THE DYNAMICS OF RESOURCE SELECTION OF HARBOUR SEALS IN A SUBARCTIC FJORD ECOSYSTEM

Ramasco V, Lindström U, & Nilssen KT

The dynamics of resource selection of harbour seals in a subarctic fjord ecosystem

Ramasco V[1*], Lindström U[1], Nilssen KT[1]

[1] *Institute of Marine Research, PoBox 6404, 9294 Tromsø, Norway*

5   *Corresponding author*: *virginie.ramasco@imr.no*

Abstract

Resource selection, the disproportional use of resources with respect to their availability, is a hierarchical, contextual and dynamic process. Selection can occur at different spatial and temporal scales, and can change over time with shifts in resource availability (*i.e.* functional response). The dynamic of resource selection was investigated for a resident harbour seals population in the Porsangerfjord, a subarctic fjord ecosystem with large seasonal fluctuations in resource distribution and abundance. 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, which could be restricted by the presence of sea ice during winter and spring. The seals foraging behaviour was investigated by assessing prey preference and the seals' behavioural response to the seasonal dynamics of prey distribution. The movement patterns of individual harbour seals (n = 10) were followed and foraging locations identified. The latter were then compared to the availability of potential prey species and size classes in the fjord. Results on the selection analyses suggested that harbour seals in Porsangerfjord had a preference for small size fish (< 25cm). Small codfish was 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 in these areas 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 and pelagic fish was preferred again. The results suggest preference for small aggregated fish close to the haulout areas and the presence of a response both in movements and haulout placement to changes in resource distribution.

Keywords: functional response, foraging, ice, preference, predation

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 chose 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 (Mysterud, Lian & Hjermann 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, that need to return to a fixed location (*e.g.* nesting birds), the placement of haulout sites is relatively dynamic for harbour seals (Lesage, Hammill & Kovacs 2004). As a result resource selection for this species can be seen as a hierarchical process operating mainly at two 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 two processes contribute to the selection of resources (see Mysterud *et al.* 1999) has not been assessed yet in seals.

Selection is also affected by the temporal dynamics of ecological processes, such as seasonal variation in resources, and may therefore 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 the constraints of the areas where the resources are located (Mysterud, Lian & Hjermann 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 therefore pointed out the importance of accounting for changes in resource availability in studies of selection (Aarts, Fieberg & Matthiopoulos 2012; Aarts *et al.* 2013; Johnson, Hooten & Kuhn 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 inhabiting the Barents Sea (Jakobsen & Ozhigin 2011). The seasonal dynamics of this system can be therefore strongly affected by drivers far outside the area. The fjord is characterized by the presence of cold Arctic deep basins in the southeastern 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 are known to 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*) are known to overwinter in the cold inner basins (Bergstad, Jørgensen & Dragesund 1987; Fernö *et al.* 1998; Jakobsen & Ozhigin 2011). A small population of currently about 200 harbour seals (KT Nilssen, Institute of Marine Research, IMR, unpublished results from 2013) is known to be resident in the fjord all year round. This partially enclosed but dynamic fjord ecosystem, subject to seasonal resource pulses and changes in environmental characteristics, offers therefore a favourable setting to study the foraging ecology of this species.

In this area harbour seals' resource selection 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 respectively in winter and spring. As a 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 therefore investigated selection at multiple spatial scales and assessed 1) resources selection conditional to the placement of the haulout sites; 2) general resources selection within the entire fjord system. We did so by fitting resource selection functions (RSF) comparing resource usage to its availability conditional to haulout sites and general for the entire fjord. We defined resources as the landscapes of harbour seals' potential prey characterizing locations in space. We therefore compared data on harbour seals individual movements to modelled biomass density maps of potential prey species. We

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then investigated changes in selection to assess the presence of a functional 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.

Material and methods

Data collection

To investigate the movements 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 position at intervals of minimum 20 min, together with dive profiles of 11 time and depth inflection points, equally spaced in time, and haulout registrations. Details on the animal catching and tagging procedures, and the tags' settings are provided in Ramasco Biuw & Nilssen (2014).

To map the spatial distribution of the resources potentially available to the seals in the study region, data on the biomasses of the fish species assumed to be potential prey were collected. The range of fish species to include in the analysis was restricted to the ones which had been observed to occur in harbour seals' diet either in literature or specifically in the results of a small diet investigation run in parallel to this study (see S1). Codfish (*Gadidae*), sandeel (*Ammodytes sp*), and small pelagic fishes, such as herring and capelin (*Mallotus villosus*), have been reported as being the most frequent components of harbour seal diet in Norwegian and adjacent waters (Olsen & Bjørge 1995; Berg, Haug & Nilssen 2002; Andersen *et al.* 2004); sculpins (*Cottidae*), pricklebacks (*Stichaeidae*) and flatfishes (*Pleuronectidae*) were additionally found to be largely present in the diet of harbour seals in this area (S1); and salmon (*Salmo salar*) has been registered occasionally in the diet of harbour seals (Middlemas *et al.* 2006).

The biomass density distribution (kg/nm^2) of the following fish species was therefore collected: cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), herring, capelin, and sculpins. The distributions of the semi-pelagic (codfish) and pelagic fish species were assumed to vary in time and were therefore surveyed using standard acoustic fish abundance methods (Bodholt, Nes & Solli 1989) during 4 periods, along

predefined transects, respectively during August 2009, February 2010, April 2010 and
August 2010 (Table 1). The sampling consisted in continuous boat-based acoustic
measurements integrated at each 1 nm of transect and scaled by the catches at pelagic
and benthic trawl stations (Figure 1, see S2 for specifications on biomass estimation
from acoustic measurements). During acoustic sampling sandeel and saithe (*Pollachius
virens*) were also caught, but the first occurred in the samples only during one season,
and, the second only at few stations each season. Despite considering these as potential
prey for harbour seals, they were not included in further analysis.

The biomass density (kg/nm^2) of sculpins was obtained from a study on benthic
epifauna in the area (Lis Jørgensen, IMR, unpublished results). The epibenthic fauna 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 (Figure 1). Registrations of pricklebacks and flatfish were present in this study
but inconsistent and did not seem suitable for prediction and extrapolation in space.
These prey groups were therefore not included in further analysis.

Given preliminary results on the length distribution of fish items in the scats (see
S1), 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 99 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 in two groups.

Data analysis

Harbour seals' individual movements and foraging behaviour

To estimate resource usage, harbour seals movements were analysed to
characterize the animals' behaviour and identify the locations used for foraging.
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), the animals' latent

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movement state was estimated as either transient or resident. The average dive

160   characteristics (time diving or at surface) and the presence of resting dives (see Ramasco *et al.* 2014) were estimated. 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 surface or while diving. The foraging segments included in the two-months periods closest to each of the 4 resource sampling dates were then

165   selected (Table 1). Out of the 12 originally tagged individuals, only 10 had data falling within these periods and were therefore retained for further analysis.

Spatial and temporal dynamics of potential prey

    The spatial biomass density distribution of the sampled potential prey was predicted for the entire study area. A prediction grid was first constructed to limit the

170   spatial extent of the area and to define the desired spatial resolution for the predictions (1 nm^2). For a more 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, run for the months of

175   March, April and May 2009 (Myksvoll *et al.* 2012). The mean of these variables was then computed for the three-months period at the spatial resolution of the prediction grid. Sea bottom depth values were predicted at the same spatial resolution by ordinary kriging from bathymetric measurements (Norwegian Mapping Authority, http://www.statkart.no/en/). Finally, the extent of the ice cover was mapped using

180   daily satellite pictures of the fjord for the period December 2009 - May 2010 (courtesy of Eirik Malnes, NORUT, Tromsø).

    The biomass density distributions (kg/nm^2) of potential prey (herring, capelin, sculpins, and the two size classes of cod and haddock, respectively > and < 25 cm) was modelled from the environmental variables mentioned above, by means of regression

185   kriging (RK, Hengl *et al.* 2007). This method consists in 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 variation in resource biomass related to the environmental variables, while the stochastic component (an ordinary kriging model) was used to predict the residuals in space, using

190   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 S3 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, Heuvelink & Stein 2003), but a single

195   iteration has been reported to give satisfactory solutions, while greatly simplifying the analysis (Hengl, Heuvelink & Rossiter 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).

       Two additional resource variables were computed as respectively an index of the

200   potential presence of salmon and the abundance of cod juveniles (0 – 2 years of age) in the sublittoral zone (5-20 m). The first index reflected the distance from the major salmon river estuaries (Lakselv, Børselv and Stabburselv, Figure 1) and was computed as a 2 levels factor (1: distance ≤ 2 km and 0: distance > 2 km). The abundance of cod juveniles was obtained through a predictive model from a parallel study in

205   Porsangerfjord, indicating a positive non-linear relationship between macroalgal coverage and juvenile cod abundance mediated by depth (courtesy of Pedersen T and Michaelsen C, see S4). Macroalgal coverage (%) in sublittoral areas was predicted from data sampled at stations along the fjord and from environmental covariates (see S4). The biomass density of cod juveniles (kg/nm^2) was then estimated by fitting the cod

210   model with respectively the predictions of macroalgal coverage and bottom depth values.

Resource selection

       We investigated the selection of resources for the different individual harbour seals at two spatial scales: a large scale, reflecting the selection of foraging areas within

215   the entire fjord system, and a smaller scale, reflecting selection conditional to the placement of the haulout sites. We built resource selection functions (RSF), which relate resource usage, represented by the seals' use of space while foraging, to resource availability, estimated by means of distribution maps of their potential prey (see Aarts *et al.* 2008). Specifically, we fitted logistic regressions to a binomial response *u*, taking the

220   value of 1 for used locations and of 0 for available locations (Figure 2). The set of

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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 Figure 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 (Matthiopoulos 2003). To estimate resource selection for the entire study area we generated an availability IPP with constant density in space (Figure 2, left column lower plot), while to estimate resource selection conditional to haulout sites 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_i, the number of times each site was used (Figure 2, left column upper plot):

$$\lambda_a \sim \sum_{i=1}^{i=N} x_i \, d_i^{-1.98}. \tag{1}$$

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 (S5). Different conditional IPPs were simulated for each time period (t), conditional to the specific 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:

$$u \sim B\,(1, h), \tag{2}$$

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

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

$$\eta = \beta_1 X_1 + \beta_2 X_2 \ldots + \beta_n X_n \tag{4}$$

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 of the two-months periods, a monthly factor was used to track potential fine scale temporal changes in selection, due to changes in area accessibility caused by the variation of ice coverage. To allow selection to vary among individuals and months, models were fitted with a 3-ways interaction term:

$$\eta = \boldsymbol{\beta X} * individual * month \tag{5}$$

where $\boldsymbol{X}$ is the matrix of covariates and $\boldsymbol{\beta}$ the vector of selection coefficients. This setup allowed estimating inter-individual variation, as well as comparing selection at a large (seasonal) and small (monthly) 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 by prediction errors. The effect 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 Figure 2 and Table 2 for the definition and value 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, 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 $s_1 * s_2$ sets of usage points, each containing $p_u * n_t$ points, where p_u is the selected number of used points per individual 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 $p_a = r * p_u$ points, 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 = $s_1 * s_2 * s_3$. For some

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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.

Functional response to changes in resource availability

The presence of a functional response in resource selection was evaluated at the population level by comparing changes in selection to changes in availability across time periods *t*. We modelled the changes in RSFs selection coefficients against the changes in the conditional and general availability of resources across time independently for each fish species analysed. We fitted linear regressions of the monthly selection coefficients, averaged across individuals and across the 1000 Monte Carlo simulation ($s_1 * s_2 * s_3$), against the mean availability per month (n = 8). A functional response in resource selection is present when the regression slope is significantly different from zero.

Changes in resource availability were estimated across the 4 sampling periods and depending on ice extent for herring, capelin, cod and haddock. For the remaining species, shifts in availability were estimated only based on the changes in ice extent along time, since these species were not resampled in different seasons. The index for salmon showed very little differences in availability along time, therefore a functional response for salmon was not estimated.

