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Predictions replaced by facts: a keystone species' behavioural responses to declining arctic sea-ice

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Since the first documentation of climate-warming induced declines in arctic sea-ice, predictions have been made regarding the expected negative consequences for endemic marine mammals. But, several decades later, little hard evidence exists regarding the responses of these animals to the ongoing environmental changes. Herein, we report the first empirical evidence of a dramatic shift in movement patterns and foraging behaviour of the arctic endemic ringed seal (*Pusa hispida*), before and after a major collapse in sea-ice in Svalbard, Norway. Among other changes to the ice-regime, this collapse shifted the summer position of the marginal ice zone from over the continental shelf, northward to the deep Arctic Ocean Basin. Following this change, which is thought to be a 'tipping point', subadult ringed seals swam greater distances, showed less area-restricted search behaviour, dived for longer periods, exhibited shorter surface intervals, rested less on sea-ice and did less diving directly beneath the ice during post-moulting foraging excursions. In combination, these behavioural changes suggest increased foraging effort and thus also likely increases in the energetic costs of finding food. Continued declines in sea-ice are likely to result in distributional changes, range reductions and population declines in this keystone arctic species.

1. Introduction

Over the past few decades, the Arctic has warmed at twice the global average and sea-ice extent and volume have declined markedly [1]. Continued declines are expected to result in an ice-free Arctic Ocean as early as 2037 [2], with transformative consequences for arctic ecosystems [3,4]. Endemic arctic animals that rely on sea-ice and the associated sympagic (ice-associated) ecosystem are expected to undergo major ecological shifts or face extinction [3].

Ringed seals are a keystone, endemic arctic species that is the principal prey of polar bears (*Ursus maritimus*) and an important resource for coastal arctic people. Their circumpolar distribution and high abundance, along with their vital roles both as a high-trophic predator and as prey in this relatively species-poor system, makes them a key link in the arctic food web. This species is intimately associated with sea-ice for most aspects of its existence [5]. Ringed seals are born on sea-ice and moult and rest on it throughout their lives, experiencing low reproductive success in years with poor ice or snow conditions [6–8].

Ringed seal biological investigations have been undertaken in Svalbard, Norway, since the 1980s, providing background data on this population [8]. In 2006, the sea-ice regime in this region underwent an unpredicted collapse that has persisted to the present. Among other changes, the southern edge of the summer arctic icecap (the marginal ice zone, MIZ) has shifted northward from its previous norm over the continental shelf to a location over the deep Arctic Ocean Basin (figure 1). A ringed seal tracking study conducted in Svalbard in

Table 1. Seal and trip metrics for 60 ringed seals tagged in 2002–2003 and 2010–2012 in Svalbard, Norway, with individual details for animals undertaking offshore excursions.

