BIOLOGY LETTERS

royalsocietypublishing.org/journal/rsbl

Research

Cite this article: Hamilton CD, Vacquié-Garcia J, Kovacs KM, Ims RA, Kohler J, Lydersen C. 2019 Contrasting changes in space use induced by climate change in two Arctic marine mammal species. *Biol. Lett.* **15**: 20180834. http://dx.doi.org/10.1098/rsbl.2018.0834

Received: 27 November 2018
Accepted: 15 February 2019

Subject Areas:
behaviour, ecology

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

Author for correspondence:
Charmain D. Hamilton
e-mail: charmain.hamilton@npolar.no

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4413419.

THE ROYAL SOCIETY PUBLISHING

Global change biology

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

Charmain D. Hamilton[1], Jade Vacquié-Garcia[1], Kit M. Kovacs[1], Rolf A. Ims[2], Jack Kohler[1] and Christian Lydersen[1]

[1]Norwegian Polar Institute, Fram Centre, Tromsø, Norway
[2]University of Tromsø, The Arctic University of Norway, Tromsø, Norway

CDH, 0000-0002-9420-8616

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

1. Background

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

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

Ringed seals (RS; *Pusa hispida*) and white whales (WW; *Delphinapterus leucas*) are Arctic marine mammals with circumpolar distributions [7]. Most populations of both species are found in areas containing sea ice throughout the year and both species forage predominantly on ice-associated prey [7].

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

species	time period	number of individuals	sex ratio (F : M)	tracking duration (days; mean ± s.d.)
ringed seal	1996–2003	28	18 : 10	82 ± 36
	2010–2016	28	14 : 14	76 ± 25
white whale	1995–2001	18	0 : 18	38 ± 26
	2013–2016	16	0 : 16	60 ± 29

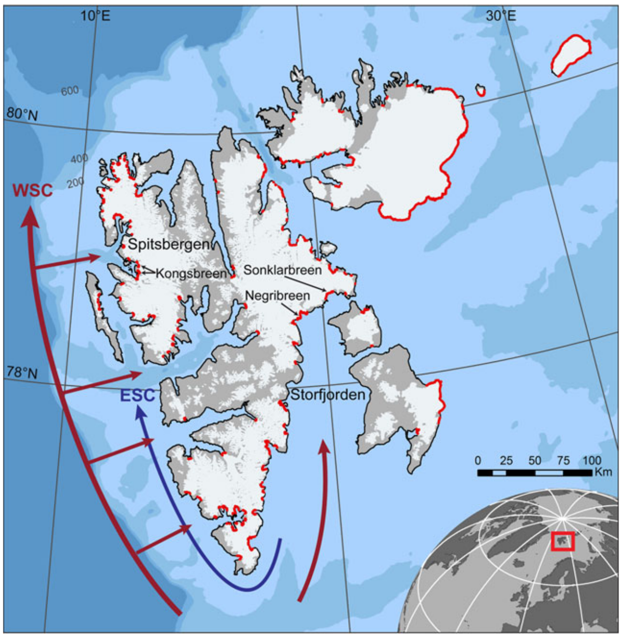

Figure 1. Svalbard, Norway, with place names and ocean currents. Glaciers (white) and tidal glacier fronts (red) in 2015 are shown. The West Spitsbergen Current (dark-red arrows) transports warm Atlantic water, while the East Spitsbergen Current (blue arrows) transports cold Arctic water.

Tidal glacier fronts are important areas for both species in some regions for foraging [8]. Both species will likely be impacted directly and indirectly (i.e. through changes in their prey base) by sea-ice reductions and glacier retraction.

RS and WW live year-round in waters surrounding Svalbard, Norway (74–81° N, 10–35° E). More than half of Svalbard's landmass is covered by glaciers and 60% of the glaciated area terminates in the sea ([8], figure 1). This archipelago has variable oceanographic regimes with the West Spitsbergen Current (WSC) transporting warm, Atlantic water northwards along the continental shelf-break in the west while eastern Svalbard is primarily influenced by Arctic water, which is transported around the southern tip of Svalbard and then northward along the west coast by the East Spitsbergen Current (ESC). Water mass exchange occurs across the polar front that forms between the WSC and ESC, resulting in intrusions of Atlantic water into west coast fjords and Storfjorden (east; figure 1) [9,10]. The magnitude of Atlantic water intrusions varies intra- and inter-annually [10].

