

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

Contrasting changes in space use induced by climate change in two Arctic marine mammal species

Authors: Charmain D. Hamilton^{1*}, Jade Vacquié-Garcia¹, Kit M. Kovacs¹, Rolf A. Ims², Jack
Kohler¹, Christian Lydersen¹

Affiliations:

¹Norwegian Polar Institute, Fram Centre, Tromsø, Norway.

²University of Tromsø, the Arctic University of Norway, Tromsø, Norway.

*Correspondence to: charmain.hamilton@npolar.no

24 **Abstract**

25 Global warming is inducing major environmental changes in the Arctic. These changes will
26 differentially affect species due to differences in climate sensitivity and behavioural plasticity.
27 Arctic endemic marine mammals are expected to be impacted significantly by ongoing
28 changes in their key habitats due to their long life cycles and dependence on ice. Herein,
29 unique biotelemetry datasets for ringed seals (*Pusa hispida*) and white whales (*Delphinapterus*
30 *leucas*) from Svalbard, Norway, spanning two decades (1995-2016) are used to investigate
31 how these species have responded to reduced sea-ice cover and increased Atlantic Water
32 influxes. Tidal glacier fronts were traditionally important foraging areas for both species.
33 Following a period with dramatic environmental change, ringed seals now spend significantly
34 more time near tidal glaciers, where Arctic prey presumably still concentrate. Conversely,
35 white whales spend significantly less time near tidal glacier fronts and display spatial patterns
36 that suggest that they are foraging on Atlantic fishes that are new to the region. Differences in
37 levels of dietary specialization and overall behavioural plasticity are likely reasons for similar
38 environmental pressures affecting these species differently. Climate change adjustments
39 through behavioural plasticity will be vital for species survival in the Arctic, given the
40 rapidity of change and limited dispersal options.

41

42 **Keywords:** *Delphinapterus leucas*, tidal glacier fronts, *Pusa hispida*, ringed seals, Svalbard,
43 white whales

44

45

46

47

48

49 **1. Background**

50 Climate change is having serious consequences for global biodiversity [1]. Long-lived,
51 high trophic level species are experiencing direct and indirect impacts of climate change, with
52 the rapid pace of change rendering genetic adaptation unfeasible [2]. Distributional changes
53 and various expressions of behavioural and dietary plasticity will likely be the first observable
54 responses within ecosystems [2,3]. However, time series of sufficient length to assess these
55 changes are rare in the Arctic [4,5].

56 The Arctic is the bellwether of climate change. Air temperatures are increasing three times
57 faster than the global average, sea-ice extents are declining and glaciers are retreating [6].
58 Climate change impacts on Arctic species will likely have far-reaching impacts across
59 ecosystems [4,7]. As long-lived species that are dependent on sea ice, and in some regions
60 glacier fronts, Arctic marine mammals are expected to be negatively affected by climate
61 change [7,8]. Due to different ecological relationships with sea ice (or glacier fronts) and
62 varying degrees of behavioural plasticity, species responses to climate change will likely vary
63 [7].

64 Ringed seals (RS; *Pusa hispida*) and white whales (WW; *Delphinapterus leucas*) are
65 Arctic marine mammals with circumpolar distributions [7]. Most populations of both species
66 are found in areas containing sea ice throughout the year and both species forage
67 predominantly on ice-associated prey [7]. Tidal glacier fronts are important areas for both
68 species in some regions for foraging [8]. Both species will likely be impacted directly and
69 indirectly (i.e. through changes in their prey base) by sea-ice reductions and glacier retraction.

70 RS and WW live year-round in waters surrounding Svalbard, Norway (74-81°N, 10-
71 35°E). More than half of Svalbard's landmass is covered by glaciers and 60% of the
72 glaciated area terminates in the sea [8, figure 1]. This archipelago has variable
73 oceanographic regimes with the West Spitsbergen Current (WSC) transporting warm, Atlantic

74 Water northwards along the continental shelf-break in the west while eastern Svalbard is
75 primarily influenced by Arctic Water, which is transported around the southern tip of
76 Svalbard and then northward along the west coast by the East Spitsbergen Current (ESC).
77 Water mass exchange occurs across the polar front that forms between the WSC and ESC,
78 resulting in intrusions of Atlantic Water into west coast fjords and Storfjorden (east; figure 1)
79 [9,10]. The magnitude of Atlantic Water intrusions vary intra- and inter-annually [10].

80 In 2006, the sea-ice regime in Svalbard unexpectedly collapsed with the altered sea-ice
81 conditions persisting to the present day. The land-fast sea-ice extent declined sharply,
82 especially along the west coast [11]. This is partly due to the increased temperature of the
83 WSC and more frequent penetration of the WSC across the polar front [10,11]. Svalbard and
84 the northern Barents Sea region have had the greatest decrease in the seasonal duration of sea-
85 ice cover in the Arctic [5]. The number of tidal glacier fronts in Svalbard is also decreasing
86 [8].

87 Biotelemetry data from RS and WW were collected between 1995-2003 to study their
88 basic ecology. The unexpected change in environmental conditions in 2006 presented the
89 opportunity for a natural experiment. Repeat sampling after 2006 created unique biotelemetry
90 datasets spanning two decades that were used herein to investigate how the large
91 environmental changes in Svalbard have impacted the space-use patterns of these two ice-
92 affiliated species during summer and autumn. These seasons are important foraging periods
93 for both species and are times when the fjords are equally accessible to both species.

94

95 **2. Materials and methods**

96 RS (28 in 1996-2003, 28 in 2010-2016) and WW (18 in 1995-2001, 16 in 2013-2016)
97 were equipped with biotelemetry devices in Svalbard waters, providing animal movement
98 data (tables 1; ESM, figure S1, tables S1, S2) [12]. Generalized additive mixed-effect models

99 (GAMMs - binomial family and logistic link) were used to investigate how the proportion of
100 time spent within 5 km of tidal glacier fronts (distance \leq 5 km=1, distance $>$ 5 km=0) changed
101 between these two periods. Linear models were used to assess if glacier front use was
102 associated with calving length or water depth. See electronic supplementary material for
103 further details.

104

105 **3. Results and Discussion**

106 Two decades ago, RS and WW spent approximately half of their time affiliated with
107 glacier fronts (figure 2) and had diets dominated by polar cod (*Boreogadus saida*) during the
108 summer and autumn [13-16]. However, these two species display contrasting responses to the
109 environmental changes that have occurred in Svalbard waters, with RS now spending
110 significantly higher proportions of time near tidal glacier fronts, while WW spent significantly
111 less time near tidal glacier fronts (figures 2, S2).

