

# Spatial overlap among an Arctic predator, prey and scavenger in the marginal ice zone

Charmain D. Hamilton<sup>1,2,\*</sup>, Kit M. Kovacs<sup>1</sup>, Rolf A. Ims<sup>2</sup>, Jon Aars<sup>1</sup>, Hallvard Strøm<sup>1</sup>, Christian Lydersen<sup>1</sup>

<sup>1</sup>Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway

<sup>2</sup>Department of Arctic and Marine Biology, The Arctic University of Norway, 9037 Tromsø, Norway

**ABSTRACT:** Conducting multi-species studies is important when assessing current ecosystem state and predicting climate change impacts, as altered biological interactions can affect the wider ecosystem. The marginal ice zone (MIZ, transition zone between the sea ice edge and areas with complete sea ice coverage) is an important foraging area for Arctic marine mammals and seabirds. The location of the MIZ has shifted northwards over the last decades due to sea ice declines. Many ringed seals *Pusa hispida*, polar bears *Ursus maritimus* and ivory gulls *Pagophila eburnea* travel from Svalbard, Norway, to the MIZ to forage during summer and autumn. These species are trophically linked: ringed seals are the primary prey of polar bears and ivory gulls scavenge on polar bear kills. Biotelemetry data (ringed seals [n = 10]: 2010–2012; polar bears [n = 24]: 2007–2014; ivory gulls [n = 29]: 2010–2013) were used to characterize the MIZ habitats of these species and to identify areas of overlap. Individuals from all 3 species travelled long distances to forage in the MIZ, with maximum distances for each species exceeding 1400 km. All 3 species selected areas with sea ice concentrations between 40 and 80%. The highest spatial overlap between August and October for this species assemblage occurred slightly north of the 50% sea ice contour, with the precise location and density of overlap varying monthly and inter-annually in relation to the location and breadth of the MIZ. Further northward retreat and the potential total disappearance of the MIZ (in summer) is likely to have serious consequences for the distribution, abundance and trophic relations among these ice-obligate species.

**KEY WORDS:** Habitat selection · Trophic interactions · Svalbard · *Pusa hispida* · *Ursus maritimus* · *Pagophila eburnea*

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Climate change is currently the most serious threat to Arctic biodiversity (Conservation of Arctic Flora and Fauna [CAFF] 2013). Warming in the Arctic region is taking place at 3 times the rate of the global average and the summer sea ice extent has declined at a rate of 11.5% per decade since 1979 (Comiso & Hall 2014). The amount of multi-year sea ice in the Arctic Ocean Basin decreased by 40% between 2005 and 2008, with the Arctic predicted to be sea ice free in the summer by as early as the 2030s (Kwok et al. 2009, Wang & Overland 2012). Sea ice is a central component of the Arctic ecosystem, influencing pro-

ductivity, exchange of individuals between populations and overall ecological dynamics in both the marine and terrestrial systems (Post et al. 2013). The consequences of Arctic sea ice declines are occurring among different species at different rates, leading to trophic mismatches as well temporal and spatial changes in trophic interactions, with consequences for ecological communities (Post et al. 2013, Hamilton et al. 2017).

Ice-obligate and ice-associated marine mammal and seabird species are dependent on sea ice for a variety of purposes. Sea ice areas provide important foraging habitat, protection from aquatic predators and storm events, a solid substrate for birthing and

\*Corresponding author: charmain.hamilton@npolar.no

nursing for ice-associated seals and a resting platform for ice-associated seals and seabirds. Sea ice is also vital in providing transit corridors for polar bears *Ursus maritimus*. This solid substrate is particularly important for females with young cubs that cannot be immersed in water for long periods (Gilchrist et al. 2008, Kovacs et al. 2011). Consequences of sea ice loss for Arctic marine mammal and seabird species are expected to be significant, with negative effects of sea ice declines already reported for some species (e.g. Moline et al. 2008, Kovacs et al. 2011, Stirling & Derocher 2012, Hamilton et al. 2015). However, the effects of sea ice decline may be hard to detect in many of these species since basic data, such as population trends, are lacking for over 70% of sub-populations or stocks of endemic marine mammals (Laidre et al. 2015a). In addition, some Arctic seabirds such as ivory gulls *Pagophila eburnea* and Arctic terns *Sterna paradisaea* exhibit inter-annual changes in breeding colony size or location, making assessing population size via colony counts difficult (Møller et al. 2006, Gilchrist et al. 2008).

Ringed seals *Pusa hispida* are an ice-obligate keystone species in the Arctic ecosystem. They have a circumpolar distribution and are found in both coastal and offshore waters over the continental shelves and in the Arctic Ocean Basin (Finley et al. 1983, Reeves 1998, Wiig et al. 1999). Ringed seals maintain breathing holes in the fast ice, above which they dig out snow lairs in the winter and spring that are used for pupping, nursing and for general rest (McLaren 1958, Smith & Stirling 1975, Lydersen & Gjertz 1986). Sea ice is also used as a resting platform throughout the year and as a moulting platform in early summer. Additionally, ringed seal foraging often targets ice-associated prey (Reeves 1998, Labansen et al. 2007).

Polar bears are top predators of the Arctic food web. They have a circumpolar distribution and are primarily found over the continental shelf areas, but are also found at low densities in the Arctic Ocean Basin (Amstrup 2003). Polar bears use sea ice as a platform to hunt ice-associated prey, which is primarily ringed seals in most areas, and they also move large distances across ice, e.g. to get between denning and feeding areas (Derocher et al. 2002, Thiemann et al. 2008, Stirling & Derocher 2012, Iversen et al. 2013).

Ivory gulls have a patchy circumpolar distribution (Gilchrist et al. 2008). Breeding colonies for this species are usually situated on nunataks, steep cliffs or on flat ground, but have also been discovered on ice floes (Gilchrist & Mallory 2005, Gilchrist et al. 2008, Boert-

mann et al. 2010). Ivory gulls are associated with drift ice year round, where they feed on fish and zooplankton. This species also scavenges at polar bear kill sites throughout the year, at harp seal *Pagophilus groenlandicus* and hooded seal *Cystophora cristata* whelping patches in the spring, as well as at human settlements, where they scavenge on blubber, blood, meat, placentas and garbage (Divoky 1976, Orr & Parsons 1982, Renaud & McLaren 1982, Mehlum & Gabrielsen 1993, Gilchrist et al. 2008, Karnovsky et al. 2009, Gilg et al. 2010, Spencer et al. 2014).

The seasonal sea ice extent in the Barents Sea has large inter-annual variation, due to a variety of factors such as the magnitude of the Atlantic Water inflow, the North Atlantic Oscillation (NAO) and the amount of solar radiation during the summer months (Gloersen et al. 1993, Vinje 2009). Historically, the summer sea ice minimum was located over the productive continental shelf of the Barents Sea, but in recent decades the sea ice extent has declined rapidly (Norwegian Ice Service – Norwegian Meteorological Institute, <http://polarview.met.no/>). The summer sea ice minimum in the Barents Sea has now shifted to a location over the less productive deep waters of the Arctic Ocean Basin (Sakshaug et al. 2009). Between 1979 and 2013, the seasonal duration of sea ice cover in the Barents Sea declined by over 20 wk, which is a 2 to 4 times greater reduction compared to other Arctic areas (Laidre et al. 2015a). Concomitant with the rapid physical changes in this region, changes in the biological realm have also occurred. A rapid 'borealization' of the Barents Sea occurred from 2004 to 2012, with boreal fish communities rapidly extending their distribution northwards, limiting Arctic shelf fish communities to deep areas bordering the Arctic Ocean Basin (Fossheim et al. 2015).

A portion of the polar bear and ringed seal populations in the Arctic archipelago of Svalbard (74 to 81° N, 10 to 35° E), Norway, travel offshore during summer and autumn to the marginal ice zone (MIZ, transition zone between the sea ice edge and areas with complete [ $>80\%$ ] sea ice coverage) of the Barents Sea (Mauritzen et al. 2002, Freitas et al. 2008a, Hamilton et al. 2015). Post-breeding ivory gulls from Greenland, Svalbard and Franz Josef Land (Russia) also travel to the MIZ in the northeast Atlantic and remain there for several months before continuing their migration to the wintering grounds (Gilg et al. 2010). The purpose of the present study was to investigate the environmental characteristics of the MIZ habitat for all 3 species and to identify the defining environmental features in areas of high spatial overlap for this species assemblage. In addition, the

monthly and inter-annual variation in the location and density of spatial overlap values were investigated. These findings are discussed in relation to the current and predicted environmental changes in the Svalbard area.

## MATERIALS AND METHODS

### Capture and biotelemetry device information

Offshore habitat use by these 3 species was the focus of the analyses in this study, so only offshore locations (when the animals were associated with the MIZ) were considered herein for each species. The tracks of the ringed seals and polar bears were divided into coastal and offshore components as per Hamilton et al. (2015) and Hamilton et al. (2017). Ivory gulls were classified as being offshore following their departure from their nesting areas. The seasonal period was restricted to 1 August to 31 October, to match the shortest offshore period, that for ringed seals.

A total of 139 adult female polar bears were captured and equipped with a satellite collar between 2007 and 2014 at several locations around Svalbard. Of these, 88 collars transmitted GPS positions (calculated at least once every 4 h) using either the Iridium (Iridium Satellite Communications) or Argos satellite systems (System Argos; Collecte Localisation Satellites [CLS] 2015). The remaining 51 collars had positions calculated by the Argos satellite system. The collars were produced by Telonics, Advanced Telemetry Systems (ATS) and SirTrack. Of these 139 polar bears, 23 displayed the offshore movement strategy during the seasonal period of interest (Table 1). For details on capture and handling, see Mauritzen et al. (2002). Body mass (kg) and body condition index of the bears were calculated following Cattet et al. (2002).