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

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

2. Material and methods

RS (28 in 1996–2003, 28 in 2010–2016) and WW (18 in 1995–2001, 16 in 2013–2016) were equipped with biotelemetry devices in Svalbard waters, providing animal movement data (table 1; electronic supplementary material, figure S1 and tables S1 and S2) [12]. Generalized additive mixed-effect models (GAMMs—binomial family and logistic link) were used to investigate how the proportion of time spent within 5 km of tidal glacier fronts (distance ≤ 5 km $= 1$, distance > 5 km $= 0$) changed between these two periods. Linear models were used to assess if glacier front use was associated with calving length or water depth. See electronic supplementary material for further details.

3. Results and discussion

Two decades ago, RS and WW spent approximately half of their time affiliated with glacier fronts (figure 2) and had diets dominated by polar cod (*Boreogadus saida*) during the summer and autumn [13–16]. However, RS and WW display contrasting responses to the environmental changes that have occurred in Svalbard waters, with RS now spending significantly higher proportions of time near tidal glacier fronts, while WW spend significantly less time near tidal glacier fronts (figure 2; electronic supplementary material, figure S2).

Negribreen was the glacier most visited by WW (both periods) and RS (first period) (figure 1; electronic supplementary material, tables S3 and S4). This glacier is large and has a long calving front that occurs in deep water. RS also heavily used Sonklarbreen (first period) and Kongsbreen (second period), which have similar characteristics to Negribreen (figure 1; electronic supplementary material, table S3). Time spent in front of other glaciers was relatively low and relative