112 Negribreen was the glacier most visited by WW (both periods) and RS (first period)
113 (figure 1, tables S3, S4). This glacier is large and has a long calving front that occurs in deep
114 water. RS also heavily used Sonklarbreen (first period) and Kongsbreen (second period),
115 which have similar characteristics to Negribreen (figure 1, table S3). Time spent in front of
116 other glaciers was relatively low and relative use of them was not explained by their
117 characteristics for RS, though for WW frontal length remained important (tables S5, S6).
118 Differences in tagging locations in the two study years (figure S1, tables S1, S2) are unlikely
119 to have impacted our results because WW move across much of the archipelago constantly
120 [16] and RS results were not dependent on tagging location in the analyses herein.

121 Concomitant with the physical changes (increased Atlantic Water intrusion and
122 decreased sea ice) that have occurred over the last decade in Svalbard waters, large ecosystem
123 changes have taken place, including a general “borealization” of the fish community. Atlantic

124 species are increasingly common and the ranges of Arctic and sub-Arctic species are shifting
125 northward [17,18]. Diets of some seabirds and marine mammals in the Svalbard area have
126 changed to include more Atlantic and less Arctic prey [19,20]. However, Arctic and sub-
127 Arctic zooplankton, which are the main prey of polar cod, still dominate the innermost parts
128 of glacial fjords [21] and polar cod are still abundant in these areas [22]. Calved glacier ice
129 pieces also provide haul-out platforms for ringed seals. Tidal glacier fronts appear to be
130 serving as Arctic “refugia” for RS, explaining why this species has increased the amount of
131 time spent near glaciers, resulting in smaller home ranges following the sea-ice collapse
132 (figures 2, S2). Foraging effort by RS has also increased following the sea-ice collapse [15].

133 In contrast to RS, WW are not retracting into Arctic glacial refugia. They have larger
134 home ranges and spent less time near glacier fronts and more time in the centre of fjords
135 (figures 2, S2) in 2013-2016 compared to 1995-2001 [16]. It is likely that they have shifted to
136 foraging on Atlantic prey such as capelin (*Mallotus villosus*) and herring (*Clupea harengus*),
137 similar to the situation in the Canadian Arctic [23]. WW have been observed milling in the
138 centre of fjords in recent years, which was never seen previously in Svalbard waters (KMK &
139 CL, unpublished data). WW tend to be dietary generalists, in contrast to RS that are more
140 commonly individual specialists [24]. Although competition between these two species cannot
141 be ruled out, a difference in dietary plasticity between them is likely the primary factor
142 influencing their contrasting responses to a shared environmental change.

143

144 **4. Conclusion**

145 The different changes observed in the space use patterns of RS and WW in Svalbard
146 waters, using unique long-term biotelemetry datasets, highlight that ecosystem changes are
147 affecting top trophic level predators differently. The flexible response shown by WW
148 improves their chances of adapting to warming conditions, while RS’ retraction into Arctic

149 refugia, which are declining in number, with an on-going dependence on prey that are also in
150 decline, reflects limited adaptability and resilience. Plasticity in foraging and other responses
151 to habitat change will be important in successfully adjusting to the on-going environmental
152 changes driven by global warming. Species and sub-populations that are not able to make
153 such changes are almost certain to decline, perhaps to extinction where refugial areas become
154 too limiting for species survival.

155

156 **Ethics.** Animal handling protocols were approved by the Norwegian Animal Research
157 Authority and the Governor of Svalbard (RIS numbers: 2014/00067-9, 2014/00067-14,
158 16/01341-4, 16/01621-3).

159

160 **Data accessibility.** Data are available at the Norwegian Polar Data Centre
161 (doi:10.21334/npolar.2019.e1cd54e1).

162

163 **Competing interests.** We have no competing interests.

164

165 **Authors' contributions.** CDH, JVG, RAI, CL and KMK conducted fieldwork. JK provided
166 glacier data. CDH and JVG analysed the data. CDH, JVG, CL and KMK interpreted the
167 results. All authors wrote the manuscript, approved the final version and agree to be
168 accountable for the manuscript contents.

169

170 **Acknowledgements.** We thank field team members.

171

172 **Funding.** Funding was provided by the Norwegian Research Council (ICE-WHALES,
173 TIGRIF, GLAERE), NPIs ICE Centre and Fram Centre's Fjord and Coast Flagship.

174

175 **References**

- 176 1. Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012 Impacts of
177 climate change on the future of biodiversity. *Ecol. Lett.* **15**, 365-
178 377.(doi:10.1111/j.1461-0248.2011.01736.x)
- 179 2. Hoffmann AA, Sgrò CM. 2011 Climate change and evolutionary adaptation. *Nature*
180 **470**, 479-485.(doi:10.1038/nature09670)
- 181 3. Gilg O *et al.* 2012 Climate change and the ecology and evolution of Arctic vertebrates.
182 *Ann. N. Y. Acad. Sci.* **1249**, 166-190.(doi:10.1111/j.1749-6632.2011.06412.x)
- 183 4. Post E *et al.* 2009 Ecological dynamics across the Arctic associated with recent
184 climate change. *Science* **325**, 1355-1358.(doi:10.1126/science.1173113)
- 185 5. Laidre KL *et al.* 2015 Arctic marine mammal population status, sea ice habitat loss,
186 and conservation recommendations for the 21st century. *Conserv. Biol.* **29**, 724-
187 737.(doi:10.1111/cobi.12474)
- 188 6. Comiso JC, Hall DK. 2014 Climate trends in the Arctic as observed from space.
189 *WIREs Clim. Change* **5**, 389-409.(doi:10.1002/wcc.277)
- 190 7. Kovacs KM, Lydersen C, Overland JE, Moore SE. 2011 Impacts of changing sea-ice
191 conditions on Arctic marine mammals. *Mar. Biodiv.* **41**, 181-194.
192 (doi:10.1007/s12526-010-0061-0)
- 193 8. Lydersen C *et al.* 2014 The importance of tidewater glaciers for marine mammals and
194 seabirds in Svalbard, Norway. *J. Mar. Syst.* **129**, 452-471.(doi:10.1016/j.jmarsys.2013.
195 09.006)
- 196 9. Skogseth R, Haugan PM, Jakobsson M. 2005 Watermass transformations in
197 Storfjorden. *Cont. Shelf Res.* **25**, 667-695.(doi:10.1016/j.csr.2004.10.005)

