188 ± 16 d (Table 1). Eleven of the tagged seals were males while 9 were females. A total of 34 345 locations were reported by the data loggers but the filtration process removed 0.5% of these locations (155 locations), leaving 34 190 locations (99.5%) for analyses (Figs. 1 & S2). Among the filtered locations, 10% (3105) were inside Charleslaguna while 90% (31 085) were located elsewhere. On average, 10.4 ± 1.0 (range: 3.4–21.5) locations were received per day for each seal. Six of the 20 individuals did not come back to the lagoon following their release (3 males and 3 females), but all animals were included in the analyses in order to portray the most realistic population-level behaviour possible. One of these 6 seals visited another lagoon (Richardlaguna on Prins Karls Forlandet, see Fig. S2) twice, for short periods, but these periods were omitted from the analyses.

Table 1. Tagging metrics for the 20 ringed seals instrumented with satellite transmitters in Charleslaguna, Svalbard, Norway during summer of 2012, 2016 and 2017

ID	Sex	Body mass (kg)	Deployment date (dd/mm/yy)	Track duration (d)	% of raw locations in the lagoon	% of time spent in the lagoon per day (mean ± SE)
ct94-M74Dusty-12	M	74	25/08/12	105.5	7	3 ± 0.9
ct94-M103Samson-12	M	102	25/08/12	191.5	25	39 ± 3
ct94-M60Alice-12	M	60	25/08/12	208.9	17	6 ± 1
ct94-M88Rocky-12	M	88	26/08/12	173.7	0	0 ± 0
ct94-M100Leo-12	M	100	25/08/12	189.5	12	13 ± 2
ct130-M53-16	M	53	24/07/16	283.2	14	6 ± 1
ct130-F58-16	F	58	24/07/16	261.6	12	8 ± 1
ct130-F65-16	F	65	24/07/16	185.2	0.1	0.3 ± 0.2
ct130-M65-16	M	65	24/07/16	30.1	16	25 ± 6
ct130-F55-16	F	55	24/07/16	122.5	35	40 ± 3
ct138-F85-17	F	85	10/08/17	255.1	36	29 ± 3
ct138-F75-17	F	75	10/08/17	44.8	72	43 ± 7
ct138-M88-17	M	88	10/08/17	237.3	0	0 ± 0
ct138-F70-17	F	70	10/08/17	187.6	3	3 ± 0.9
ct138-M75-17	M	75	10/08/17	267.4	3	1 ± 0.5
ct138-M89-17	M	89	10/08/17	203.3	13	10 ± 2
ct138-F72-17	F	72	10/08/17	229.5	0	0 ± 0
ct138-F78-17	F	78	10/08/17	241.8	0	0 ± 0
ct138-M80-17	M	80	10/08/17	193.9	0	0 ± 0
ct138-F77-17	F	77	10/08/17	144.9	0	0 ± 0