seal ID	trip	sex	mass (kg)	tagging date	departure date	return date	trip duration (d)	total distance travelled (km)	tracking duration (d)
F31–02	1	F	31	21 July 2002	22 July 2002	29 Aug. 2002	39	1587	172
F33–02	2	F	33	21 July 2002	26 July 2002	6 Sept. 2002	43	1447	127
F36–02	3	F	36	21 July 2002	29 July 2002	2 Sept. 2002	36	1509	126
F37–02	4	F	37	20 July 2002	23 Aug. 2002	21 Nov. 2002	91	2203	187
F57–02	5	F	57	19 July 2002	1 Aug. 2002	1 Sept. 2002	32	1422	169
F59–02	6	F	59	21 July 2002	1 Aug. 2002	25 Aug. 2002	25	990	78
F59–02	7	F	59	21 July 2002	15 Sept. 2002	30 Sept. 2002	16 ^a	534 ^a	78
M50–02	8	M	50	19 July 2002	23 July 2002	20 Oct. 2002	90 ^a	2413 ^a	96
F34–03	9	F	34	19 July 2003	24 July 2003	11 Aug. 2003	19	734	129
F34–03	10	F	34	19 July 2003	18 Aug. 2003	8 Sept. 2003	22	949	129
F37–03	11	F	37	22 July 2003	7 Aug. 2003	18 Sept. 2003	43	1391	243
<i>mean ± s.d.</i>			42 ± 11				39 ± 21	1359 ± 432	139 ± 50
F34–10	12	F	34	3 Aug. 2010	5 Aug. 2010	5 Oct. 2010	62	2048	193
F40–10	13	F	40	25 July 2010	2 Aug. 2010	30 Sept. 2010	60	1677	235
M36–10	14	M	36	26 July 2010	31 July 2010	12 Nov. 2010	105	5393	129
F52–10	15	F	52	3 Aug. 2010	17 Aug. 2010	9 Sept. 2010	24	1009	224
F60–10	16	F	60	29 July 2010	31 July 2010	2 Sept. 2010	34	1703	202
F60–10	17	F	60	29 July 2010	3 Oct. 2010	19 Oct. 2010	17	970	202
M62–10	18	M	62	1 Aug. 2010	15 Aug. 2010	4 Sept. 2010	21	844	197
M90–11	19	M	90	3 Aug. 2011	6 Aug. 2011	1 Sept. 2011	27	1540	166
F35–12	20	F	35	30 July 2012	12 Aug. 2012	27 Aug. 2012	16	677	306
F40–12	21	F	40	1 Aug. 2012	13 Aug. 2012	29 Sept. 2012	48	2182	178
M46–12	22	M	46	1 Aug. 2012	4 Aug. 2012	6 Aug. 2012	3 ^a	299 ^a	6
<i>mean ± s.d.</i>			50 ± 17				41 ± 28	1804 ± 1362	185 ± 74
other tagged seals									
<i>mean ± s.d.</i>	41 seals	20 F : 21 M	62 ± 20						165 ± 66

^aData transmission terminated while offshore (not included in the mean).

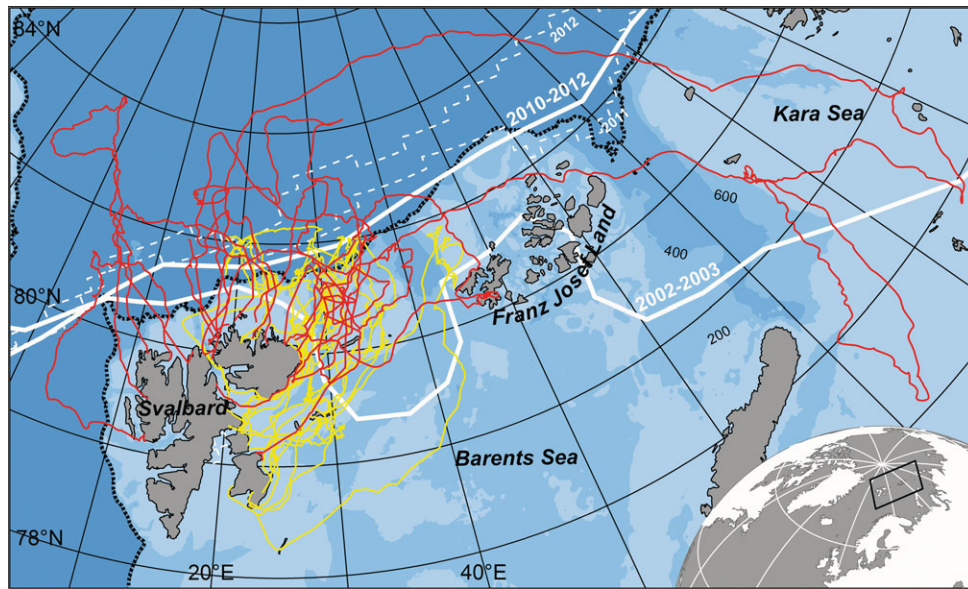


Figure 1. Offshore trips undertaken by ringed seals in 2002–2003 (yellow) and 2010–2012 (red) in Svalbard, Norway. White lines show the average (solid) and minimum (dashed) September sea-ice extent (National Snow and Ice Data Center, Boulder, CO). The black dotted line denotes the continental shelf.