royalsocietypublishing.org/journal/rsbl *Biol. Lett.* **15**: 20180834

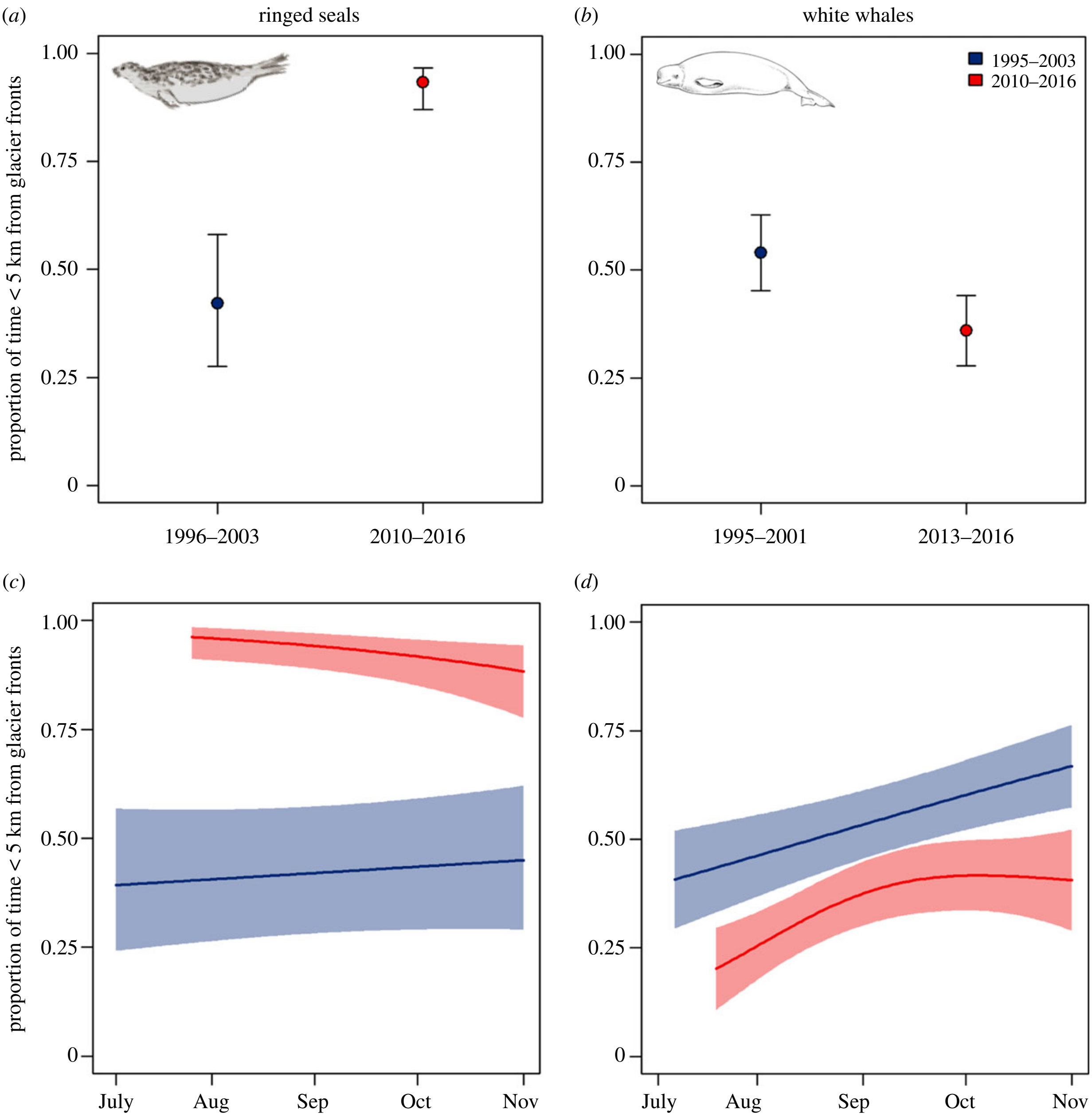

Figure 2. Proportion of time spent within 5 km of tidal glacier fronts by (*a*) ringed seals (RS) and (*b*) white whales (WW), and GAMM results according to day of the year for (*c*) RS and (*d*) WW equipped with biotelemetry devices before and after a major environmental change in Svalbard, Norway.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

use of them was not explained by their characteristics for RS, though for WW frontal length remained important (electronic supplementary material, tables S5 and S6). Differences in tagging locations in the two study years (electronic supplementary material, figure S1 and tables S1 and S2) are unlikely to have impacted our results because WW move across much of the archipelago constantly [16] and RS results were not dependent on tagging location in the analyses herein.

Concomitant with the physical changes (increased Atlantic water intrusion and decreased sea ice) that have occurred over the last decade in Svalbard waters, large ecosystem changes have taken place, including a general 'borealization' of the fish community. Atlantic species are increasingly common and the ranges of Arctic and subarctic species are shifting northward [17,18]. Diets of some seabirds and marine mammals in the Svalbard area have changed to include more Atlantic and less Arctic prey [19,20]. However, Arctic and subarctic zooplankton, which are the main prey of polar cod, still dominate the innermost parts of glacial fjords [21] and polar cod are still abundant in these areas [22]. Calved glacier ice pieces also provide haul-out platforms for RS. Tidal glacier fronts appear to be serving as Arctic 'refugia' for RS, explaining why this species has increased the amount of time spent near glaciers, resulting in smaller home ranges following the sea-ice collapse (figure 2; electronic supplementary material, figure S2). Foraging effort by RS has also increased following the sea-ice collapse [15].

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

4. Conclusion

The different changes observed in the space-use patterns of RS and WW in Svalbard waters, using unique long-term bio-telemetry datasets, highlight that ecosystem changes are affecting top trophic level predators differently. The flexible response shown by WW improves their chances of adapting to warming conditions, while RS's retraction into Arctic refugia, which are declining in number, with an ongoing dependence on prey that are also in decline, reflects limited adaptability and resilience. Plasticity in foraging and other responses to habitat change will be important in successfully adjusting to the ongoing environmental changes driven by global warming. Species and subpopulations that are not able to make such changes are almost certain to decline, perhaps to extinction where refugial areas become too limiting for species survival.

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

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

Authors' contributions. C.D.H., J.V.-G., R.A.I., C.L. and K.M.K. conducted fieldwork. J.K. provided glacier data. C.D.H. and J.V.-G. analysed the data. C.D.H., J.V.-G., C.L. and K.M.K. interpreted the results. All authors wrote the manuscript, approved the final version and agree to be accountable for the manuscript contents.

Competing interests. We have no competing interests.

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

Acknowledgements. We thank field team members.

