

Selection and foraging response of harbour seals in an area of changing prey resources

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ABSTRACT: Resource selection is a hierarchical and dynamic process. Selection can occur at different spatial and temporal scales, and can change over time with shifts in resource availability. The temporal dynamic of selection was investigated for a harbour seal *Phoca vitulina* population in Porsangerfjord, Norway, a subarctic fjord with large seasonal fluctuations in resource distribution. The availability of potential harbour seal prey was assumed to be dependent on the prey's biomass densities, distance from the seals' haulout sites and accessibility of the areas where prey was located, restricted by the presence of sea ice during winter and spring. The foraging behaviour of seals was investigated by assessing their preference and foraging response to the seasonal dynamics of prey distribution. The movement and dive patterns of individual seals ($n = 10$) were tracked with GPS devices. Foraging locations were compared to the availability of potential prey species in the fjord. Results suggested that harbour seals in Porsangerfjord had a preference for small-sized fish (<25 cm). Small codfish were preferred during autumn, but a response to the presence of pelagic fish was seen when the latter aggregated to overwinter in cold deep waters in the inner parts of the fjord. The formation of ice during late winter, however, provoked a shift in preference for small codfish, due to the sudden inaccessibility of pelagic fish. A strong reversed trend was observed in spring when the ice melted. The results indicate preference for small aggregated fish and the presence of a foraging response to changes in resource distribution.

KEY WORDS: Feeding response · Resource selection function · Resource availability · Preference · Predator–prey overlap · Home range · Haulout · Ice coverage · *Phoca vitulina*

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INTRODUCTION

Resource selection is defined as a disproportional use of resources with respect to their availability and can be seen as a hierarchical process occurring at different spatial and temporal scales (Manly et al. 2002). Animals can choose among prey items within a foraging patch, select foraging patches within a given home range or decide to shift their home range based, for example, on life history requirements or trade-off situations (Myysterud et al. 1999). Harbour seals *Phoca vitulina*, being central place foragers, perform regular trips to foraging grounds from their haulout sites. The availability of resources in space is therefore conditional to the placement of haulout

sites, since foraging locations have a decreasing accessibility with distance from the sites (Matthiopoulos 2003). However, unlike other central place foraging species, which need to return to a fixed location (e.g. nesting birds), the placement of haulout sites is relatively dynamic for harbour seals (Lesage et al. 2004). As a result, resource selection for this species can be seen as a hierarchical process operating mainly at 2 spatial scales: the choice of foraging areas and home ranges within the total potentially exploitable area, and the choice of foraging locations conditional to the position of the haulout sites. The way in which these 2 processes contribute to the selection of resources (see Myysterud et al. 1999) has not yet been assessed in seals.

Selection is also affected by the temporal dynamics of ecological processes, such as seasonal variation in resources, and may vary with time as animals experience changes in resource availability (McLoughlin et al. 2010). Availability varies with the density and spatial distribution of the resources, but also depends on the accessibility and constraints of the areas where the resources are located (Mysterud et al. 1999, Matthiopoulos 2003). Selection can therefore be seen as a context-dependent and dynamic process both in space and time (Beyer et al. 2010). Increasing numbers of studies have pointed out the importance of accounting for changes in resource availability in studies of selection (Aarts et al. 2012, 2013, Johnson et al. 2013) and assessing the response of animals to such changes (i.e. functional response sensu Mysterud & Ims 1998), in order to better understand the foraging ecology of animals in dynamic environments.

We examined resource selection by a resident population of harbour seals in the Porsangerfjord, a subarctic fjord in northern Norway. This fjord is a highly complex and dynamic system which is connected at its outer edge to the open Barents Sea. The area serves as breeding, spawning, nursery and overwintering grounds for several fish species, sea birds and sea mammals (Jakobsen & Ozhigin 2011). The seasonal dynamics of this system can be strongly affected by drivers far outside the area. The fjord is characterized by the presence of cold-water deep basins in the southeast inner parts, while the outer areas are characterized by the influx of Atlantic waters from the north (Myksvoll et al. 2012). During late winter and spring, ice covers the inner areas (Myksvoll et al. 2012). Fish resources vary seasonally, with Atlantic fish species entering the fjord following the inflow of warmer Atlantic waters in the summer, while in winter large concentrations of young herring *Clupea harengus* overwinter in the cold inner basins (Bergstad et al. 1987, Fernö et al. 1998, Jakobsen & Ozhigin 2011). A small population of about 200 harbour seals (K.T. Nilssen unpublished) resides in the fjord year round. This partially enclosed but dynamic fjord ecosystem, subject to seasonal resource pulses and changes in environmental characteristics, offers a favourable setting to study the foraging ecology of this species.

In this area, resource selection by harbour seals was expected to change in response to the seasonal changes in resource distribution and the changes in the accessibility of the inner areas, due to the formation and retreat of ice in winter and spring, respectively. In response, seals can alter their preference by selecting foraging locations with certain resource

characteristics, but also move their general home range (foraging area and haulout sites) to increase the accessibility of certain resources. We investigated selection at multiple spatial scales and assessed (1) resource selection conditional upon the placement of the haulout sites; and (2) general resource selection within the entire fjord system. We did so by fitting resource selection functions (RSFs) comparing resource usage to availability conditional to haulout sites and to general availability for the entire fjord. We defined resources as the biomass densities of harbour seals' potential prey species present at harbour seals' locations in space. We compared data on harbour seal movements to modelled biomass density maps of potential prey species. We then investigated temporal changes in selection to assess the presence of a behavioural response of the seals to the temporal dynamics of the system. These were expected to be seasonal changes in resource distribution and shifts in area accessibility associated with the presence of ice in the inner parts of the fjord in winter and spring.

MATERIALS AND METHODS

Data collection

To investigate the foraging behaviour of individual harbour seals from the resident population in Porsangerfjord, GPS phone tags (SMRU Instrumentation, University of St Andrews, UK) were deployed on 12 animals in the fall of 2009 and 2010. The tags recorded irregular series of GPS positions at intervals of minimum 20 min, together with dive profiles of 11 time and depth inflection points, equally spaced in time, and haulout events. Details on the capture of animals and tagging procedures and the tag settings are provided by Ramasco et al. (2014).

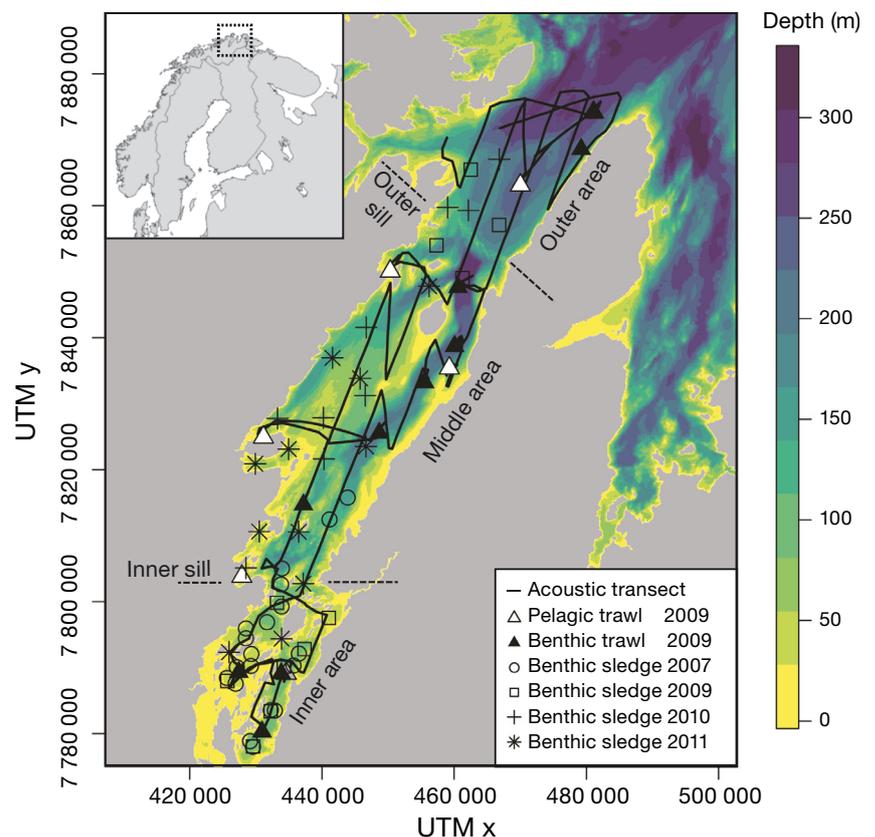
We mapped the spatial distribution of resources available to the seals in the study region. These resources included the biomass of potential prey species, collected over multiple seasons and, when possible, during harbour seal tag deployment periods. Only fish species known to occur in the harbour seal diet, identified in the literature or through a concurrent diet study (see Fig. S1 and text in the Supplement at www.int-res.com/articles/suppl/m581p199_supp.pdf), were included. These species include codfish (Gadidae), sandeel (*Ammodytes* spp.), and small pelagic fishes, such as herring and capelin *Mallotus villosus*, sculpins (Cottidae), pricklebacks (Stichaeidae) and flatfishes (*Pleuronectidae*) (Olsen & Bjørge 1995, Berg et al. 2002, Andersen et al. 2004).