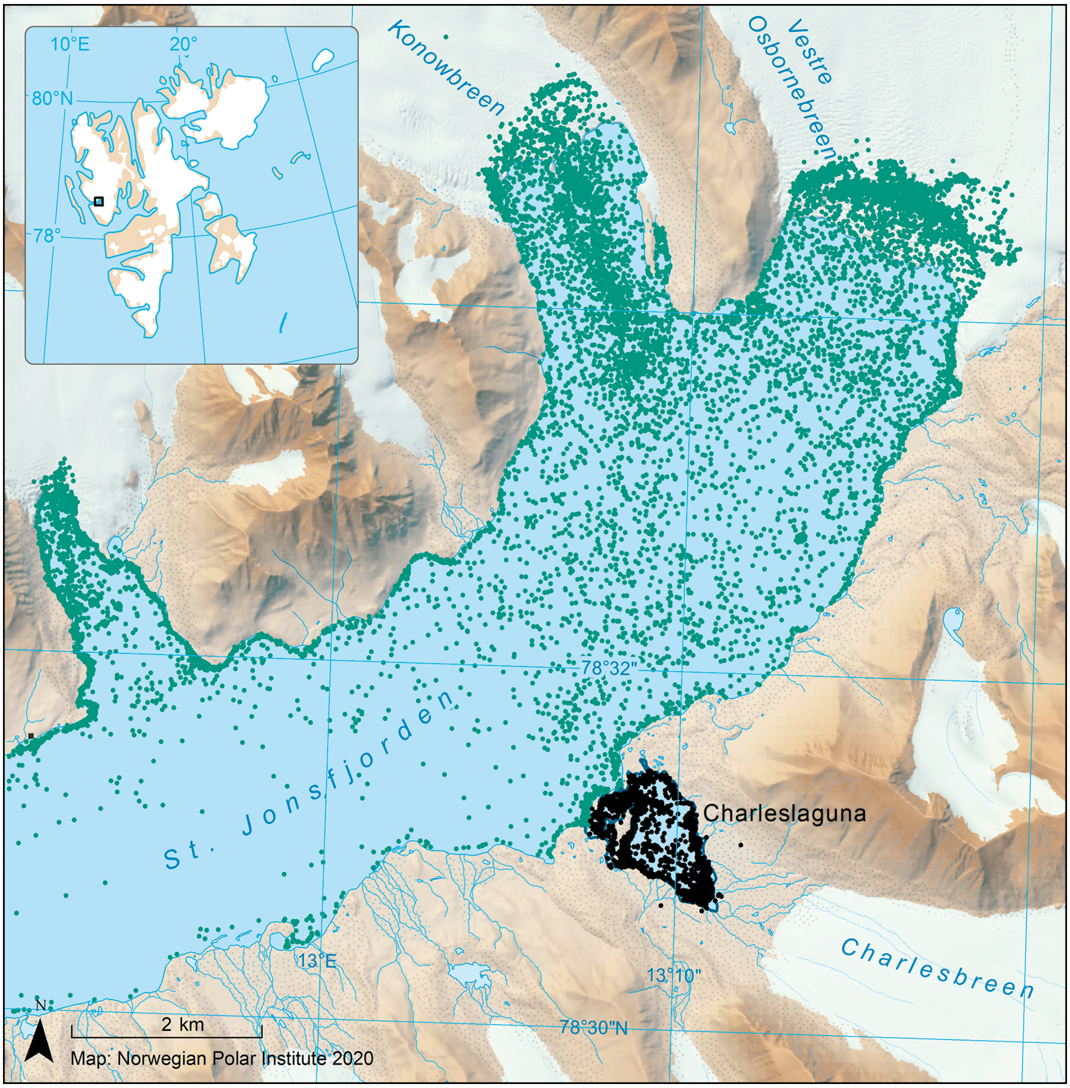

Fig. 1. Filtered locations for 20 ringed seals instrumented with GPS-linked satellite transmitters in Charleslaguna, Svalbard, Norway, in 2012, 2016 and 2017. Green dots: seal locations outside the lagoon; black dots: inside the lagoon

After the 1 h interpolation process, a total of 88 345 locations were extracted, involving 7840 (9.7 %) interpolated locations within Charleslaguna and 80 505 (90.3 %) locations outside the lagoon. The total proportion of tracking time ringed seals spent in the lagoon was on average 8.9 ± 0.4 % d^{-1}, but lagoon use varied markedly through the year (Fig. 2, Table 2), with visitation to the lagoon occurring from the time of tagging in July through until February; the seals did not use the lagoon from March to May and no data were available for June because the seals moult the tags along with their hair toward the end of the breeding period (late May/early June; see Fig. 2, Table 2). Time spent in the lagoon per day peaked in late summer and in autumn (monthly mean time spent in the lagoon per day ranged between 8 and 18 % between July and January); minimum values, excluding the months with no visitation to the lagoon, were detected in February (mean proportion of time spent in the lagoon per day = 7 % in this month; Fig. 2). The durations of individual trips to the lagoon were on average 20.9 ± 3.3 h, with the longest registered stay inside the lagoon by an individual seal being 43 d, starting at the end of November.

Of the 6 h summary periods, a total of 9329 were reported by the tags. Of these, 552 were classified as IN (i.e. all filtered locations of the period within the limits of the lagoon) and 5879 as OUT (i.e. all filtered locations of the period outside the limits of the lagoon), while the remaining 2898 periods included

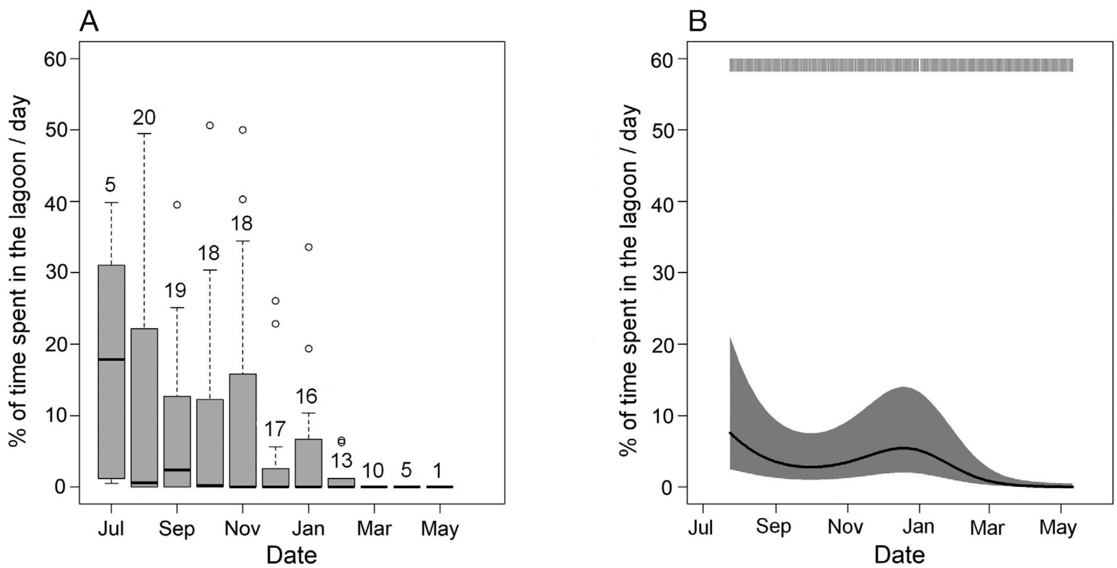

Fig. 2. Seasonal change in the proportion of time ringed seals instrumented with GPS-linked satellite transmitters spent per day in Charleslaguna, Svalbard, Norway, in 2012, 2016 and 2017. (A) Monthly distribution of the mean proportion of time spent in the lagoon per day for tracked individuals; (B) corresponding generalized additive mixed model output comparing the proportion of time spent in the lagoon per day vs. date. Bold lines in (A): median of the mean proportions of time spent per day in the lagoon per individual for each month; boxes: 25th–75th quartiles; thin lines: maximum and minimum values; circles: outliers. Shaded area in (B) represents the 95% CIs. Sample sizes (number of ind. mo^{-1}) are detailed in (A)

positions inside and outside the lagoon, which were not analysed further. Overall, animals spent more of their time diving when outside the lagoon compared to when they were inside the lagoon (mean per 6 h period: 60 vs. 31%), while inside the lagoon they spent more of their time hauled out (mean per 6 h period: 31 vs. 9%) or swimming at the surface (mean per 6 h period: 43 vs. 31%) compared to when they were outside the lagoon (Fig. 3, Table 2). In the lagoon, the percent of time spent hauled out per 6 h period was higher in summer and at the beginning of the winter (January) than in autumn or winter (February), while the percent of time spent diving and swimming at the surface per 6 h period was higher in autumn than in summer or at the beginning of the winter (Fig. 3, Table 2). Outside the lagoon, the per-