- 198 10. Tverberg V, Skogseth R, Cottier F, Sundfjord A, Walczowski W, Inall ME, Falck E,
199 Pavlova O, Nilsen F. 2018 The Kongsfjorden Transect: seasonal and inter-annual
200 variability in hydrography. *Polar Res.* in press.
- 201 11. Pavlova O, Gerland S, Hop H. 2018 Changes in sea-ice extent and thickness in
202 Kongsfjorden, Svalbard (2003-2016). *Polar Res.* in press.
- 203 12. Hamilton CD, Vacquié-Garcia J, Kovacs KM, Lydersen C. 2019 Data from:
204 Contrasting changes in space use induced by climate change in two Arctic marine
205 mammal species. Norwegian Polar Institute.(doi:10.21334/npolar.2019.e1cd54e1)
- 206 13. Dahl TM, Lydersen C, Kovacs KM, Falk-Petersen S, Sargent J, Gjertz I, Gulliksen B.
207 2000 Fatty acid composition of the blubber in white whales (*Delphinapterus leucas*).
208 *Polar Biol.* **23**, 401-409.(doi:10.1007/s003000050461)
- 209 14. Labansen AL, Lydersen C, Haug T, Kovacs KM. 2007 Spring diet of ringed seals
210 (*Phoca hispida*) from Spitsbergen, Norway. *ICES J. Mar. Sci.* **64**, 1246-
211 1256.(doi:10.1093/icesjms/fsm090)
- 212 15. Hamilton CD, Lydersen C, Ims RA, Kovacs KM. 2016 Coastal habitat use by ringed
213 seals *Pusa hispida* following a regional sea-ice collapse. *Mar. Ecol. Prog. Ser.* **545**,
214 261-277.(doi:10.3354/meps11598)
- 215 16. Vacquié-Garcia J, Lydersen C, Ims RA, Kovacs KM. 2018 Habitats and movement
216 patterns of white whales *Delphinapterus leucas* in Svalbard, Norway. *Mov. Ecol.* **6**,
217 21.(doi:10.1186/s40462-018-0139-z)
- 218 17. Berge J, Heggland K, Lønne OJ, Cottier F, Hop H, Gabrielsen GW, Nøttestad L,
219 Misund OA. 2015 First records of Atlantic mackerel (*Scomber scombrus*) from the
220 Svalbard Archipelago, Norway. *Arctic* **68**, 54-61.(doi:10.14430/arctic4455)

- 221 18. Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV.
222 2015 Recent warming leads to a rapid borealization of fish communities in the Arctic.
223 *Nature Clim. Change* **5**, 673-677.(doi:10.1038/nclimate2647)
- 224 19. Descamps S, Aars J, Fuglei E, Kovacs KM, Lydersen C, Pavlova O, Pedersen ÅØ,
225 Ravolainen V, Strøm H. 2017 Climate change impacts on wildlife in a High Arctic
226 archipelago. *Glob. Change Biol.* **23**, 490-502.
227 (doi:10.1111/gcb.13381)
- 228 20. Vihtakari M, Welcker J, Moe B, Chastel O, Tartu S, Hop H, Bech C, Descamps S,
229 Gabrielsen GW. 2018 Black-legged kittiwakes as messengers of Atlantification in the
230 Arctic. *Sci. Rep.* **8**, 1178.(doi:10.1038/s41598-017-19118-8)
- 231 21. Dalpadado P, Hop H, Rønning J, Pavlov V, Sperfeld E, Buchholz F, Rey A, Wold A.
232 2016 Distribution and abundance of euphausiids and pelagic amphipods in
233 Kongsfjorden, Isfjorden and Rijpfjorden (Svalbard). *Polar Biol.* **39**, 1765-
234 1784.(doi:10.1007/s00300-015-1874-x)
- 235 22. Fey DP, Węśławski JM. 2017 Age, growth rate, and otolith growth of polar cod
236 (*Boreogadus saida*) in two fjords of Svalbard. *Oceanologia* **59**, 576-
237 584.(doi:10.1016/j.oceano.2017.03.011)
- 238 23. Watt CA, Orr J, Ferguson SH. 2016 A shift in foraging behaviour of beluga whales
239 *Delphinapterus leucas* from the threatened Cumberland Sound population may reflect
240 a changing Arctic food web. *Endang. Species Res.* **31**, 259-270.
241 (doi:10.3354/esr00768)
- 242 24. Yurkowski DJ, Ferguson S, Choy ES, Loseto LL, Brown TM, Muir DCG, Semeniuk
243 CAD, Fisk AT. 2016 Latitudinal variation in ecological opportunity and intraspecific
244 competition indicates differences in niche variability and diet specialization of Arctic
245 marine predators. *Ecol. Evol.* **6**, 1666-1678.(doi:10.1002/ece3.1980)

246 **Table 1.** Tagging metrics for 56 ringed seals and 34 white whales equipped with biotelemetry
 247 devices in Svalbard, Norway. Note that the tracking duration ends on 01 November or when
 248 the animal leaves the west coast of Svalbard or Storfjorden.

Species	Time period	Number of individuals	Sex ratio (F:M)	Tracking duration (days; mean \pm SD)
Ringed seal	1996-2003	28	18:10	82 \pm 36
	2010-2016	28	14:14	76 \pm 25
White whale	1995-2001	18	0:18	38 \pm 26
	2013-2016	16	0:16	60 \pm 29

249

250

251 **Figure 1.** Svalbard, Norway, with place names and water currents. Glaciers (light-grey) and
 252 tidal glacier fronts (red) in 2015 are shown. The West Spitsbergen Current (WSC; dark-red
 253 arrows) transports warm Atlantic Water while the East Spitsbergen Current (ESC; blue
 254 arrows) transports cold Arctic Water.

255

256 **Figure 2.** Proportion of time spent within 5 km of tidal glacier fronts by (a) ringed seals and
 257 (b) white whales and GAMM results according to day of the year for (c) ringed seals and (d)
 258 white whales equipped with biotelemetry devices before and after a major environmental
 259 change in Svalbard, Norway. (Mean \pm 95% CI).