Table 1. Overview of the data types and sampling sizes of harbour seal *Phoca vitulina* movement and dive data for different 2 mo periods ($t = 1-4$) closest to the acoustic sampling dates. Acoustic sampling: timing and duration of the 4 sampling efforts together with the number of trawl hauls for the estimations of the potential prey resources. Dates are given as dd.mm.yyyy

Animal data					Period $t = 1$	Period $t = 2$	Period $t = 3$	Period $t = 4$
Individual	Sex	Length (cm)	Weight (kg)	Tagging duration (from-to)	01.09.2009 to 31.10.2009	01.01.2010 to 28.02.2010	01.04.2010 to 31.05.2010	01.09.2010 to 31.10.2010
					No. of GPSs	No. of dives	No. of GPSs	No. of GPSs
pv30-01-09	M	87	21	01.09.2009 10.07.2010	1713	23221	1448	23903
pv30-05-09	M	105	30	04.09.2009 30.03.2010	2169	15210	1440	31976
pv30-06-09	F	104	31	02.09.2009 28.05.2010	1441	28879	1595	22612
pv30-11-09	F	93	22	06.09.2009 09.06.2010	1468	36894	1774	34709
pv30-12-09	M	100	24	08.09.2009 20.12.2009	2052	31576	1947	31304
pv30-02-09	M	94	24	20.09.2010 04.07.2011				1503 27409
pv30-03-09	M	108	41	19.09.2010 31.01.2011				1469 29535
pv30-08-09	M	101	25	10.09.2010 22.06.2011				750 36500
pv30-09-09	F	90	20	03.09.2010 30.06.2011				2181 39351
pv30-13-09	F	101	28	22.09.2010 10.06.2011				1497 24486
Acoustic sampling					No. of seal individuals per period (n_t)			
					$n = 5$ $t = 1$	$n = 4$ $t = 2$	$n = 3$ $t = 3$	$n = 5$ $t = 4$
Transect start					18.08.2009	02.02.2010	27.04.2010	17.08.2010
Transect end					20.08.2009	04.02.2010	29.04.2010	19.08.2010
No. of pelagic trawl hauls					7	0	4	6
No. of benthic trawl hauls					10	8	8	9

The distribution of potential prey was surveyed using standard acoustic methods for the estimation of fish abundance (Bodholt et al. 1989). Surveys were run along predefined transects, during 4 periods: August 2009, February 2010, April 2010 and August 2010 (Table 1). The sampling consisted of continuous boat-based acoustic measurements integrated at each 1 nautical mile (n mile) of transect (Fig. 1). The biomass density (kg n mile^{-2}) of cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, her-

Fig. 1. Study area and bathymetry (colour scale), and design for sampling potential prey of harbour seals *Phoca vitulina*. The Porsangerfjord can be roughly divided into 3 areas, delimited by an inner and an outer fjord sill. An average acoustic transect for the sampling of pelagic and semi-pelagic fish species is illustrated, as is the placement of benthic and pelagic trawl stations for the calibration of the acoustic survey (those from August 2009 are shown as an example) and the benthic sledge stations from different years for the sampling of bottom-dwelling fish species



ring and capelin along the transects was estimated by scaling the acoustic measurements by the catches at pelagic and benthic trawl stations (Fig. 1, see the Supplement for specifications on estimation methods). Sandeel and saithe *Pollachius virens* were also caught, but the former occurred in the samples only during 1 season, and the latter at few stations each season and could not be included in further analysis.

The acoustic methods described above were not adapted for estimating the biomass densities of benthic fish species. The biomass density of sculpins was therefore obtained from a study on benthic epifauna in the area (L. Jørgensen unpublished results). The epibenthic fauna biomass was sampled at 49 stations distributed throughout the fjord, by towing a benthic sledge (2 m width, 4 mm mesh size) for 5 min (towing speed 1.5 knots) in June 2007, 2009, 2010 and 2011 (Fig. 1). Registrations of pricklebacks and flatfish were logged in this study, but they were inconsistent and not suitable for prediction and extrapolation in space and were not included in further analysis.

Given preliminary results on the length distribution of fish items in the scats (see the Supplement), all potential prey species from the acoustic and benthic samplings were divided into different size classes in order to investigate potential size selection within a species. Two size classes were defined, respectively for specimens larger and smaller than 25 cm (the upper 99th percentile of fish length in the diet samples). In practice, only cod and haddock presented specimens belonging to the larger size class (>25 cm) and were therefore split into 2 size groups.

Data analysis

Individual movements and foraging behaviour of harbour seals

To estimate resource usage, movements and diving patterns of harbour seals were analysed to characterize the animals' behaviour and identify the locations used for foraging. First, switching state-space models (SSSMs) (*bsam* package, Jonsen et al. 2005, R Development Core Team 2014) were fitted, separately for each individual, and probability distributions of locations were obtained at regular time intervals (20 min). For each trajectory segment (time period within 2 successive animal locations), an animal's latent movement state was estimated as either transient or resident. Subsequently, the averages of dive characteristics (time diving or at the surface) and the presence of resting dives were estimated. Resting

dives were identified as those with a very slow and constant descent phase, as if driven by negative buoyancy and indicative of prolonged downward gliding (see Ramasco et al. 2014 for more detail). Animals were considered foraging during resident trajectory segments, unless these included a haulout event or had more than 50% of the time spent resting either at the surface or while diving. We selected the foraging segments that occurred within 2 mo periods centred on each of the 4 resource sampling dates (Table 1). Out of the 12 originally tagged individuals, only 10 had data falling within these periods and were used in the analysis.

Spatial and temporal dynamics of potential prey

The spatial distribution of the potential prey biomass sampled along the transects was predicted for the entire study area by means of regression kriging (RK) models (Hengl et al. 2007). A prediction grid was first constructed to limit the spatial extent of the area and to define the desired spatial resolution for the predictions (1 n mile²). For robust estimation of fish distribution outside the sampled areas (e.g. extrapolation to the fjord's edges), environmental variables were used to inform the predictive models. Estimates of bottom water temperature, salinity and tidal current speed were extracted from a hydrodynamic model of the fjord at the spatial resolution of the 1 n mile² prediction grid (Myksvoll et al. 2012). The model was run separately for the months of March, April and May 2009, and the 3 final prediction fields were averaged. Sea bottom depth values were predicted at the same spatial resolution by ordinary kriging from bathymetric measurements (Norwegian Mapping Authority, www.statkart.no/en/). Finally, the extent of the ice cover was mapped using daily satellite pictures of the fjord for the period December 2009 to May 2010 (courtesy of E. Malnes, NORUT, Tromsø).

The biomass densities (kg n mile⁻²) of potential prey (herring, capelin, sculpins, and the 2 size classes of cod and haddock, i.e. >25 and <25 cm) were extrapolated from the acoustic measurements along the transects for the entire study area from the environmental variables mentioned above, by means of RK. This method involves constructing a geostatistical model with both a deterministic and a stochastic component. The deterministic component of the model, a linear regression, was used to model the spatial variation in resource biomass related to the environmental variables, while the stochastic compo-

ment (an ordinary kriging model) was used to predict the residuals in space, using their spatial correlation structure. Visual exploration of the relationship between resource biomass and environmental variables showed a log linear relationship. Resource biomasses were thus log-transformed prior to RK (see the Supplement for more detail on the RK analysis). In RK, an iterative process is required for an unbiased estimation of the variance of the regression parameters (Hengl et al. 2003), but a single iteration has been reported to give satisfactory solutions, while greatly simplifying the analysis (Hengl et al. 2007). As a result, the simplified approach was chosen for this study. All geostatistical analyses were performed using the R package *gstat* (Pebesma & Wesseling 1998).

ment of the haulout sites. We defined resources as the biomass densities of potential prey present at any location in space, estimated by means of modelled distribution maps. We then built RSFs by relating resource usage, represented by the resource biomasses at the locations visited by the seals while foraging, to resource availability, represented by the resource biomasses at locations available to the seals (see Aarts et al. 2008). Specifically, we fitted logistic regressions to a binomial response u , taking the value of 1 for used locations and of 0 for available locations (Fig. 2). The set of telemetry observations, representing the used locations, can be seen as an inhomogeneous Poisson point process (IPP) in space, with rate λ_u (point density per unit surface, where u stands for usage) proportional to the unknown underlying spatial probability density function of usage (Aarts 2007) (see Fig. 2 right column plot). In order to evaluate selection as the disproportional usage of resources with respect to availability, the IPP of usage can be compared to a simulated IPP of availability, the rate of which can be constant in space or set as a function based on assumptions about the potentially unequal accessibility of different areas (Matthio-

Resource selection

We investigated the selection of resources for the different individual harbour seals at 2 spatial scales: a large scale, reflecting the selection of foraging areas within the entire fjord system, and a smaller scale, reflecting selection conditional to the place-