Results

Resource distribution and dynamics

The distribution of the harbour seals' potential prey species showed variability in both time and space (Figure 3 for selected species and S6 for the remaining ones). The highest biomass concentrations were found during summer and spring, while a general reduction in resource biomasses was registered in winter. The back transformed mean log biomass density cumulated for the pelagic and semi-pelagic fish species in the study area was 63 kg/nm^2 in August 2009, 9 kg/nm^2 in February 2010, 77 kg/nm^2 in April 2010, and 224 kg/nm^2 August 2010, indicating the presence of seasonal dynamics in resource density in the fjord. The semi-pelagic species (cod and haddock) showed high

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biomass concentrations in the outer areas, dynamically extending to the inner parts of the fjord depending on the season, showing a positive relationship with temperature, depth, current and, for the large size class, salinity (see S7 for environmental variable distribution and S8 for the RK model parameters). Concentrations of the small size class of codfish reached areas further in the fjord. The small pelagic species (herring and capelin) were most abundant in the inner Arctic areas in all seasons, but were more patchily distributed throughout the fjord in the summer season. Sculpins were highly concentrated in the inner parts of the fjord. Both small pelagic species and sculpins showed positive association with number of days of ice cover (see S8). The deterministic component of the RK models (linear regression between prey biomass and environmental variables) explained very little variance for the pelagic species (adjusted R^2 herring = 0.13, capelin = 0.06), but was slightly better for the semi-pelagic (adjusted R^2 cod <25 cm = 0.20, cod >25 cm = 0.50, haddock <25 cm = 0.34, haddock >25 cm = 0.54) and benthic species (adjusted R^2 sculpins = 0.59, see S8). However, a high correlation was present between observed and predicted values (corr range 0.66 – 0.92 depending on the species), indicating the RK models were predicting well at the sampling locations. The highest densities of macroalgae (see S4) were found in the fjord's outer edges, but medium densities were found over wide areas in the inner western part of the fjord and in the middle along the eastern coast. Cod juveniles, being related to medium coverage, were therefore predicted to be abundant in these areas (Figure 3). The predictive model for macroalgal coverage, however, performed poorly (corr. predicted and observed values = 0.20), suggesting the derived predictions of cod juvenile densities should be interpreted with care.

Harbour seals movements and behaviour

From the analysis of harbour seals movements (SSSMs), between 7 and 47 % of the locations were classified as being in transient movement state, and 53 – 93 % in resident movement state, depending on the individual. Among the points in 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 (Figure

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4). Changes in ice cover during late winter and early spring rendered large parts of the
345   inner areas inaccessible, limiting the harbour seals movements southwards. Usage was
however 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 (Figure
5).

Resource selection

350   The resource selection coefficients at the population level (*i.e.* considering the
parameters distribution of all individuals and simulations) showed no distinctive
pattern along time and across potential prey species at the small spatial scale
(conditional to the placement of haulout sites). The vast majority of the 95% confidence
intervals of the coefficients in fact overlapped zero and the coefficients' variance was
355   larger than any of the changes along time (Figure 6). At the scale of the entire study area
(*i.e.* large spatial scale), a general avoidance of the large size classes of codfish (>25 cm)
was observed consistently across seasons, reflected by the negative selection
coefficients' means. A general avoidance of the river estuaries at any time period was
observed at both spatial scales analysed (*i.e.* consistently negative coefficients for
360   salmon).

At the large spatial scale, selection showed some degree of variation across
seasons. During autumn harbour seals showed a tendency to increase 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.
365   An opposite trend was found for capelin, with a slightly negative preference in autumn.
During early winter 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
370   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 of avoidance of sculpins at the
small spatial scale, with negative coefficients on average. This indicates the non

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375   preference for this species when choosing foraging locations relative to their availability
from the haulout sites.

Although some trends in the coefficients were evident, the large variance in the
population estimates did not allow finding patterns with strong significance. When
partitioning the variance among the different sources of variation, a difference of about
380   one order of magnitude was found between the different sources, with the largest one
being associated with individual preferences (variance associated to individuals ~ 0.1,
resource predictions ~ 0.01, subset selection ~ 0.001, location error ~ 0.0001, see S9 for
individual coefficients and S10 for the partitioning of the sources of variance).

Functional response to changes in resource availability

385   The functional response in resource selection due to changes in conditional
availability from the haulout sites was not significant for any potential prey species,
since the slopes of the regressions were not significantly different from zero (Figure 7).
At the large scale, a positive functional response was found for small cod and a negative
response was found for capelin.

390   **Discussion**

The dynamics of resources in Porsangerfjord

The harbour seals' potential prey resources in Porsangerfjord displayed seasonal
fluctuations in both biomass and distribution. The lowest total biomasses were observed
in winter, with a gradual increase throughout spring and summer for all species
395   analysed. Large codfish (> 25 cm) was 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 (S8). The codfish present in the study
area comprises both long-range migrant species (*e.g.* North East Arctic cod and
400   haddock), and resident local populations (*e.g.* Coastal cod, Jakobsen 1987). The long-
range migrants spawn along the coast of Norway, mostly below 68-69°N (Bergstad,
Jørgensen & Dragesund 1987), and to some extent along the coast of Finnmark (Sunnanå
K, IMR, pers. comm.). In summer they migrate towards feeding grounds following the

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Norwegian coastal current either to the open Barents Sea or into the fjords (Bergstad, Jørgensen & Dragesund 1987). Smaller codfish (< 25 cm, 0-group codfish) was distributed both in the outer areas and in areas further into the fjord, the latter being probably a result of larval drifting southward from local spawning areas in middle of the fjord (*i.e.* Smørfjorden, see Myksvoll *et al.* 2012). The Arctic inner parts of the fjord showed high densities of sculpins. The areas within the innermost fjord sill (see Figure 1) are in fact known to host a productive environment with high biomasses of benthic organisms (Fuhrmann *et al. submitted*). High densities of pelagic planctivorous fish (*i.e.* capelin and herring) were found mainly in the inner Arctic areas during winter and spring, but were distributed throughout the fjord during summer. Juvenile herring is in fact known to enter the fjords of northern Norway in the autumn, overwinter in cold waters, and emigrate the following spring (Fernö *et al.* 1998; Jakobsen & Ozhigin 2011). Overwintering in cold water is assumed to be a strategy for energy saving and predator avoidance when foraging is at its lowest (Huse & Ona 1996).

In general, the spatial predictions of the semi-pelagic (*i.e.* codfish) and benthic fishes (*i.e.* sculpins) were better compared to pelagic species (*i.e.* herring and capelin). This was also true within the different size classes of the same species, since the 0- and 1-group of codfish (< 25 cm), which were less well predicted than the larger size class, are mostly pelagic (Bergstad, Jørgensen & Dragesund 1987). This is likely due to the expected higher temporal and spatial variability in biomass of fish species in the pelagic environment with respect to bottom dwelling ones (Bjørkvoll *et al.* 2012). The less good model fit of the pelagic species suggests that either important predictors were missing (*e.g.* chlorophyll concentration) or that the temporal resolution of the hydrographical variables, which were not sampled simultaneously as the fish biomasses, was too coarse. In addition, the largest predictive errors for fish distribution were related to the presence of ice in winter and spring, which prevented form sampling in the innermost areas. Despite the use of regression kriging, which generally improves extrapolation, it is therefore likely that the biomass of pelagic fish overwintering in the vicinity of the ice was underestimated. Data sampled during winter and spring previous to this study period (February and May 2009), when the inner parts of Porsangerfjord were free of ice, revealed high densities of herring and capelin in the deep Arctic basins in the inner

435   eastern part of the fjord (Lindström U, IMR, & Pedersen T, University of Tromsø, UiT, unpublished results).

Resource selection at multiple spatial scales

The harbour seals' in this study appeared to select, at the large spatial scale, areas with higher densities of either small sized fish species (herring, capelin, sculpins) or small 440   size classes of larger species (codfish), depending on the season. In contrast, no clear preference was found when considering the use of resources with respect to their availability conditional to the haulout sites (*i.e.* selection at the small spatial scale). This can be interpreted as harbour seals being opportunistic feeders at the level of individual trips from the haulout sites, but selective in the location of their home range within the 445   fjord.

Several studies have shown that harbour seals prefer to feed on small fish specimens (mostly < 30 cm, Olsen & Bjørge 1995; Tollit & Thompson 1996; Tollit, Greenstreet & Thompson 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 450   available (Tollit, Greenstreet & Thompson 1997; Brown *et al.* 2001). In this study the preference for smaller size 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. All individuals tagged in this study foraged primarily in the inner parts of the fjord, where the larger size classes of codfish did not occur. Size selection was also 455   confirmed in the harbour seal diet study (S1), where 99% of all specimens in the diet were below 25 cm.

At the large scale, a positive selection for sculpins was found in late spring as a consequence of the high usage of the inner Arctic areas, where benthic prey is abundant. This prey was however slightly avoided at the small spatial scale. This may indicate that 460   the large scale preference for sculpins was an artefact of the increased usage of the areas with high density of other preferred prey (*i.e.* herring and capelin). Sculpins have in fact generally lower energetic density value compared to pelagic fish (Ball, Esler & Schmutz 2007). However, sculpins were found in high proportions and frequencies in the autumn diet of harbour seals in the fjord (see S1), suggesting a relatively high degree of 465   predation on these fishes. Additionally, the lipid content of pelagic fish decreases

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drastically during winter and spring (January - April) due to the combined effect of reduced feeding and increased energy usage in relation to spawning (Henderson, Sargent & Hopkins 1984; Mårtensson *et al.* 1996). We therefore suggest the possibility that sculpins in Porsangerfjod are used opportunistically as incidental prey (as described for harbour seals and flatfish in the UK, Hall *et al.* 1998), because these are highly accessible in areas of other preferred prey, such as pelagic schooling fish. Moreover, since the latter are preferred in a period of relatively low energy density, we argue that their distributional characteristics, such as their high aggregative behaviour in winter and spring, may play a role in their preference. Such a hypothesis should be investigated further.

While our results indicate that harbour seals prey on both benthic and pelagic species in the same season (see also, Ramasco *et al.* 2015), other studies have suggested the presence of a seasonally dominant strategy (either benthic or pelagic) depending on the main preferred prey (Tollit, Greenstreet & Thompson 1997). Selection in this study was estimated by the comparison of the location of foraging areas and biomass density fields of potential prey. It should therefore be remembered that these data did not provide information on the actual prey selection among the ones encountered at the foraging patch (*e.g.* herring vs. sculpins). To gain better understanding on the extent of benthic and pelagic foraging and on other responses to the vertical migration of fishes (*e.g.* due to daylight or season), resource selection patterns of harbour seals should therefore be explored in 3 dimensions by including the vertical perspective.

The resource selection analysis in this study did not account for all the spectrum of potential prey available in the area. The diet study (S1) suggests in fact that harbour seals in Porsangerfjord fed on more species than the ones accounted for in this study, such as saithe, flatfish and pricklebacks, which were not possible to estimate robustly by acoustic methods.

Large biomasses of saithe were measured in the trawl samples (IMR, unpublished results), but could not be used for extrapolation in space. Saithe is a relatively fast swimming codfish and is known to avoid trawls, thus being often underestimated (Godø, Somerton & Totland 1999). In addition, beach seine data from the area have shown large quantities of juvenile saithe in the sublittoral zone (IMR, unpublished results). A few specimens of saithe were found in the diet of harbour seals in Porsangerfjord, but the

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majority of the codfish specimens was not identified at finer taxonomic resolution, due to otolith degradation (see S1). The proportion of the different species of codfish in the diet of this seal population is therefore unknown, but previous studies in other areas along the coast of Norway have shown that harbour seals may feed extensively on small size classes of saithe (Berg, Haug & Nilssen 2002; Ramasco 2008).

Flatfish was found to be abundant in the middle and outer parts of the fjord at depths > 50 m (IMR, unpublished results). Flatfish has been recorded occurring in the harbour seal's diet in other areas (*e.g.* Härkönen 1987; Pierce *et al.* 1991), but never as a preferential prey, and some species have been recorded having a seasonal appearance in the diet in association with their migration to shallower waters for spawning (Hall, Watkins & Hammond 1998). The middle and outer parts of Porsangerfjord were not extensively used by the tagged seals therefore a general preference for this prey type can be disregarded in this study. Pricklebacks were mostly registered in the inner parts of fjord, in the shallower western areas. Foraging on this prey group may therefore be assumed to occur during the seasons when the inner areas are free of ice cover and highly used.

Among the total number of fish items analysed in the harbour seals' diet investigation for this area (S1), 76 % were included as potential prey species in this study. This suggests that, despite the impossibility of covering the complete spectrum of potential prey species in this study, the results included the main fish species eaten by harbour seals in the fjord.

The harbour seals' response to changes in resources availability and distribution

The analysis of large scale selection patterns in time revealed seasonal shifts following the major movements of resource biomass in the fjord. The largest shifts in preference occurred between the autumn and the remaining seasons, and within the winter and spring seasons, between the months with respectively low and high ice coverage. In the autumn months and in the months with maximal ice coverage (*i.e.* late winter and early spring) a tendency to positive selection for small codfish was observed, while after ice retreat a strong preference for pelagic forage fish and sculpins emerged.