Table 2. GAMM model output summaries investigating presence in the lagoon (% of time spent in the lagoon), the proportion of time spent in different activities inside (Lagoon) or outside (Outside) the lagoon (% of time spent hauling out, % spent at the surface and % spent diving) as well as the diving and hauling out behaviour inside and outside the lagoon (Mean dive duration, Mean dive depth, haul-out duration) as a function of the date (day). The intercept estimates, *t*-values and p-values are shown for the linear predictor variables and the estimated degrees of freedom (edf), *F* and p-values are shown for the predictor variables included in the smooth function in each model. The level of temporal autocorrelation (Phi value) is also given

Response variable	Estimate	*t*	p	Location (In or outside the lagoon)	edf	*F*	p	Phi
% spent in the lagoon	−3.57	−6.95	<0.001	s(day)	3.51	11.93	<0.001	0.54
% spent hauling out	−2.48	−27.21	<0.001	s(day):Lagoon	4.97	79.07	<0.001	0.36
				s(day):Outside	3.78	33.51	<0.001	
% spent at the surface	−0.54	−11.30	<0.001	s(day):Lagoon	4.94	54.42	<0.001	0.35
				s(day):Outside	1.00	1.09	0.30	
% spent diving	0.46	5.40	<0.001	s(day):Lagoon	4.99	155.65	<0.001	0.41
				s(day):Outside	4.18	25.73	<0.001	
Mean dive duration	242.71	22.3	<0.001	s(day):Lagoon	2.99	59.24	<0.001	0.3
				s(day):Outside	2.93	26.97	<0.001	
Mean dive depth	20.02	7.90	<0.001	s(day):Lagoon	2.99	135.61	<0.001	0.49
				s(day):Outside	2.89	7.02	<0.001	
Haul-out duration	4.21	67.56	<0.001	s(day):Lagoon	2.93	28.64	<0.001	0.2
				s(day):Outside	2.89	10.36	<0.001	