Between 2010 and 2012, 38 ringed seals were captured and equipped with Satellite-Relay Data Loggers (SRDLs, Sea Mammal Research Unit Instrumen-

tation, University of St Andrews) at several locations around Svalbard following the annual moult. The SRDLs transmitted data using the Argos satellite system, which also calculated the locations of the seals. Ten of these tagged seals took offshore trips during the autumn (Table 1). For details on capture and handling, see Hamilton et al. (2016).

A total of 40 ivory gulls were captured using baited traps or, when sitting on the nest, with a nylon loop attached at the end of a fishing rod, between 2010 and 2013 in several colonies on Barentsøya, Svalbard. Following capture, they were weighed and equipped with a solar-powered satellite Platform Transmitter Terminal (PTT, produced by Microwave Telemetry and North Star Science and Technology) by means of either a harness (2010 to 2012) or a leg-loop (2013). Locations for the ivory gulls were computed by the Argos satellite system. Following the breeding period, 29 of the ivory gulls went offshore; PTTs on the remaining 11 birds either terminated transmissions during the breeding season or did not transmit locations during the seasonal period of interest (Table 1). Therefore, all of the ivory gulls for which information is available travelled to the MIZ. All animal-handling protocols for all 3 species were approved by the Governor of Svalbard and the Norwegian Animal Research Authority.

### Location data

Locations from both polar bears and ringed seals were pre-filtered using the speed-distance-angle (SDA) filter with maximum speeds of 2.78 (10 km h<sup>-1</sup>) and 2 m s<sup>-1</sup>, respectively (Freitas et al. 2008b). Additionally, a small number of obviously erroneous locations (e.g. ringed seal positions inland) were manually removed. Locations were subsequently filtered using the CRAWL package in R 3.1.3, with a stopping model incorporated for ringed seals to account for time spent hauled out (Johnson et al. 2008, R Core

Team 2015). A position from every fourth hour was extracted from each individual's CRAWL model.

Ivory gull locations were filtered using the SDA filter with a maximum speed of 40 m s<sup>-1</sup> (highest recorded speed of an ivory gull is 28 m s<sup>-1</sup>, Spencer et al. 2014). The default angles were lowered to 5 and 15 and the default distances were raised to 5000 and 10000, meaning that all spikes with angles smaller than 5 and

Table 1. Information about the offshore ringed seals *Pusa hispida*, polar bears *Ursus maritimus* and ivory gulls *Pagophila eburnea* equipped with biotelemetry devices between 2007 and 2014 in Svalbard, Norway. The number of locations represent the number of locations used in the statistical analyses

	No. of tagged animals	No. of offshore animals	No. of offshore locations	No. of offshore locations per animal (mean ± SD)	Years of tagging
Ringed seal	38	10	2387	239 ± 164	2010–2012
Polar bear	139	23	8596	374 ± 164	2007–2014
Ivory gull	40	29	6424	222 ± 140	2010–2013

15 degrees that had lengths greater than 5000 and 10 000 m, respectively, were removed (see Freitas et al. 2008b for details). A position from every fourth hour was linearly interpolated from the SDA-filtered tracks.

### Offshore habitat

Environmental variables of interest were assigned to each point along the animals' offshore tracks. Included variables were sea ice concentration, distance to the 15% ice contour (approximate location of the sea ice edge), distance to the 50% ice contour (intermediate between complete sea ice coverage and open water), distance to the nearest coastline, distance from the tagging location and bathymetric depth. Daily sea ice concentration data at 10 × 10 km resolution were obtained from the Ocean and Sea Ice SAF High Latitude Processing Centre's Global Sea Ice Concentration archive (OSI SAF HL, <http://osisaf.met.no/>), and were used to assign sea ice concentration and the distance to the 15% and 50% sea ice contours. Distance to the nearest coastline was calculated using a coastline shapefile obtained from the Norwegian Polar Institute ([www.npolar.no](http://www.npolar.no)). Bathymetric depth data at 500 m spatial resolution were obtained from the International Bathymetric Chart of the Arctic Ocean Version 3.0 (IBCAO, Jakobsson et al. 2012). Biological data assessed included mass (ringed seals and ivory gulls), sex (ringed seals and ivory gulls), body condition index (polar bears) and reproductive status (polar bears: whether a female was alone, was with cub[s] of the year or yearling[s]).

The average distances from the coast and the tagging location were bootstrapped using 1000 replicates with the *boot* package in R (Canty & Ripley 2016). The percentage of locations that individuals of each species were in areas with a water depth of ≥600 m depth (i.e. approximate depth of the continental shelf break), were in areas with ≥15%, 50% and 90% ice concentration and were within 10 km of the 15% and 50% ice contours were calculated to characterize the offshore habitat of each species. Linear mixed effects models with the identity link and Gaussian family were used to test for potential changes in association with each environmental variable (by month) for each species using the *nlme* package in R (Pinheiro et al. 2016). Animal ID was included as a random effect. The response variable was transformed when needed to fulfil model assumptions. Model validation was carried out as recommended by Zuur et al. (2009).

### Species-specific habitat selection

In order to identify the habitat selected by each species in the offshore environment, the environmental characteristics of locations along the offshore tracks (utilized habitat) were compared to the environmental characteristics of areas the animal could have travelled to (available habitat). As biotelemetry data only gives presence information, correlated random walks were simulated for each individual, using characteristics of each individual's track, to generate pseudo-absences (see Žydelis et al. 2011, Raymond et al. 2015). Binomial generalized additive models (GAMs) with the logistic link function were used to identify the selected environmental characteristics. A response variable value of 1 indicated points along the actual track and 0 indicated points along the simulated tracks.

A total of 75 correlated random walks were simulated for each individual using Weibull distributed step lengths and Von Mises distributed turning angles (Žydelis et al. 2011, Raymond et al. 2015). The correlated random walks for each individual had the same number of steps as their offshore track and the same starting location. The step lengths and turning angles from each individual's track were used to create the relevant distributions for its simulated tracks, and the maximum step length from each individual's track was used to place an upper limit on the step length selected by the correlated random walk. The simulated tracks of polar bears and ivory gulls were allowed to cross land, but the simulated tracks of ringed seals were constrained to the ocean (see Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m573p045\\_supp.pdf](http://www.int-res.com/articles/suppl/m573p045_supp.pdf)).

Mean ice concentration and distance to the 15% and 50% ice contours were extracted for each point along the offshore tracks and simulated tracks. Data exploration, via checking for outliers, collinearity and relationships between the response and predictor variables and amongst the predictor variables, was carried out as recommended by Zuur et al. (2010). Distance to the 15% and 50% ice contours were highly correlated and thus the 2 variables were not included simultaneously in the same model. Additionally, correlated predictor variables can cause GAM smooth curves to behave erratically (Zuur 2012); variables that showed this behaviour were not included in the same model. Data exploration showed that the biological variables either had little effect or were highly unbalanced, and thus they were not included in the statistical analyses.

To select the number of simulated offshore tracks to use, binomial GAMs were run using 1 to 75 of the simulated tracks for each species using the *mgcv* package in R (Wood 2006). Each of the environmental variables were included as a cubic regression smooth curve, and month and ID were included as random effects using the type 're' smooth curve (Wood 2006). The chi-square values of the smooth curves, as well as the associated area under the curve (AUC), were plotted against the sequential number of simulated tracks (Żydelis et al. 2011); in general, these values stabilized at approximately 50 simulated tracks for each species (see Figs. S2, S3, & S4 in the Supplement). Thus, 55 simulated tracks were used in the analyses.

GAMs were run for each species using the above parameters. Mean ice concentration and distance to the 15% or 50% ice contours were included as possible predictor variables. The Bayesian Information Criterion (BIC) was used to guide model selection and to assess whether a variable should be included linearly or as a smooth term. As residuals from binomial models are difficult to interpret, the fitted values, raw data, deviance and normalized residuals were grouped by day and individual to assess model fit (Zuur et al. 2009). Each smooth term was also applied to the deviance residuals with an increased  $k$  to ensure that the  $k$ -value was high enough (Wood 2016). The BIC-selected model for each species was used to predict the habitat selection of the species within the offshore area north of Svalbard from August to October using ice data from 2010 to 2012.

### Inter-specific spatial overlap

In order to conduct an interspecies comparison, the predicted habitat selection values resulting from the GAM models were transformed into habitat importance values (HI) using the quantiles of the predicted values for each species and month. For example, grid cells that had a predicted value beneath the 10% quantile were assigned an HI of 0, grid cells that had a predicted value between the 10% and 20% quantile were assigned an HI of 10, etc., with the final HIs ranging between 0 and 100 (see Raymond et al. 2015 for more details). The HIs of the 3 species were multiplied together in order to identify the areas with the highest spatial overlap for each month. A cross-validation procedure was performed where the percentage change in overlap values was calculated for each grid cell when 1 individual was randomly left out of the analyses (Raymond et al. 2015).

## RESULTS

### Polar bears

Out of the 139 tracked polar bears, 23 (17%) were classified as being offshore between August and October (Fig. 1, Table 1, see Table S1 in the Supplement).