260

261

262

263

264

265

266

267



268

269 **Figure 1**

270

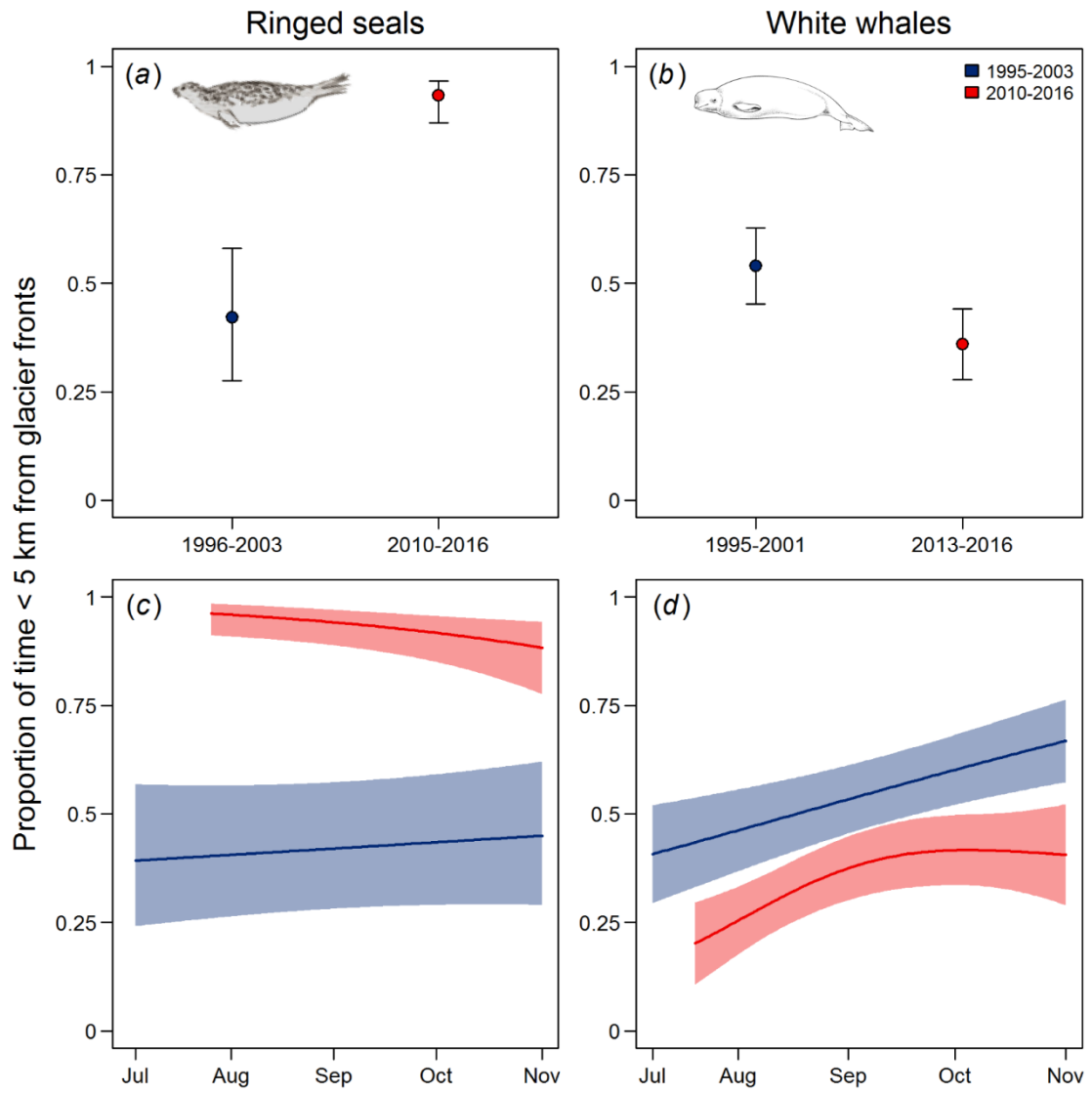
271

272

273

274

275



276

277 **Figure 2**

Supplementary material

Materials and methods

(a) Capture

Fifty-six ringed seals and 34 male white whales were caught with shore-set nets in the Svalbard Archipelago before (ringed seals=28 (1996-2003), white whales=18 (1995-2001)) and after (ringed seals=28 (2010-2016), white whales=16 (2013-2016)) a major collapse in sea-ice conditions occurred in 2006 (electronic supplementary material, tables S1, S2, figure S1). Only male white whales are considered herein due to the low number of female white whales tagged in each time period (two in both 1995-2001 and 2013-2016). Seals in 1996 were equipped with 0.5-W Satellite Linked Dive Recorders (SLDR; SDR-T6, Wildlife Computers, Redmond, USA). The rest of the ringed seals (2002-2016) and all of the white whales (1995-2016) were equipped with Satellite Relay Data Loggers (SRDLs, Sea Mammal Research Unit, University of St Andrews, St Andrews, Scotland; see [15,16,25] for more details). All animal-handling and tagging protocols were approved by the Norwegian Animal Research Authority and the Governor of Svalbard.

(b) Statistical Analysis

All data analyses were conducted using R 3.3.3 [26]. Six (or the maximum number of transmissions that day if $n < 6$) locations were randomly selected every second day from ringed seals tagged in 2002-2016 to match the transmission frequency of seals tagged in 1996. The locations from all seals were filtered, first with the SDA filter and subsequently with the continuous-time correlated random walk (crawl) model, with a stopping model incorporated for the seals from 2002-2016 to account for the time spent hauled out [27,28] (haul-out data was not available for ringed seals tagged in 1996). One daily position was extracted from the crawl models for each seal, due to the low transmission frequency of the tags on seals in 1996.

Only time periods in which the ringed seals were close to the coast (see [15] for further details) were used in the analyses herein. White whale positions were filtered with the SDA filter [27]. Hourly locations were extracted from the SDA-filtered tracks using linear interpolation.

Ringed seal and white whale positions were compared to the locations of tidal glacier fronts in areas with Atlantic Water inflows (i.e. the west coast of Spitsbergen and Storfjorden, figure 1). Only summer and autumn data are considered in this study because these time periods are important foraging periods for both species and are times when the fjords are equally accessible to both species. Glacial meltwater plumes entrain large volumes of water as they rise to the surface, causing advection of production toward the glacier front. Lower trophic organisms in these areas also might become pushed to the surface or trapped along the bottom (below the fresh water), making these areas important for Arctic marine mammals and seabirds for foraging [8]. Glaciers in Svalbard are retreating, and thus different sets of shapefiles, from 2001-2009 and from 2015, were used for the ringed seals and white whales tagged in 1995-2003 and 2010-2016, respectively [29,30]. The proportion of time spent within 5 km of a tidal glacier front (distance ≤ 5 km = 1, distance > 5 km = 0) for each species was analysed using generalized additive mixed-effect models (GAMM, mgcv package [31]). Although in reality animals frequenting glacier fronts are much closer than this, five km was used to account for uncertainty in the yearly position of quickly retreating glacier fronts and the errors inherent in Argos location estimates [32]. Fifteen ringed seals and two white whales also transmitted Fastloc GPS positions. Comparisons between GPS and Argos data showed that 85% of the Argos locations from both ringed seals and white whales were within 5 km of the corresponding GPS location.

Proportion of time spent within 5 km of a glacier front was included in the GAMM models as the response variable using the logit link function and the binomial error was used

to account for residual variance. Possible predictor variables included time period (i.e. before and after the collapse in sea-ice conditions), day of year, sex (ringed seals only) and mass (ringed seals only). A separate day of year smooth curve was made for each time period, by including time period as a “by” variable in the day of the year smooth term [31]. Individual ID was included as both a random effect and as a grouping factor in the temporal autocorrelation structure order one (corAR1) term. Model selection took place using p-values and model validation was conducted as recommended by [33].