A high variance was registered in the confidence intervals for the selection coefficients resulting in few significant selection patterns at the population level.

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Differences in individual preferences were found to be the major source of variance in the population parameters (see S9 and S10). However the largest source of variation attributable to uncertainty in the data was the prediction error of the resource distributions. Improvements in resource selection analysis should therefore be addressed by increasing the precision in the distribution of resources, for example by sampling them with a higher spatial resolution. In this study in fact, the error associated with animal movement (*i.e.* GPS locations), requiring a complex modelling framework to be accounted for (*i.e.* state space-models, Jonsen *et al.* 2013), was negligible compared with the other sources.

The positive and negative functional response at the large spatial scale (*sensu* Mysterud & Ims 1998), towards small cod and capelin respectively, suggests that harbour seals feed in areas with high densities of small cod when this is abundant (*i.e.* summer), while they prefer capelin when this is less abundant in the fjord (*i.e.* in the winter/spring season). No significant response was found at the small spatial scale, again suggesting no response at the level of single trips from the haulout sites.

Despite seasonal changes in preference for haddock and herring, no significant functional response to changes in availability was detected for these species. However, the strong positive selection for pelagic prey in late spring was associated to a clear movement response towards the deep Arctic basin in the inner eastern Porsangerfjord. This was visible in the southward shift in average haulout latitude and main trip direction, and in the spatial patterns of space usage during January and May 2010 (Figure 4 and 5), suggesting a strong interest of the tagged individuals for the resources made accessible by ice retreat. As mentioned above, the biomass of overwintering pelagic fish species have been most likely underestimated in the deep basins in the inner eastern part of the fjord because the area was not sampled in winter and spring, resulting in a possible undetected high usage of herring during the winter months as well.

The general movement patterns of the tagged individuals showed increased home ranges (*i.e.* longer distances from haulout sites) during autumn. During winter and spring harbour seals showed a northward shift in haulout placement and trip directionality with increasing ice extent, but a sharp shift to southward trip direction and southward movement of the haulout sites in late spring at the time of ice retreat

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(Figure 4 and 5). A similar pattern can be seen in early winter, before ice formation. In this case the pattern is less clear due to individual differences in the timing of the southward movement response. Other studies of harbour seals at high latitude have reported that the animals are expanding their home ranges and exhibiting a more offshore behaviour with ice formation (Lowry *et al.* 2001; Lesage, Hammill & Kovacs 2004; Bajzak *et al.* 2012; Blanchet *et al.* 2014). This is a consequence of the ice being a hinder in the movements between feeding grounds and haulout sites. However, in Porsangerfjord the haulout sites themselves are shifted northward in late winter and early spring (Figure 5) and the ice does not prevent the access to open water at any time; the southward movements of harbour seals individuals in this area are therefore most likely a reflection of the targeted resource. This is an additional confirmation of the increased interest of this local population in the fish resources in the cold and ice-covered areas of the Porsangerfjord during winter and spring.

Although positive selection was found for capelin and not for herring during the winter months, we argue that harbour seals in this area are most likely feeding to a large extent on overwintering pelagic species in general during both winter and spring. Harbour seals have been observed to respond to changes in seasonal pulses of pelagic schooling fish, depending on the fishes migratory behaviour (Pierce *et al.* 1991; Brown & Pierce 1998; Berg, Haug & Nilssen 2002) and energetic content (Thomas *et al.* 2011). In the Shetland adult herring is preyed upon during the summer months when passing through the area on their annual spawning migration (Brown & Pierce 1998). In the Moray Firth on the other hand 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 have seemed to drive the composition of the harbour seals' winter diet and, as a consequence, the extent of predation on other prey such as codfish (Tollit & Thompson 1996). Since the latter situation is very similar in north Norwegian fjords, we therefore suggest that variation in the abundance of pelagic schooling fish in the inner areas of the Porsangerfjord may have a significant effect on the predation on juvenile cod at least in the winter and spring months.

No functional response was registered for sculpins, cod juveniles in the sublittoral zone, or salmon. It should be noted however that the only source of variability in the availability of these resources across seasons was given by the changes

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in ice extent, since no seasonal estimates were available for those species. In the case of salmon the differences in availability with ice extent were so small that the regression was not fitted (Figure 7). A certain degree of variation in biomasses was however expected for cod juveniles and salmon. Cod settles in shallow waters in July-August, therefore the highest concentrations of juveniles in the sublittoral zone should be expected during summer and autumn (Godø *et al.* 1989). Mature salmons enter the rivers between June and August, while smolts leave the rivers in July (Orell *et al.* 2007), therefore larger concentrations of salmon were expected in the estuary areas in the summer months. Despite the absence of variation in the data for these variables, a response to such prey density changes could have been seen in differential usage of such areas across seasons, but this was not the case. An aggregative movement response of harbour seals to the presence of salmon in estuaries has been reported in Scotland (Middlemas *et al.* 2006). In Porsangerfjord the population did not show preference or increased usage of the estuaries during May or September (*i.e.* the months analyzed closest to the summer), but the lack of data on the seals' behaviour at the exact timing of the salmons migration did not allow for robust conclusions.

General constraints affecting the harbour seal population of Porsangerfjorden

The seals used the inner areas to a much wider extent than the outer areas of the fjord with the highest fish biomasses. The outer areas of the fjord were rarely used even though fully accessible (*i.e.* well within the ranges of distances that the species can afford travelling, >500 km, Lowry *et al.* 2001) and despite the presence of suitable haulout places in the outer edges of the fjord (*e.g.* sites used by grey seals, Nilssen & Haug 2007). This suggests that the resources present in the inner areas are enough to support the population all year round, at least at this demographic state. In fact, intra-specific competition can be assumed to be relatively low, due to the decline of the population in the last years as a result of hunting (Nilssen *et al.* 2010).

Harbour seals select their haulout sites in the vicinity of their foraging areas (Bjørge *et al.* 1995). The selection of haulout site is however also affected by the availability of suitable sites with respect to tide, exposure to weather, accessibility from and to the sea, disturbance and predation risk (Da Silva & Therune 1988; Grellier, Thompson & Corpe 1996; Lesage, Hammill & Kovacs 2004). One question that arises

from the results of this study is whether foraging in the inner part of Porsangerfjord is a

625   consequence of the presence of suitable haulout sites or of preferential prey. The movement response to changes in prey distribution and environment in Porsangerfjord has occurred to a certain extent at the level of haulout sites (Figure 5). However, harbour seals in this fjord have been recorded to haul out in these areas for several decades (Henriksen 1995), suggesting that the seasonal shift between haulout sites

630   occurs within a limited set of suitable locations. This has occurred despite large changes in the abundance of codfish in the last decades (ICES 2013). It is therefore not yet clear if, under the hypothesis of a large increase of the seals' population in the fjord, the animals will move their haulout sites closer to areas of higher prey concentrations, possibly towards the outer regions of the fjord, or if the individual home ranges will

635   have to expand drastically due to a limited flexibility in the choice of haulout sites. The latter hypothesis can be supported by recent findings of the presence of different forms of resting behaviour at sea (Ramasco, Biuw & Nilssen 2014), which could allow the individuals to balance the costs of travelling further away from the haulout regions.

In summary, harbour seals in Porsangerfjord exhibit size preference in terms of

640   selection of areas with the highest concentrations of small prey species or small size classes of larger fish species. In addition they show a clear movement response to the concentration of pelagic schooling fish with predictable seasonal patterns (*i.e.* herring and capelin in winter and spring). They are however opportunistic at the small spatial scale (*i.e.* single trips from the haulout sites).

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Tables

Table 1 Overview of the data types and sampling sizes for the different periods (t = 1 - 4) for the seal movement and dive data, and for the prey resources.

Animal data

Individual	Sex	Length (cm)	Weight (kg)	Tagging duration (from-to)		Period t=1 n GPS	n dives	Period t=2 n GPS	n dives	Period t=3 n GPS	n dives	Period t=4 n GPS	n dives
from						01.09.2009		01.01.2010		01.04.2010		01.09.2010	
to						31.10.2009		28.02.2010		31.05.2010		31.10.2010	
pv30-01-09	m	87	21	01.09.2009	10.07.2010	1713	23221	1448	23903	2232	32557		
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	1677	19396		
pv30-11-09	f	93	22	06.09.2009	09.06.2010	1468	36894	1774	34709	1947	31304		
pv30-12-09	m	100	24	08.09.2009	20.12.2009	2052	31576						
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
Nr of seal individuals per period (n_t)						5		4		3		5	

Prey resources: acoustic transects and trawls

	Period t=1	Period t=2	Period t=3	Period t=4
from	18.08.2009	02.02.2010	27.04.2010	17.08.2010
to	20.08.2009	04.02.2010	29.04.2010	19.08.2010
n **pelagic trawls**	7	0	4	6
n **benthic trawls**	10	8	8	9

Table 2 Definition and values of the parameters used in building RSFs.