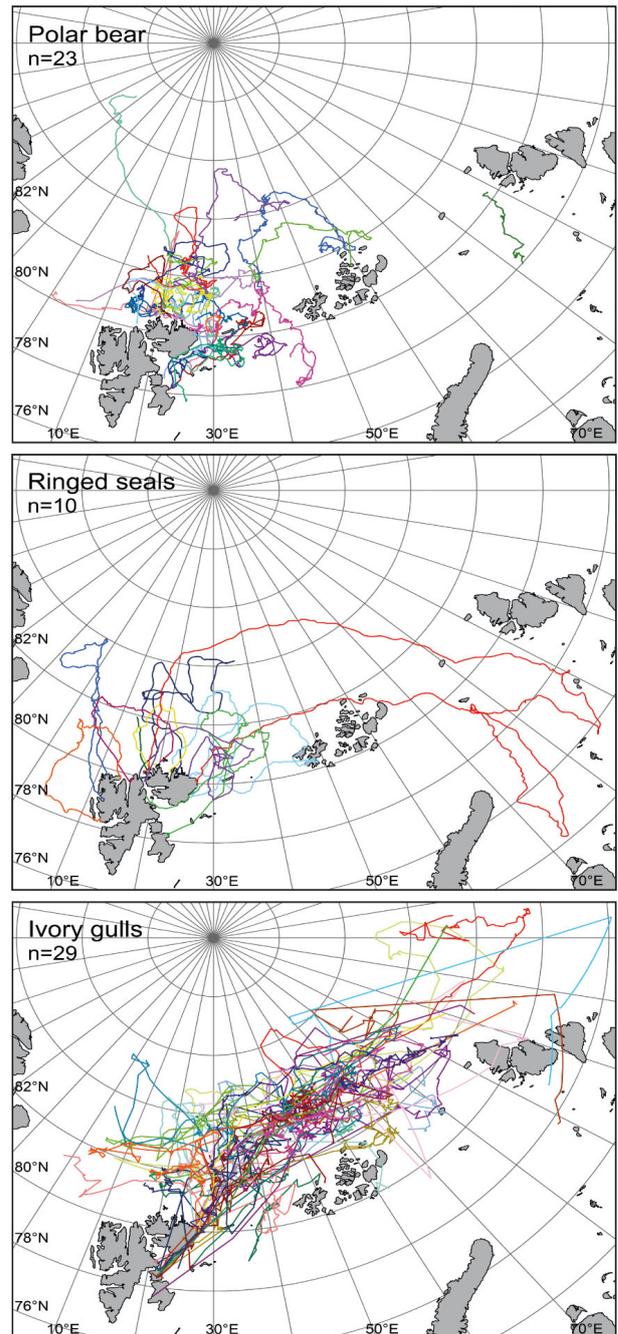


Fig. 1. Offshore tracks of polar bears *Ursus maritimus*, ringed seals *Pusa hispida* and ivory gulls *Pagophila eburnea* (from 1 August to 31 October) equipped with biotelemetry devices between 2007 and 2014 in Svalbard, Norway

The northernmost location was 87.0°N, while the easternmost location was 95.5°E. The furthest a bear travelled from its tagging location was 1662 km (great circle distance). The bears were on average 100 (73 to 128) km and 368 (245 to 494) km from the nearest coastline and their tagging location, respectively. Almost all (22 out of 23, 96%) of the bears spent the majority of their time ( $\geq 50\%$ ) in areas with sea ice concentrations  $\geq 15\%$  (Fig. 2), and 16 out of the 23 bears (70%) spent the majority of their time in areas with sea ice concentrations  $\geq 50\%$  (Fig. 2). There were no seasonal patterns in the association of the polar bears with any of the environmental variables included herein.

### Ringed seals

Following their annual moult, 10 of the 38 (26%) tagged ringed seals took offshore trips (Fig. 1, Table 1, see Table S2 in the Supplement). The northernmost and easternmost locations were 85.1°N and 90.5°E, respectively. The furthest distance a seal travelled from the tagging location was 1434 km (great circle distance). The ringed seals were on average 132 (105 to 159) and 359 (218 to 506) km from the nearest coastline and the tagging location, respectively. All but 1 (9 out of 10, 90%) of the tagged seals spent the majority of their time ( $\geq 50\%$ ) in areas with  $\geq 15\%$  sea ice concentration (Fig. 2), and 6 out of 10 (60%) of the seals spent the majority of their time in areas with sea ice concentrations  $\geq 50\%$  (Fig. 2). There was a decrease in the percentage of locations in areas with  $\geq 15\%$  (estimate =  $-0.215$ , SE = 0.093,  $t = -2.308$ ,  $p = 0.044$ ) and  $\geq 50\%$  sea ice concentration (estimate =  $-0.254$ , SE = 0.090,  $t = -2.815$ ,  $p = 0.018$ ) and a decrease in the percentage of locations deeper than 600 m (estimate =  $-0.251$ , SE = 0.096,  $t = -2.599$ ,  $p = 0.027$ ) from August to October.

### Ivory gulls

All ivory gulls that transmitted locations between August and October travelled offshore following the breeding period

(Fig. 1, Table 1, see Table S3 in the Supplement). The northernmost location was 86.5°N, while the easternmost locations was 126.0°E. The furthest an individual travelled from its tagging location was 2024 km (great circle distance). The ivory gulls were on average 207 (181 to 233) km and 754 (657 to 851) km from the nearest coastline and the tagging location,

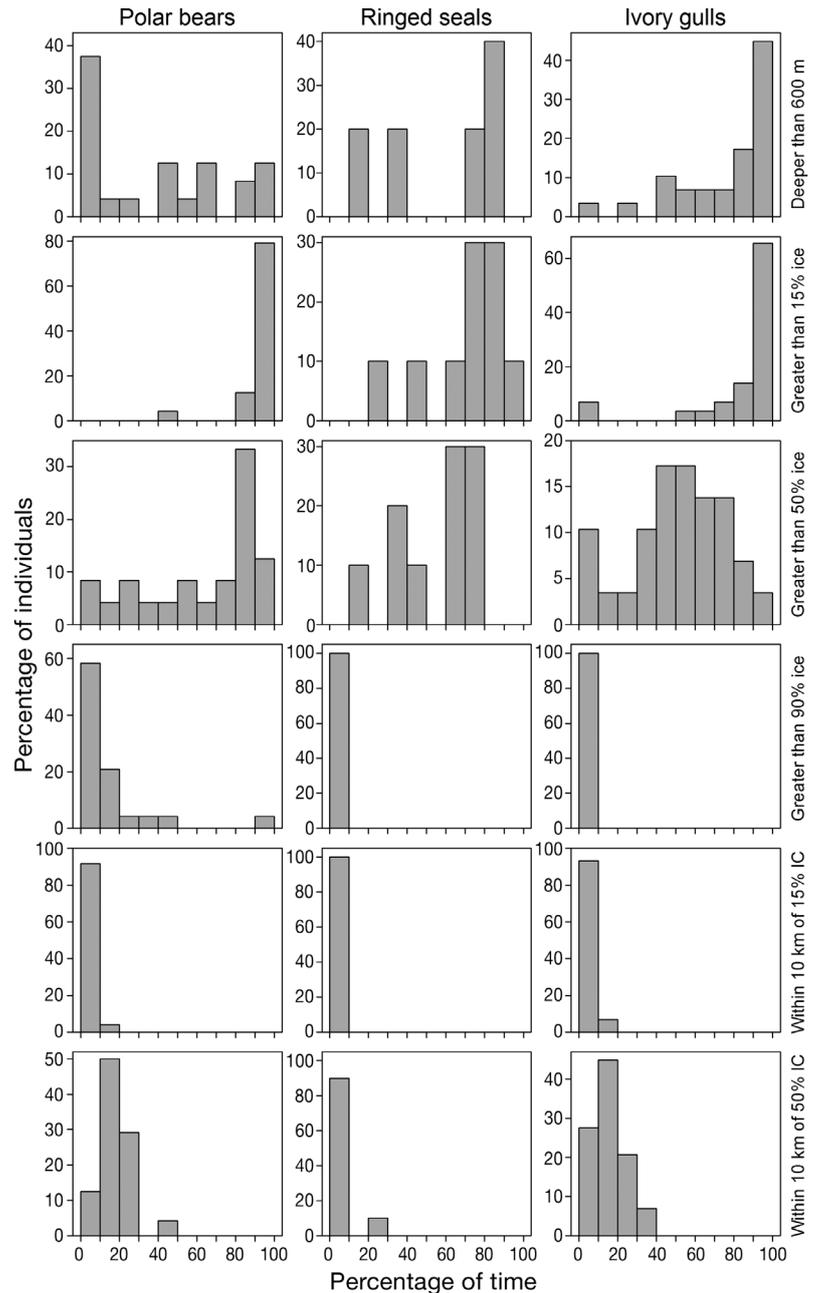


Fig. 2. Percentage of time spent in areas with water depths  $\geq 600$  m, in areas with sea ice concentrations  $\geq 15\%$ , 50% and 90%, and within 10 km of the 15% and 50% ice contour (IC) for 23 offshore polar bears *Ursus maritimus* (left column), 10 offshore ringed seals *Pusa hispida* (centre column) and 29 offshore ivory gulls *Pagophila eburnea* (right column) equipped with biotelemetry devices from 2007 to 2014 in Svalbard, Norway

respectively. Most (27 out of 29, 93 %) spent the majority of their time ( $\geq 50\%$ ) in areas with sea ice concentrations  $\geq 15\%$  (Fig. 2), and 17 out of the 29 birds (59%) spent the majority of their time in areas with sea ice concentrations  $\geq 50\%$  (Fig. 2). There was a decrease in the percentage of locations in  $\geq 50\%$  sea ice concentration (estimate =  $-0.202$ , SE =  $0.048$ ,  $t = -4.238$ ,  $p < 0.001$ ) and a decrease in the percentage of locations deeper than 600 m (estimate =  $-0.159$ , SE =  $0.049$ ,  $t = -3.234$ ,  $p = 0.003$ ) from August to October.

### Species-specific habitat selection

GAM models were used to predict the habitat selection for each species using ice data from 2010 to 2012 for the areas they frequented north of Svalbard and Franz Josef Land. The predicted values were transformed into HI values to facilitate inter-species comparisons (Fig. 3, see Figs. S5 & S6 and Table S4 in the Supplement). All 3 species selected areas with sea ice concentrations between 40% and 80% (Fig. 4). Only mean ice concentration was retained in the ringed seal model due to high correlation between this variable and the distances to the 15% and 50% ice contours (Fig. 4).