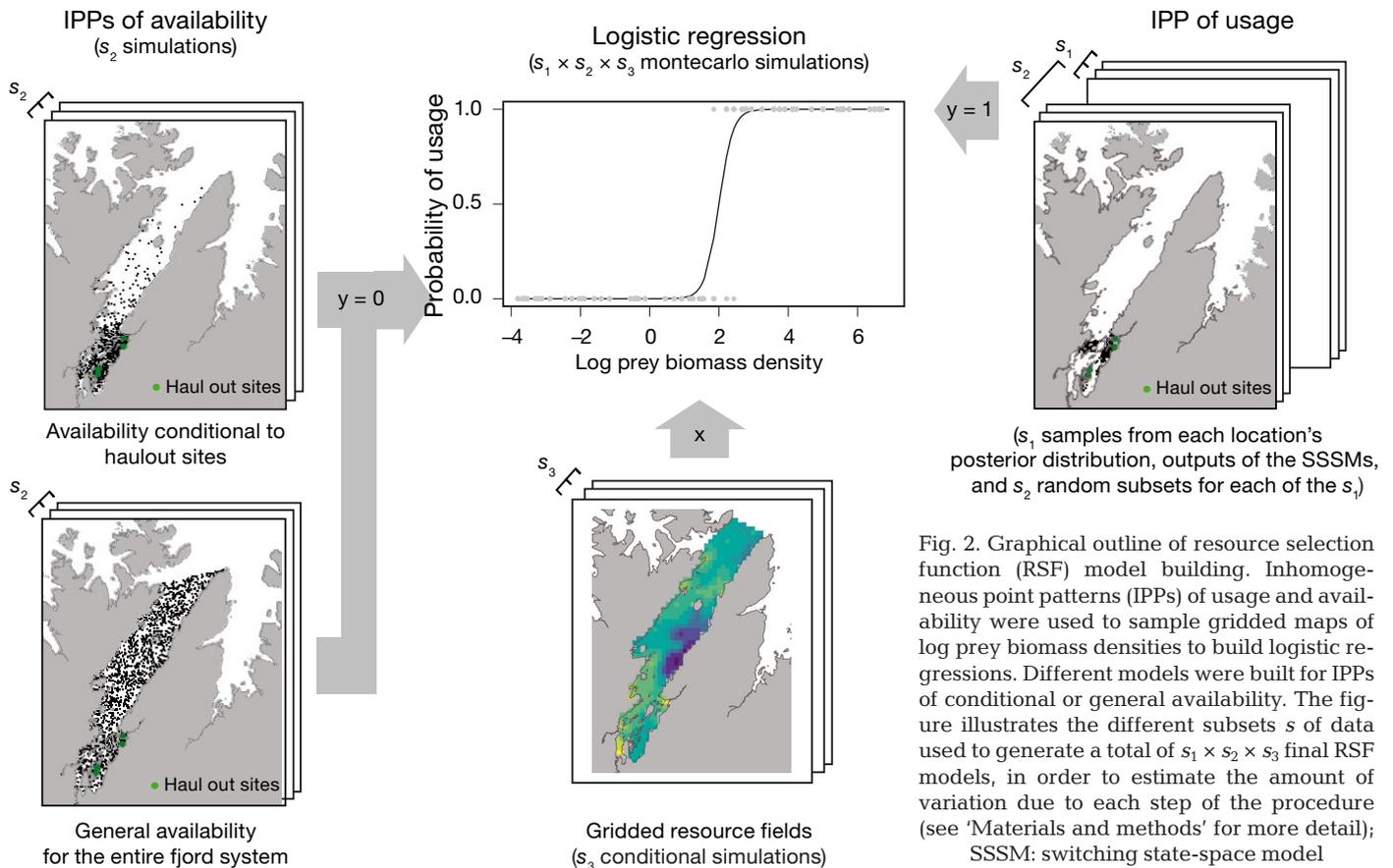


Fig. 2. Graphical outline of resource selection function (RSF) model building. Inhomogeneous point patterns (IPPs) of usage and availability were used to sample gridded maps of log prey biomass densities to build logistic regressions. Different models were built for IPPs of conditional or general availability. The figure illustrates the different subsets s of data used to generate a total of $s_1 \times s_2 \times s_3$ final RSF models, in order to estimate the amount of variation due to each step of the procedure (see 'Materials and methods' for more detail); SSSM: switching state-space model

poulos 2003). To estimate resource selection for the entire study area, we generated an availability IPP with constant density in space (Fig. 2, left column lower plot), while to estimate resource selection conditional to haulout site placement, we assumed accessibility to decrease with distance d_i from each haulout site i . In the latter case, the density of points λ_a per unit surface (where a stands for availability) of the simulated IPP was set to be proportional to an inverse power function of d_i (Matthiopoulos et al. 2004), weighted by x_{ji} the number of times each site was used (Fig. 2, left column upper plot):

$$\lambda_a \sim \sum_{i=1}^{i=N} x_i d_i^{-1.98} \quad (1)$$

Since the function was originally derived from a movement model for grey seals *Halichoerus grypus*, the range of distances obtained in the simulated point pattern was compared to the ones observed in this study to assess the validity of this function for harbour seals (see Fig. S2 in the Supplement). Different conditional IPPs were simulated for each of the 4 time periods (t), conditional to all haulout sites used by the individuals during each period. Both the general and conditional IPPs were simulated in the areas within the fjord accessible to the animals, delimited by the coastline and the ice edge (when present).

The obtained response variable u was then modelled as a Bernoulli process with probability h :

$$u \sim B(1, h) \quad (2)$$

$$h = \text{logit}^{-1}(\eta) \quad (3)$$

where the predictor η is a linear function of n resource covariates X :

$$\eta = \beta_1 X_1 + \beta_2 X_2 \dots + \beta_n X_n \quad (4)$$

and β are the selection coefficients. When $\beta > 0$, usage of a resource is expected to be proportionally higher than availability, representing positive selection, and vice versa.

RSFs were fit independently for the 4 time periods, since different individuals were followed during the different periods (Table 1). For each model (corresponding to a 2 mo period), a monthly factor was used to track potential finer-scale temporal changes in selection, due to large changes in area accessibility, caused by the relatively quick changes in ice extent. To allow selection to vary among individuals and months, each of the 4 models was fitted with a 3-way interaction term:

$$\eta = \beta X * \text{individual} * \text{month} \quad (5)$$

where X is the matrix of covariates and β the vector of selection coefficients. This setup allowed estimation of inter-individual variation, as well as comparison of selection at a seasonal (across models) and monthly (across factor levels) temporal scale.

Monte Carlo simulations were performed in order to estimate the variance of the selection parameters. The animal locations were characterized by observation errors, while resource distributions were characterized by prediction errors. The effects of the different error sources on the final selection parameters were estimated by simulating a series of datasets to which RSFs were fit. The following procedure was implemented identically for each time period t (see Fig. 2 and Table 2 for the definitions and values of the parameters mentioned in the following paragraph). To account for animal location error, s_1 random points were sampled from the locations' posterior distributions, the output of the SSSMs. To reduce the intrinsic autocorrelation among animal locations and approximate an IPP of independent points, s_2 random sets of points were subsampled among the ones being classified as foraging for each of the s_1 datasets. We thus obtained $s_1 \times s_2$ sets of usage points, each containing $p_u \times n_t$ points, where p_u is the selected number of used points ind.⁻¹ and n_t is the number of individuals followed during each time period t (Table 1). For each of the s_2 usage datasets, an availability dataset was simulated, consisting of a number of availability

Table 2. Definitions and values of the parameters used in building resource selection functions

Parameter	Description	Value
s_1	Number of random resampling of locations from posterior distribution	10
s_2	Number of random subsamples of used locations (classified as foraging) and of random simulations of availability samples	10
s_3	Number of resource prediction conditional simulations	10
p_u	Number of used points sampled per individual	200
p_a	Number of available points simulated per individual (a multiple of p_u)	$r p_u$
r	Proportion of availability points with respect to used points	2
t	Time period	1–4
n_t	Number of individuals per time period	3–5

points $p_a = r \times p_{ui}$, where r (the proportion of availability vs. used points) was chosen equal to 2 as suggested by Aarts et al. (2008). The usage and availability point datasets were used to sample the value of the resources at those locations. To account for the variability in resource predictions, s_3 possible realizations of resource density distributions were generated for each potential prey species by conditional simulation from their respective predictive models. To estimate the partial effects of the different sources of variance, models were fitted to all combinations of simulated datasets with a total number of Monte Carlo simulations = $s_1 \times s_2 \times s_3$. For some simulations (2% of the runs), the logistic regression models showed separation (Albert & Anderson 1984), although convergence was reached, implying a potential bias in the variance estimates of the parameters. The selection coefficient estimates of these outputs were excluded from the results.

Foraging response to changes in resource availability

The presence of a response in foraging behaviour to changes in resources was evaluated at the population level by assessing if changes in resource availability across time periods t would affect resource selection. We fitted linear regressions of the monthly selection coefficients, averaged across individuals and across the 1000 Monte Carlo simulation ($s_1 \times s_2 \times s_3$), against the mean resource availability per month ($n = 8$), both conditional and general, independently for each fish species analysed. A response was detected when the regression slope was significantly different from 0.

Differences in resource availability across the 4 sampling periods were dependent on the different distributions of prey and on ice extent for herring, capelin, cod and haddock. For the remaining species, shifts in availability over time were only based on the temporal changes in ice extent, since the biomass densities of these species were not resampled in different seasons.