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

Figures
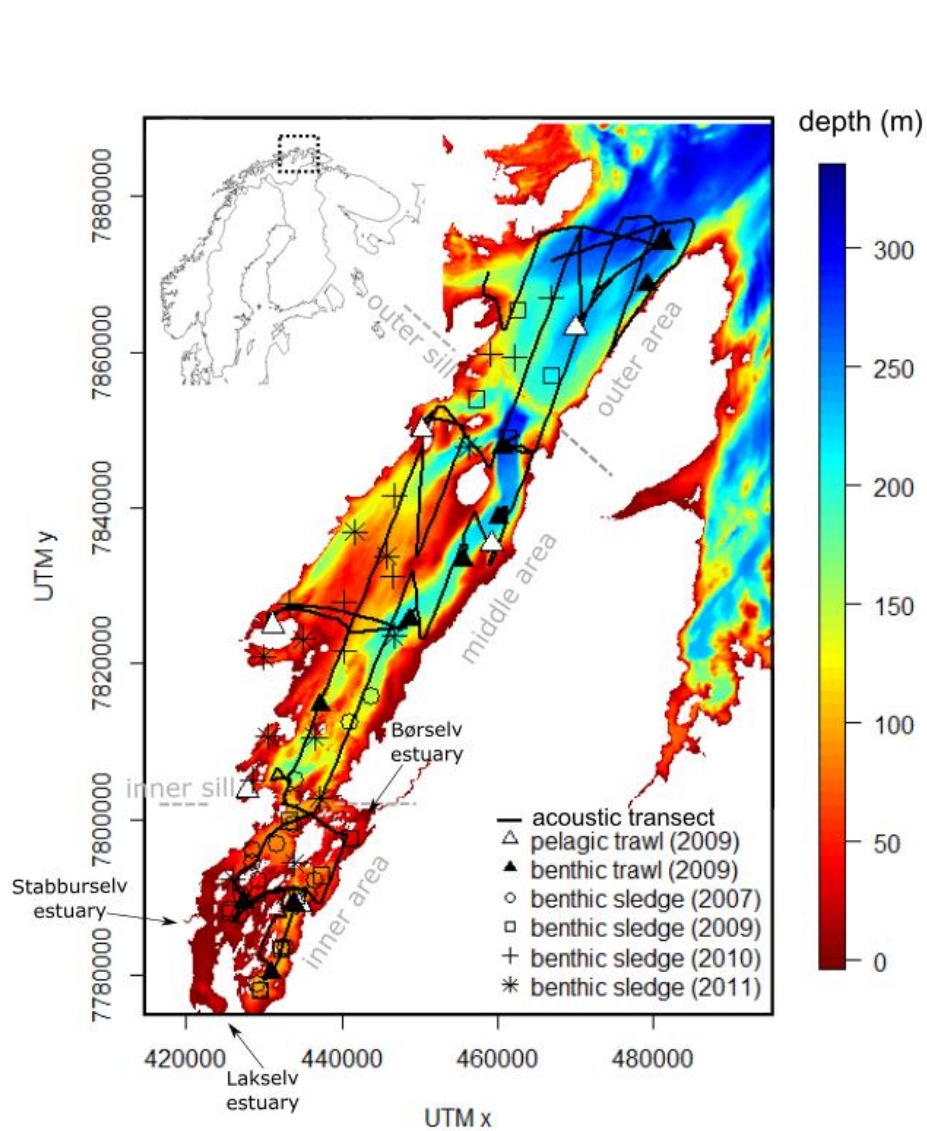
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Figure 1 The study area and its bathymetry (colour scale), and the sampling design for harbour seals' potential prey. The Porsangerfjord can be roughly divided into 3 areas, delimited by an inner and an outer fjord sill. Three main rivers flow into the fjord (Lakselv, Stabburselv and Børselv). The figure illustrates an average acoustic transect for the sampling of pelagic and semi-pelagic fish species; the placement of the
830 benthic and pelagic trawl stations for the calibration of the acoustic survey (the ones from August 2009 are shown as an example); the benthic sledge stations from different years for the sampling of the bottom dwelling fish species.
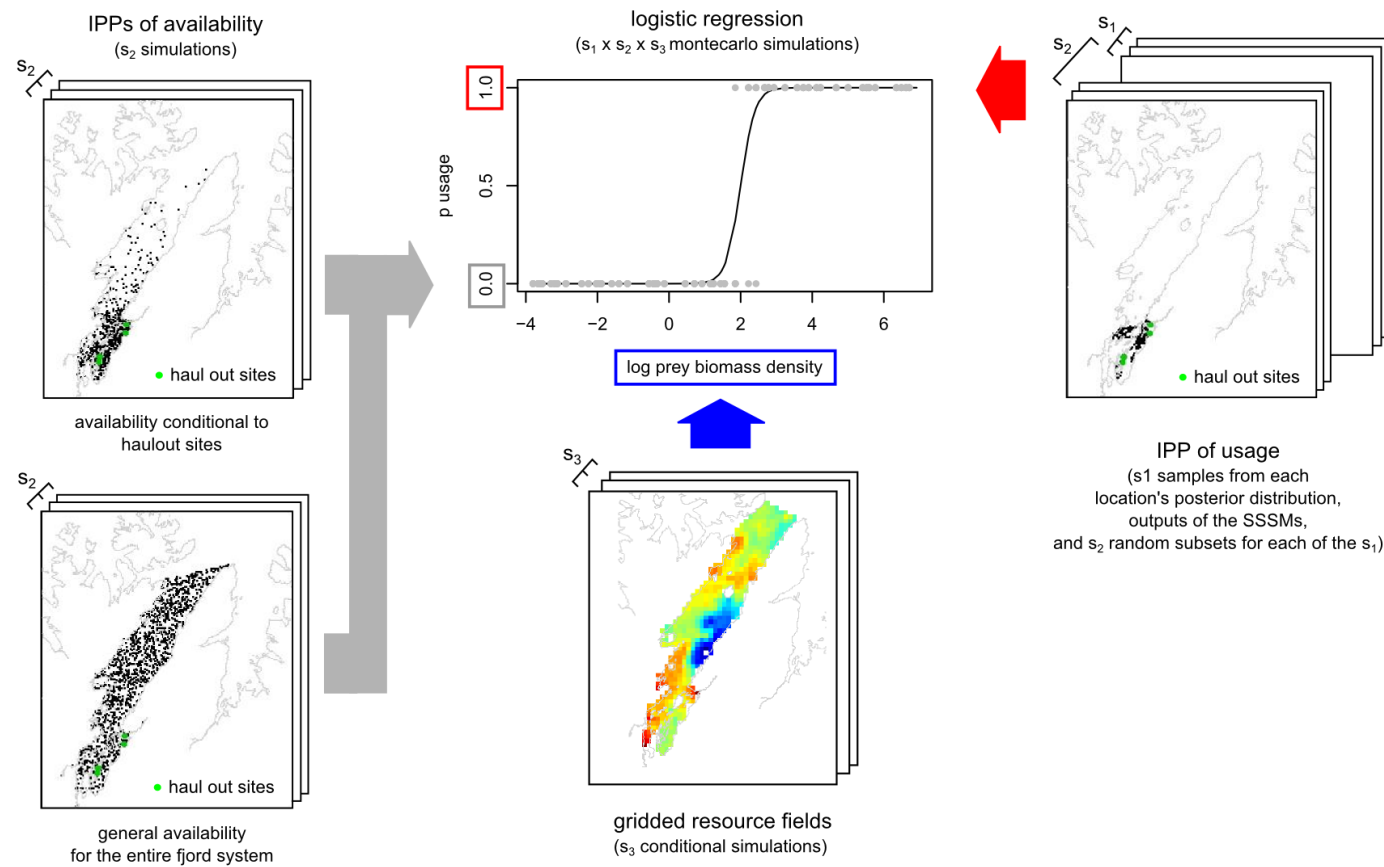
Figure 2 Resource Selection Functions were built by fitting logistic regressions to sets of used (= 1, red arrow) and available points (= 0, grey arrow) at two spatial scales (general and conditional to the haulout sites). Animal locations were predicted at regular times from a set of GPS positions by means of Switching State Space models. Inhomogeneous point patterns (IPPs) of usage were generated by re-sampling s_1 times from the predicted distribution of locations. For each of these sets of locations, s_2 random subsets were generated, producing $s_1 * s_2$ IPPs of usage. Availability datasets were generated by simulating s_2 IPPs both for the conditional and general availability. S_3 gridded resource fields of log biomass densities of potential prey were produced by conditional simulations from regression kriging models. Models were fitted to all possible combinations of outputs ($s_1 * s_2 * s_3$) in order to estimate the amount of variation due to each step of the procedure (see Material and Methods for more detail).

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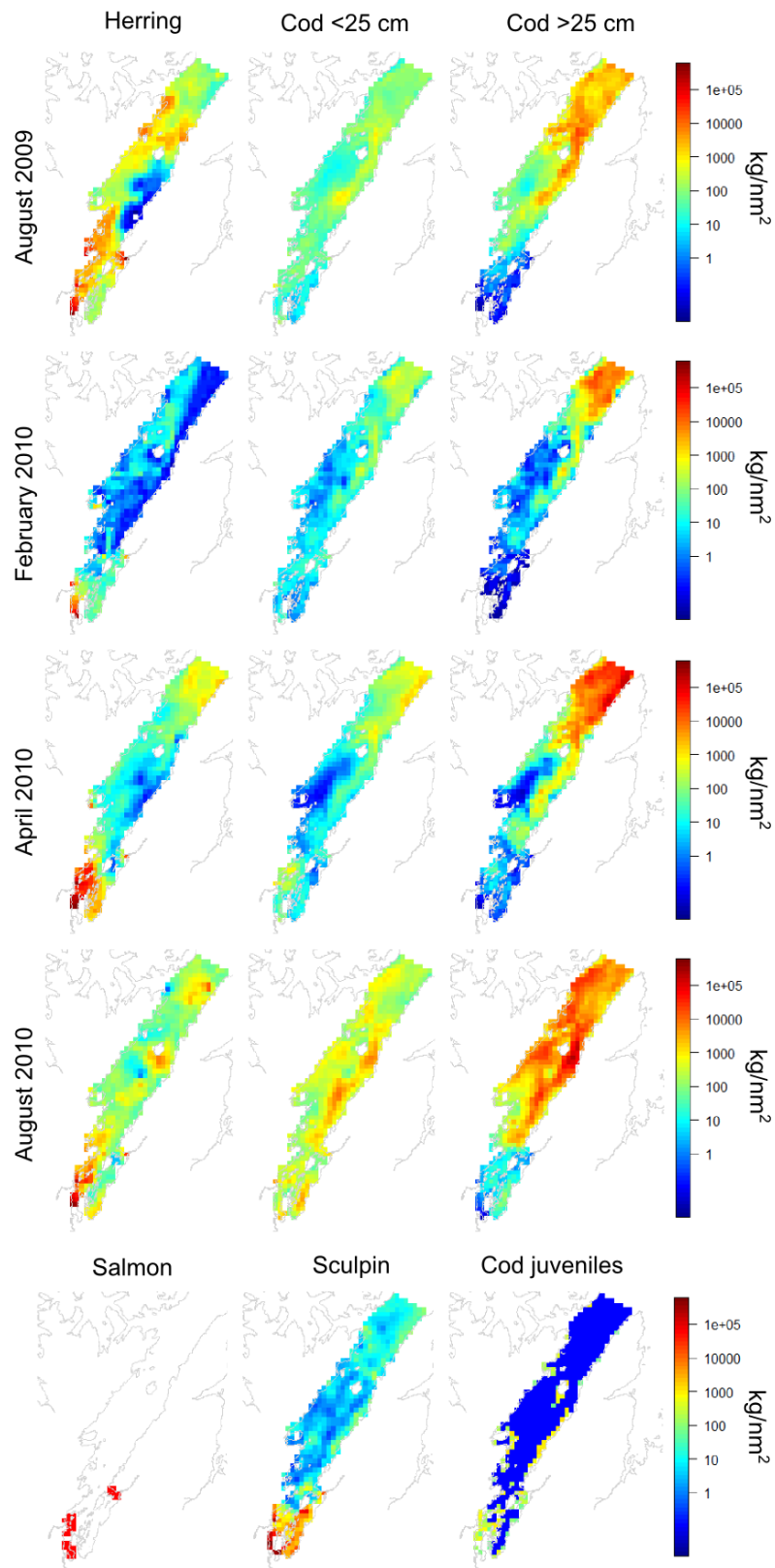
Figure 3 Average prediction maps of biomass (colours, in log scale) of selected potential prey resources. For herring, and the two size classes of cod (< 25 cm and > 25 cm), the distribution is shown for the 4 sampling periods (August 2009 – August 2010). For sculpins, cod juveniles and salmon average annual predictions are shown. Maps of the potential prey not shown in this figure (capelin, haddock < 25 cm, and haddock > 25 cm) are presented in S6.

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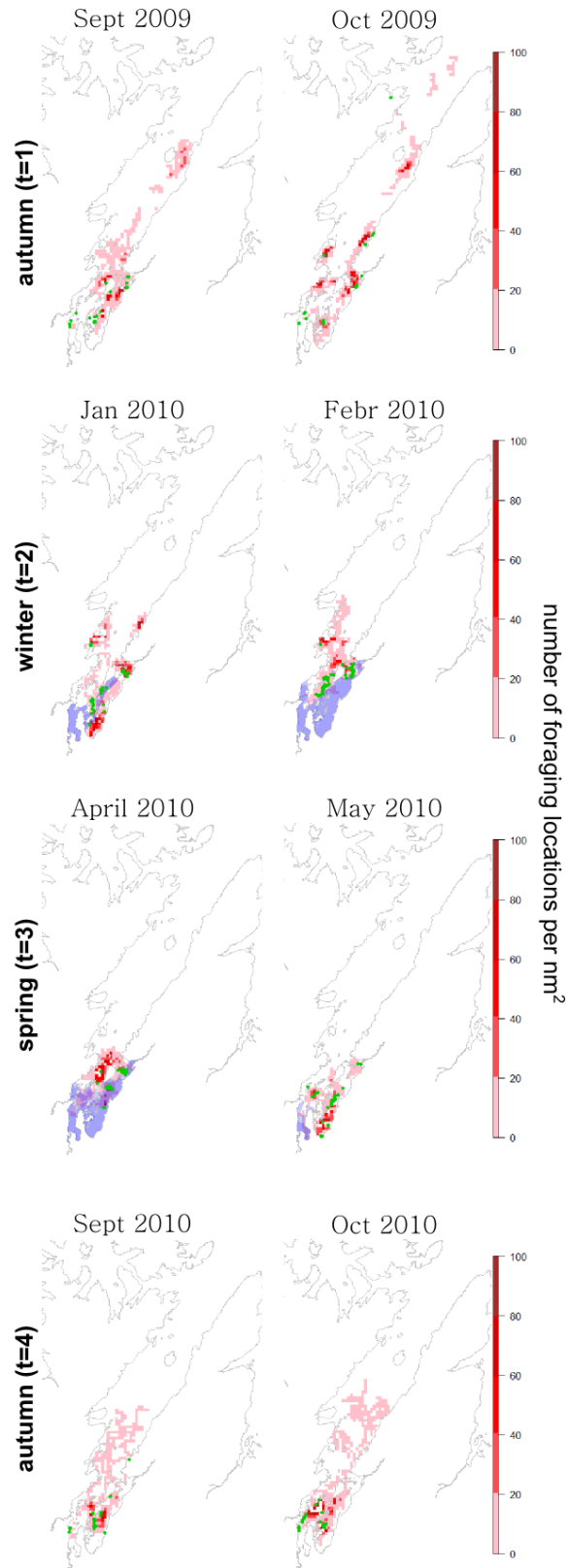
Figure 4 Harbour seals ($n = 3 – 5$, see Table 1) foraging intensity (number of foraging locations per nm^2) for each month of the 4 periods analysed ($t = 1 – 4$). The extent of the average ice cover per month in winter and spring is shown as a blue shade. The used haulout sites during each month are shown (green dots).