### Inter-specific spatial overlap

The most important habitat areas in terms of overlap within the species assemblage were areas slightly north of the 50% ice contour in all of the months considered (August to October, Fig. 5). The cross-validation procedure showed that the uncertainty (percentage change) in overlap values when 1 individual was randomly left out of the analyses were generally small (see Fig. S7 in the Supplement).

## DISCUSSION

All of the ivory gulls, 26% of the ringed seals and 17% of the polar bears equipped with biotelemetry devices in the Svalbard region travelled to the MIZ of the Barents Sea during late summer and early autumn. The Svalbard population of ringed seals has been estimated to contain approximately 7500 individuals during the peak moulting season, but this is believed to be an underestimate of the total population size of the region (Krafft et al. 2006). Ringed seals also breed in the drifting pack ice of the Barents

Sea. Not much is known about this group but they likely also inhabit the MIZ during the summer and autumn (Wiig et al. 1999). Thousands of ringed seals are thus expected to be present in the MIZ north of Svalbard during the summer and autumn. Similarly, although only 17% of the tagged polar bears travelled to the MIZ in this study, population surveys indicate that the large majority of the approximately 2500 bears in the Barents Sea are found in the MIZ with only a few hundred remaining on land within the Svalbard Archipelago when the MIZ retreats north of Svalbard (Aars et al. 2009, Lone et al. 2017). The MIZ is thus an important foraging habitat for all 3 species. This important foraging habitat has retreated in recent years from being located over the productive continental shelf of the Barents Sea to being located over the less productive, deep Arctic Ocean Basin (Norwegian Ice Service – Norwegian Meteorological Institute, <http://polarview.met.no/>), but animals still make this migration. Individuals from each of the 3 species in this study selected areas with sea ice concentrations between 40% and 80% within the ice pack. Only a minority of locations from each species occurred in areas with heavy sea ice coverage (concentrations  $\geq 90\%$ ), similar to what has been found in other studies on these 3 species (Fretitas et al. 2008a, Durner et al. 2009, Hamilton et al. 2015, Laidre et al. 2015b, Gilg et al. 2016). The areas of highest spatial overlap for this species assemblage in the MIZ from August to October fluctuated on a monthly and yearly basis, but were generally associated with the 50% ice contour. The highest density of overlap values were found in years and months when the MIZ was narrow (i.e. the zone between the sea ice edge and heavy sea ice concentration was limited in area). This is likely to be due to concentration of the animals within areas that have suitable sea ice characteristics.

The MIZ in the Barents Sea is an important feeding area for a wide variety of marine mammal and sea bird species. A phytoplankton bloom follows the retreat of the seasonal sea ice cover as it melts in the spring and summer with a time delay of about 2 wk, providing a continuous food source for animals that are able to track its progression (Engelsen et al. 2002). Even though the annual primary production in the northern seasonally sea ice covered portion of the Barents Sea is less than half of that in southern areas of the Barents Sea that are not covered by sea ice, productivity in the MIZ is still high and it is spatially concentrated and predictable (Sakshaug et al. 2009). The bloom also starts 6 to 8 wk earlier in the ice-covered portion of the Barents Sea compared to

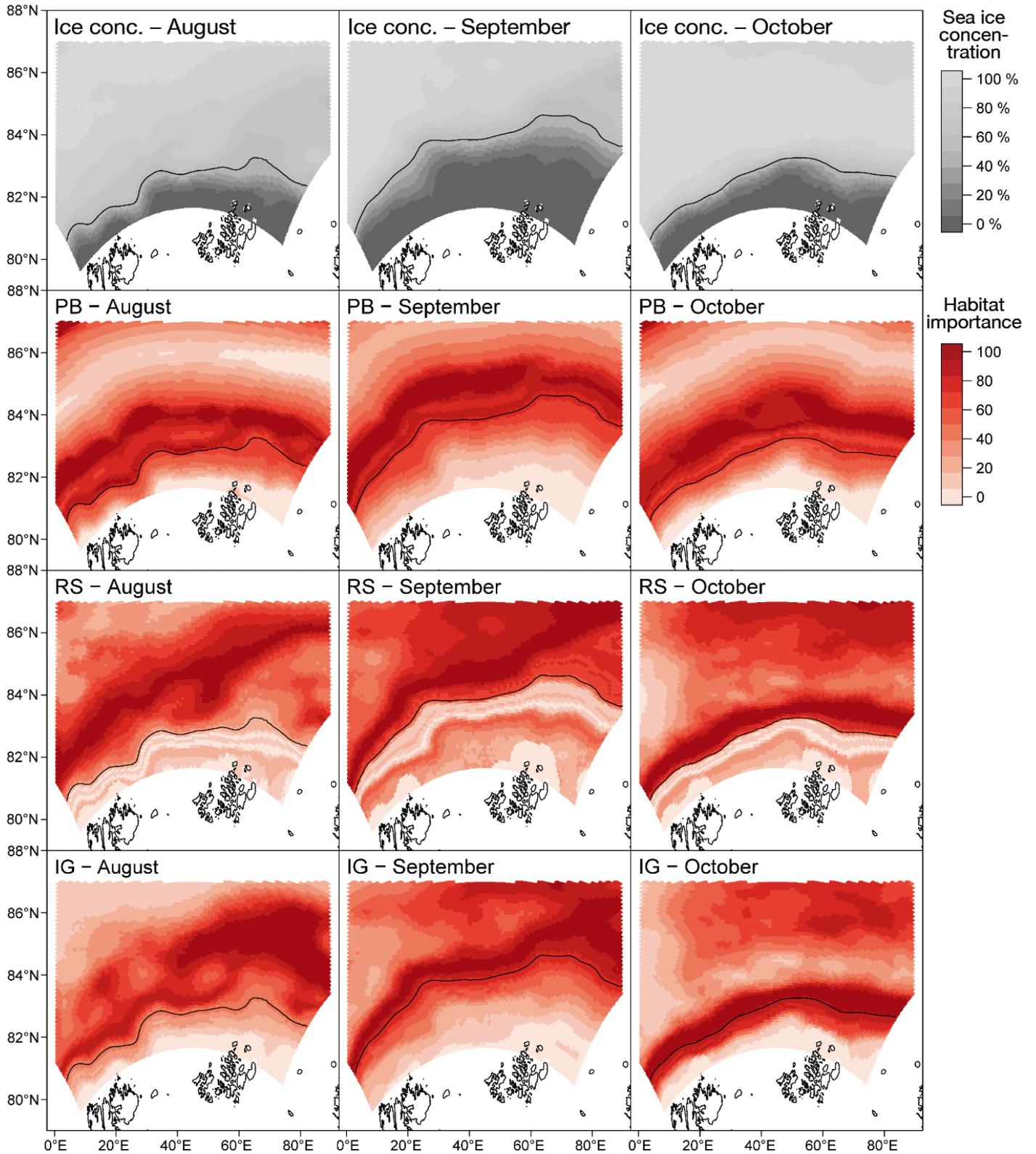


Fig. 3. Monthly mean sea ice concentrations (0 to 100%) and habitat importance values (0 indicates least important habitat and 100 indicates most important habitat) for 2012 for polar bears *Ursus maritimus* (PB), ringed seals *Pusa hispida* (RS) and ivory gulls *Pagophila eburnea* (IG) equipped with biotelemetry devices from 2007 to 2014 in Svalbard, Norway for August to October. Black line: position of the average 50% ice contour for each month