RESULTS

Resource distribution and dynamics

The distribution of the harbour seals' potential prey species showed variability in both time and space (Fig. 3 and Fig. S3 in the Supplement). The highest biomass concentrations were found during summer and spring, while a general reduction in resource biomass was registered in winter. The back-transformed mean log biomass density summed for the

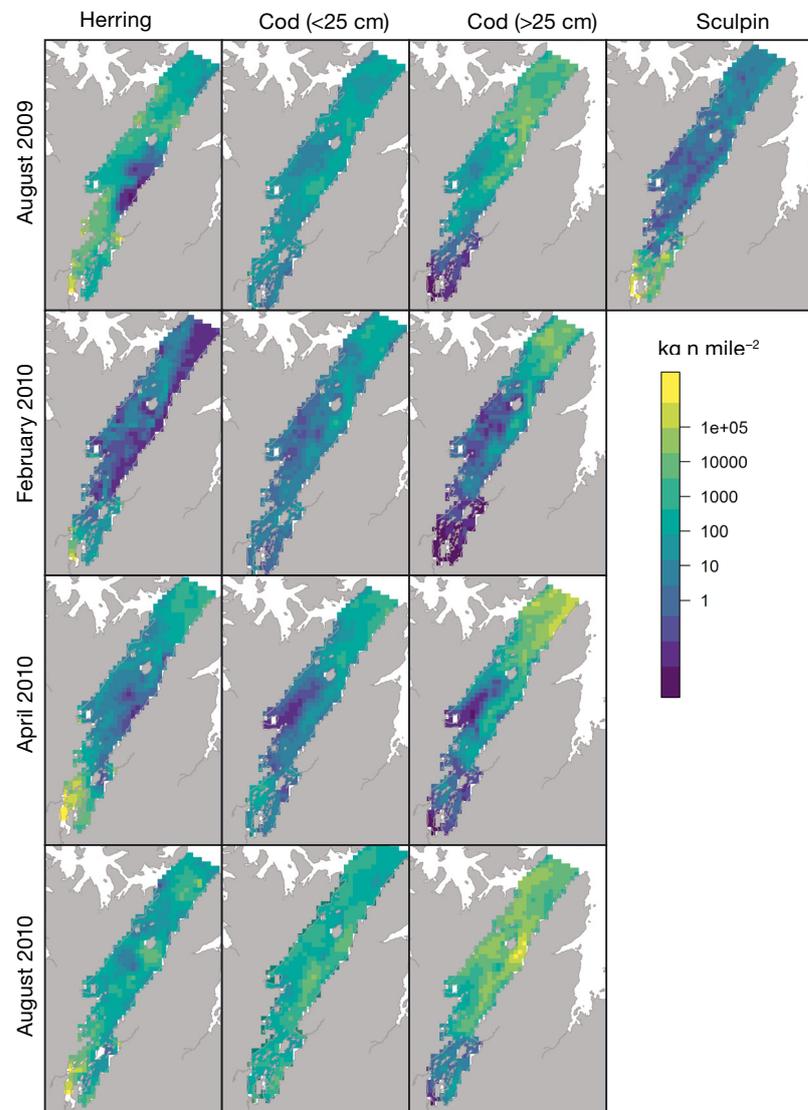


Fig. 3. Average prediction maps of biomass (colours, in log scale) of selected potential prey resources. For herring and the 2 size classes of cod (<25 and >25 cm), the distribution is shown for the 4 sampling periods (August 2009–August 2010). For sculpins, average annual predictions are shown. Maps of the potential prey not shown here (capelin, haddock <25 cm and haddock >25 cm) are presented in Fig. S3 in the Supplement at www.int-res.com/articles/suppl/m581p199_supp.pdf

pelagic and semi-pelagic fish species in the study area was $63 \text{ kg n mile}^{-2}$ in August 2009, 9 kg n mile^{-2} in February 2010, $77 \text{ kg n mile}^{-2}$ in April 2010 and $224 \text{ kg n mile}^{-2}$ in August 2010, indicating the presence of seasonal dynamics in resource density in the fjord. Cod and haddock (semi-pelagic species) showed high biomass concentrations in the outer areas, dynamically extending to the inner parts of the fjord depending on the season (see Fig. S4 for environmental variable distribution and Table S1 for the relationship between prey biomasses and environmental parameters in the Supplement). Concentrations of the small size class of codfish reached areas further in the fjord. Herring and capelin (small pelagic species) were concentrated in the inner cold water areas in winter and spring, but were more patchily distributed throughout the fjord in the summer season. Sculpins were highly

concentrated in the inner cold water areas of the fjord. The deterministic component of the RK models (linear regression between prey biomass and environmental variables) explained very little variance for the pelagic species, but was slightly better for the semi-pelagic and benthic species (see Table S1 for R^2 values). However, a high correlation was present between observed and predicted values (correlation range 0.66–0.92 depending on the species), indicating that the RK models were predicting well at the sampling locations.

Harbour seal movements and behaviour

From the analysis of harbour seal movements (SSSMs), 7–47% of the locations were classified as

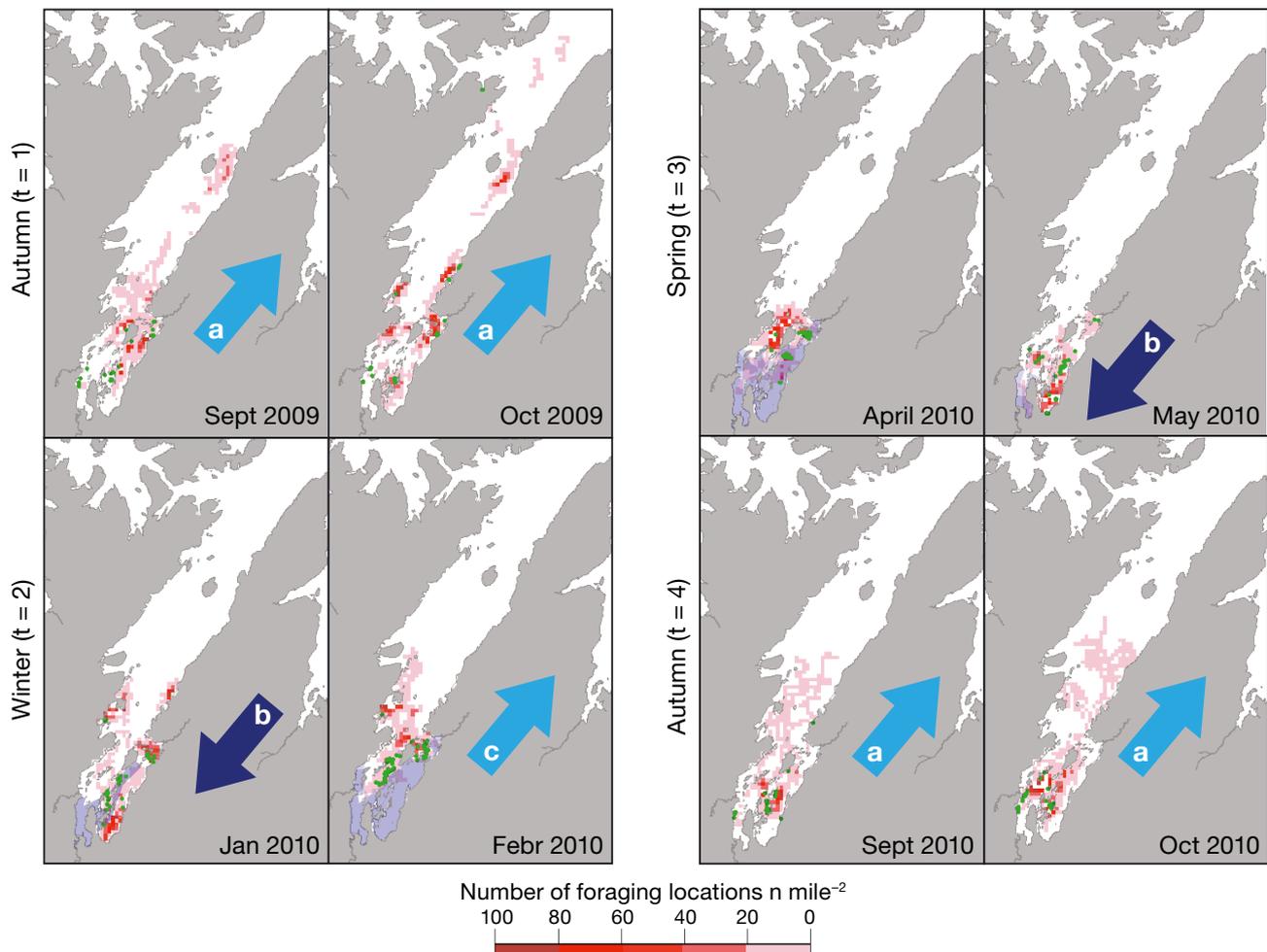


Fig. 4. Foraging intensity (number of foraging locations per n mile^2) of harbour seals *Phoca vitulina* ($n = 3-5$, see Table 1) for each month of the 4 periods analysed ($t = 1-4$). The extent of the average ice cover per month in winter and spring is shown as blue shading. The used haulout sites during each month are shown (green dots). Light blue arrows (a, c) indicate movements of haulout locations or trip direction towards the outside part of the fjord, dark blue arrows (b) towards the inside of the fjord

being in a transient movement state, and 53–93% in a resident movement state, depending on the individual. Among the points in the resident state, 57–81% were described as foraging behaviour, while the remaining were considered resting (either at the haulout sites or at sea). The tagged individuals used the inner parts of the fjord during all seasons, the middle part during autumn and winter, and performed occasional trips to the outer edges of the study area in autumn (Fig. 4). Changes in ice cover during late winter and early spring rendered large parts of the inner areas inaccessible, limiting the harbour seals' movements southwards. Usage was frequent along the ice edge during these periods, while a general tendency to expand the home range southwards was observed when ice was at a minimum (Fig. 5).