Table 2. Offshore-trip metrics for 19 ringed seals tagged in 2002–2003 and 2010–2012 in Svalbard, Norway.

	no. individuals	no. trips	total distance travelled (km)	no. tracking days	no. locations transmitted	no. dives transmitted
2002–2003	9	11	12 232	350	7140	13 961
2010–2012	10	11	18 043	414	8581	12 744

2002–2003 [9] documented extensive offshore summer excursions to the MIZ by subadult seals during the post-moulting period when they acquire most of their annual energy intake [10]. The unpredicted regional sea-ice collapse that occurred several years after this study has created the possibility for a natural experiment exploring the impact of this dramatic environmental change on the behaviour of this species, via repeating tracking efforts on this population. Such knowledge will greatly improve our predictive capacity regarding global warming impacts on this keystone species because the changes occurring currently in Svalbard are predicted to spread throughout the Arctic.

2. Material and methods

Ringed seals (22 before (2002–2003) and 38 after (2010–2012) the sea-ice collapse) were equipped with Satellite-Relay Data Loggers (<http://www.smru.st-andrews.ac.uk/Instrumentation/Overview/>) that provided information on seal movements and behaviour. Nineteen seals in the two periods (nine in 2002–2003 and 10 in 2010–2012) undertook offshore excursions during the post-moulting period (table 1). These excursions are the subject of this study.

We used a generalized linear model with the binomial family and a logistic link to investigate the probability of taking an offshore trip. Possible explanatory variables included mass, sex and time period. We also conducted first-passage time (FPT) analysis on each offshore excursion to identify the spatial scale of area-restricted search (ARS) behaviour, which is associated with intense feeding activity in many species [11], and employed linear-mixed effects models to explore whether diving and movement behaviour varied between the two time periods. Trip number was included as a random effect to account for

non-independence of observations within trips. Bayesian information criterion (BIC) was used for backward model selection; p -values ≤ 0.05 in the BIC-selected model indicated significance. A nested random effect of trip number within year was also considered but was not retained after model selection. See the electronic supplementary material for further details.

3. Results and Discussion

During offshore excursions, 19 seals transmitted over 25 000 dives over 764 tracking days (table 2; electronic supplementary material, figure S1 and S2). Body mass measurements clearly show that smaller animals (i.e. subadults) had a higher probability of undertaking offshore movements (table 1; electronic supplementary material, tables S1 and S2). Time period did not impact the probability of undertaking offshore trips, which are foraging–migratory movements rather than dispersal movements; the seals return to Svalbard in time for the traditional land-fast ice formation.

Seals in the two time periods undertook offshore trips of similar duration ($p = 0.831$, table 1), but they encountered sea-ice for the first time approximately 1° of latitude further north in 2010–2012 than in 2002–2003 ($p = 0.004$), and thus spent more time further from land ($p = 0.003$) and a greater proportion of time over the Arctic Ocean Basin ($p = 0.072$; figures 1 and 2; electronic supplementary material, tables S3 and S4). Seals in both periods occupied areas with similar sea-ice concentrations ($p = 0.605$) and similar proportions of first-year ice versus multiyear ice ($p = 0.943$; electronic supplementary material, table S3), suggesting that they sought this particular habitat, despite having to travel farther to reach it and despite its location shifting from being over the