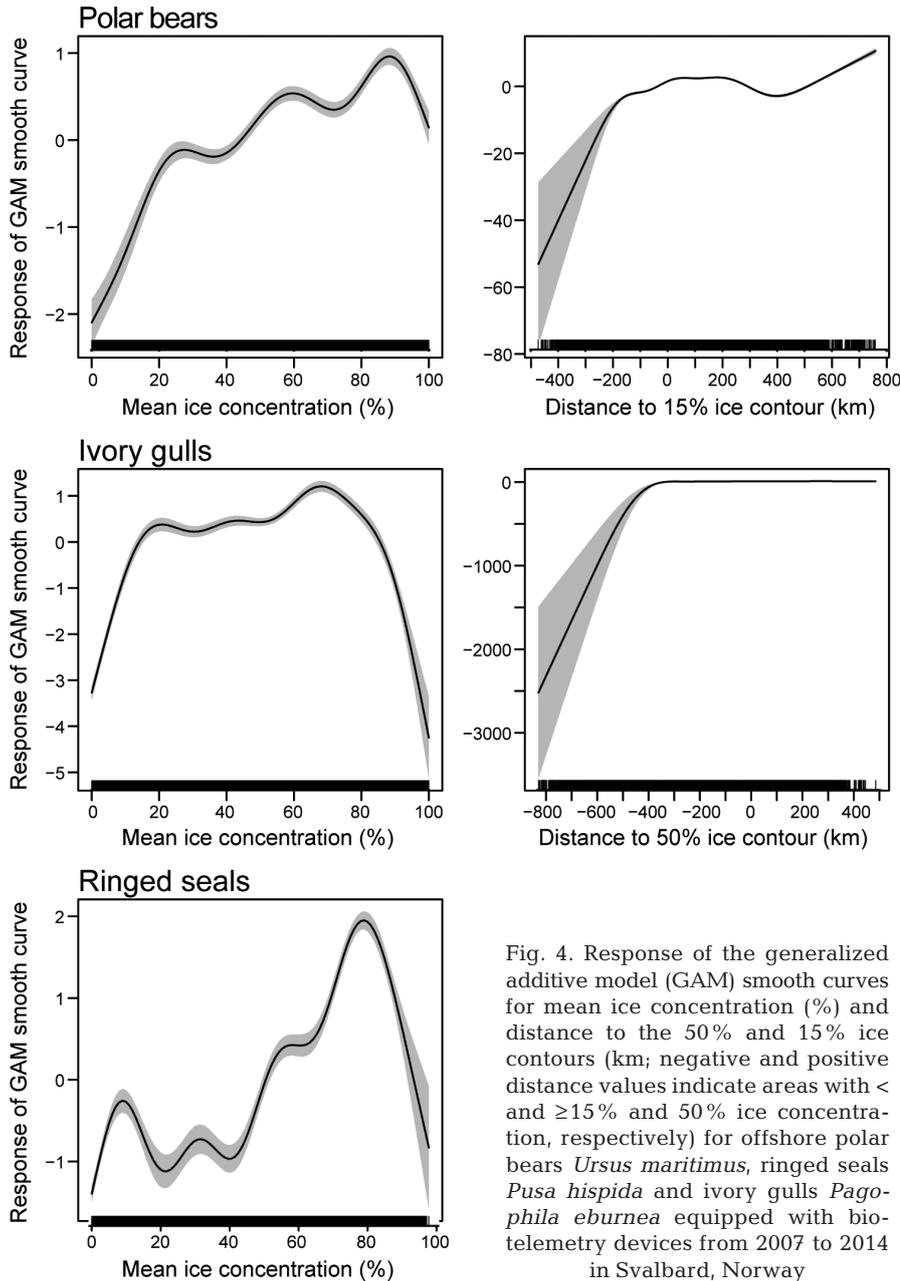


Fig. 4. Response of the generalized additive model (GAM) smooth curves for mean ice concentration (%) and distance to the 50% and 15% ice contours (km; negative and positive distance values indicate areas with < and  $\geq 15\%$  and 50% ice concentration, respectively) for offshore polar bears *Ursus maritimus*, ringed seals *Pusa hispida* and ivory gulls *Pagophila eburnea* equipped with biotelemetry devices from 2007 to 2014 in Svalbard, Norway

open-water areas, due to earlier stratification caused by melt water from the sea ice (Sakshaug et al. 2009). Sympagic fauna (i.e. fish and invertebrates associated with the underside of the sea ice) are important prey for numerous marine mammal and bird species, including ivory gulls, ringed seals, harp seals and black guillemots *Cepphus grylle* (Gulliksen & Lønne 1989, Mehlum 1990, Mehlum & Gabrielsen 1993, Arndt et al. 2009). Ice algae are estimated to produce 16 to 22% of the primary production in the northern Barents Sea and the sub-ice ecosystem is home to a variety of ice-associated fauna, including a number of

amphipod species and the younger age-classes of polar cod *Boreogadus saida*. Multi-year sea ice and sea ice with a rough underside that includes brine channels, holes and crevices has greater densities of sympagic fauna than first-year sea ice or sea ice with a flat underside (Lønne & Gulliksen 1989, 1991, Hegseth 1998, Arndt et al. 2009, von Quillfeldt et al. 2009).

The summer and autumn are important foraging periods for ringed seals as this is when they regain mass that they lost in the spring and early summer during the breeding and moulting periods (Freitas et al. 2008a, Young & Ferguson 2013, Hamilton et al. 2015). Travelling offshore to the MIZ is one of the 2 movement strategies for Svalbard ringed seals: individuals that travel offshore are primarily juveniles, while larger, older individuals stay coastal and are mainly associated with tidal glacier fronts (Freitas et al. 2008a, Hamilton et al. 2015). High intraspecific competition in areas at tidal glacier fronts likely results in smaller, younger ringed seals being displaced and travelling to the MIZ, which, due to its large spatial extent and high and extended productivity, is an important alternate foraging area. Ringed seals in other Arctic regions also travel offshore in the summer and autumn (Born et al. 2004, Kelly et al. 2010, Crawford et al. 2012, Harwood et al. 2012, Martinez-Bakker et al. 2013). However, in other

regions, such as Hudson Bay and western Greenland, ringed seals stay close to their tagging locations throughout the year, potentially reflecting ample food sources locally or excessive distances to reach suitable offshore areas (Born et al. 2004, Luque et al. 2014).

One of the 2 movement strategies of polar bears in the Barents Sea sub-population is also to move offshore in the summer and autumn, following the retreating summer sea ice edge, while other bears in this sub-population remain coastal in Svalbard (Mauritzen et al. 2002). Polar bears use offshore ice exten-

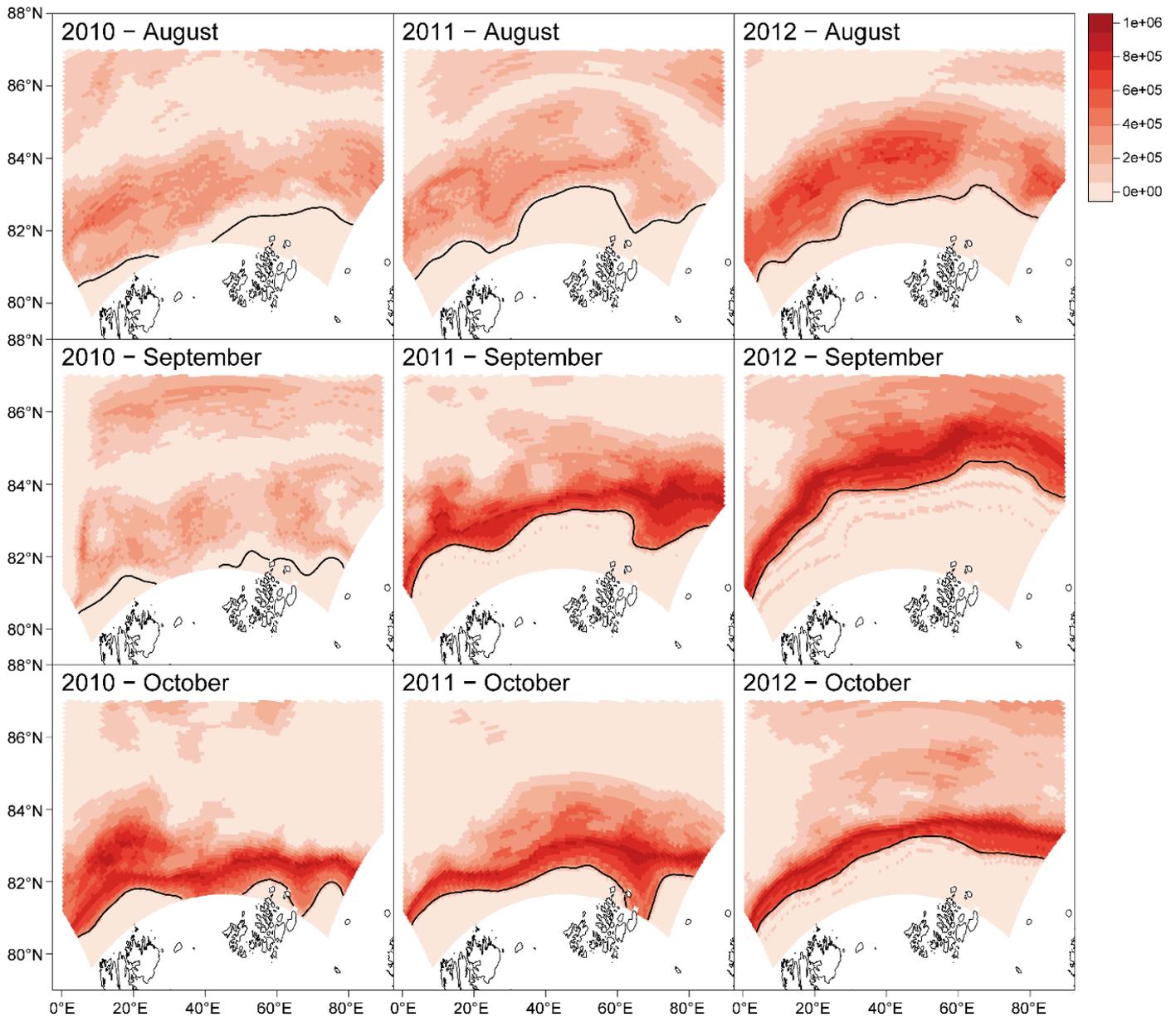


Fig. 5. Overlap of important habitat areas for 2010 to 2012 for polar bears *Ursus maritimus*, ringed seals *Pusa hispida* and ivory gulls *Pagophila eburnea* equipped with biotelemetry devices from 2007 to 2014 in Svalbard, Norway. Black line: position of the average 50% ice contour for each month

sively throughout the year in the circumpolar Arctic (Stirling et al. 1993, Durner et al. 2009, Laidre et al. 2015b, Wilson et al. 2016). Declines in Arctic sea ice have led to polar bears increasingly using land during the summer, which has been linked to declines in condition, survival of different age classes and abundance for several sub-populations (Stirling & Derocher 2012, Rode et al. 2014, 2015, Atwood et al. 2016). Investigations into condition and cub production of polar bears in Svalbard have found no consis-

tent trends, although these metrics have been linked to the value of the Arctic Oscillation (i.e. high AO values—milder weather with less sea ice—correspond to reduced condition and decreased cub production the following spring, Andersen & Aars 2016).

In the MIZ, Svalbard polar bears hunt ice-associated seals. Ringed seals, bearded seals *Erignathus barbatus* and harp seals feed in the MIZ of the Barents Sea in the summer and autumn (Derocher et al. 2002, Freitas et al. 2008a, Nordøy et al. 2008, Hamil-

ton et al. 2015). Individual bears in Svalbard normally specialize in one of the 2 movement strategies, repeating the same movement pattern every year if possible (Mauritzen et al. 2001). However, early retreat of sea ice can affect the ability of females to go offshore in some years, turning bears that normally use the offshore movement strategy into coastal bears (J. Aars unpubl. data). Polar bears in the Barents Sea have their maternity dens on land, and the sea ice arrival and departure dates affects the ability of polar bears to reach different denning areas (Derocher et al. 2011, Aars 2013).