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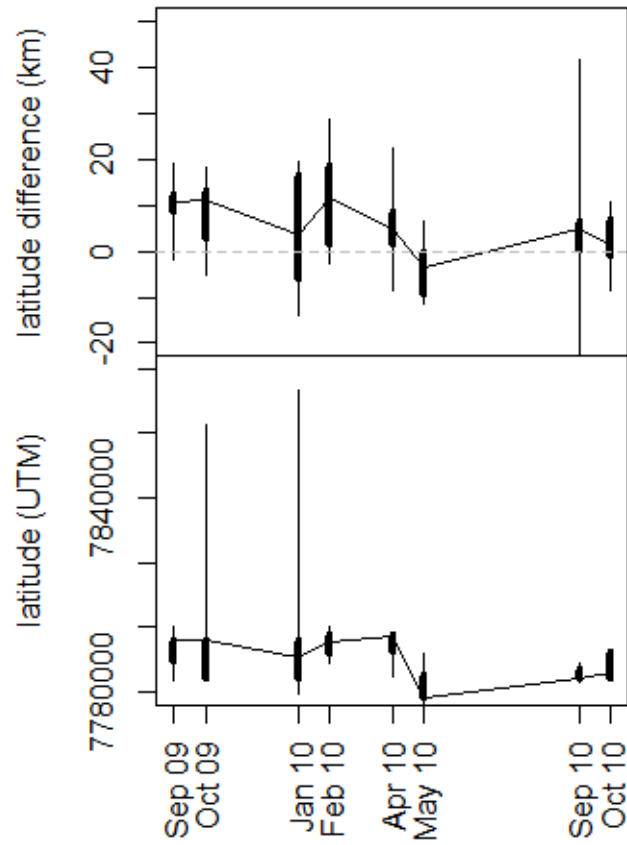
Figure 5 The north-south movement response in trip directionality (expressed in km distance from the haulout site, upper plot) and haulout site placement (lower plot) at the population level across the months and periods analysed (median: horizontal line; range of 50% and 95% of data: respectively thick and thin black vertical lines).

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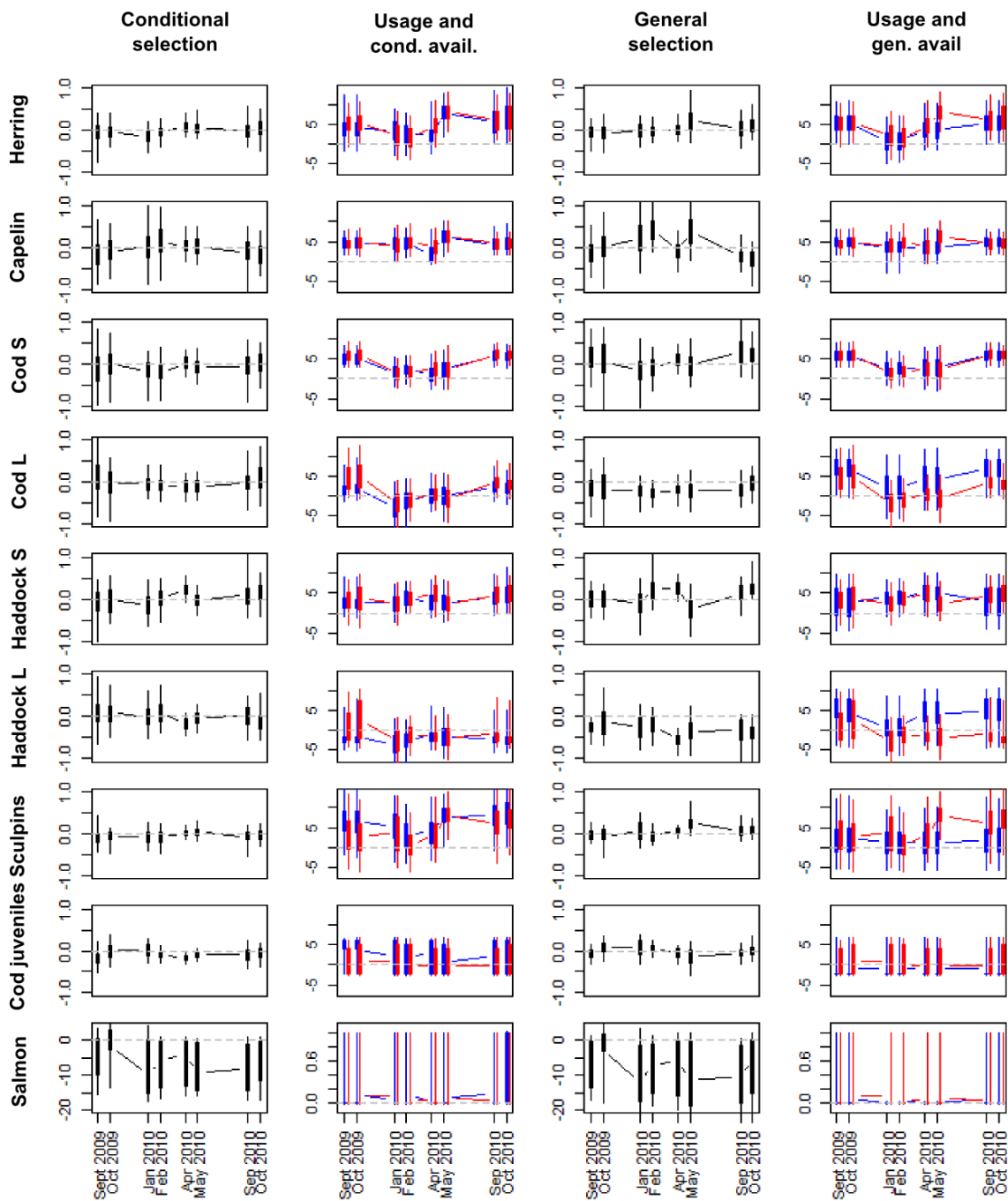
Figure 6 Temporal patterns in conditional and general resource selection coefficients (black boxplots), resource usage (red boxplots) and availability (blue boxplots) for the potential prey species analysed (horizontal dashed line = zero selection). The boxplots show the distribution of the population values across simulations (range of 50% and 95% of data: respectively thick and thin vertical lines). While resource coefficients are unitless, resource usage and availability are expressed in log biomass (kg/nm^2).
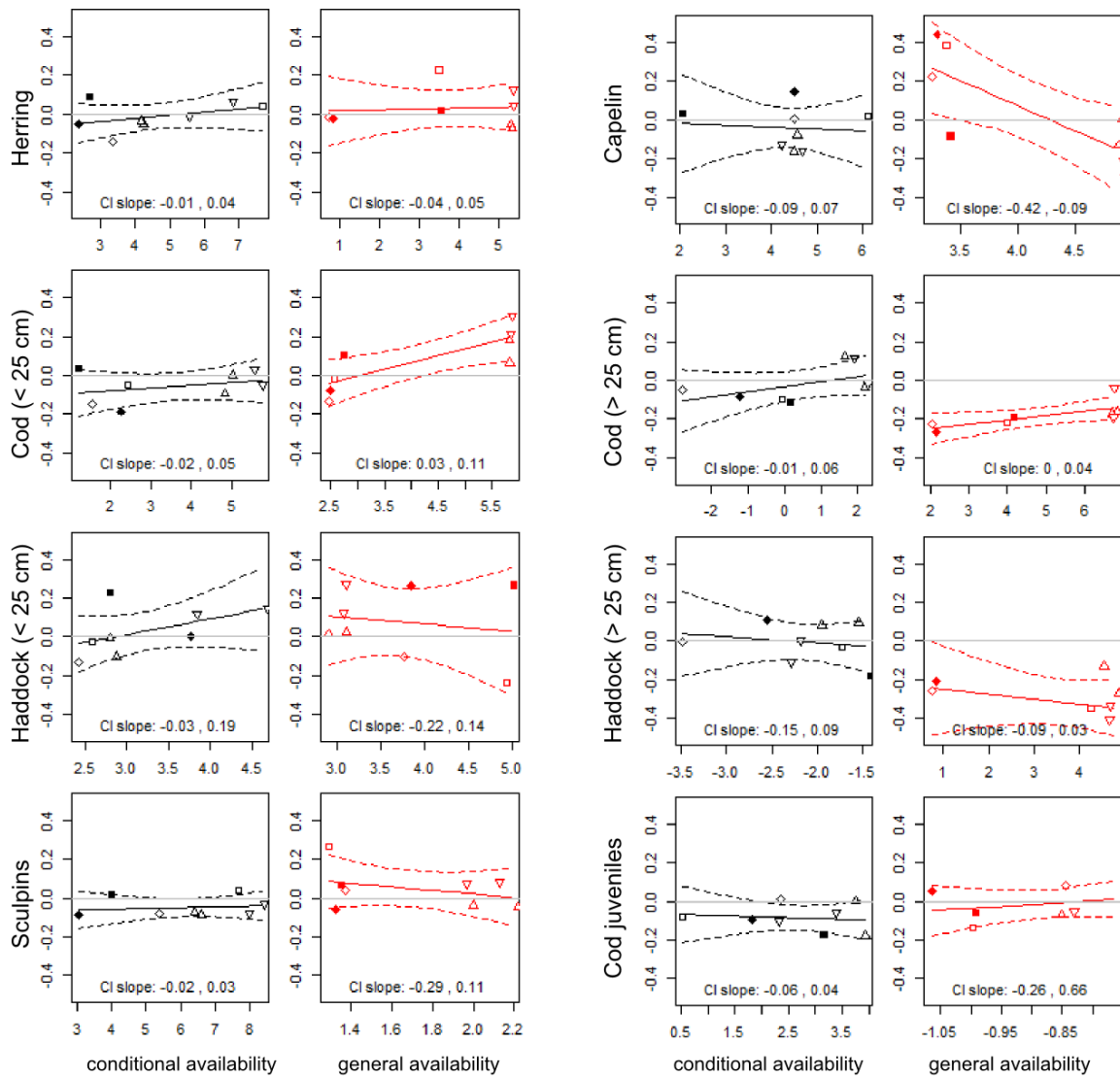
Figure 7 Functional response in resource selection to changes in availability, conditional to the haulout sites (black) and general for the entire fjord area (red). Linear models were fit on the population's mean resource selection coefficients (y-axis) against the conditional or general availability (in log biomass density, kg/nm^2) for each month during the 4 periods analyzed ($\triangle$ summer, $\diamond$ winter, $\square$ spring, colour-filled when ice cover was large). The regression's 95% confidence bands (dashed lines) and the zero line of no selection (grey line) are shown. The confidence intervals of each regression slope (CI slope) are printed on the bottom of each plot. No functional response was analysed for salmon (see Methods).

Supplementary material

S1 Harbour seals scat sampling in Porsangerfjord

In order to investigate the diet of harbour seals in Porsangerfjord, known haulout sites in the area were repetitively visited for scat collection during the tagging attempts, in the falls of 2009 and 2010. Otoliths were extracted for taxonomic recognition to the lower possible level (Härkönen 1986). The number of prey items in each scat was estimated from the number of otolith pairs (left or right side) of each species in each scat. Fish length was estimated from the mean length of otolith pairs using species-specific regressions taken from literature (Breiby 1985; Härkönen 1986; Leopold *et al.* 2001; Svetocheva, Stasenkova & Fooks 2007) or other unpublished data sources (catch data from the Barents Sea, IMR; data on sculpins from Porsangerfjord, courtesy of Källgren E, UiT). Different regressions were used for different ranges of otolith lengths for gadoids to account for decreasing growth rates with age. When taxonomic recognition could not be performed down to the species level, the regressions of the most common species belonging to that taxonomic group and present in the area were used and the results averaged.

A total of 48 harbour seals scats (37 of which were found in 2010) were sampled from a single site in inner Porsangerfjord (Lat 70.152° Lon 25.151°) despite several sites were visited. Not all otoliths could be recognized down to species level during analysis due to partial digestion in the scats and some species have been therefore grouped at the family level.

Codfish (Gadidae) had the highest frequency of occurrence in the scats (present in 85% of the scats), with sculpins (Cottidae, 60%), herring (*Clupea harengus*, 56%) and pricklebacks (Stichaeidae, 50%) (Figure A1 upper plot). The forenamed groups made up 93% of the fish items in the total population diet (Figure A1 lower plot).