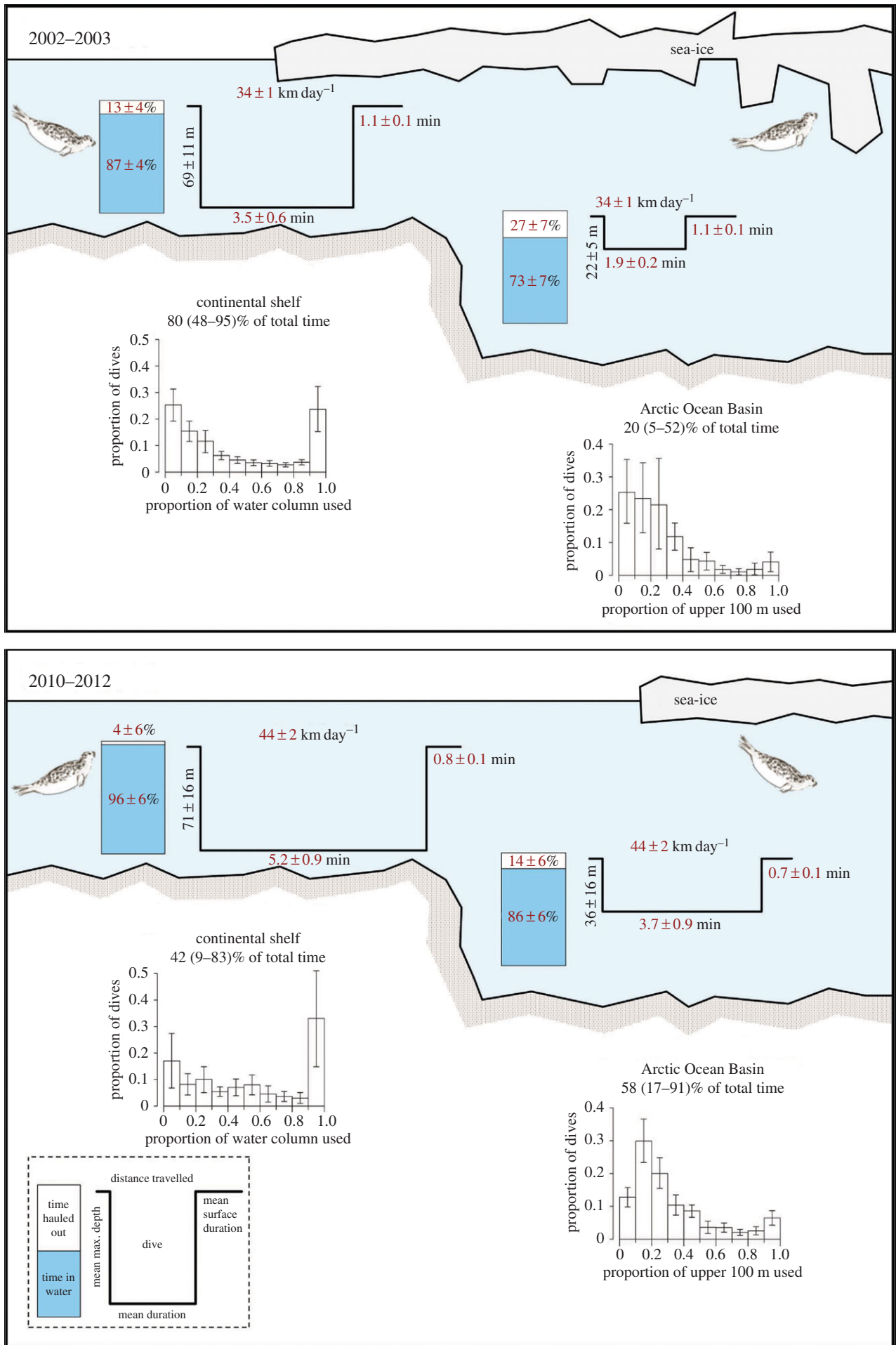


Figure 2. Behaviour metrics for ringed seals in Svalbard, Norway, during offshore trips in 2002–2003 and 2010–2012. Values in red indicate significant differences between the two time periods. Barplots over the Arctic Ocean Basin only consider the upper 100 m of the water column. Error bars in the graphs indicate 95% confidence intervals.

productive continental shelf to being over the less-productive Arctic Ocean Basin [12]. However, when they arrived in areas with these ice conditions significant changes in their behaviour were detected. The seals moved greater distances daily (even in areas with high sea-ice concentrations) and spent less time resting on sea-ice in 2010–2012 (figure 2; electronic supplementary material, table S4). Resting time is likely kept to a minimum if the animals are not finding sufficient food to be satiated. Seals in 2010–2012 also had longer dive durations and shorter surface intervals compared with seals in 2002–2003 (figure 2; electronic supplementary material, table S4). These findings suggest that energetic costs associated with finding food have increased in the latter period. Time-at-depth also suggests that sympagic feeding was replaced by pelagic and benthic feeding modes in 2010–2012.