Ivory gulls are associated with offshore pack ice most months of the year (Gilchrist et al. 2008, Gilg et al. 2010, 2016, Spencer et al. 2014, 2016). Three populations of ivory gulls in the northeast Atlantic (north Greenland, Svalbard and Franz Josef Land) travel to the MIZ of the Barents Sea post-breeding, with some Svalbard individuals also taking trips to the MIZ from the breeding colonies during the breeding season (Gilg et al. 2010, H. Strøm unpubl. data). In Canada, ivory gulls remain within the Arctic Archipelago post-breeding before moving to wintering areas in the Davis Strait (Spencer et al. 2014). In the MIZ, they forage on ice-associated zooplankton and fish, and also scavenge on polar bear kills (Ryder 1957, Divoky 1976, Orr & Parsons 1982, Renaud & McLaren 1982, Mehlum & Gabrielsen 1993, Gilchrist et al. 2008, Karnovsky et al. 2009, Gilg et al. 2010, Lydersen et al. 2014). The spatial overlap between ivory gulls and ringed seals in the MIZ is likely due in part to a shared food source, as both ivory gulls and ringed seals forage on the same ice-associated prey. It is not known how important scavenging is in terms of overall energy gain or if there are different individual foraging strategies, but the regular occurrence of ivory gulls at polar bear kills indicates that it may be significant, at least for some individuals or for some parts of the year. Stable isotope analyses of ivory gulls in the North Water Polynya have suggested that scavenging on marine mammal carcasses is important and that ivory gulls have a higher trophic position than most other Arctic seabirds, with the exception of glaucous gulls *Larus hyperboreus* (Karnovsky et al. 2009, Hobson & Bond 2012). The energy content of ringed seal blubber (close to 100% fat) is up to 10 times higher than that of many potential fish or invertebrate prey (ringed seal fat: 34–39 kJ g<sup>-1</sup> wet wt, Stirling & McEwan 1975; polar cod: 4–7 kJ g<sup>-1</sup> wet wt, Harter et al. 2013, Hop & Gjørseter 2013; *Themisto libellula*: 4 kJ g<sup>-1</sup> wet wt, Hop et al. 1997), highlighting the energetic profitability of scavenging seal carcasses.

The shift in the MIZ from over the continental shelf to over the deep waters of the Arctic Ocean Basin in the Barents Region has already been shown to have negative consequences for ringed seals (Hamilton et al. 2015) and thus this is also likely for the whole species assemblage. Ringed seals that travelled to the MIZ during late summer and autumn were shown to move greater distances per day, had dives of longer duration, spent less time at the surface between dives and spent less time hauled out after the summer sea ice edge shifted to over the Arctic Ocean Basin (Hamilton et al. 2015). Spending less time hauled out and expending greater effort foraging is expected to have negative impacts on ringed seal condition, and less time spent resting on the surface likely reduces their availability to hunting bears. Fewer kills by polar bears will naturally affect both the energy balance of the bears in the MIZ and the scavenging habits of ivory gulls.

Sex, age and reproductive status were found to have little or no effect on the habitat selection models for the 3 species in this study, although other studies have found variations in habitat selection, home range size and movement patterns in the MIZ between unaccompanied female polar bears and females with cub(s) of the year or yearling(s) (Stirling et al. 1993, Mauritzen et al. 2001, 2003, Laidre et al. 2013). However, only 6 of the 23 female polar bears that went offshore in this study had dependent young (i.e. cub[s] of the year or yearling[s]), which might have reduced the ability of the model to detect any potential differences. All of the bears in this study were females, as no data from males are available from Svalbard for this time period. However, Laidre et al. (2013) found that male and female polar bears in East Greenland had similar patterns of sea ice habitat selection. The ringed seals that took offshore trips were primarily juveniles (Hamilton et al. 2015), which is likely the reason why mass and sex did not have an effect in the habitat selection models. Mass and sex also had no effect in the ivory gull habitat selection models. As 21 of the 29 ivory gulls were males, this bias may have impacted the ability of the model to detect any potential differences, although sex was not found to have an effect on stable isotope results and habitat selection analyses of ivory gulls elsewhere in the Arctic (Hobson & Bond 2012, Gilg et al. 2016).

### Future outlook

Summer sea ice extent is predicted to retreat further north and ultimately disappear; this retreat has

already had a multitude of serious consequences for Arctic ecosystems (Wang & Overland 2012, Post et al. 2013). Currently, the MIZ represents a predictable location for successful foraging for marine mammals and seabird species. Recent warming in the Barents Sea has shifted the polar shelf fish community northwards, limiting these species to deep areas bordering the Arctic Ocean Basin, but deeper bathymetric depths might limit further northward movement of this community (Fossheim et al. 2015). Although young year-classes of polar cod and ice-associated invertebrates are found throughout the Arctic Ocean, they have higher abundances in coastal regions, in thick, old ice and in areas with high sea ice concentration (Gulliksen & Lønne 1989, David et al. 2016). It is currently unknown what will replace the ice-associated fauna in the diets of marine mammals and sea birds in a seasonally sea ice free Arctic Ocean.

As sea ice declines continue, the main overlap areas between ringed seals, polar bears and ivory gulls are likely to track the sea ice northwards, remaining in association with the 50% sea ice contour, at least to some distance from the Svalbard coastline. A modelling study of Svalbard ringed seals predicted that offshore foraging-migration trips will continue to be energetically profitable as long as the summer sea ice edge is within 600 to 700 km of the Svalbard coastline (i.e. sea ice edge situated approximately around 86° N), given that there are adequate food resources in the MIZ (Freitas et al. 2008c). A concern for polar bears is whether the southern sea ice edge is within swimming distance of the coast. Taking long distance swims (>50 km) increases the mortality rate of dependent cubs and puts polar bears at risk from storm events (Monnett & Gleason 2006, Durner et al. 2011, Pagano et al. 2012). Ivory gulls are likely to continue travelling to the MIZ in the post-breeding period as long as sea ice occurs at this time of year. The extra distance travelled is unlikely to have large energetic consequences given their lower cost of movement and their capacity for long distance migration (Gilg et al. 2010, Spencer et al. 2014). However, the proportion of seal blubber in their diet may be reduced, depending on the number of polar bears and ringed seals that are left in the MIZ and whether or not the proportion of time that ringed seals spend hauled out (i.e. exposed to predation) continues to decrease as the sea ice retreats northwards (Hamilton et al. 2015).

When the Arctic Ocean becomes seasonally sea ice free, the spatial overlap between these 3 species in this area will naturally cease to exist. Ringed seals and ivory gulls that use the MIZ as a profitable foraging area will have to move elsewhere in their search

for food. The success of a future offshore strategy for ringed seals and ivory gulls depends on their ability to locate accessible prey patches of sufficient quantity and quality in the quickly changing Barents Sea ecosystem (Fossheim et al. 2015). Whether or not they can spend multiple months offshore without resting platforms is still an uncertainty.

The polar bear, ringed seal, ivory gull species assemblage also currently exists along the Svalbard coastline, primarily associated with tidal glacier fronts (Freitas et al. 2008a, Lydersen et al. 2014, Hamilton et al. 2015, 2017). The magnitude of the predator-prey relationship between polar bears and ringed seals has already been impacted by the earlier disappearance of fast ice in these areas (Hamilton et al. 2017).

After the disappearance of the MIZ, both inter- and intraspecific competition for ringed seals and ivory gulls is likely to increase in tidal glacier front areas (Lydersen et al. 2014). However, tidal glacier front areas in Svalbard are also disappearing, as glaciers here are in negative mass-balance, and both the number and total length of tidal glacier fronts have already decreased in recent decades (Kohler et al. 2007, Błaszczuk et al. 2009). The continued disappearance of these coastal foraging 'hotspots' and the sea ice cover in these areas will lead to further increases in competition, with consequences for the population sizes and distribution of polar bears, ringed seals and ivory gulls in Svalbard. Additionally, calved pieces of glacier ice frozen into annual fast ice create conditions suitable for ringed seals to make snow lairs, which are vital for pup survival (Lydersen & Gjertz 1986). The decline in the number of calved pieces of glacier ice as well as the deterioration of sea ice and snow conditions in the spring will lead to increased predation pressure on the pups with further consequences for Svalbard ringed seal recruitment and abundance. (Lydersen & Smith 1989, Smith & Lydersen 1991).

The disappearance of both the MIZ and tidal glacier fronts on Svalbard pose serious threats to the various marine mammal and seabird species that forage in these traditionally 'hotspot' areas. Changes in the abundance and distribution of a single species can affect many other species through altered biological interactions, with the potential for broad ramifications for Arctic terrestrial and marine ecosystems. This study highlights the importance of conducting multi-species studies when assessing the current state of the ecosystem and when predicting the consequences of climate change. Including biological interactions in ecological investigations will improve prediction accuracy and the success of management efforts in this time of rapid change.

**Acknowledgements.** We thank Magnus Andersen, Vidar Bakken, Lars Boehme, Heinrich Eggenfellner, Mike Fedak, Carla Freitas, Nils Christian Ravnas Heen, Audun Igesund, Rupert Krapp, Hans Lund, Benjamin Merkel and Bobben Severinsen for their assistance tagging the various animals in the field and Benjamin Merkel for preparation of the polar bear location data. This study was supported by the Norwegian Polar Institute's Centre for Ice, Climate and Ecosystems (ICE), the Norwegian Research Council, the World Wildlife Fund (WWF), Statoil and the Norwegian seabird monitoring program SEAPOP ([www.seapop.no](http://www.seapop.no)). C.D.H. is funded by the VISTA Scholar's programme, a collaboration between the Norwegian Academy of Science and Letters and Statoil.