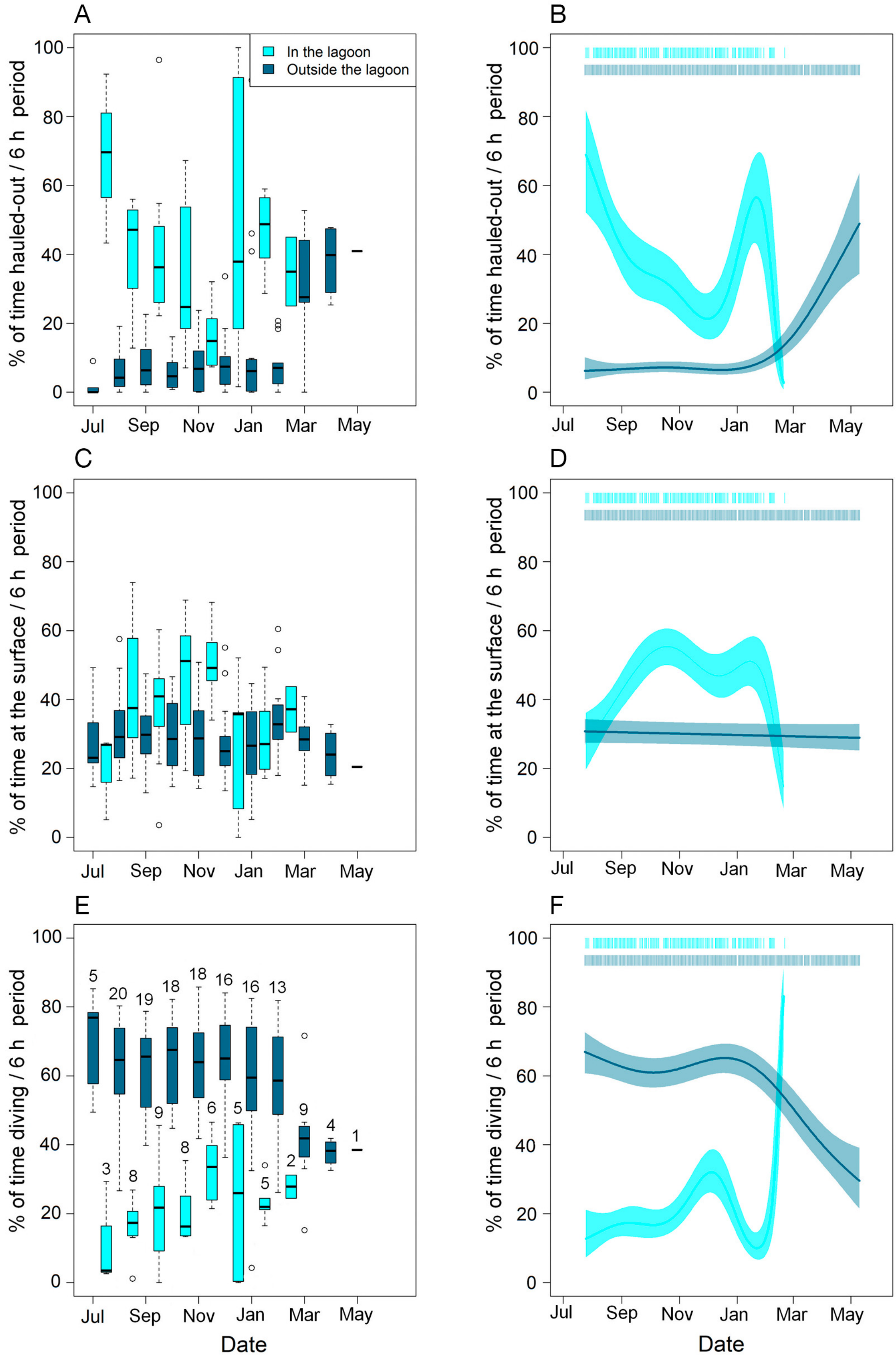

Fig. 3. Seasonal change in the proportion of time spent in different activities by GPS-linked satellite tagged ringed seals, per 6 h period, inside and outside Charleslaguna, Svalbard, Norway, in 2012, 2016 and 2017. Panels on the left represent monthly distribution of the mean proportion of time spent per 6 h period (A) hauling out, (C) at the surface and (E) diving. Panels on the right represent the corresponding generalized additive mixed model outputs comparing the proportion of time spent per 6 h period (B) hauling out, (D) at the surface and (F) diving vs. date. Bold lines in (A,C,E) represent the median of the mean proportions of time spent hauling out, at the surface or diving per 6 h period inside or outside the lagoon (per individual) for each month; boxes: 25th–75th quartiles; thin lines: minimum and maximum values; circles: outliers. Shaded areas in (B,D,F) represent the 95% CIs. Sample size (number of ind. mo^{-1}) are detailed in (E)

cent of time spent hauled out per 6 h period was low in summer, autumn and winter but high in spring (Fig. 3A,D, Table 2). Conversely, the percent of time diving was relatively high most of the time in summer, autumn and winter, while it was low in spring (Fig. 3C,F, Table 2). The percent of time spent at the surface outside the lagoon was stable throughout the study period (Fig. 3B,E, Table 2). The seals dove deeper and for longer periods when they were outside the lagoon (means per 6 h period: 19.1 ± 0.3 m and 4.0 ± 0.1 min, respectively; mean maximum depth per 6 h period: 46.9 ± 0.6 m; mean maximum duration: 9.6 ± 0.1 min) compared to when they were inside the lagoon (means per 6 h period: 7.0 ± 0.3 m and 2.5 ± 0.1 min; mean maximums per 6 h period: 19.8 ± 1.0 m and 8.1 ± 0.2 min) (Fig. 4, Table 2). The mean dive depths and dive durations outside the lagoon were relatively stable from July to February before they decreased in March. Inside the lagoon, animals dove deeper and for longer periods in the autumn and winter (February) compared to other seasons (Fig. 4, Table 2).