FPT analyses easily defined a common spatial scale for ARS during offshore excursions in 2002–2003 [9]. But, fewer seals performed clear ARS behaviour in 2010–2012 (electronic supplementary material, figure S3, $p = 0.016$), suggesting that the sea-ice extent retreating north of the continental shelf resulted in fewer areas where the seals could feed intensively. Two seals tagged in 2010–2012 employed strategies not seen in 2002–2003. One travelled to a glacier front in Franz Josef Land, Russia, and the other swam to the eastern Kara Sea in the Russian Arctic (total trip length of approx. 5400 km; figure 1; electronic supplementary material, figure S2). Both seals travelled to these areas via routes over the Arctic Ocean Basin. Given it is unlikely that ringed seals bypass productive foraging areas, it is probable that they did not find sufficient food along their tracks, closer to Svalbard, and thus continued to search further afield.

Ringed seals are opportunistic predators but they do show a preference for polar cod (*Boreogadus saida*) and lipid-rich pelagic crustaceans [5,13]. Polar cod are found in cold water masses in the Barents Sea, occupying sympagic, pelagic and benthic environments [14]. Larval and juvenile polar cod are directly affiliated with sea-ice, occupying small cracks where they are afforded some predator-protection [14]. Regionally, polar cod abundance has decreased and the 0-age class has shifted its distribution northeastward over the last decade [15], part of the rapid 'borealization' of the fish community of this region [16]. Polar cod occur at lower densities in the Arctic Ocean Basin compared with the arctic shelf seas [17] and the more than 40% decrease in arctic multiyear sea-ice from 2005 to 2008 [18] has likely decreased habitat quality for these fish and other ice-associated lower trophic organisms. These factors are almost certainly related to the increased foraging effort and less spatially concentrated foraging activity we document herein for ringed seals during 2010–2012.

Ringed seals in other arctic areas also undertake late-summer foraging trips [19]. But, in these other regions sea-ice changes have been much less dramatic compared with

Svalbard. The Barents Sea region has experienced the largest declines in seasonal duration of arctic sea-ice cover, with more than 20 weeks fewer with ice cover from 1979 to 2013 (two to four times the reduction in other arctic areas [20]). Future retractions of summer sea-ice extent are expected [1,2]; in these conditions, ringed seals will have to travel further into the Arctic Ocean Basin to find sea-ice, further increasing energetic costs of their important post-moult foraging trips. Alternatively, they could remain in near-shore habitats, but in Svalbard this would increase competition with the older animals that remain coastal, associated with tidewater glaciers [9,21]. Such areas are spatially restricted compared to the MIZ and glaciers in Svalbard are also in negative mass-balance, with the total length of tidewater glacier fronts having already markedly decreased in recent decades [22]. A further decrease in the number of these coastal 'hot-spots' would be critical for ringed seals in Svalbard.

Our study has shown that past predictions [3] regarding climate change impacts on ringed seals were correct—sea-ice extent declines are affecting their movement patterns and foraging behaviour. The northward retreat of the sea-ice edge has markedly increased foraging effort for subadult ringed seals. If these costs are not compensated for by increased energetic returns, this will affect growth, reproduction and mortality rates. Data documenting changes in these parameters would give additional scope to our findings; however, such data are difficult to obtain in areas such as Svalbard where little hunting takes place. But condition declines concomitant with sea-ice declines elsewhere in the Arctic strongly suggest that plasticity is limited. The behavioural changes we document all suggest that energetic costs have increased, and as sea-ice continues to retreat ringed seals will be further challenged. Shifts in the distribution and abundance of this keystone species are likely to have repercussions throughout the arctic marine ecosystem.

Ethics. Animal handling protocols were approved by the Norwegian Animal Research Authority (permit no. 10/45416) and the Governor of Svalbard (permit no. 2010/00093-19).

Data accessibility. The data are available at the Norwegian National Polar Data Centre (data.npolar.no). Contact person Kit M. Kovacs (kit.kovacs@npolar.no).

Authors' contributions. K.M.K. and C.L. conceived the study. K.M.K., C.L. and C.D.H. conducted the fieldwork. All authors analysed and interpreted the data, wrote the manuscript, approved the final version and agree to be held accountable for the manuscripts contents.

Competing interests. We have no competing interests.

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