## LITERATURE CITED

- Aars J, Marques TA, Buckland ST, Andersen M, Belikov S, Boltunov A, Wiig Ø (2009) Estimating the Barents Sea polar bear subpopulation size. *Mar Mamm Sci* 25:35–52
- ✦ Aars J (2013) Variation in detection probability of polar bear maternity dens. *Polar Biol* 36:1089–1096
- Amstrup SC (2003) Polar bear (*Ursus maritimus*). In: Feldhammer GA, Thompson BC, Chapman JA (eds) *Wild mammals of North America: biology, management and conservation*, 2nd edn. Johns Hopkins University Press, Baltimore, MD, p 587–610
- ✦ Andersen M, Aars J (2016) Barents Sea polar bears (*Ursus maritimus*): population biology and anthropogenic threats. *Polar Res* 35:26029
- Arndt CE, Gulliksen B, Lønne OJ, Berge J (2009) Sea-ice fauna. In: Sakshaug E, Johnsen G, Kovacs K (eds) *Ecosystem Barents Sea*. Tapir Academic Press, Trondheim, p 303–322
- ✦ Atwood TC, Peacock E, McKinney MA, Lillie K and others (2016) Rapid environmental change drives increased land use by an Arctic marine predator. *PLOS ONE* 11:e0155932
- Błaszczyk M, Jania JA, Hagen JO (2009) Tidewater glaciers of Svalbard: recent changes and estimates of calving fluxes. *Pol Polar Res* 30:85–142
- ✦ Boertmann D, Olsen K, Gilg O (2010) Ivory gulls breeding on ice. *Polar Rec (Gr Brit)* 46:86–88
- ✦ Born EW, Teilmann J, Acquarone M, Riget FF (2004) Habitat use of ringed seals (*Phoca hispida*) in the North Water Area (North Baffin Bay). *Arctic* 57:129–142
- Canty A, Ripley B (2016) boot: Bootstrap R (S-Plus) functions. R package version 1.3-18
- ✦ Cattet MRL, Caulkett NA, Obbard ME, Stenhouse GB (2002) A body-condition index for ursids. *Can J Zool* 80:1156–1161
- Collecte Localisation Satellites (CLS) (2016) Argos user's manual. [www.argos-system.org/manual/](http://www.argos-system.org/manual/) (accessed 8 Feb 2016)
- ✦ Comiso JC, Hall DK (2014) Climate trends in the Arctic as observed from space. *Wiley Interdiscip Rev Clim Change* 5:389–409
- Conservation of Arctic Flora and Fauna (CAFF) (2013) Arctic biodiversity assessment. Status and trends in Arctic biodiversity: synthesis. Arctic Council, Stel
- ✦ Crawford JA, Frost KJ, Quakenbush LT, Whiting A (2012) Different habitat use strategies by subadult and adult ringed seals (*Phoca hispida*) in the Bering and Chukchi seas. *Polar Biol* 35:241–255
- ✦ David C, Lange B, Krumpfen T, Schaafsma F, van Franeker JA, Flores H (2016) Under-ice distribution of polar cod *Boreogadus saida* in the central Arctic Ocean and their association with sea-ice habitat properties. *Polar Biol* 39:981–994
- Derocher AE, Wiig Ø, Andersen M (2002) Diet composition of polar bears in Svalbard and the western Barents Sea. *Polar Biol* 25:448–452
- ✦ Derocher AE, Andersen M, Wiig Ø, Aars J, Hansen E, Biuw M (2011) Sea ice and polar bear den ecology at Hopen Island, Svalbard. *Mar Ecol Prog Ser* 441:273–279
- ✦ Divoky GJ (1976) The pelagic feeding habits of ivory and Ross' gulls. *Condor* 78:85–90
- ✦ Durner GM, Douglas DC, Nielson RM, Amstrup SC and others (2009) Predicting 21st-century polar bear habitat distribution from global climate models. *Ecol Monogr* 79:25–58
- ✦ Durner GM, Whiteman JP, Harlow HJ, Amstrup SC, Regehr EV, Ben-David M (2011) Consequences of long-distance swimming and travel over deep-water pack ice for a female polar bear during a year of extreme sea ice retreat. *Polar Biol* 34:975–984
- ✦ Engelsen O, Hegseth EN, Hop H, Hansen E, Falk-Petersen S (2002) Spatial variability of chlorophyll-*a* in the Marginal Ice Zone of the Barents Sea, with relations to sea ice and oceanographic conditions. *J Mar Syst* 35:79–97
- Finley KJ, Miller GW, Davis RA, Koski WR (1983) A distinctive large breeding population of ringed seals (*Phoca hispida*) inhabiting the Baffin Bay pack ice. *Arctic* 36:162–173
- ✦ Fosshem 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 Chang* 5:673–677
- ✦ Freitas C, Kovacs KM, Ims RA, Fedak MA, Lydersen C (2008a) Ringed seal post-moulting movement tactics and habitat selection. *Oecologia* 155:193–204
- ✦ Freitas C, Lydersen C, Fedak MA, Kovacs KM (2008b) A simple new algorithm to filter marine mammal Argos locations. *Mar Mamm Sci* 24:315–325
- ✦ Freitas C, Kovacs KM, Ims RA, Lydersen C (2008c) Predicting habitat use by ringed seals (*Phoca hispida*) in a warming Arctic. *Ecol Modell* 217:19–32
- ✦ Gilchrist HG, Mallory ML (2005) Declines in abundance and distribution of the ivory gull (*Pagophila eburnea*) in Arctic Canada. *Biol Conserv* 121:303–309
- Gilchrist HG, Strøm H, Gavrilov MV, Mosbech A (2008) International ivory gull conservation strategy and action plan. CAFF International Secretariat, Circumpolar Seabird Group (CBird), CAFF Technical Report No. 18
- ✦ Gilg O, Strøm H, Aebischer A, Gavrilov MV, Volkov AE, Miljeteig C, Sabard B (2010) Post-breeding movements of northeast Atlantic ivory gull *Pagophila eburnea* populations. *J Avian Biol* 41:532–542
- ✦ Gilg O, Istomina L, Heygster G, Strøm H and others (2016) Living on the edge of a shrinking habitat: the ivory gull, *Pagophila eburnea*, an endangered sea-ice specialist. *Biol Lett* 12:20160277
- ✦ Gloersen P, Campbell WJ, Cavalieri DJ, Comiso JC, Parkinson CL, Zwally HJ (1993) Satellite passive microwave observations and analysis of Arctic and Antarctic sea ice, 1978–1987. *Ann Glaciol* 17:149–154
- Gulliksen B, Lønne OJ (1989) Distribution, abundance, and ecological importance of marine sympagic fauna in the Arctic. *Rapp P-V Reun Cons Int Explor Mer* 188:133–138
- ✦ Hamilton CD, Lydersen C, Ims RA, Kovacs KM (2015) Predictions replaced by facts: a keystone species' behav-