The group Gadidae included species as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*). Within the group Cottidae, the following species were identified with a certain degree of uncertainty: Bull rout (*Myoxocephalus scorpius*), Moustache sculpin (*Triglops murrayi*), Ribbed sculpin (*Triglops pingelii*) and Polar sculpin (*Cottunculus microps*). The last species, though belonging to the Psychrolutidae family, closely related to Cottidae, was grouped together with the other sculpins in this analysis.

Ninety nine % of the fish items in the data had an estimated length < 25 cm. Fish size estimation was not corrected for partial or total digestion in this analysis, potentially underestimating the size of prey. However the size of this bias was evaluated as small (Wilson 2014) and not altering the interpretation of the results.
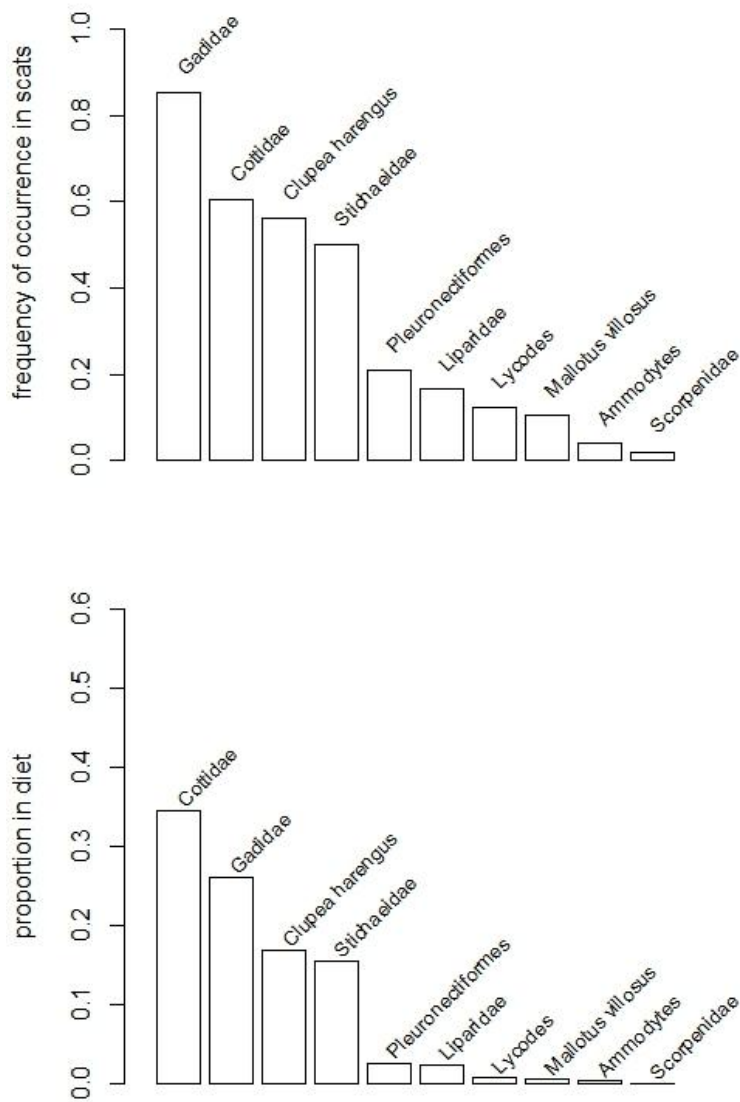
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Figure S1: Frequency of occurrence (incidence) of prey items in scats (upper plot) and proportion of prey items in the population's diet (lower plot).

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S2 Fish biomass estimation from acoustic sampling

Continuous acoustic recordings of area backscattering coefficients (*SA*), from ca. 10 m below surface to the sea bottom, were made using a 38 kHz Simrad EK-500 splitbeam echosounding system (Bodholt, Nes & Solli 1989). The conversion of *SA* values into abundance estimates was carried out on the basis of the acoustic character of species and the partitioning of species in trawl samples. Benthic trawl hauls were taken at predetermined stations along the fjord, whereas pelagic trawl hauls we taken in response to large changes in the echo sounder registrations. For pelagic trawling, a 14 fathom trawl (Harstad, Norway) fitted with a Scanmar depth recorder was used, while a Super Campelin 1400 mesh shrimp trawl was used for demersal trawling. Both trawls were fitted with an 8 mm net inside the codend thereby making it possible to sample juvenile fish as well. Pelagic and demersal trawling was standardized to 30 and 20 min duration respectively and the trawling speed was approximately 3 knots. The recorded *SA* values, averaged over one square nautical mile (nm²) and 10 m depth strata, were converted to abundances (ρ) according to the relation:

$$\rho_i = \frac{SA_i}{4 \cdot \pi \cdot 10^{0.1 \cdot TS_i}} \tag{1}$$

where TS_i is the mean target strength of species *i*, which varies with species and body length (McLennan & Simmonds 1992). Abundances were then transformed into biomasses by multiplying them with species specific mean body weight from the trawl hauls. The final fish biomass estimates per depth interval were cumulated for the entire water column.

S3 Details on regression kriging for the predictions of fish biomass distributions

For the variable resources (herring, capelin, cod and haddock), we assumed the relationship of each species with the environmental variables to be invariant with time, while we considered this not to be the case for their spatial covariance structure, which was therefore allowed to vary across time periods. We therefore fitted linear models, separately for each species and size group, of biomass density against all covariates using pooled data across time periods and then kriged the model residuals separately for each time period, allowing the variograms to change. The final biomass density distribution was computed as the sum of the predicted average biomass from the linear model and the krieged residuals. For sculpins, stations sampled in different years and different locations were pooled together in one RK analysis to obtain a better spatial coverage, assuming both the relationship with covariates and the spatial characteristics were invariant with time.

For the stochastic model component, we computed the empirical variograms with a threshold maximum distance of 20 km (width of the fjord) and distance lags of 2 km for the species sampled with acoustic transects (comparable to the integration distance along transects = 1 nm or 1.8 km) and 500 m for the sculpins, given some of the benthic stations were very close in space. We then fitted exponential models to the empirical variograms.

S4 Mapping macroalgal coverage and predicting cod juvenile biomass density

Macroalgal forests are an important refuge and feeding habitat for the juvenile stages of cod and saithe (0-2 years). A study on the abundance of cod juveniles along the coast of Porsangerfjord and Ullsfjord has shown that the highest concentrations of cod juveniles are in areas of high to intermediate macroalgal coverage and around 10-20 m depth (Michaelsen 2012). Cod juvenile biomass was therefore estimated for the sublittoral zone (5 - 20 m) of Porsangerfjord using a non-linear model with macroalgal coverage (%) and depth as predictors (courtesy of Pedersen T & Michaelsen C, UiT, Figure S2).
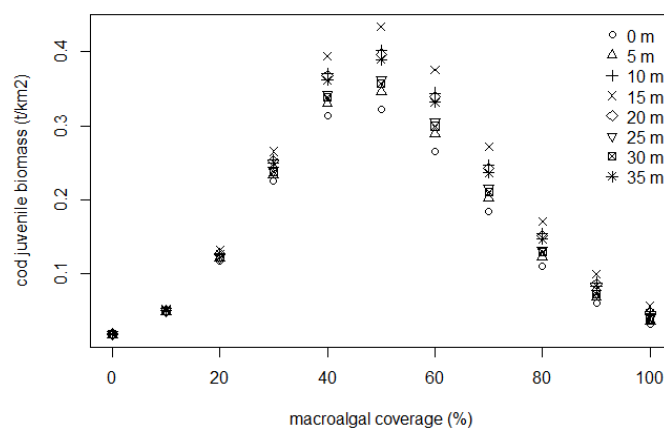
Figure S2 The relationship between macroalgal coverage and cod juvenile biomass density mediated by depth (symbols) in Porsangerfjord and Ullsfjord.

First, macroalgal coverage was mapped across the entire fjord using two available sources of macroalgal data. Dataset A consisted in the biomass density (kg/m^2) of different macroalgal species sampled in the intertidal zone by collecting and weighing macroalgae in 1 m^2 grids at each station (courtesy of Sivertsen K, Finnmark University College, FUC, Figure S3). Dataset B consisted in measures of macroalgal coverage (%) from 5 to 20 m depth (sublittoral zone) sampled by towing a video camera along linear transects perpendicular to the coastline (courtesy of Steen H, IMR). Coverage was then visually estimated for every 3 m depth intervals along the video transects (Figure S3). Dataset A was collected at a higher spatial resolution and with stations distributed all along the coast of the fjord (N$_A$ = 776), while dataset B was collected in the middle and

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outer fjord areas only, and at much fewer locations (N_B = 94, Figure S4). Both datasets also recorded the density of sea urchins, *Strongylocentrotus droebachiensis*, which has been reported as one of the main grazer of kelp forests (Norderhaug & Christie 2009). Macroalgal coverage was therefore expected to be related, not only to the environmental conditions at each location (Bekkby *et al.* 2009), but also to the grazing pressure, which varied consistently along the fjord. Due to the lack of coverage data (B) in the inner parts of Porsangerfjord, extrapolation of predictions based solely on dataset B would have resulted in unrealistic predictions for these areas. Macroalgal biomass and sea urchins density in the intertidal zone (A) were then used, together with environmental covariates, to help predicting coverage more robustly in particular in the inner areas of Porsangerfjord.

Percentage of macroalgal coverage (y_{ij}) for each depth interval *j* and transect *i* in B was modelled by logistic regression using the following predictors: macroalgal biomass and sea urchins density in the intertidal zone (A), depth, slope, curvature, light exposure, current, and salinity. The biomass values from A were suggested to relate to coverage through a power function (Sivertsen K, FUC, *pers. comm.*), hence the square root of biomass density was used in the model. Macroalgal density in the intertidal zone close to each of the B transects was estimated by averaging the values of the A stations situated within a 0.5 nm distance range of each of the start location of the B transects (n = 93, 1 transect start location did not have any A station within its range). A Digital Terrain Model (DTM) was generated from sea bottom depth point measurements (data courtesy of The Norwegian Mapping Authority) by kriging (raster cell resolution of 100 x 100 m). Slope and terrain orientation (in degrees) were calculated from the DTM using the algorithms in Horn (1981). A two-levels light condition index was derived from terrain orientation (0 = 22° ± 90, 1 = 202° ± 90, as in Økland 1990, 1996). Terrain curvature was computed as the difference between the depth at one cell and the average depth in the 8 neighbouring cells (Wilson *et al.* 2007). Water current, temperature and salinity estimates were extracted from a geophysical model for the months of March, April, and May 2009 (Myksvoll *et al.* 2012). Absolute values of current were averaged over the 3 months. Temperature and salinity were highly non-linearly correlated (corr. (salinity, 1/temperature) = - 0.90), therefore only salinity was used in the models.
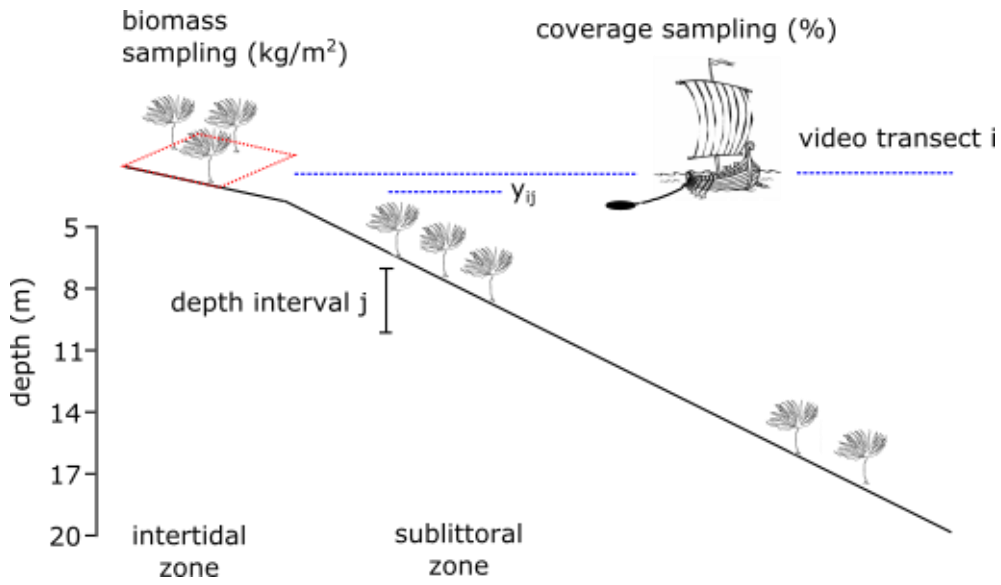
Figure S3 Sampling scheme for kelp biomass density (kg/m^2) in the intertidal zone (dataset A) and coverage (%) along transects from 5 to 20 m depth (dataset B). Coverage y_{ij} was measured for each for transect i and depth interval j (3 m).
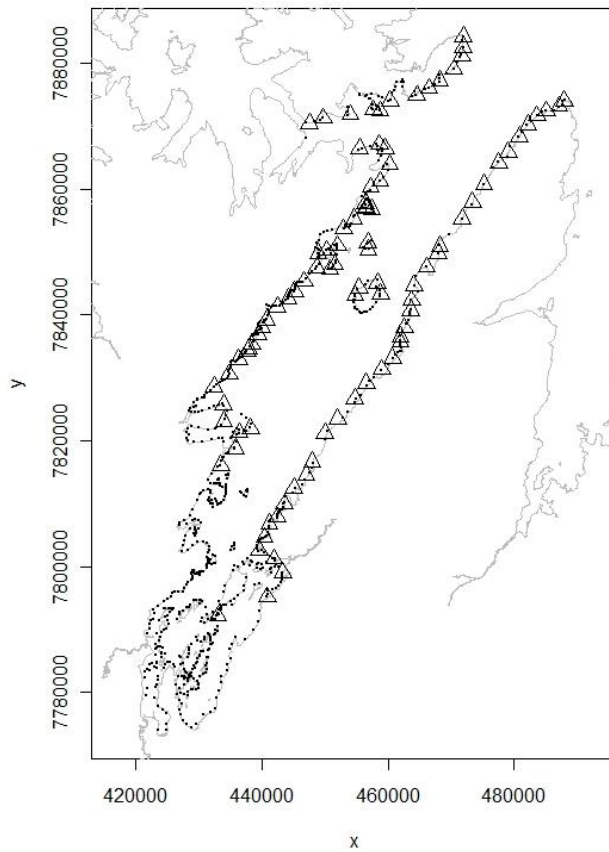
Figure S4 Sampling stations for macroalgal biomass density in the intertidal zone (dataset A, dots, n = 776) and video transects for macroalgal coverage in the sublittoral zone (dataset B, triangles, n = 94). Macroalgal coverage (B) was not sampled in the inner part of Porsangerfjord. Latitude and longitude are expressed in UTM coordinates.