Resource selection

The resource selection coefficients at the population level (i.e. considering the parameter distributions across individuals and simulations) showed no distinctive pattern over time and across potential prey species at the small spatial scale (conditional to the placement of haulout sites), since the vast majority of the 95% confidence intervals of the coefficients overlapped 0 (Fig. S5 in the Supplement).

At the large spatial scale (i.e. of the entire study area), selection showed some degree of variation across seasons (Fig. 6). A general avoidance of the large size classes of codfish (>25 cm) was observed consistently across seasons, reflected by the means of the negative selection coefficients. Size selection was also confirmed in the harbour seal diet study (see the Supplement), where 99% of all specimens in the diet were below 25 cm. During autumn (September–October), harbour seals showed a tendency for increased preference for small cod (in both years) and small haddock (in 2010 only). These were the periods of peak fish biomasses, and both usage and availability of small codfish species were high. An opposite trend was found for capelin, with a slight avoidance in autumn. During early winter (January), no particular patterns of selection were evident. During late winter and early spring (February and April), when ice cover was at its maximum and resource availability at its minimum, the harbour seals appeared to prefer capelin and small haddock. The most significant changes occurred in late spring (May 2010) following ice retreat, with a sharp increase in both usage and preference of areas with higher biomass densities of

sculpins and pelagic species (herring and capelin). Despite a general high usage of areas with high densities of sculpins, in particular during spring and autumn 2010, there was a tendency to avoid sculpins at the small spatial scale, with negative coefficients on average. This indicates the non-preference for this species when choosing foraging locations relative to their availability from the haulout sites.

Although trends were evident, none of the patterns at the population level was significant. When partitioning the variance among the different sources of

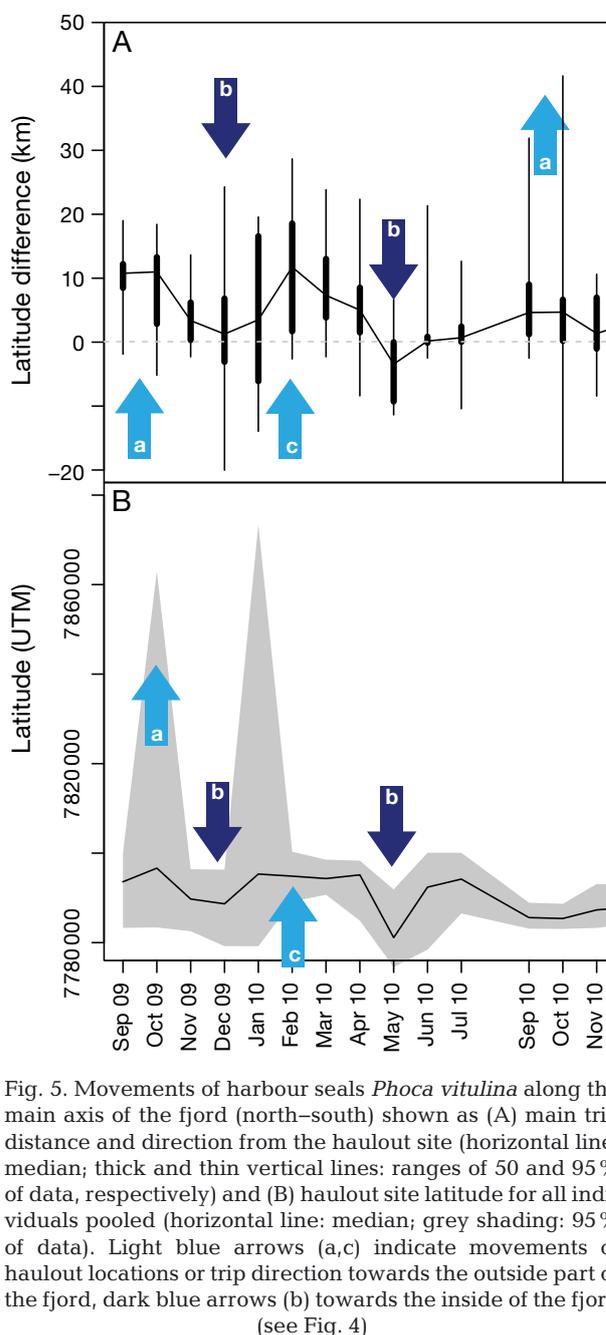


Fig. 5. Movements of harbour seals *Phoca vitulina* along the main axis of the fjord (north–south) shown as (A) main trip distance and direction from the haulout site (horizontal line: median; thick and thin vertical lines: ranges of 50 and 95% of data, respectively) and (B) haulout site latitude for all individuals pooled (horizontal line: median; grey shading: 95% of data). Light blue arrows (a,c) indicate movements of haulout locations or trip direction towards the outside part of the fjord, dark blue arrows (b) towards the inside of the fjord (see Fig. 4)

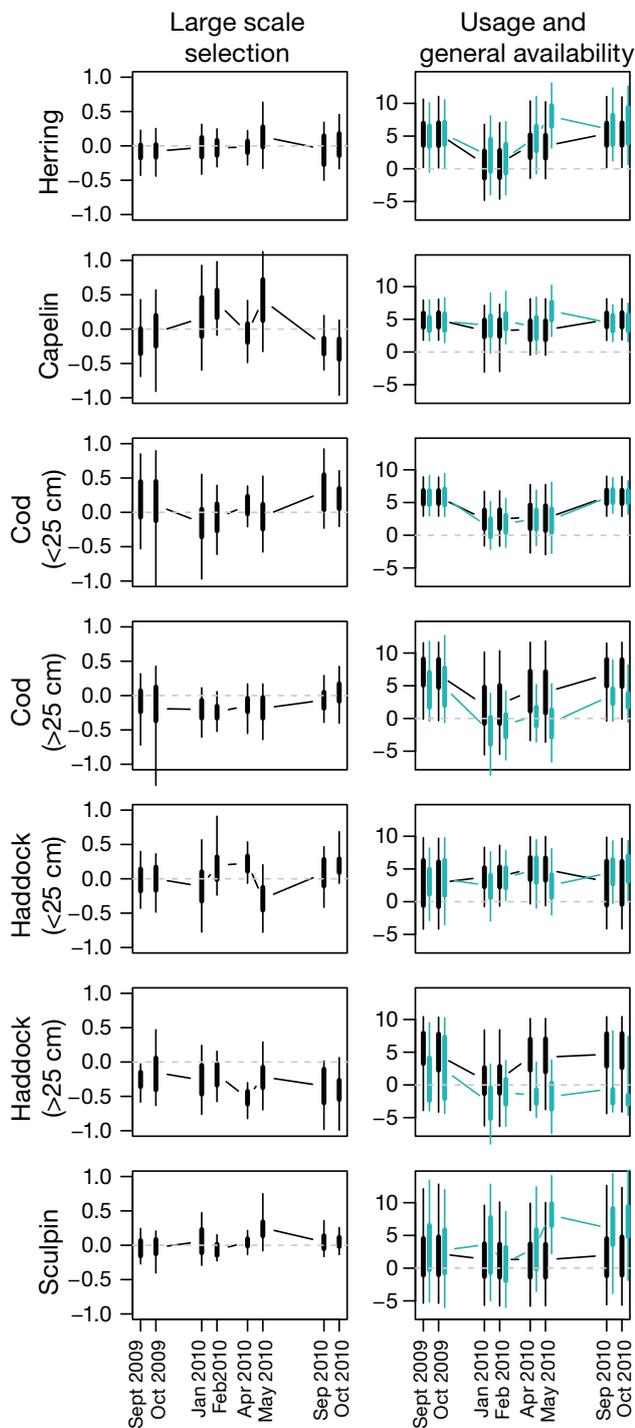


Fig. 6. Temporal patterns in large-scale resource selection (left column), and usage and general availability (black and green boxplots, respectively, right column). The boxplots show the range of the selection coefficients across individuals and simulations (thick and thin vertical lines: range of 50 and 95% of data, respectively). Positive and negative selection is represented by selection coefficient values above and below 0 (horizontal dashed line). While resource coefficients are unitless, resource usage and availability are expressed in log biomass (kg n mile^{-2})

variation, a difference of about 1 order of magnitude was found between the different sources, with the largest being associated with individual preferences (variance associated with individuals ~ 0.1 , resource predictions ~ 0.01 , subset selection ~ 0.001 , location error ~ 0.0001 , see Fig. S6 for individual coefficients and Fig. S7 for the partitioning of the sources of variance in the Supplement).