Linear Models (LM) were used to test whether the subject species preferred glaciers with longer calving lengths, greater surface areas or deeper water depths in both of the study periods. The closest glacier and its associated calving length, area and water depth were identified for all locations within 5 km of a tidal glacier front. The length of the calving fronts was calculated from the glacier front shapefiles used to calculate distance in each time period (see above) and the water depth in front of the tidal glacier fronts were extracted from an updated version of the S800 bathymetry data [34]. Glacier surface area strongly influences the amount of glacial discharge at the glacier front (J.K., unpublished data). Because glacier area was highly correlated with calving length (>70%), only calving length and water depth were included as possible predictor variables in the LMs (correlation between these latter two variables was <30%). The identity link was used for the response variable in the LMs (i.e. proportion of locations in front of each tidal glacier front) and the Gaussian family was used to assess residual variance. The response variable was log-transformed to meet model assumptions. AICc was used for model selection [35] and model validation was conducted as recommended by [33].

To test if locations occurring on land, due to Argos error, were affecting the results, positions on land were corrected using their associated Argos error following a simplified particle filter adapted from [36]. For each on-land position, 50 particles were created based on

the associated Argos error with each particle classified as on-land or at-sea (Argos errors based on [32,37] for animals tagged in 1995-2011 and 2012-2016, respectively). The geographic averages of the at-sea particles were used to correct each on-land location. On-land locations where the geographic average of at-sea particles occurred on land or locations that had only on-land particles were deleted. Model results did not differ based on whether locations were corrected or not, so only original (uncorrected) positions were used in the analyses herein.

To graphically illustrate the changes in space use of ringed seals and white whales shown herein, home ranges were created for areas of high use for each species that had data available for both time periods. For ringed seals, locations within St Jonsfjorden and on the northern coast of Isfjorden (encompassing Nansenbreen, Borebreen, Wahlenbergbreen and Sveabreen) were selected and for white whales, locations near Negribreen and Heuglibreen were selected (see tables S3 and S4). A utilization distribution for each area was created using kernelUD with the smoothing parameter “href”. A 75% home range was extracted from each utilization distribution (adehabitatHR package) [38].

Spatial analyses in this study are restricted to 2-dimensional versions of space use because the large developments in biotelemetry devices that have taken place since 1995 and the realities of scale in small areas make more analytically complex comparison of the two time periods impossible. The white whales tagged in 1995-2001 and the ringed seals tagged in 1996 did not transmit comparable dive data to the biotelemetry devices used in later deployments. Therefore, analyses investigating differences in diving behaviour could not be conducted across the whole time frame of this study (differences in ringed seal diving behaviour between 2002-2003 and 2010-2013 have been published [see 15]). The small spatial scale of Svalbard’s fjords, combined with Argos error, also breaks key assumptions of other spatial analyses, such as first passage time and behavioural switching correlated random

walk models [39,40]. For example, a circle with a 5 km radius encompasses both tidal glacier fronts and central areas of most fjords in Svalbard and key assumptions separating travelling and foraging in animal movement models (i.e. that travelling takes place in straight lines) are broken when attempted to deal with fine spatial scales.

References

25. Gjertz I, Kovacs KM, Lydersen C, Wiig  . 2000 Movements and diving of adult ringed seals (*Phoca hispida*) in Svalbard. *Polar Biol.* **23**, 651-656.
(doi:10.1007/s003000000143)
26. R Development Core Team. 2013 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
<http://www.R-project.org>
27. 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. (doi:10.1111/j.1748-7692.2007.00180.x)
28. 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)
29. K nig M, Kohler J, Nuth C. 2013 Glacier area outlines – Svalbard [Data set]. Norwegian Polar Institute. (doi:10.21334/npolar.2013.89f430f8)
30. Kohler J, K nig M, Nuth C, Villaflor G. 2018 Svalbard tidewater glacier front database [Data set]. Norwegian Polar Institute. (doi:10.21334/npolar.2018.7cd67b1a)
31. Wood SN. 2006 *Generalized Additive Models: An Introduction With R*. Boca Raton, FL: Chapman & Hall/CRC.

32. Costa DP *et al.* 2010 Accuracy of ARGOS locations of pinnipeds at-sea estimated using Fastloc GPS. *PLoS ONE* **5**, e8677. (doi:10.1371/journal.pone.0008677)
33. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009 *Mixed Effects Models And Extensions In Ecology With R*. New York, NY: Springer-Verlag.
34. Hattermann T, Isachsen PE, von Appen WJ, Albretsen J, Sundfjord A. 2016 Eddy-driven recirculation of Atlantic water in Fram Strait. *Geophys. Res. Lett.* **43**, 3406-3414. (doi:10.1002/2016GL068323)
35. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer-Verlag.
36. Tremblay Y, Robinson PW, Costa DP. 2009 A parsimonious approach to modeling animal movement data. *PLoS ONE* **4**, e4711. (doi:10.1371/journal.pone.0004711)
37. Lowther AD, Lydersen C, Fedak MA, Lovell P, Kovacs KM. 2015 The Argos-CLS Kalman filter: error structures and state-space modelling relative to Fastloc GPS data. *PLoS ONE* **10**, e0124754. (doi:10.1371/journal.pone.0124754)
38. Calenge C. 2006 The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Model.* **197**, 516-519. (doi:10.1016/j.ecolmodel.2006.03.017)
39. Fauchald P, Tveraa T. 2003 Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* **84**, 282-288. (doi:10.1890/0012-9658(2003)084[0282:UFPTIT]2.0.CO;2)
40. Jonsen ID, Flemming JM, Myers RA. 2005 Robust state-space modeling of animal movement data. *Ecology* **86**, 2874-2880. (doi:10.1890/04-1852)