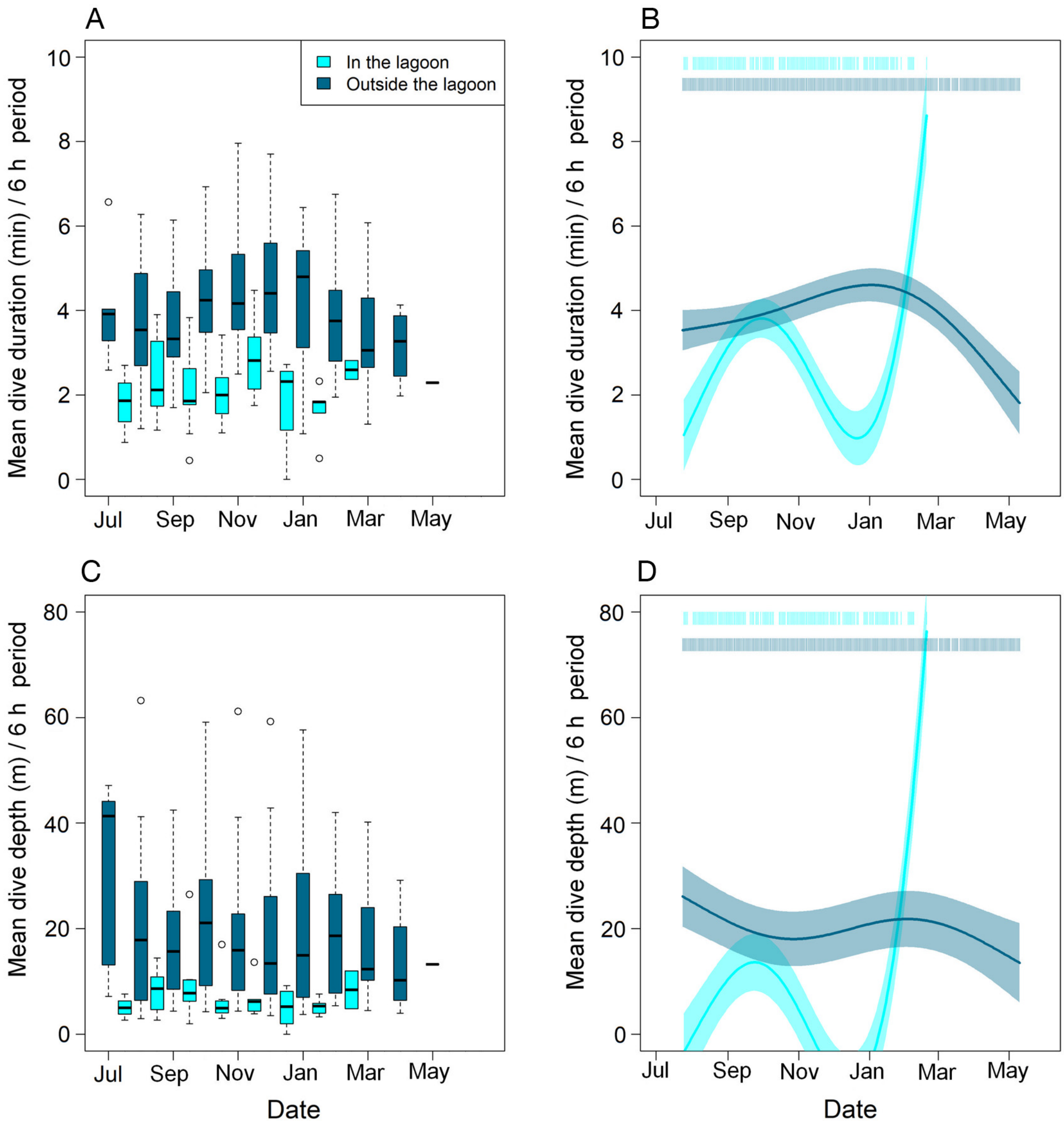

Fig. 4. Seasonal change in the mean dive duration and mean dive depth per 6 h period, inside and outside Charleslaguna, Svalbard, Norway, for ringed seals instrumented with GPS-linked satellite transmitters in 2012, 2016 and 2017. (A,C) Monthly distribution of the mean dive duration and the mean dive depth per 6 h period; (B,D) corresponding generalized additive mixed model (GAMM) outputs comparing the mean dive duration and mean dive depth per 6 h period vs. date. Bold lines represent the median of the mean dive depth (A) or dive duration (C) per 6 h period inside or outside the lagoon (per individual) for each month; boxes: 25th–75th quartiles; thin lines: minimum and maximum values; circles: outliers. Shaded areas in (B) and (D) represent the 95% CIs around the GAMM outputs. Sample sizes are the same as those in Fig. 3

After calculating locations at 1 min intervals, a total of 5 300 282 interpolated locations were extracted, with 470 864 (8.9 %) interpolated locations inside the lagoon and 4 829 418 (91.1 %) outside the lagoon. A total of 3433 haul-out periods were identified, 971 of which took place inside the lagoon and 2421 that were outside the lagoon; the exact locations of the other 41 haul-out periods were intermediate (likely in the mouth of the lagoon) and were removed from the analyses. The haul-out periods retained for analyses lasted on average 2.5 ± 0.1 h, and their durations varied seasonally and by location (Fig. 5, Table 2). Haul-out durations were shortest in summer and longest in winter/spring, both inside and outside the lagoon. However, while the duration of haul-out periods was similar in summer and autumn inside and outside the lagoon, in winter, reported haul-outs were significantly longer inside the lagoon than outside (Fig. 5, Table 2). No haul-outs were recorded inside the lagoon during the ice-free summer months (July and August) in 2012, but some of the seals did haul out inside the lagoon in the summers of both 2016 and 2017 when there was no ice (i.e. they were using shorelines).

4. DISCUSSION

Investigating habitat use within unique nature types, such as lagoons, is crucial to understanding ecosystem function and potential climate change responses by marine animals. This is especially true in polar environments, where environmental change is already severe and is expected to have dramatic consequences on habitat use by marine animals. The present study represents a novel achievement, describing an Arctic endemic marine mammal's seasonal use of a lagoon system over multiple years.

Among 20 ringed seals instrumented inside the lagoon, 14 individuals returned to use the lagoon in the 3 study years. Charleslaguna was used by ringed seals from summer (tagging in July–August) until the beginning of the following spring (February). During that period, the seals spent a monthly average of 7–18 % of their time per day inside this small lagoon (circa 1 km^2), suggesting that this habitat was a favourable location for the seals. One must of course bear in mind that all of the seals were initially caught inside the lagoon and may therefore not be representative for the whole Svalbard ringed seal population, since sampling is biased towards the fraction (of unknown size) that are aware of this habitat and living close enough to utilize it. However, there is also the possibility that capture and tagging could have caused some of the seals to terminate their use of the lagoon; 6 seals did not return to the lagoon after being released post-tagging. Alternatively, these 6 seals might have been one-time visitors to the site. It is impossible to ascertain which of these scenarios might be true.