Foraging response to changes in resource availability

The changes in resource selection due to changes in conditional availability from the haulout sites were not significant for any potential prey species, since the slopes of the regressions were not significantly different from 0 (Fig. S8 in the Supplement). At the large scale, an increase in preference for small cod was found with the increase in their availability, while the opposite was found for capelin (Fig. 7). No changes in preference with availability were registered for sculpins across seasons. It should be noted, however, that the only source of variability in the availability of this resource across seasons was given by the changes in ice extent, since no seasonal estimates were available for this species.

DISCUSSION

Dynamics of resources in Porsangerfjord

The potential prey resources of harbour seals in Porsangerfjord displayed seasonal fluctuations in both biomass and distribution. Large codfish (>25 cm) were limited to the outer areas during winter and progressively extended into the fjord towards summer, most likely in association with the inflow of warmer Atlantic waters from the fjord's mouth, as suggested by its association with warmer and more saline waters (Table S1). The codfish present in the study area comprised both long-range migrant species (e.g. northeast Arctic cod and haddock), and resident local populations (e.g. coastal cod, Jakobsen 1987). Smaller codfish (<25 cm, 0-group) were distributed both in the outer areas and in areas further into the fjord, the latter being probably local coastal cod spawning in the fjord (i.e. Smørfjorden, see Myksvoll et al. 2012). Pelagic planktivorous fishes (i.e. capelin and herring) were found to have higher levels of aggregation in the inner coldwater areas during winter and spring, rather than in summer.

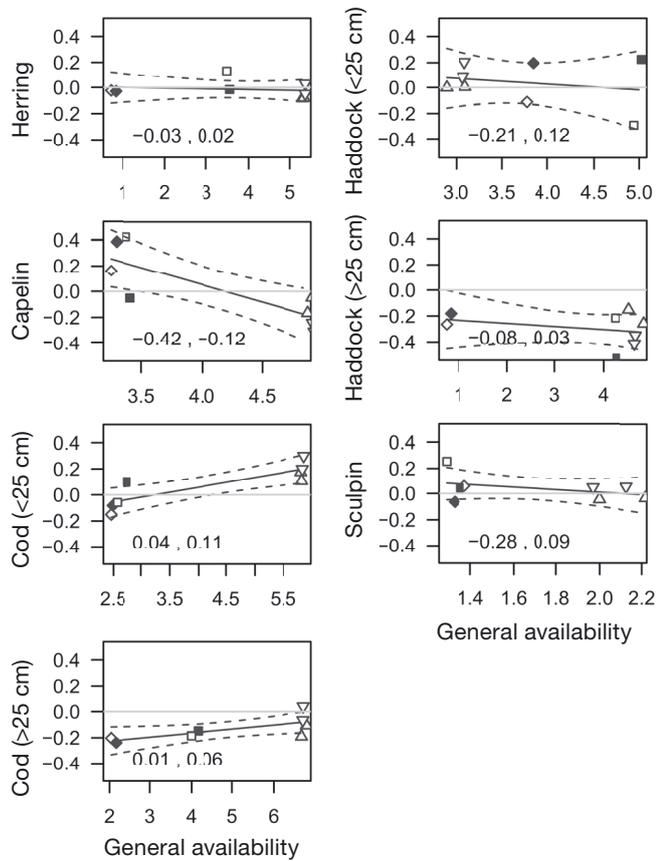


Fig. 7. Foraging response to changes in resource availability for the entire fjord area. Linear models were fit on the population's mean large-scale resource selection coefficients (y-axis) against the general prey availability (in log biomass density, kg n mile^{-2}) for each month during the 4 periods analysed (Δ : summer 2009; ∇ : summer 2010; \diamond : winter; \square : spring, black-filled when ice cover was large). The regression's 95% confidence bands (dashed lines) and the 0 line of no selection (grey line) are shown. The confidence intervals of each regression slope (CI slope) are shown at the bottom of each plot

The largest predictive errors for fish distribution were related to the presence of ice in the innermost areas of the fjord, which could not be sampled in winter and spring. Despite the use of RK, which generally improves extrapolation, it is likely that the biomass of pelagic fish overwintering in the vicinity of the ice was underestimated.

Harbour seal resource selection and response to resource changes

At the large spatial scale, the harbour seals in this study appeared to select areas with higher densities of either small-sized fish species (herring, capelin, sculpin) or small size classes of larger species (cod-

fish), depending on the season. In this study, the preference for smaller-sized fish was related to the differential size distribution of the fishes along the fjord, with the small size classes occurring further in and closer to the haulout sites. Grey seals are known to haul out and feed in the outer parts of the fjord (Nilssen & Haug 2007). Size selection in this area could be seen as a consequence of area selection due to interspecific competition. The preference of harbour seals for small fish specimens is widely acknowledged (mostly <30 cm, Olsen & Bjørge 1995, Tollit & Thompson 1996, Tollit et al. 1997, Berg et al. 2002, Andersen et al. 2004, Ramasco 2008), although some have argued for the selection of larger fishes within the young age classes available (Tollit et al. 1997, Brown et al. 2001). On the other hand, grey seals are known to generally feed on slightly larger size classes of codfish and herring (Bowen et al. 1993). A certain degree of niche partitioning on prey size is present between these seals, even though their diet overlaps to a wide extent in the targeted species. Competition between the 2 species exists for prey and haulout sites in some areas (Bowen et al. 2003, Duck et al. 2013), while spatial segregation in the usage of foraging habitats occurs in other systems (Jones et al. 2015). In Porsangerfjord, the 2 species do not compete for haulout sites, and their preferred resources show a good degree of spatial segregation, hence the overall competition is likely to be small, at the current population status.

In this study, harbour seals showed seasonal shifts in the large-scale selection patterns following the major movements of resource biomass in the fjord and their accessibility. In autumn and in the months with maximal ice coverage, a tendency to positive selection for small codfish was observed, while a strong preference for sculpins and pelagic forage fish emerged right before ice formation (capelin only) and after ice retreat (both capelin and herring). As previously mentioned, the biomass of overwintering pelagic fish species was likely underestimated in the inner deep basins, resulting in a possible undetected presence and high usage of herring during the winter months as well. The general interest in the resources located in the cold and ice-covered inner areas of the fjord was also reflected in the sharp southward shift in average haulout latitude and main trip direction both in December 2009 and May 2010, right before ice formation and after ice retreat, respectively (Figs. 4 & 5, pattern b). Additionally, the analysis of the response to changes in resource availability showed, at the large scale, an increase in preference for small cod with increased availability, and

the opposite trend for pelagic schooling fish (i.e. capelin), which were preferred when least abundant (Fig. 7).

Since total biomass seemed not to be driving the alternation between preference for codfish and pelagic fish, the question arises: What are the factors influencing this? Despite codfish having been documented to be a major component of the diet of harbour seals in many areas, the shift to preference for schooling prey has been seen in the areas and seasons when pulses of such resources occur (Pierce et al. 1991, Brown & Pierce 1998, Berg et al. 2002) or in relation to their energetic content (Thomas et al. 2011). In the Shetland Islands, adult herring are preyed upon during the summer months as they pass through the area on their annual spawning migration (Brown & Pierce 1998). In the Moray Firth, clupeids gather close to shore to overwinter (Pierce et al. 1991). In this area, large inter-annual variations in the concentration of pelagic schooling fish appear to drive the composition of the harbour seals' winter diet, as codfish are found to be part of the winter diet only in years of low clupeid abundance (Thompson et al. 1996).

In Porsangerfjord, pelagic forage fish did not have the highest total biomasses or the highest energetic values in winter and spring (Henderson et al. 1984, Mårtensson et al. 1996), when preferred by harbour seals, but showed the highest levels of aggregation when concentrating in cold waters to overwinter (see Fig. 3). We argue that aggregation was the factor most likely affecting the increased interest for the resources gathered in the ice-covered areas in the inner part of the fjord. A preference for certain distributional characteristics of prey (e.g. aggregation) rather than of the species itself has been suggested earlier for harbour seals (Tollit et al. 1997). Other predators have been found to respond rather to general characteristics of prey distribution than to the specific biomasses of single species (Benoit-Bird et al. 2013).

Herring have high aggregative behaviour when overwintering, in particular during daytime, when moving to deeper layers to avoid visual predators (Huse & Ona 1996, Huse & Korneliussen 2000). Ramasco et al. (2015) described a dominance of benthic foraging during daylight in winter and spring for the animals in this study, supporting the preference for aggregated schooling fish in these seasons. A similar pattern of increased benthic diving activity was found for harbour seals feeding on overwintering herring in the Moray Firth (Thompson et al. 1991). The presence of a high level of aggregation of prey, even though at depth, was in this case hypothesised

to be a factor of greater importance for the seals than accessibility of the prey from the surface, as previously described for other pinnipeds (Watanabe et al. 2003) or for harbour seals in other systems (Womble et al. 2014). In the inner part of the Porsangerfjord, depth is not a limiting factor with respect to the diving capabilities of the seals, because it is generally shallow (mostly <50 m).