- ournal responses to declining Arctic sea-ice. *Biol Lett* 11: 20150803
- Hamilton CD, Lydersen C, Ims RA, Kovacs KM (2016) Coastal habitat use by ringed seals *Pusa hispida* following a regional sea-ice collapse: importance of glacial refugia in a changing Arctic. *Mar Ecol Prog Ser* 545: 261–277
- Hamilton CD, Kovacs KM, Ims RA, Aars J, Lydersen C (2017) An Arctic predator-prey system in flux: climate change impacts on coastal space use by polar bears and ringed seals. *J Anim Ecol*, doi:10.1111/1365-2656.12685
- Harter BB, Elliott KH, Divoky GJ, Davoren GK (2013) Arctic cod (*Boreogadus saida*) as prey: fish length-energetics relationships in the Beaufort Sea and Hudson Bay. *Arctic* 66:191–196
- Harwood LA, Smith TG, Auld JC (2012) Fall migration of ringed seals (*Phoca hispida*) through the Beaufort and Chukchi Seas, 2001–02. *Arctic* 65:35–44
- Hegseth EN (1998) Primary production of the northern Barents Sea. *Polar Res* 17:113–123
- Hobson KA, Bond AL (2012) Extending an indicator: year-round information on seabird trophic ecology from multiple-tissue stable-isotope analyses. *Mar Ecol Prog Ser* 461:233–243
- Hop H, Gjørseter H (2013) Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Mar Biol Res* 9: 878–894
- Hop H, Tonn WM, Welch HE (1997) Bioenergetics of Arctic cod (*Boreogadus saida*) at low temperatures. *Can J Fish Aquat Sci* 54:1772–1784
- Iversen M, Aars J, Haug T, Alsos IG, Lydersen C, Bachmann L, Kovacs KM (2013) The diet of polar bears (*Ursus maritimus*) from Svalbard, Norway, inferred from scat analysis. *Polar Biol* 36:561–571
- Jakobsson M, Mayer L, Coakley B, Dowdeswell JA and others (2012) The International Bathymetric Chart of the Arctic Ocean (IBCAO) Version 3.0. *Geophys Res Lett* 39: L12609
- Johnson DS, London JM, Lea MA, Durban JW (2008) Continuous-time correlated random walk model for animal telemetry data. *Ecology* 89:1208–1215
- Karnovsky NJ, Hobson KA, Brown ZW, Hunt GL Jr (2009) Distribution and diet of ivory gulls (*Pagophila eburnea*) in the North Water Polynya. *Arctic* 62:65–74
- Kelly BP, Badajos OH, Kunnsaranta M, Moran JR, Martinez-Bakker M, Wartzok D, Boveng P (2010) Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biol* 33:1095–1109
- Kohler J, James TD, Murray T, Nuth C and others (2007) Acceleration in thinning rate on western Svalbard glaciers. *Geophys Res Lett* 34:L18502
- Kovacs KM, Lydersen C, Overland JE, Moore SE (2011) Impacts of changing sea-ice conditions on Arctic marine mammals. *Mar Biodivers* 41:181–194
- Krafft BA, Kovacs KM, Andersen M, Aars J, Lydersen C, Ergon T, Haug T (2006) Abundance of ringed seals (*Pusa hispida*) in the fjords of Spitsbergen, Svalbard, during the peak molting period. *Mar Mamm Sci* 22: 394–412
- Kwok R, Cunningham GF, Wensnahan M, Rigor I, Zwally HJ, Yi D (2009) Thinning and volume loss of the Arctic Ocean sea ice cover: 2003–2008. *J Geophys Res* 114:C07005
- Labansen AL, Lydersen C, Haug T, Kovacs KM (2007) Spring diet of ringed seals (*Phoca hispida*) from north-western Spitsbergen, Norway. *ICES J Mar Sci* 64: 1246–1256
- Laidre KL, Born EW, Gurarie E, Wiig Ø, Dietz R, Stern H (2013) Females roam while males patrol: divergence in breeding season movements of pack-ice polar bears (*Ursus maritimus*). *Proc R Soc B* 280:20122371
- Laidre KL, Stern H, Kovacs KM, Lowry L and others (2015a) Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conserv Biol* 29:724–737
- Laidre KL, Born EW, Heagerty P, Wiig Ø and others (2015b) Shifts in female polar bear (*Ursus maritimus*) habitat use in East Greenland. *Polar Biol* 38:879–893
- Lone K, Merkel B, Lydersen C, Kovacs KM, Aars J (2017) Sea ice resource selection models for polar bears in the Barents Sea subpopulation. *Ecography* doi:10.1111/ecog. 03020
- Lønne OJ, Gulliksen B (1989) Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1773), in ice covered waters. *Polar Biol* 9:187–191
- Lønne OJ, Gulliksen B (1991) On the distribution of sympatric macro-fauna in the seasonally ice covered Barents Sea. *Polar Biol* 11:457–469
- Luque SP, Ferguson SH, Breed GA (2014) Spatial behaviour of a keystone Arctic marine predator and implications of climate warming in Hudson Bay. *J Exp Mar Biol Ecol* 461:504–515
- 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, Smith TG (1989) Avian predation on ringed seal *Phoca hispida* pups. *Polar Biol* 9:489–490
- 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
- Martinez-Bakker ME, Sell SK, Swanson BJ, Kelly BP, Tallmon DA (2013) Combined genetic and telemetry data reveal high rates of gene flow, migration, and long-distance dispersal potential in Arctic ringed seals (*Pusa hispida*). *PLOS ONE* 8:e77125
- Mauritzen M, Derocher AE, Wiig Ø (2001) Space-use strategies of female polar bears in a dynamic sea ice habitat. *Can J Zool* 79:1704–1713
- Mauritzen M, Derocher AE, Wiig Ø, Belikov S, Boltunov A, Hansen E, Garner GW (2002) Using satellite telemetry to define spatial population structure in polar bears in the Norwegian and western Russian Arctic. *J Appl Ecol* 39: 79–90
- Mauritzen M, Belikov SE, Boltunov AN, Derocher AE and others (2003) Functional responses in polar bear habitat selection. *Oikos* 100:112–124
- McLaren IA (1958) The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. *Bull Fish Res Board Can* 118
- Mehlum F (1990) Seabird distribution in the northern Barents Sea marginal ice-zone during late summer. *Polar Res* 8:61–65
- Mehlum F, Gabrielsen GW (1993) The diet of High-Arctic seabirds in coastal and ice-covered, pelagic areas near the Svalbard archipelago. *Polar Res* 12:1–20
- Moline MA, Karnovsky NJ, Brown Z, Divoky GJ and others (2008) High latitude changes in ice dynamics and their impact on polar marine ecosystems. *Ann NY Acad Sci* 1134:267–319

- Møller AP, Flensted-Jensen E, Mardal W (2006) Dispersal and climate change: a case study of the Arctic tern *Sterna paradisaea*. *Glob Chang Biol* 12:2005–2013
- Monnett C, Gleason JS (2006) Observations of mortality associated with extended open-water swimming by polar bears in the Alaskan Beaufort Sea. *Polar Biol* 29: 681–687
- Nordøy ES, Folkow LP, Potelov V, Prischemikhin V, Blix AS (2008) Seasonal distribution and dive behaviour of harp seals (*Pagophilus groenlandicus*) of the White Sea–Barents Sea stock. *Polar Biol* 31:1119–1135
- Orr CD, Parsons JL (1982) Ivory gulls, *Pagophila eburnea*, and ice edges in Davis Strait and the Labrador Sea. *Can Field Nat* 96:323–328
- Pagano AM, Durner GM, Amstrup SC, Simac KS, York GS (2012) Long-distance swimming by polar bears (*Ursus maritimus*) of the southern Beaufort Sea during years of extensive open water. *Can J Zool* 90:663–676
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2016) nlme: linear and nonlinear mixed effects models. R package version 3.1-125. <http://CRAN.R-project.org/package=nlme>
- Post E, Bhatt US, Bitz CM, Brodie JF and others (2013) Ecological consequences of sea-ice decline. *Science* 341: 519–524
- R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Raymond B, Lea MA, Patterson T, Andrews-Goff V and others (2015) Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography* 38:121–129
- Reeves RR (1998) Distribution, abundance and biology of ringed seals (*Phoca hispida*): an overview. NAMMCO Scientific Publications 1:9–45
- Renaud WE, McLaren PL (1982) Ivory gull (*Pagophila eburnea*) distribution in late summer and autumn in eastern Lancaster Sound and western Baffin Bay. *Arctic* 35: 141–148
- Rode KD, Regehr EV, Douglas DC, Durner G, Derocher AE, Thiemann GW, Budge SM (2014) Variation in the response of an Arctic top predator experiencing habitat loss: feeding and reproductive ecology of two polar bear populations. *Glob Chang Biol* 20:76–88
- Rode KD, Wilson RR, Regehr EV, St. Martin M, Douglas DC, Olson J (2015) Increased land use by Chukchi Sea polar bears in relation to changing sea ice conditions. *PLOS ONE* 10:e0142213
- Ryder RA (1957) Avian-pinniped feeding associations. *Condor* 59:68–69
- Sakshaug E, Johnsen G, Kristiansen S, von Quillfeldt C, Rey F, Slagstad D, Thingstad F (2009) Phytoplankton and primary production. In: Sakshaug E, Johnsen G, Kovacs K (eds) *Ecosystem Barents Sea*. Tapir Academic Press, Trondheim, p 167–208
- Smith TG, Lydersen C (1991) Availability of suitable land-fast ice and predation as factors limiting ringed seal populations, *Phoca hispida*, in Svalbard. *Polar Res* 10:585–594
- 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
- Spencer NC, Gilchrist HG, Mallory ML (2014) Annual movement patterns of endangered ivory gulls: the importance of sea ice. *PLOS ONE* 9:e115231
- Spencer NC, Gilchrist HG, Strøm H, Allard KA, Mallory ML (2016) Key winter habitat of the ivory gull *Pagophila eburnea* in the Canadian Arctic. *Endang Species Res* 31: 33–45
- Stirling I, Derocher AE (2012) Effects of climate warming on polar bears: a review of the evidence. *Glob Chang Biol* 18:2694–2706
- Stirling I, McEwan EH (1975) The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behavior. *Can J Zool* 53:1021–1027
- Stirling I, Andriashek D, Calvert W (1993) Habitat preferences of polar bears in the western Canadian Arctic in late winter and spring. *Polar Rec (Gr Brit)* 29:13–24
- Thiemann GW, Iverson SJ, Stirling I (2008) Polar bear diets and arctic marine food webs: insights from fatty acid analysis. *Ecol Monogr* 78:591–613
- Vinje T (2009) Sea-ice. In: Sakshaug E, Johnsen G, Kovacs K (eds) *Ecosystem Barents Sea*. Tapir Academic Press, Trondheim, p 65–82
- von Quillfeldt CH, Hegseth EN, Johnsen G, Sakshaug E, Syvertsen EE (2009) Ice algae. In: Sakshaug E, Johnsen G, Kovacs K (eds) *Ecosystem Barents Sea*. Tapir Academic Press, Trondheim, p 285–302
- Wang M, Overland JE (2012) A sea ice free summer Arctic within 30 years: an update from CMIP5 models. *Geophys Res Lett* 39:L18501
- Wiig Ø, Derocher AE, Belikov SE (1999) Ringed seal (*Phoca hispida*) breeding in the drifting pack ice of the Barents Sea. *Mar Mamm Sci* 15:595–598
- Wilson RR, Regehr EV, Rode KD, St Martin M (2016) Invariant polar bear habitat selection during a period of sea ice loss. *Proc Biol Sci* 283:20160380
- Wood S (2006) *Generalized additive models: an introduction with R*. Chapman & Hall/CRC, Boca Raton, FL
- Wood S (2016) choose.k. In: Package 'mgcv', version 1.8-16, p 17–20. <https://cran.r-project.org/web/packages/mgcv/mgcv.pdf>
- Young BG, Ferguson SH (2013) Seasons of the ringed seal: pelagic open-water hyperphagy, benthic feeding over winter and spring fasting during molt. *Wildl Res* 40:52–60
- Zuur AF (2012) *A beginner's guide to generalized additive models with R*. Highland Statistics, Newburgh
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer-Verlag, New York, NY
- Zuur AF, Ieno EN, Elphick CS (2010) *A protocol for data exploration to avoid common statistical problems*. *Methods Ecol Evol* 1:3–14
- Żydelis R, Lewison RL, Shaffer SA, Moore JE and others (2011) Dynamic habitat models: using telemetry data to project fisheries bycatch. *Proc Biol Sci* 278:3191–3200