seal ID	sex	mass (kg)	tagging date	tagging latitude (�N)	tagging longitude (�E)	tracking duration (d)
8568	F	68.5	1996-07-01	78.5	12.8	5
14747	F	51	1996-07-04	78.5	12.9	119
14748	M	69.5	1996-07-05	78.5	13.1	115
14749	F	60	1996-07-06	78.5	13.1	115
14750	F	52.5	1996-07-06	78.5	13.1	109
14751	F	52	1996-07-08	78.5	13.1	73
14752	F	68.5	1996-07-10	78.5	13.1	113
14753	M	54	1996-07-23	77.8	15.7	5
F31-02	F	31	2002-07-21	78.7	20.2	62
F33-02	F	33	2002-07-21	78.7	20.2	99
F36-02	F	36	2002-07-21	78.7	20.2	101
F37-02	F	37	2002-07-20	78.7	20.2	32
F57-02	F	57	2002-07-19	78.7	20.2	101
M28-02	M	28	2002-07-20	78.7	20.2	102
M34-02	M	34	2002-07-19	78.7	20.2	32
M50-02	M	60	2002-07-19	78.7	20.2	1
M65-02	M	65	2002-07-20	78.7	20.2	101
M72-02	M	72	2002-07-21	78.7	20.2	39
F28-03	F	28	2003-07-20	78.7	20.2	102
F34-03	F	34	2003-07-19	78.7	20.2	102
F37-03	F	37	2003-07-22	78.7	20.2	98
F53-03	F	53	2003-07-21	78.7	20.2	101
F58-03	F	58	2003-07-19	78.7	20.2	103
F59-03	F	59	2003-07-20	78.7	20.2	102
F89-03	F	89	2003-07-20	78.7	20.2	100
M40-03	M	40	2003-07-22	78.7	20.2	98
M57-03	M	57	2003-07-21	78.7	20.2	79
M59-03	M	59	2003-07-24	78.7	20.2	98
F34-10	F	34	2010-08-03	79.8	21.7	24
F52-10	F	52	2010-08-03	79.8	21.7	51
F61-11	F	61	2011-07-28	78.9	12.4	94
F66-11	F	66	2011-07-30	78.9	12.4	92
F72-11	F	72	2011-08-03	78.9	12.4	88
F73-11	F	73	2011-07-22	78.9	12.4	100
F76-11	F	76	2011-07-30	78.9	12.4	72
F99-11	F	99	2011-07-29	78.9	12.4	93
M55-11	M	55	2011-07-28	78.9	12.4	94
M57-11	M	57	2011-08-03	78.9	12.4	88
M81-11	M	81	2011-07-24	78.9	12.4	98
M90-11	M	90	2011-08-03	78.9	12.4	88
M100-11	M	100	2011-07-20	78.9	12.4	102
M44-12	M	44	2012-07-29	79.8	21.7	4
F61a-12	F	61	2012-08-15	78.9	12.4	68
F61b-12	F	61	2012-08-17	78.9	12.4	74
F64-12	F	64	2012-08-18	78.9	12.4	73
M60a-12	M	60	2012-08-25	78.5	12.6	62
M60b-12	M	60	2012-08-15	78.9	12.4	76
M74-12	M	74	2012-08-25	78.5	12.6	66
M88-12	M	88	2012-08-26	78.5	12.6	65
M100-12	M	100	2012-08-25	78.5	12.6	66
M103-12	M	103	2012-08-25	78.5	12.6	66
F55-16	F	55	2016-07-25	78.5	13.1	97
F58-16	F	58	2016-07-26	78.5	13.1	96
F65-16	F	65	2016-07-26	78.5	13.1	94
M53-16	M	53	2016-07-26	78.5	13.1	96
M65-16	M	65	2016-07-26	78.5	13.1	28

Table S1. Tagging metrics for 56 ringed seals equipped with biotelemetry devices from 1996-2016 in Svalbard, Norway, including tagging date, tagging location and tracking duration. Note that the tracking duration ends either on 01 November or when the seals left the west coast of Svalbard or the Storfjorden area.

whale ID	sex	tagging date	tagging latitude (�N)	tagging longitude (�E)	tracking duration (d)
1995-1	M	1995-07-07	77.8	16.9	31
1995-2	M	1998-07-09	77.9	16.3	30
1995-3	M	1995-07-08	77.8	15.7	58
1996-1	M	1996-07-20	77.5	16.0	7
1997-1	M	1997-08-04	77.8	16.0	54
1997-2	M	1997-08-04	77.8	16.0	34
1997-3	M	1997-08-04	77.8	16.0	82
1998-7	M	1998-09-01	78.5	18.9	7
1999-3	M	1999-08-21	78.5	18.9	72
1999-4	M	1999-08-21	78.5	18.9	13
1999-5	M	1999-08-18	78.5	18.9	63
1999-6	M	1999-08-18	78.5	18.9	68
1999-7	M	1999-08-18	78.5	18.9	55
1999-8	M	1999-08-19	78.5	18.9	65
2000-2	M	2000-10-18	78.5	18.9	13
2001-1	M	2000-10-17	78.5	18.9	10
2001-2	M	2000-10-18	78.5	18.9	13
2001-3	M	2000-10-19	78.5	18.9	12
2013-1	M	2013-08-16	79.8	12.2	76
2013-2	M	2013-08-23	78.4	17.3	70
2013-3	M	2013-08-23	78.3	15.7	69
2014-1	M	2014-08-11	77.0	16.4	20
2014-2	M	2014-08-14	77.0	16.4	51
2014-3	M	2014-08-14	77.0	16.4	78
2014-4	M	2014-08-03	78.5	18.9	81
2014-5	M	2014-08-11	77.0	16.4	81
2014-8	M	2014-08-18	77.5	14.7	21
2015-5	M	2015-07-19	79.3	11.7	19
2015-8	M	2015-07-19	79.2	11.6	2
2016-1	M	2016-08-14	78.4	17.0	78
2016-2	M	2016-08-04	78.1	14.0	88
2016-3	M	2016-08-09	78.0	14.2	82
2016-4	M	2016-07-19	78.5	11.7	56
2016-5	M	2016-08-04	78.0	14.1	88

Table S2. Tagging metrics for 34 male white whales equipped with biotelemetry devices from 1995-2016 in Svalbard, Norway, including tagging date, tagging location and tracking duration. Note that the tracking duration ends either on 01 November or when the whales left the west coast of Svalbard or the Storfjorden area.

Glacier ID	Glacier name	Percentage used 1996-2003	Percentage used 2010-2016
15404	Aavatsmarkbreen	0.30	8.01
15515	Blomstrandbreen	0.45	11.84
14901	Borebreen	0.15	1.44
15412	Comfortlessbreen	3.87	NA
15512	Conwaybreen	NA	13.14
15319	Dahlbreen	0.89	1.44
14903.1	Esmarkbreen	0.15	NA
15316	Gaffelbreen	7.75	5.00
11406	Inglefieldbreen	4.32	NA
11106.1	Johansenbreen	1.34	NA
15511.1	Kongsbreen	0.15	19.03
15314.1	Konowbreen	2.53	10.34
15511.2	Kronebreen	0.15	10.13
14902	Nansenbreen	0.30	0.55
11105.1	Negribreen	25.93	NA
11502.2	Nuddbreen/Strongbreen	1.19	NA
15313.2	Osbornebreen	0.15	7.32
11101	Peda�enkobreen	1.34	NA
11503.1	Perseibreen	2.68	NA
11106.2	Petermannbreen	7.45	0.21
11103	Sonklarbreen	29.66	NA
15107.2	S�re Buchananisen	1.64	NA
14803	Sveabreen	NA	0.55
15312	Vintervegen	0.89	6.02
14805.1	Wahlenbergbreen	0.15	2.26

Table S3. Proportion of locations that were within 5 km of the different tidal glacier fronts for 56 ringed seals equipped with biotelemetry devices in Svalbard, Norway from 1996-2016. Only glaciers that had use percentages >1.00% or are labelled in figure S2 were included; an additional 28 glaciers were excluded.