Positive selection for sculpins was registered in the same periods as the preference for pelagic forage fish, due to the overlapping distribution of sculpins with pelagic fish in the inner cold areas of the fjord (Fig. 3). On the other hand, a slight avoidance of this prey species was registered at the small scale (Fig. S5). Preference for sculpins could therefore be an artefact of the increased usage of the areas with high density of highly aggregated, hence more profitable, prey. Sculpins generally have lower energetic density than pelagic fish (Ball et al. 2007), but they were present in high proportions and frequencies in the autumn diet of these seals (Fig. S1 in the Supplement), indicating a relatively high degree of predation on these fishes during this time of the year. Sculpins may therefore be opportunistically preyed upon because they are highly accessible in areas of preferred prey. This type of behaviour has been called 'incidental predation' and has been described in harbour seals foraging on flatfish in the UK (Hall et al. 1998).

Home range shifts with changes in resource availability

While a selection pattern appeared in the general resource use within the fjord, no clear preference was found conditional to the haulout placements (i.e. small spatial scale). This can be interpreted as harbour seals being opportunistic foragers at the level of individual trips from the haulout sites. This also indicates that shifts in large-scale preference were driven by shifts in haulout location and total trip distances (Fig. 5). In addition, the seals used the inner areas to a much wider extent than the outer areas of the fjord with the highest fish biomasses. A question that arises from these observations is: To what extent do suitable haulout sites and the changes in resource availability affect home range size and location, and trip direction?

Harbour seals select their haulout sites in the vicinity of their foraging areas to reduce the cost of swimming between foraging and resting areas (Bjørge et al. 1995). The selection of haulout sites is also af-

ected by the availability of suitable sites with respect to tides, exposure to weather, accessibility from and to the sea, disturbance, presence of conspecifics and predation risk (Da Silva & Terhune 1988, Grellier et al. 1996, Lesage et al. 2004). In this study, both home range size and location showed seasonal patterns (Figs. 4 & 5, patterns a–c). The tagged individuals foraged towards the outer areas during autumn by either increasing home range size, or in some cases by hauling out in the outer parts of the fjord, depending on the individual (Fig. 5, see the differences in pattern a between 2009 and 2010, different sets of individuals tagged). When ice extent increased, harbour seals showed a northward shift in both haulout placement and trip directionality (Fig. 5, pattern b), with an opposite trend when ice was at a minimum (pattern c). Other studies of harbour seals at high latitudes have reported that ice formation tends to hinder movements between feeding grounds and haulout sites; hence, the animals tend to expand their home ranges and exhibit a more offshore behaviour as ice forms (Lowry et al. 2001, Lesage et al. 2004, Bajzak et al. 2013, Blanchet et al. 2014). In Porsangerfjord, the haulout sites are moved northward and the ice does not prevent access to open water; therefore, the changes in home range size are most likely a reflection of the targeted resources.

The home range sizes observed were small compared to other regions, and the outer areas of the fjord were rarely used despite being fully accessible (i.e. well within the ranges of distances that the species can afford to travel, >500 km, Lowry et al. 2001). This suggests that the resources present in the inner areas are enough to support the population year round, at the present demographic state. A large increase in seal abundance would require movement to areas of higher prey concentrations, such as the outer regions of the fjord. This could be achieved either by increasing the travelling distances and energetic cost of foraging, or alternatively by moving the haulout sites north. Despite observing a certain degree of flexibility in haulout location in this area, historical observations suggest that the sites in the inner areas of the fjord have been used for many decades, indicating a high degree of site fidelity (Henriksen 1995), even during periods with large changes in codfish abundance (ICES 2013). This suggests that the seasonal shift between haulout sites, in response to resource changes, occurs within a limited set of suitable locations and that other factors play an important role in the choice of haulout area. The usage of a limited set of locations is likely aimed at increasing the probability of gathering with con-

specifics for socialization and to reduce predator risk (Da Silva & Terhune 1988). It is therefore probable that the animals will expand their individual home ranges, rather than moving their haulout sites to the outer parts of the fjord. This hypothesis can be supported by recent findings of the presence of different forms of resting behaviour at sea (Ramasco et al. 2014), which would allow the individuals to balance the costs of travelling further away from the haulout regions.

Methodological issues

The resource selection analysis in the present work was based on the methodological framework of spatial point process models (Aarts et al. 2012). An extension of this framework exists, able to model the temporal autocorrelation of the data as part of the selection process (i.e. space–time point processes, Johnson et al. 2013). These temporally dynamic models are of great interest when both the animal movements and the available resources are sampled in time at relatively high resolution, or when resources do not change. In the present study, resources were sampled at different points in time, and the RSF analyses were based on the assumption of the relative stability of the resource distribution during 2 mo periods around the sampling dates. This assumption, though based on field knowledge of the specific system, may be the cause of the lack of significant selection patterns at the small scale, which may have shown some degree of selection if the temporal resolution of the analysis had been higher.

In this study, the error associated with animal movement (i.e. GPS locations), which required a complex modelling framework to be accounted for (i.e. state-space models, Jonsen et al. 2013), was negligible compared with the other sources. A common methodological challenge and limitation in studies of animal foraging in the wild is, in fact, the resource sampling resolution, since current technology is able to provide high-quality animal movement data (Kuhn et al. 2015). Improvements in resource selection analysis should be addressed by increasing the precision in the distribution of resources. Our results, tracking the propagation of error in the analysis, support this view, with spatial prediction error in resources being one of the main measured sources of uncertainty in the selection coefficients (Fig. S7).

Prey selection in the marine environment is a 3-dimensional process, since different resources may be found at different depths. Integrating the vertical

dimension in future analysis of this dataset may therefore provide additional insight in the selection processes. Preliminary investigations on the vertical distribution of prey indicated the presence of complex dynamics in distribution (e.g. diel patterns and size-class vertical segregation), which should be investigated further and in conjunction with the seals' behavioural patterns. The results of the present work additionally suggest that harbour seals tend to respond to more generic prey characteristics rather than to prey species, such as size class, distribution characteristics and concentration thresholds. Further work is therefore suggested to investigate thresholds of aggregation (e.g. Piatt 1990), distance to haulout sites (or central place, as in Burke & Montevecchi 2009) and other distributional characteristics of prey determining the preference switches.

CONCLUSIONS

Harbour seals in Porsangerfjord exhibit prey size preferences by selecting foraging areas with the highest concentrations of small prey species or small size classes of larger fish species. They show a clear foraging response to the concentration of aggregations of pelagic schooling fish with predictable seasonal patterns (i.e. herring and capelin in winter and spring). A similar response has been described for harbour seals in an extensively studied population (i.e. the Moray Firth; Pierce et al. 1991, Thompson et al. 1996) and is argued to be a common driving factor, determining the shifts in harbour seal preference and consequently influencing the impact of this predator on alternative preferred prey, such as cod.

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LITERATURE CITED

Aarts G (2007) Modelling space-use and environmental preference from wildlife telemetry data. PhD dissertation, University of St. Andrews

- ✦ Aarts G, MacKenzie M, McConnell B, Fedak M, Matthiopoulos J (2008) Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* 31:140–160
- ✦ Aarts G, Fieberg J, Matthiopoulos J (2012) Comparative interpretation of count, presence-absence and point methods for species distribution models. *Methods Ecol Evol* 3:177–187
- ✦ Aarts G, Fieberg J, Brasseur S, Matthiopoulos J (2013) Quantifying the effect of habitat availability on species distributions. *J Anim Ecol* 82:1135–1145
- ✦ Albert A, Anderson J (1984) On the existence of maximum likelihood estimates in logistic regression models. *Biometrika* 71:1–10
- ✦ Andersen SM, Lydersen C, Grahl-Nielsen O, Kovacs KM (2004) Autumn diet of harbour seals (*Phoca vitulina*) at Prins Karls Forland, Svalbard, assessed via scat and fatty-acid analyses. *Can J Zool* 82:1230–1245
- ✦ Bajzak CE, Bernhardt W, Mosnier A, Hammill MO, Stirling I (2013) Habitat use by harbour seals (*Phoca vitulina*) in a seasonally ice-covered region, the western Hudson Bay. *Polar Biol* 36:477–491
- ✦ Ball JR, Esler D, Schmutz JA (2007) Proximate composition, energetic value, and relative abundance of prey fish from the inshore eastern Bering Sea: implications for piscivorous predators. *Polar Biol* 30:699–708
- ✦ Benoit-Bird KJ, Battaile BC, Heppell SA, Hoover B and others (2013) Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLOS ONE* 8:e53348
- ✦ Berg I, Haug T, Nilssen KT (2002) Harbour seal (*Phoca vitulina*) diet in Vesteralen, north Norway. *Sarsia* 87: 451–461
- ✦ Bergstad OA, Jørgensen T, Dragesund O (1987) Life history and ecology of the gadoid resources of the Barents Sea. *Fish Res* 5:119–161
- ✦ Beyer HL, Haydon DT, Morales JM, Frair JL, Hebblewhite M, Mitchell M, Matthiopoulos J (2010) The interpretation of habitat preference metrics under use-availability designs. *Philos Trans R Soc Lond B Biol Sci* 365:2245–2254
- ✦ Bjørge A, Thompson D, Hammond P, Fedak M and others (1995) Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway. *Dev Mar Biol* 4: 211–223
- ✦ Blanchet MA, Lydersen C, Ims RA, Lowther AD, Kovacs KM (2014) Harbour seal *Phoca vitulina* movement patterns in the high-Arctic archipelago of Svalbard, Norway. *Aquat Biol* 21:167–181
- ✦ Bodholt H, Nes H, Solli H (1989) A new echo-sounder system. *Proc Inst Acoust* 11:123–130
- ✦ Bowen D, Lawson JW, Beck B (1993) Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian Shelf. *Can J Fish Aquat Sci* 50:1768–1778
- ✦ Bowen D, Ellis S, Iverson S, Boness D (2003) Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *J Zool* 261:155–163
- ✦ Brown EG, Pierce GJ (1998) Monthly variation in the diet of harbour seals in inshore waters along the southeast Shetland (UK) coastline. *Mar Ecol Prog Ser* 167:275–289
- ✦ Brown EG, Pierce GJ, Hislop JRG, Santos MB (2001) Inter-annual variation in the summer diets of harbour seals *Phoca vitulina* at Mousa, Shetland (UK). *J Mar Biol Assoc UK* 81:325–337