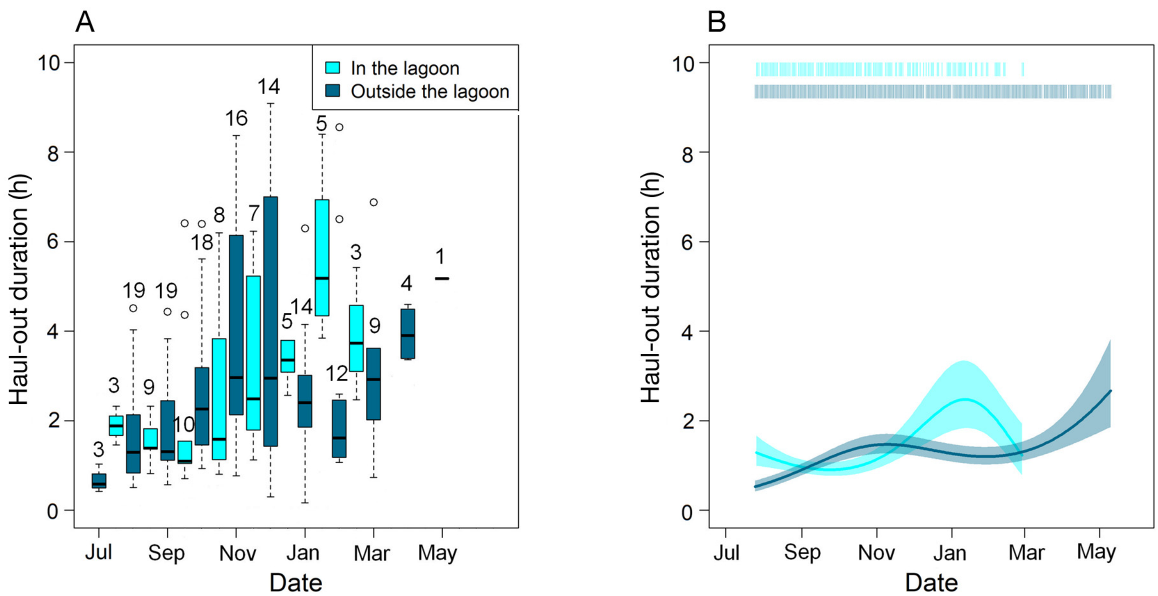

Fig. 5. Seasonal change in haul-out duration inside and outside Charleslaguna for ringed seals instrumented with GPS-linked satellite transmitters in 2012, 2016 and 2017. (A) Average haul-out duration vs. month; (B) corresponding generalized additive mixed model (GAMM) output comparing the haul-out duration vs. date. Bold lines represent the median of the mean haul-out durations per individual; boxes: 25^{th}–75^{th} quartiles; thin lines: maximum and minimum values; circles: outliers. Shaded area in (B) represents the 95 % CIs around the GAMM outputs. Sample sizes (number of ind. mo^{-1}) are detailed in (A)

All of the seals that used the lagoon in summer, autumn and into the winter stopped using it after February, despite the continued presence of sea ice in the lagoon. Nine of the tags continued to report until mid-May; all of these seals spent March–May in ice-covered areas outside the lagoon. The breeding period for ringed seals in Svalbard occurs during this period, with peak pupping in the first week of April (Lydersen & Gjertz 1986, Lydersen 1998), followed by a relatively long lactation period of about 40 d (Hammill et al. 1991). Thus, it is clear that the tagged ringed seals did not make use of the lagoon for breeding. Ideal breeding habitat for ringed seals in Svalbard is land-fast ice, deep inside fjords, where they maintain several breathing holes, and in areas where enough snow accumulates on the sea ice; they dig out lairs (small snow caves) above their breathing holes. Females give birth within such lairs, providing the pup with thermal shelter and also some protection against predators such as polar bears *Ursus maritimus* (Stirling 1974, Smith & Stirling 1975, Lydersen & Gjertz 1986). In the Svalbard Archipelago, the best breeding habitat occurs in fjords that have terminal glaciers, because glacier pieces frozen into the land-fast ice enhance snow accumulation in this Arctic desert (Lydersen & Gjertz 1986, Lydersen et al. 2014, Hamilton et al. 2016).

Charleslaguna was a glacier site historically, but the glacier has retracted onto shore and no longer calves ice pieces into the sea; thus, it is not currently a favourable site for pupping for ringed seals because snow accumulation is unlikely to be deep enough to accommodate lair construction. Another potential issue is that the lactation period is very energetically demanding. Seals must eat circa 2 kg of polar cod (or other food items with corresponding energy density) to balance their energy budgets while remaining within their breeding territories (Lydersen & Kovacs 1999). Although food resource availability in Charleslaguna is not known, it is not likely that it could support many seals full time over extended periods. It is not known if the lagoon was historically a breeding area, but the ice in the lagoon has been used for haul-out in spring and into summer for at least some decades (K. M. Kovacs & C. Lydersen pers. obs.). This continues to be the case, with the ringed seals spending most of their time in the lagoon hauled out, especially toward the end of the summer (July–September) and early in the winter (December–January). Due to runoff of freshwater as well as less wave action inside the lagoons, the lagoon freezes up earlier and the ice stays longer than in the adjacent fjords, which then gives ringed seals access to sea-ice platforms in the lagoon for haul-out earlier in the season in autumn/winter and for longer periods into the late spring/early summer. Use of this lagoon is known to start during the moult, in late May/early June, when many seals have been documented hauled out on the ice in this area (K. M. Kovacs & C. Lydersen pers. obs.). The present study does not document this early seasonal use because tagging was not done until July due to the challenges of setting nets in areas with deteriorated ice and the fact that instrument deployment must be done some weeks after moulting when the new hair is established and strong enough to withstand the weight/drag of the tag. When ringed seals go through their annual replacement of hair, they prefer to do so out of the water to reduce heat loss (Carlens et al. 2006). In recent years, very few places on the west coast of Svalbard retained sea ice into early summer and thus the ice in lagoons is likely a sought-after haul-out habitat. Charleslaguna is also one of a small handful of sites in Svalbard where ringed seals have recently (since circa 2016) begun to haul-out on shore after the sea ice has melted (Lydersen et al. 2017). The sites where this is known to occur are all areas where ringed seals now overlap with harbour seals *Phoca vitulina*; terrestrial haul-out is the norm for this largely temperate seal species and it seems likely that ringed seals have learnt this behaviour from them (see Lydersen et al. 2017 for more details).