Glacier ID	Glacier name	Percentage used 1995-2001	Percentage used 2010-2015
12505	Vestre Torrellbreen	0.44	2.80
12420	Hansbreen	1.82	2.32
12418.1	Paierlbreen	0.23	1.12
12412	Storbreen	0.66	3.10
12407.2	Samarinbreen East	0.71	1.98
12202.1	Vasilievbreen	0.52	1.41
12413	Hyrnebreen	0.37	1.21
12408	Chomjakovbreen	1.39	3.35
12202.3	Vasilievbreen	0.55	2.26
11503.1	Perseibreen	1.07	0.97
11412.1	Thomsonbreen	0.34	2.41
11411.2	Ingerbreen	0.52	1.83
12104.1	Hambergbreen	1.06	0.83
13213.1	Zawadzki breen	1.75	0.06
13214.1	Nathorstbreen	1.27	0.03
12405.1	Petersbreen	0.57	1.68
12404	K��rberbreen	1.24	3.20
12407.1	Samarinbreen West	0.77	1.40
12503.1	Austre Torellbreen	0.35	3.39
13708	Fridtjovbreen	0.11	2.10
12102	Markhambreen	0.49	1.64
12101.1	Crollbreen	0.34	1.13
11505.1	Jemelianovbreen	0.57	1.47
11106.2	Petermannbreen	7.50	1.85
11105.1	Negribreen	56.97	17.41
11106.1	Johansenbreen	2.42	0.52
11103	Sonklarbreen	0.64	1.90
11101	Pedasjenkobreen	0.35	1.41
11201.1	Heuglinbreen	2.82	3.02
11201.4	Hayesbreen S	1.30	0.36
11407	Arnesenbreen	0.26	1.59
11408.1	Beresnikovbreen	0.48	2.98
11206.1	Ulvebreen	0.31	1.43
13116	Recherchebreen	NA	2.93
16111.1	Raudfjordbreen	NA	1.61

Table S4. Proportion of locations that were within 5 km of the different tidal glacier fronts for 34 male white whales equipped with biotelemetry devices in Svalbard, Norway from 1995-2016. Only glaciers that had use percentages >1.00% or are labelled in figure S2 were included; an additional 81 glaciers were excluded.

Species	Model	AICc	Δ AICc	AICcw
Ringed seal	Depth	274.38	0.00	0.40
	Depth*TimePeriod+FrontLength	275.58	1.20	0.22
	Depth+TimePeriod	276.52	2.14	0.14
	Depth+TimePeriod+FrontLength	276.62	2.24	0.13
	FrontLength	276.86	2.48	0.12
White whale	Depth+TimePeriod+FrontLength	623.09	0.00	0.17
	TimePeriod+FrontLength	623.37	0.28	0.15
	Depth+TimePeriod*FrontLength	623.89	0.80	0.12
	FrontLength	624.04	0.94	0.11
	Depth+FrontLength	624.09	0.99	0.10
	TimePeriod*FrontLength	624.29	1.19	0.09
	Depth*TimePeriod+FrontLength	624.64	1.55	0.08
	Depth*FrontLength+TimePeriod	624.95	1.86	0.07
	Depth*TimePeriod+FrontLength* TimePeriod	625.13	2.04	0.06
	Depth*FrontLength+TimePeriod* FrontLength	625.59	2.49	0.05

Table S5. AICc table showing the AICc value, difference in AICc values and AICc weight for the top five and ten linear models for the glacier characteristics analyses for 56 ringed seals and 34 white whales, respectively, equipped with biotelemetry devices from 1995-2016 in Svalbard, Norway. The AICc selected model for each species is bolded.

Species	Predictor variable	Estimate	Std. Error	t value	p value
Ringed seal (all glaciers)	Intercept	-5.745	0.326	-17.637	<0.001
	Depth	0.054	0.020	2.678	0.009
Ringed seal (without largest glaciers)	Intercept	-5.583	0.335	-16.658	<0.001
	Depth	0.035	0.023	1.565	0.122
White whale (all glaciers)	Intercept	-6.388	0.156	-40.920	<0.001
	Front length	0.0002	0.00003	5.716	<0.001
White whale (without largest glaciers)	Intercept	-6.290	0.175	-35.980	<0.001
	Front length	2×10^{-4}	4×10^{-5}	3.612	<0.001

Table S6. Results of the linear models examining the glacier characteristics for 56 ringed seals and 34 white whales equipped with biotelemetry devices from 1995-2016 in Svalbard, Norway. "Largest glaciers" refers to Negribreen (both species) and Sonklarbreen (ringed seals only); these two glaciers had frontal lengths and depths over two times larger than the next largest glacier.