- Burke CM, Montevecchi WA (2009) The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *J Zool* 278:354–361
- Da Silva J, Terhune J (1988) Harbour seal grouping as an anti-predator strategy. *Anim Behav* 36:1309–1316
- Duck CD, Morris CD, Thompson D (2013) The status of UK harbour seal populations in 2012. Species Committee on Seals (SCOS) Briefing Paper 13-03. www.smru.st-and.ac.uk/documents/1803.pdf
- Fernö A, Pitcher TJ, Melle W, Nøttestad L, Mackison S, Hollingworth C, Misund OA (1998) The challenge of the herring in the Norwegian Sea: making optimal collective spatial decisions. *Sarsia* 83:149–167
- Grellier K, Thompson PM, Corpe HM (1996) The effect of weather conditions on harbour seal (*Phoca vitulina*) haulout behaviour in the Moray Firth, northeast Scotland. *Can J Zool* 74:1806–1811
- Hall AJ, Watkins J, Hammond PS (1998) Seasonal variation in the diet of harbour seals in the south-western North Sea. *Mar Ecol Prog Ser* 170:269–281
- Henderson R, Sargent J, Hopkins C (1984) Changes in the content and fatty acid composition of lipid in an isolated population of the capelin *Mallotus villosus* during sexual maturation and spawning. *Mar Biol* 78:255–263
- Hengl T, Heuvelink GBM, Stein A (2003) Comparison of kriging with external drift and regression-kriging. ITC Tech Note. www.itc.nl/library/Papers_2003/misc/hengl_comparison.pdf
- Hengl T, Heuvelink GBM, Rossiter DG (2007) About regression-kriging: from equations to case studies. *Comput Geosci* 33:1301–1315
- Henriksen G (1995) Distribution, habitat use and status of protection of harbour seals *Phoca vitulina* and grey seals *Halichoerus grypus* in Finnmark, North Norway. *Fauna Norv Ser A* 16:11–18
- Huse I, Korneliussen R (2000) Diel variation in acoustic density measurements of overwintering herring (*Clupea harengus* L.). *ICES J Mar Sci* 57:903–910
- Huse I, Ona E (1996) Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring. *ICES J Mar Sci* 53:863–873
- ICES (International Council for the Exploration of the Sea) (2013) Cod in Subareas I and II (Norwegian coastal waters cod). Report of the ICES Advisory Committee. ICES, Copenhagen
- Jakobsen T (1987) Coastal cod in Northern Norway. *Fish Res* 5:223–234
- Jakobsen T, Ozhigin V (eds) (2011) *The Barents Sea: ecosystem, resources, management*. Tapir Academic Press, Trondheim
- Johnson DS, Hooten MB, Kuhn CE (2013) Estimating animal resource selection from telemetry data using point process models. *J Anim Ecol* 82:1155–1164
- Jones EL, McConnell BJ, Smout S, Hammond PS and others (2015) Patterns of space use in sympatric marine colonial predators reveal scales of spatial partitioning. *Mar Ecol Prog Ser* 534:235–249
- Jonsen ID, Flemming JM, Myers RA (2005) Robust state-space modeling of animal movement data. *Ecology* 86:2874–2880
- Jonsen ID, Basson M, Bestley S, Bravington MV and others (2013) State-space models for bio-loggers: a methodological road map. *Deep Sea Res II* 88-89:34–46
- Kuhn CE, Sterling JT, Zeppelin TK (2015) Linking northern fur seal behavior with prey distributions: the impact of temporal mismatch between predator studies and prey surveys. *Anim Biotelem* 3:26
- Lesage V, Hammill MO, Kovacs KM (2004) Long-distance movements of harbour seals (*Phoca vitulina*) from a seasonally ice-covered area, the St. Lawrence River estuary, Canada. *Can J Zool* 82:1070–1081
- Lowry LF, Frost KJ, Hoep JM, Delong RA (2001) Movements of satellite-tagged subadult and adult harbor seals in Prince William Sound, Alaska. *Mar Mamm Sci* 17:835–861
- Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) *Resource selection by animals: statistical analysis and design for field studies*. Kluwer, Dordrecht
- Mårtensson P, Lager Gotaas A, Norddy E, Blix A (1996) Seasonal changes in energy density of prey of Northeast Atlantic seals and whales. *Mar Mamm Sci* 12:635–640
- Matthiopoulos J (2003) The use of space by animals as a function of accessibility and preference. *Ecol Model* 159:239–268
- Matthiopoulos J, McConnell B, Duck C, Fedak M (2004) Using satellite telemetry and aerial counts to estimate space use by grey seals around the British Isles. *J Appl Ecol* 41:476–491
- McLoughlin PD, Morris DW, Fortin D, Vander Wal E, Contasti AL (2010) Considering ecological dynamics in resource selection functions. *J Anim Ecol* 79:4–12
- Myksvoll MS, Sandvik AD, Skarøhamar J, Sundby S (2012) Importance of high resolution wind forcing on eddy activity and particle dispersion in a Norwegian fjord. *Estuar Coast Shelf Sci* 113:293–304
- Mysterud A, Ims RA (1998) Functional responses in habitat use: availability influences relative use and trade-off situations. *Ecology* 79:1435–1441
- Mysterud A, Lian LB, Hjermand DØ (1999) Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter. *Can J Zool* 77:1486–1493
- Nilssen KT, Haug T (2007) Status of grey seals (*Halichoerus grypus*) in Norway. *NAMMCO Sci Publ* 6:23–31
- Olsen M, Bjørge A (1995) Seasonal and regional variations in the diet of harbour seal in Norwegian waters. In: Blix AS, Walloe L, Ulltang Ø (eds) *Whales, seals, fish and man*. Elsevier, Amsterdam, p 271–285
- Pebesma EJ, Wesseling CG (1998) Gstat, a program for geostatistical modelling, prediction and simulation. *Comput Geosci* 24:17–31
- Piatt JF (1990) The aggregative response of common murre and Atlantic puffins to schools of capelin. *Stud Avian Biol* 14:36–51
- Pierce GJ, Thompson PM, Miller A, Diack JSW, Miller D, Boyle PR (1991) Seasonal-variation in the diet of common seals (*Phoca vitulina*) in the Moray-Firth area of Scotland. *J Zool* 223:641–652
- R Development Core Team (2014) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Ramasco V (2008) *Habitat use and feeding behaviour of harbour seals in Vesterålen*. MSc thesis, University of Tromsø
- Ramasco V, Biuw M, Nilssen KT (2014) Improving time budget estimates through the behavioural interpretation of dive bouts in harbour seals. *Anim Behav* 94:117–134
- Ramasco V, Barraquand F, Biuw M, McConnell B, Nilssen KT (2015) The intensity of horizontal and vertical search in a diving forager: the harbour seal. *Mov Ecol* 3:15

- Thomas AC, Lance MM, Jeffries SJ, Miner BG, Acevedo-Gutiérrez A (2011) Harbor seal foraging response to a seasonal resource pulse, spawning Pacific herring. *Mar Ecol Prog Ser* 441:225–239
- Thompson PM, Pierce GJ, Hislop JRG, Miller D, Diack JSW (1991) Winter foraging by common seals (*Phoca vitulina*) in relation to food availability in the inner Moray Firth, N.E. Scotland. *J Anim Ecol* 60:283–294
- Thompson PM, McConnell BJ, Tollit DJ, Mackay A, Hunter C, Racey PA (1996) Comparative distribution, movements and diet of harbour and grey seals from Moray Firth, N. E. Scotland. *J Appl Ecol* 6:1572–1584
- Tollit DJ, Thompson PM (1996) Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. *Can J Zool* 74:1110–1121
- Tollit DJ, Greenstreet SPR, Thompson PM (1997) Prey selection by harbour seals, *Phoca vitulina*, in relation to variations in prey abundance. *Can J Zool* 75:1508–1518
- Watanabe Y, Mitani Y, Sato K, Cameron MF, Naito Y (2003) Dive depths of Weddell seals in relation to vertical prey distribution as estimated by image data. *Mar Ecol Prog Ser* 252:283–288
- Womble JN, Blundell GM, Gende SM, Horning M, Sigler MF, Csepp DJ (2014) Linking marine predator diving behavior to local prey fields in contrasting habitats in a subarctic glacial fjord. *Mar Biol* 161:1361–1374

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