Although it is clear that the lagoon is primarily used for haul-out, the ringed seals still spent a lot of their time (monthly mean up to 14–38% of their time per 6 h period) diving in this location. There was some seasonality to this behaviour, with the highest values occurring during the autumn and winter (October to November and in February). This supports the fact that ringed seals must spend a lot of time foraging in this period to regain energy losses accumulated over the spring and early summer when breeding and moulting take place, respectively, and when ringed seals feed little (Ryg & Øritsland 1991, Lydersen 1998, Lydersen & Kovacs 1999, Carlens et al. 2006). This is confirmed by the mean dive depths and durations documented in this study, which suggest that the seals do some foraging in the lagoon; their diving activity is deeper and of longer duration (mean maximum dive depth from the 6 h periods inside the lagoon was 20 m) than what would be expected for transport to and from haul-out areas. Charleslaguna has been described as a shallow lagoon (Haug & Myhre 2016), but in actuality, no depth measurements are available. The ringed seal dive records inside the lagoon in this study had a mean maximum depth (from the 6 h periods) of 20 m, and dives deeper than 50 m were registered as having taken place within the lagoon. However, this value should be treated with caution and the actual depth of the lagoon should be verified.

Many fish species occur in Arctic lagoons, including polar cod (Craig 1984), which is the main prey species for ringed seals in Svalbard (Gjertz & Lydersen 1986, Labansen et al. 2007, Bengtsson et al. 2020). However, another fat-rich fish species that could be of special interest to ringed seals in the summer months in lagoons is the anadromous form of the Arctic charr, which migrates from the lakes out into the ocean where they forage during the summer (Gulseth & Nilssen 2001). Charr are routinely caught by local sport fishermen in various lagoons in Svalbard during July and August (G. N. Christensen unpubl. data).

Although it is likely that some foraging does take place in the lagoon, the contrast between the ringed seals' diving behaviour inside and outside the lagoon confirms that most of their feeding takes place in the fjord(s). When the ringed seals were outside the lagoon from July–February, they spent a monthly mean of 57–70% of the time diving and less than 10% of their time hauled out (per 6 h period). Dives done out in the fjord were also on average 3 times deeper and twice as long as the dives performed inside the lagoon. Water depths in the lagoon are undoubted a factor, but it is also possible that they are targeting different prey species (or age classes of particular prey) inside and outside the lagoon.

Svalbard has experienced anomalously rapid increases in both air and sea water temperatures during the past 2 decades (Pavlov et al. 2013, Nordli et al. 2014, Onarheim et al. 2014), and this area has had the greatest decrease in the seasonal duration of sea-ice cover within the circumpolar Arctic (Laidre et al. 2015). Concomitant with these physical changes, large ecosystem changes have taken place, including a general 'borealization' (i.e. expansion of boreal species and decline of Arctic species) of the fish community (Fossheim et al. 2015), particularly on the westside of Svalbard (Berge et al. 2015). The ringed seals' response to these changes has been to decrease their home range size, focussing on areas close to tidewater glaciers where conditions remain most 'Arctic' (Hamilton et al. 2019). Most glaciers in Svalbard are currently retracting because of a warmer climate (Kohler et al. 2007), and thus more lagoons are likely to be formed (Haug & Myhre 2016). The regular, opportunistic sightings of ringed seals in lagoons around the archipelago, in combination with the quantitative data in this study on habitat use by ringed seals in Charleslaguna, suggests that lagoons may serve as refugia areas that provide sheltered areas for haul-out and some food resources. However a greater understanding of the physical and biological attributes of these areas would be valuable, and trends in the use of lagoons by ringed seals should be monitored on a broad spatial scale in Svalbard to see if these habitats are of increasing importance as sea ice continues to decline.

Acknowledgements. The authors thank Oddmund Isakksen, Charmain Hamilton and Karen Lone for help with the seal captures. The study was financed by the Norwegian Research Council (GLAERE project), VISTA, the Svalbard Environmental Fund and the Norwegian Polar Institute.

LITERATURE CITED

Bengtsson O, Lydersen C, Lindström U, Kovacs KM (2020) Ringed seal (*Pusa hispida*) diet on the west coast of Spitsbergen, Svalbard, Norway: during a time of ecosystem change. Polar Biol 43:773–788

Berge J, Heggland K, Lønne OJ, Cottier F and others (2015) First records of Atlantic mackerel (*Scomber scombrus*) from the Svalbard archipelago, Norway, with possible explanations for the extension of its distribution. Arctic 68:54–61

Carlens H, Lydersen C, Krafft BA, Kovacs KM (2006) Spring haul-out behavior of ringed seals (*Pusa hispida*) in Kongsfjorden, Svalbard. Mar Mamm Sci 22:379–393

Craig PC (1984) Fish use of coastal waters of the Alaskan Beaufort Sea: a review. Trans Am Fish Soc 113:265–282

de Wit R (2011) Biodiversity of coastal lagoon ecosystems and their vulnerability to global change. In: Grillo O, Venore G (eds) Ecosystems biodiversity. InTechOpen Publishers, London

Fedak M, Lovell P, McConnell B, Hunter C (2002) Overcoming the constraints of long range radio telemetry from animals: getting more useful data from smaller packages. Integr Comp Biol 42:3–10

Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan M, Dolgov AV (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. Nat Clim Chang 5:673–677

Freitas C (2012) argosfilter: Argos locations filter. R package version 0.62. https://cran.r-project.org/package=argosfilter