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For each raster cell between 0 and 50 m depth, macroalgal biomass and sea urchins density in the intertidal zone was extracted from the nearest A station. Macroalgal coverage was extrapolated for the entire fjord using the predictive model (Figure S5). Prediction uncertainties were computed by bootstrapping the data, fitting the model and calculating the predictions 100 times. The final predictions were then averaged at the spatial resolution of 1 nm^2 in order to estimate cod juvenile biomass at the same resolution as the other potential prey species used in the study (see Methods).
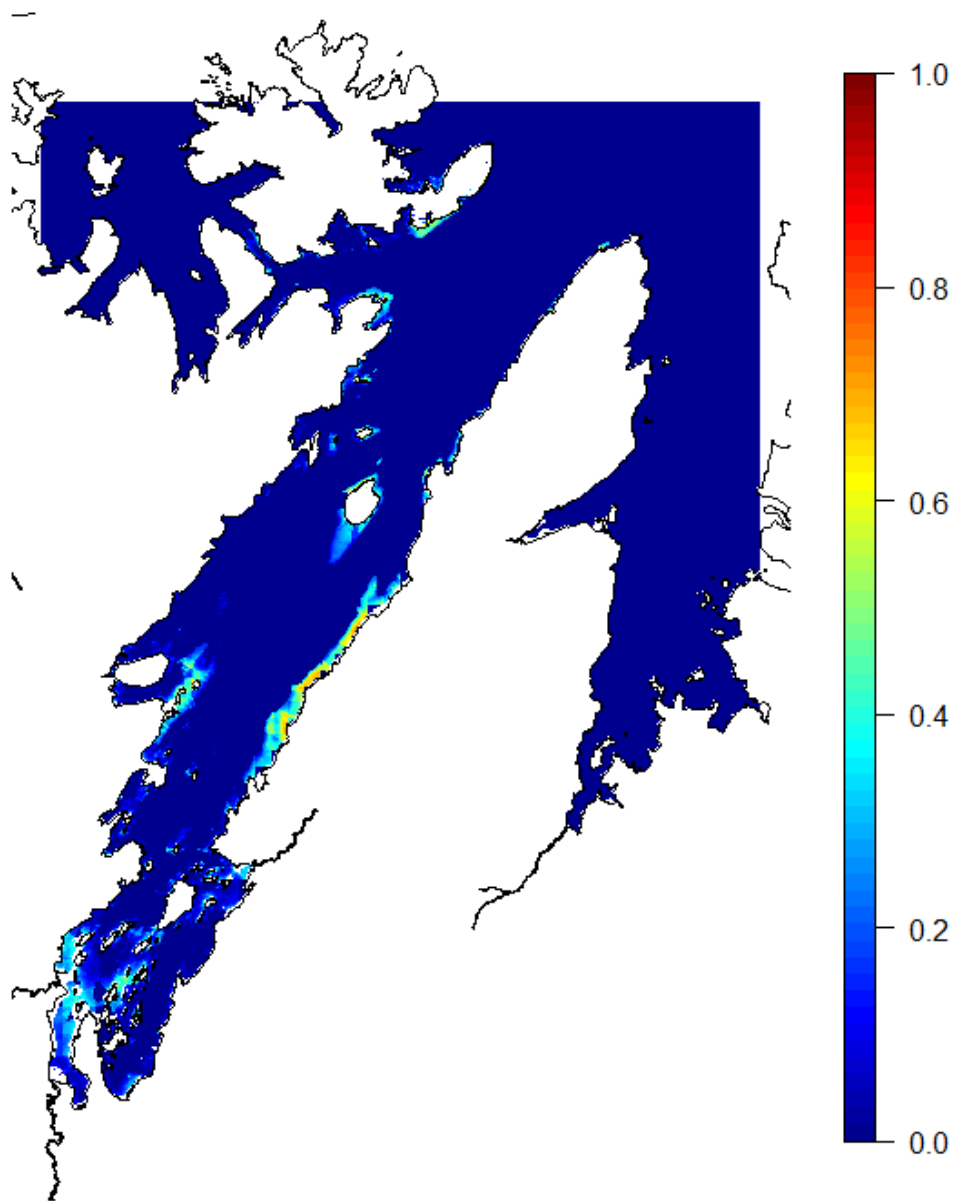
Figure S5 Model predictions of macroalgal coverage (colour scale = proportions from 0 to 1) for the entire Porsangerfjord.

# S5 Validation of the usage of the distance distribution model for grey seals (*Halichoerus grypus*)
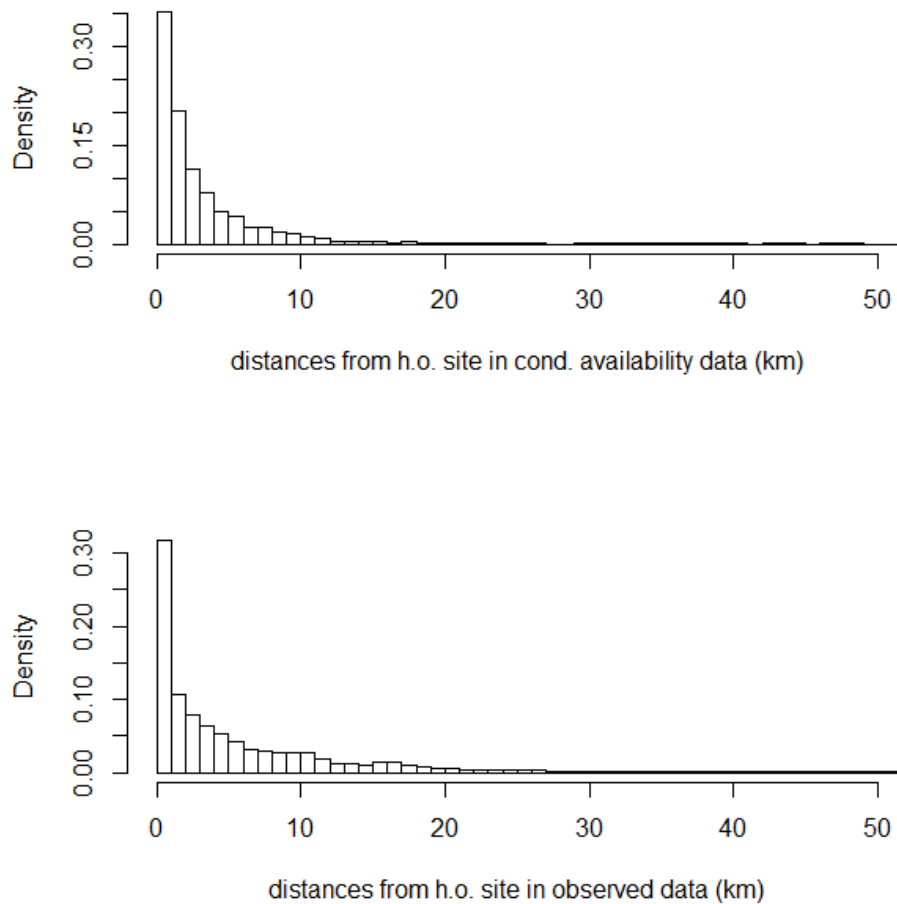
Figure S6 The distribution of distances from the haulout site for simulated points of conditional availability, derived from a model for grey seals (upper plot), and for observed harbour seals data (lower plot). Simulated distances were expected to be larger than the range of movements observed for harbour seals, since grey seals generally move faster and further away from the coast. Contrary to expectations, the upper 95 percentile of the distribution of simulated points was smaller (13 km) than the one observed (32 km). The grey seal model therefore does not overestimate availability of resources far from the haulout sites as expected and can be considered valid for harbour seals.