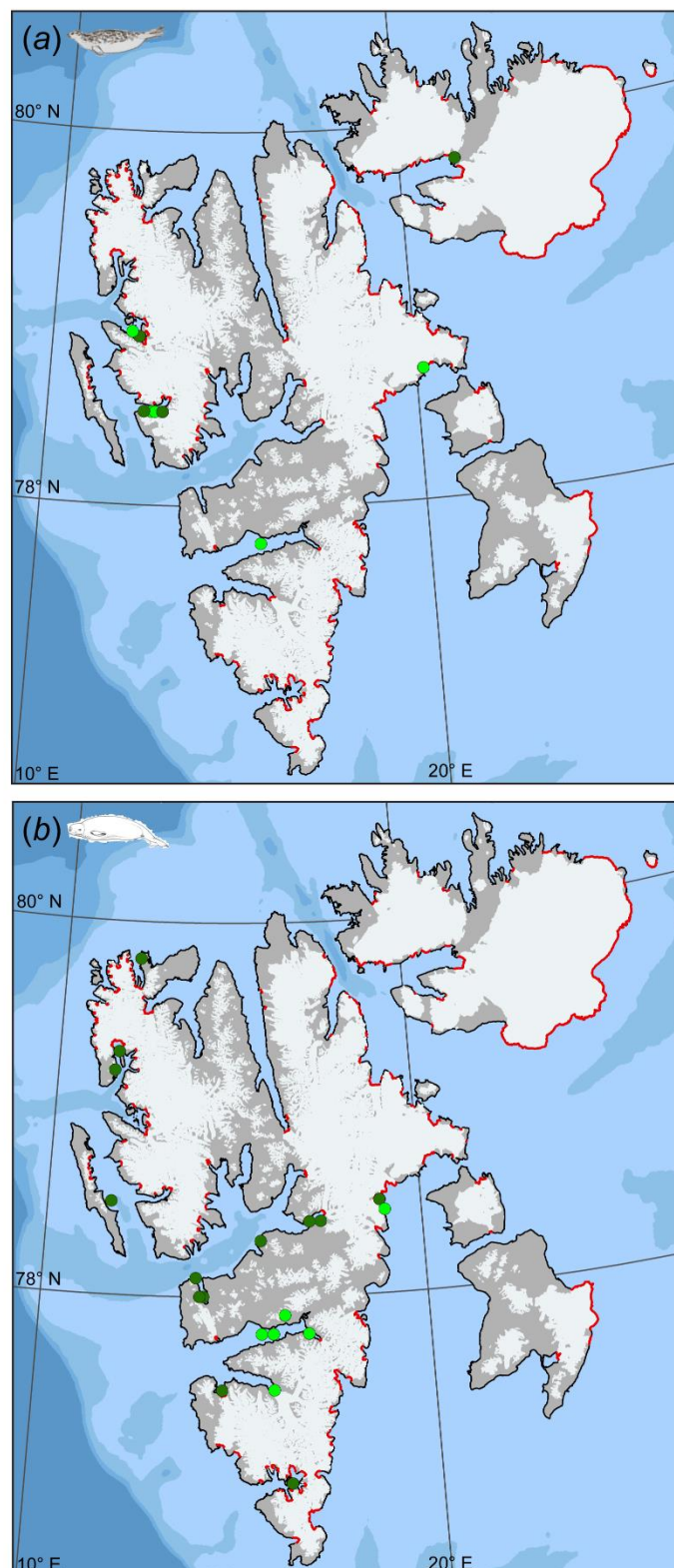


Figure S1. Tagging locations for (a) 56 ringed seals and (b) 34 white whales equipped with biotelemetry devices in 1995-2003 (light-green) and 2010-2016 (dark-green) in Svalbard, Norway. Tidal glacier fronts (red), glaciers (white) and land (grey) in 2015 are shown.

Title: Contrasting changes in space use induced by climate change in two Arctic marine mammal species

Authors: C.D. Hamilton, J. Vacqu -Garcia, K.M. Kovacs, R.A. Ims, J. Kohler, C. Lydersen

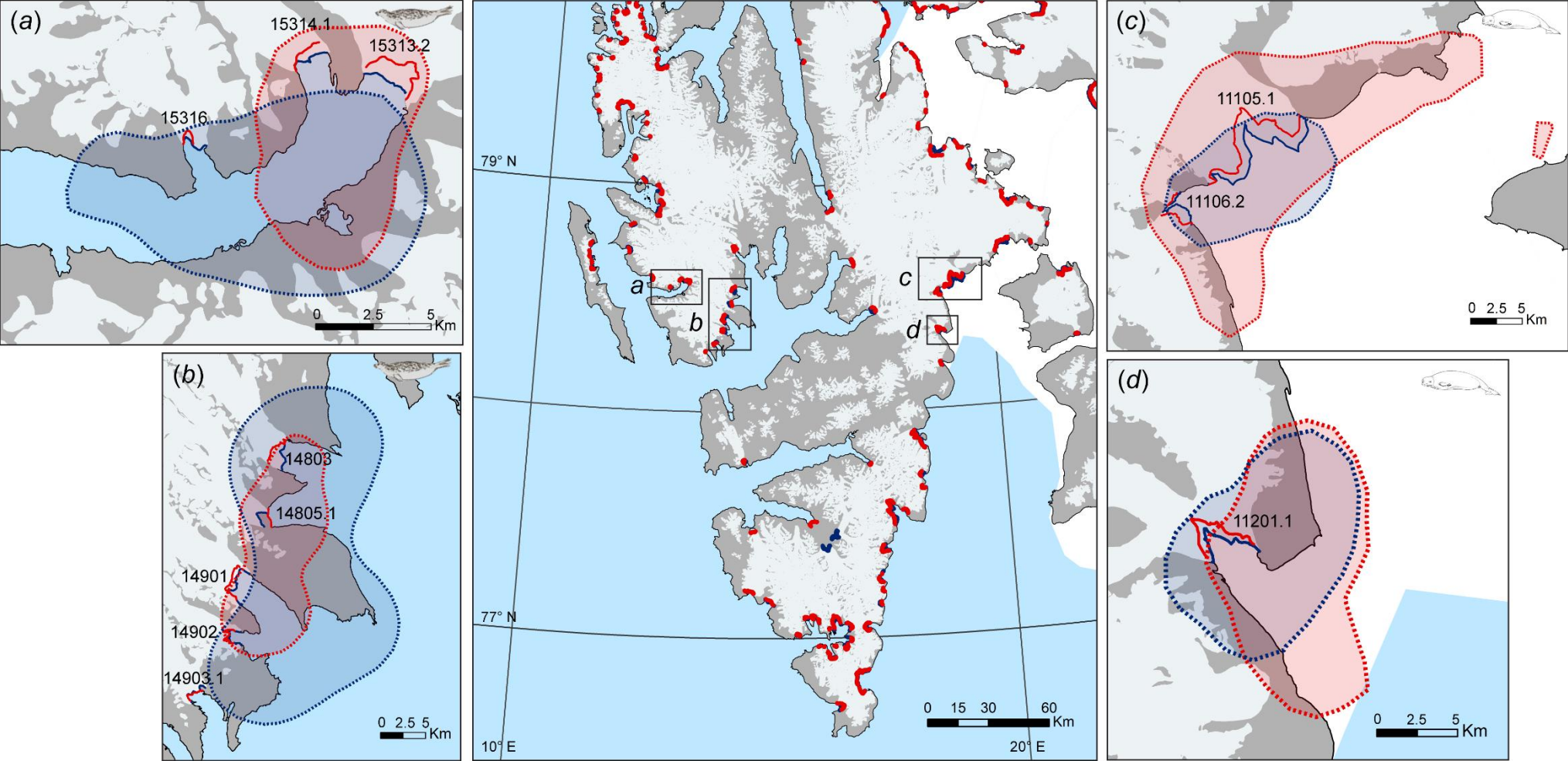


Figure S2. Changes in glacier front locations, sea-ice extent and home range size for selected areas (based on data availability in both time periods) for (a,b) 56 ringed seals and (c,d) 34 white whales equipped with biotelemetry devices from 1995-2016 in Svalbard, Norway. Tidal glacier fronts in 2010 (dark-blue solid lines) and 2015 (red solid lines), sea-ice concentration $\geq 10\%$ in October 2003 (white), glaciers (light-grey; 2010) and land (dark-grey; 2010) are shown. Sea ice with $\geq 10\%$ concentration was largely absent from these areas in the summer and autumn in 2010-2016. The shaded areas (with dotted outlines) indicate the 75% home range sizes of animals in these areas in 1995-2003 (dark-blue) and 2010-2016 (red). The 75% home range sizes changed from (a) 98 km^2 in 1996-2003 to 60 km^2 in 2010-2016, (b) 541 km^2 in 1996-2003 to 189 km^2 in 2010-2016, (c) 146 km^2 in 1995-2001 to 443 km^2 in 2013-2016 and (d) 114 km^2 in 1995-2001 to 132 km^2 in 2013-2016. Home ranges also became more and less concentrated around tidal glacier fronts for ringed seals and white whales, respectively, between 1995-2003 and 2010-2016. The numbers in the inset maps correspond to the glacier IDs in tables S3 and S4.