References

1. Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012 Impacts of climate change on the future of biodiversity. *Ecol. Lett.* **15**, 365–377. (doi:10.1111/j.1461-0248.2011.01736.x)
2. Hoffmann AA, Sgrò CM. 2011 Climate change and evolutionary adaptation. *Nature* **470**, 479–485. (doi:10.1038/nature09670)
3. Gilg O *et al.* 2012 Climate change and the ecology and evolution of Arctic vertebrates. *Ann. N. Y. Acad. Sci.* **1249**, 166–190. (doi:10.1111/j.1749-6632.2011.06412.x)
4. Post E *et al*. 2009 Ecological dynamics across the Arctic associated with recent climate change. *Science* **325**, 1355–1358. (doi:10.1126/science.1173113)
5. Laidre KL *et al*. 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)
6. Comiso JC, Hall DK. 2014 Climate trends in the Arctic as observed from space. *WIREs Clim. Change* **5**, 389–409. (doi:10.1002/wcc.277)
7. Kovacs KM, Lydersen C, Overland JE, Moore SE. 2011 Impacts of changing sea-ice conditions on Arctic marine mammals. *Mar. Biodivers.* **41**, 181–194. (doi:10.1007/s12526-010-0061-0)
8. Lydersen C *et al*. 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)
9. Skogseth R, Haugan PM, Jakobsson M. 2005 Watermass transformations in Storfjorden. *Cont. Shelf Res.* **25**, 667–695. (doi:10.1016/j.csr.2004.10.005)
10. Tverberg V, Skogseth R, Cottier F, Sundfjord A, Walczowski W, Inall ME, Falck E, Pavlova O, Nilsen F. In press. The Kongsfjorden Transect: seasonal and inter-annual variability in hydrography. *Polar Res.*
11. Pavlova O, Gerland S, Hop H. In press. Changes in sea-ice extent and thickness in Kongsfjorden, Svalbard (2003–2016). *Polar Res.*
12. Hamilton CD, Vacquié-Garcia J, Kovacs KM, Lydersen C. 2019 Data from: Contrasting changes in space use induced by climate change in two Arctic marine mammal species. Norwegian Polar Institute. (doi:10.21334/npolar.2019.e1cd54e1)
13. Dahl TM, Lydersen C, Kovacs KM, Falk-Petersen S, Sargent J, Gjertz I, Gulliksen B. 2000 Fatty acid composition of the blubber in white whales (*Delphinapterus leucas*). *Polar Biol.* **23**, 401–409. (doi:10.1007/s003000050461)
14. Labansen AL, Lydersen C, Haug T, Kovacs KM. 2007 Spring diet of ringed seals (*Phoca hispida*) from Spitsbergen, Norway. *ICES J. Mar. Sci.* **64**, 1246–1256. (doi:10.1093/icesjms/fsm090)
15. 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. (doi:10.3354/meps11598)
16. Vacquié-Garcia J, Lydersen C, Ims RA, Kovacs KM. 2018 Habitats and movement patterns of white whales *Delphinapterus leucas* in Svalbard, Norway. *Mov. Ecol.* **6**, 21. (doi:10.1186/s40462-018-0139-z)
17. Berge J, Heggland K, Lønne OJ, Cottier F, Hop H, Gabrielsen GW, Nøttestad L, Misund OA. 2015 First records of Atlantic mackerel (*Scomber scombrus*) from the Svalbard Archipelago, Norway. *Arctic* **68**, 54–61. (doi:10.14430/arctic4455)
18. Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV. 2015 Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat. Clim. Change* **5**, 673–677. (doi:10.1038/nclimate2647)
19. Descamps S, Aars J, Fuglei E, Kovacs KM, Lydersen C, Pavlova O, Pedersen ÅØ, Ravolainen V, Strøm H. 2017 Climate change impacts on wildlife in a High Arctic archipelago. *Glob. Change Biol.* **23**, 490–502. (doi:10.1111/gcb.13381)
20. Vihtakari M, Welcker J, Moe B, Chastel O, Tartu S, Hop H, Bech C, Descamps S, Gabrielsen GW. 2018 Black-legged kittiwakes as messengers of Atlantification in the Arctic. *Sci. Rep.* **8**, 1178. (doi:10.1038/s41598-017-19118-8)
21. Dalpadado P, Hop H, Rønning J, Pavlov V, Sperfeld E, Buchholz F, Rey A, Wold A. 2016 Distribution and abundance of euphausiids and pelagic amphipods in Kongsfjorden, Isfjorden and Rijpfjorden (Svalbard). *Polar Biol.* **39**, 1765–1784. (doi:10.1007/s00300-015-1874-x)
22. Fey DP, Węsławski JM. 2017 Age, growth rate, and otolith growth of polar cod (*Boreogadus saida*) in two fjords of Svalbard. *Oceanologia* **59**, 576–584. (doi:10.1016/j.oceano.2017.03.011)
23. Watt CA, Orr J, Ferguson SH. 2016 A shift in foraging behaviour of beluga whales *Delphinapterus leucas* from the threatened Cumberland Sound population may reflect a changing Arctic food web. *Endang. Species Res.* **31**, 259–270. (doi:10.3354/esr00768)
24. Yurkowski DJ, Ferguson S, Choy ES, Loseto LL, Brown TM, Muir DCG, Semeniuk CAD, Fisk AT. 2016 Latitudinal variation in ecological opportunity and intraspecific competition indicates differences in niche variability and diet specialization of Arctic marine predators. *Ecol. Evol.* **6**, 1666–1678. (doi:10.1002/ece3.1980)