S6 Biomass distribution of capelin and haddock
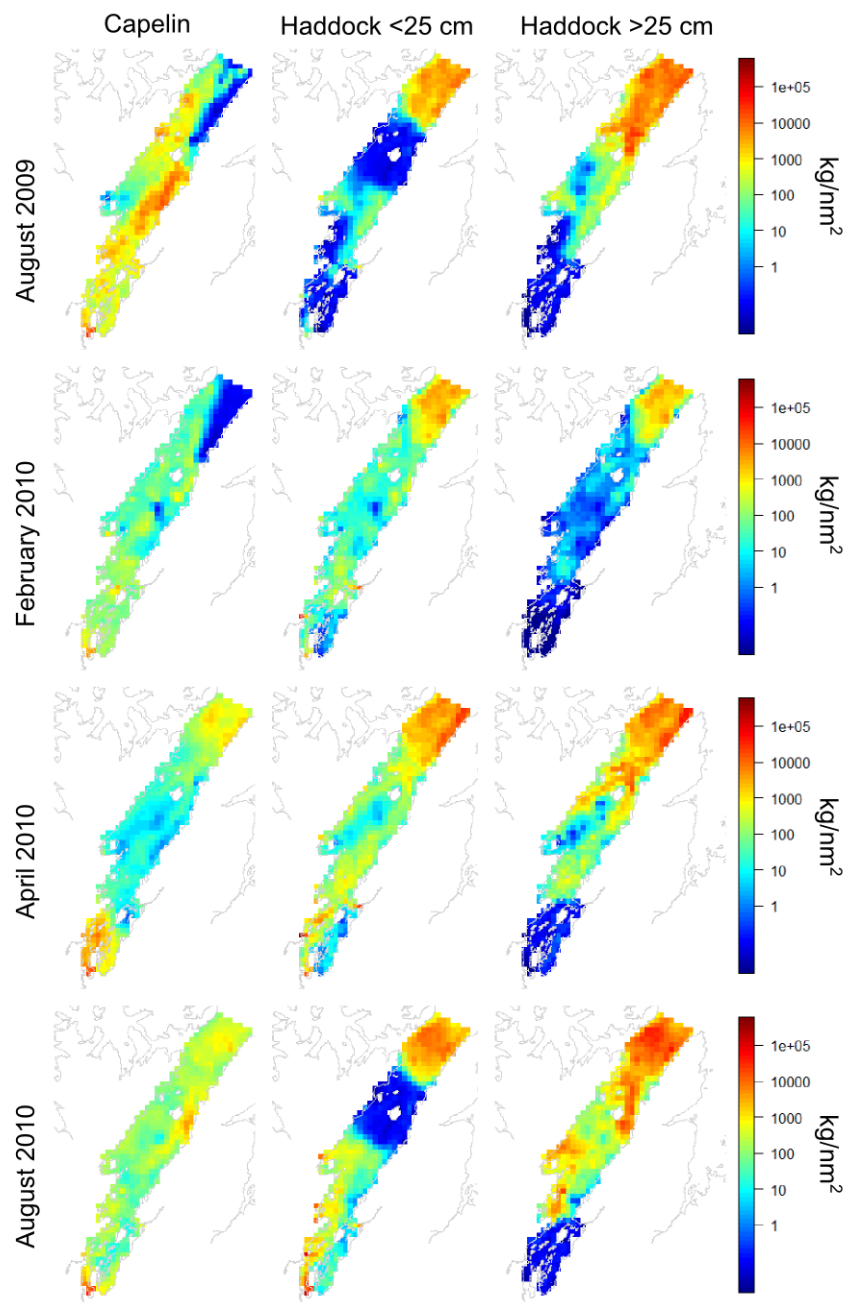
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Figure S7 Average prediction maps of log biomass (colour scale) of capelin, and the two size classes of haddock (< 25 cm and > 25 cm). The distribution is shown for the 4 sampling periods (August 2009 – August 2010).
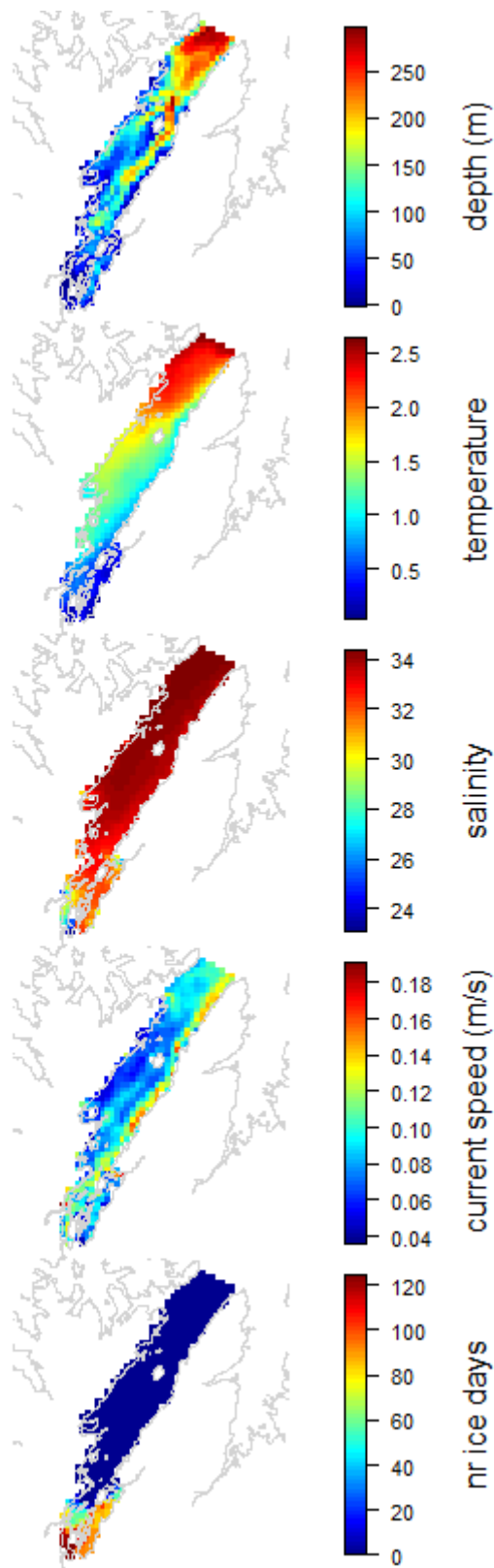
S7 Environmental characteristics of Porsangerfjord

Figure S8 Spatial patterns of the environmental variables used as predictors for the potential prey resources in the deterministic component (linear regression) of the regression kriging analysis (RK).

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S8 Regression kriging parameters

Table S1 The parameters for the deterministic component (linear regression) of the regression kriging analysis.

	Herring		Capelin		Cod (< 25 cm)		Cod (>25 cm)		Haddock (<25 cm)		Haddock (>25 cm)		Cottidae	
	Estimate	Std. Error	Estimate	Std. Error	Estimate	Std. Error	Estimate	Std. Error	Estimate	Std. Error	Estimate	Std. Error	Estimate	Std. Error
(Intercept)	52.744	5.583	24.081	4.830	16.243	4.030	-21.464	5.196	28.652	5.485	-31.712	5.227	-5.581	3.227
temperature	1.444	0.213	-0.205	0.184	0.137	0.154	1.229	0.198	2.756	0.209	2.091	0.199	1.664	2.273
depth	0.004	0.001	0.006	0.001	0.013	0.001	0.018	0.001	0.009	0.001	0.016	0.001	-0.009	0.012
current	-20.572	3.400	-18.352	2.941	10.367	2.442	19.402	3.149	33.660	3.324	26.474	3.168	59.613	26.797
salinity	-1.491	0.169	-0.555	0.146	-0.448	0.122	0.619	0.157	-0.986	0.166	0.826	0.158	6.01E-17	5.80E-15
ice days	0.025	0.004	0.008	0.004	-0.018	0.003	-0.025	0.004	-0.016	0.004	-0.009	0.004	0.113	0.019
Adjusted R^2	0.13		0.06		0.20		0.50		0.34		0.54		0.59	

S9 Individual variation in resource selection
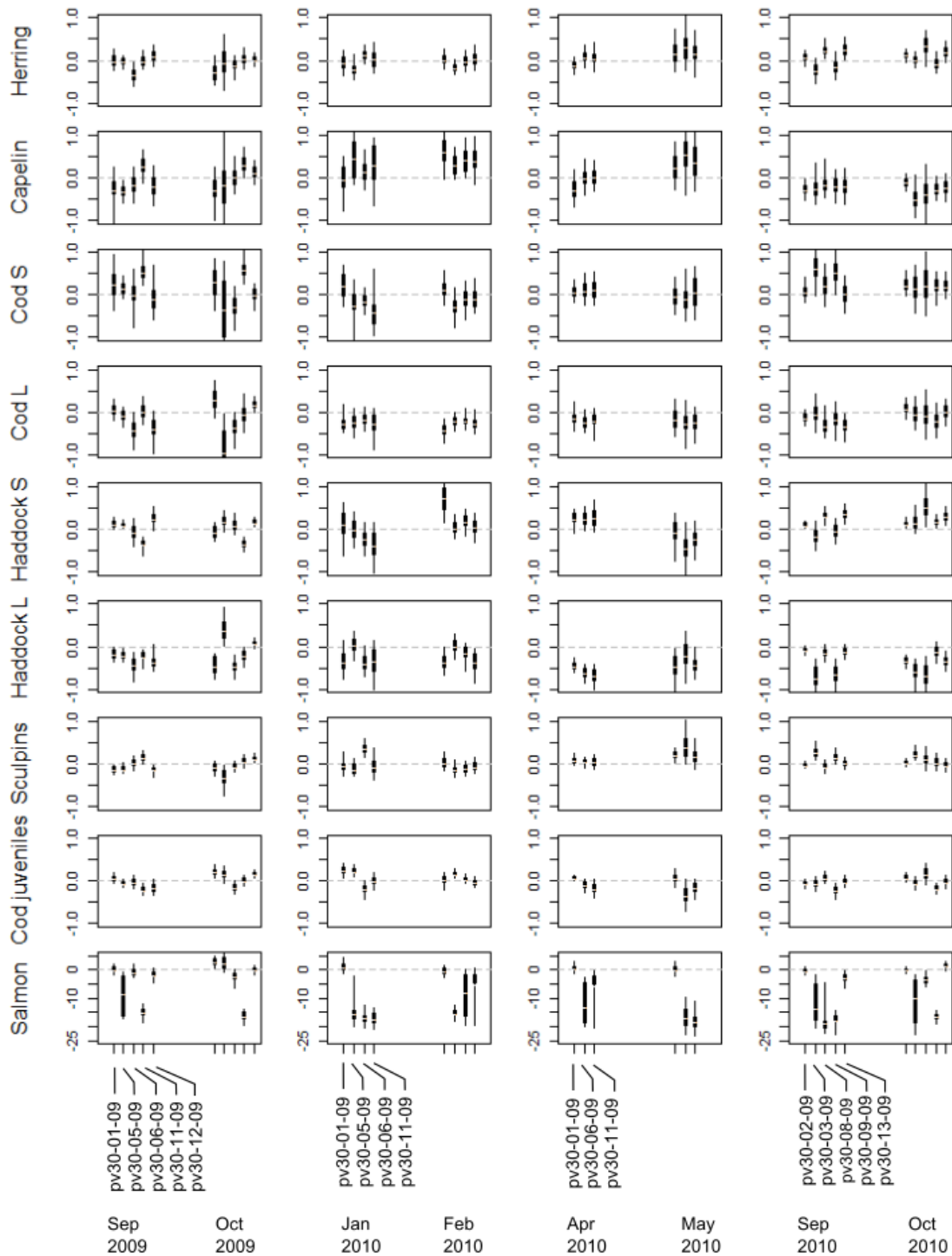
Figure S9 General resource selection coefficients for individual harbour seals during each of the two-months periods (x axis). Boxplots show the distribution of selection coefficients across simulations for the different potential prey species (plot lines), for the 4 periods analysed (plot columns). Mean (horizontal white lines), 50% (thick vertical lines) and 95% confidence intervals (thin vertical lines), and the level of zero selection (horizontal dashed line) are shown.

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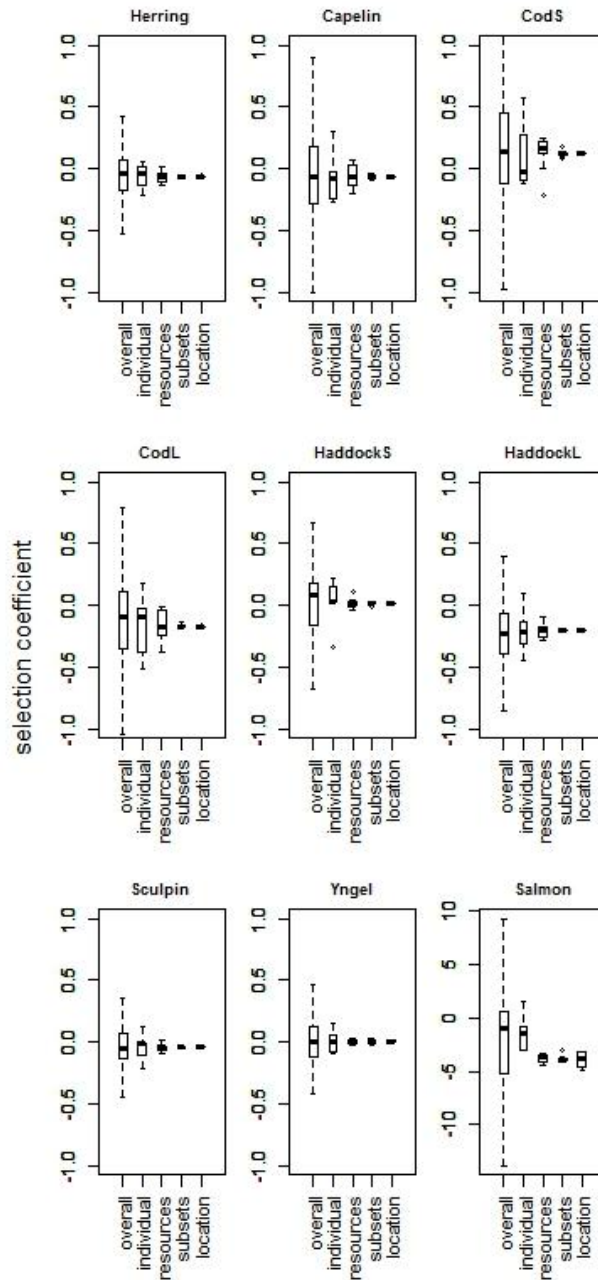## S10 Sources of variation in resource selection

Figure S7 The overall variance in selection coefficient estimates for the population and the specific variance attributable to the different sources of variation. The coefficients were estimated by Montercarlo simulations across all possible combinations of datasets, generated by modulating one source of variation at the time, keeping the others constant. The variance of selection coefficients is therefore represented by their spread along the y axis (extent of the boxplots). The different sources of variation are shown on the x axis in order of decreasing importance (respectively individual, resource prediction error, random subset selection and location error). The coefficients are shown for all potential prey species for period 1 only (Autumn 2009).