Freitas C, Lydersen C, Fedak MA, Kovacs KM (2008) A simple new algorithm to filter marine mammal Argos locations. Mar Mamm Sci 24:315–325

Garrido J, Pérez-Bilbao A, Benetti SJ (2011) Biodiversity and conservation of coastal lagoons. In: Grillo O, Venore G (eds) Ecosystems biodiversity. InTechOpen Publishers, London, p 1–28

Gjertz I, Lydersen C (1986) The ringed seal (*Phoca hispida*) spring diet in northwestern Spitsbergen, Svalbard. Polar Res 4:53–56

Gulseth OA, Nilssen KJ (2001) Life-history traits of charr, *Salvelinus alpinus*, from a High Arctic watercourse on Svalbard. Arctic 54:1–11

Halvorsen R, Skarpaas O, Bryn A, Bratli H, Erikstad L, Simensen T, Lieungh E (2020) Towards a systematics of ecodiversity: the EcoSyst framework. Glob Ecol Biogeogr 29:1887–1906
Hamilton CD, Lydersen C, Ims RA, Kovacs KM (2016) Coastal habitat use by ringed seals *Pusa hispida* following a regional sea-ice collapse. Mar Ecol Prog Ser 545: 261–277
Hamilton CD, Vacquié-Garcia J, Kovacs KM, Ims RA, Lydersen C (2019) Contrasting changes in space use induced by climate change in two Arctic marine mammal species. Biol Lett 15:20180834
Hammill MO, Lydersen C, Ryg M, Smith TG (1991) Lactation in the ringed seal (*Phoca hispida*). Can J Fish Aquat Sci 48:2471–2476
Haug FD, Myhre PI (2016) Naturtyper på Svalbard: laguner og pollers betydning, med katalog over lokaliteter. Brief Report No. 40. Norwegian Polar Institute, Tromsø (in Norwegian)
Heck KL Jr, Hays G, Orth RJ (2003) A critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 253:123–136
Johnson L (1980) The Arctic charr, *Salvelinus alpinus*. In: Balon EK (ed) Charrs, salmonid fishes of the genus *Salvelinus*. Dr W Junk, The Hague, p 15–98
Kathiresan K, Bingham BL (2001) Biology of mangroves and mangrove ecosystems. Adv Mar Biol 40:81–251
Kennish MJ, Paerl HW (2010) Coastal lagoons: critical habitats of environmental change. In: Kennish MJ, Paerl HW (eds) Coastal lagoons: critical habitats of environmental change. CRC Press, Boca Raton, FL, p 1–16
Kjerfve B (1994) Coastal lagoons. In: Kjerfve B (ed) Coastal lagoon processes. Elsevier Oceanographic Series, Amsterdam, p 1–8
Kohler J, James TD, Murray T, Nuth C and others (2007) Acceleration in thinning rate on western Svalbard glaciers. Geophys Res Lett 34:L18502
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
Laidre KL, Stern H, Kovacs KM, Lowry L and others (2015) Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conserv Biol 29:724–737
Lydersen C (1998) Status and biology of ringed seals (*Phoca hispida*) in Svalbard. NAMMCO Sci Publ 1:46–62
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
Lydersen C, Kovacs KM (1999) Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lactation period. Mar Ecol Prog Ser 187:265–281
Lydersen C, Assmy P, Falk-Petersen S, Kohler J and others (2014) The importance of tidewater glaciers for marine mammals and seabirds in Svalbard, Norway. J Mar Syst 129:452–471
Lydersen C, Vacquie-Garcia J, Lydersen E, Christensen GN, Kovacs KM (2017) Novel terrestrial haul-out behaviour by ringed seals (*Pusa hispida*) in Svalbard, in association with harbour seals (*Phoca vitulina*). Polar Res 36:1374124
McConnell BJ, Chambers C, Fedak MA (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarct Sci 4:393–398
Meredith M, Sommerkorn M, Cassotta S, Derksen C and others (2019) Polar regions. In: Pörtner HO, Roberts DC, Masson-Delmotte V, Zhai P and others (eds) IPCC special report on the ocean and cryosphere in a changing climate. IPCC, Geneva, p 203– 320
Nordli O, Prybylak 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
Onarheim IH, Smedsrud LH, Ingvaldsen RB, Nilsen F (2014) Loss of sea ice during winter north of Svalbard. Tellus 66:23933
Paiva VH, Ramos JA, Martins J, Almeida A, Carvalho A (2008) Foraging habitat selection by little terns *Sternula albifrons* in an estuarine lagoon system of southern Portugal. Ibis 150:18–31
Pavlov AK, Tverberg V, Ivanov BV, Nilsen F, Falk-Petersen S, Granskog MA (2013) Warming of Atlantic water in two West Spitsbergen fjords over the last century (1912–2009). Polar Res 32:11206
R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Ryg M, Øritsland NA (1991) Estimates of energy expenditure and energy consumption of ringed seals (*Phoca hispida*) throughout the year. Polar Res 10:595–601
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
Stirling I (1974) Midsummer observations on the behavior of wild polar bears (*Ursus maritimus*). Can J Zool 52: 1191–1198
Wood SN (2017) Generalized additive models: an introduction with R, 2nd edn. CRC/Taylor & Francis, Boca Raton, FL
Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY

Editorial responsibility: Rory Wilson, Swansea, UK
Reviewed by: L. Irvine and 2 anonymous referees

Submitted: March 21, 2021
Accepted: July 7, 2021
Proofs received from author(s): September 20, 2021