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## RESEARCH ARTICLE

# Foraging habits of Northwest Atlantic hooded seals over the past 30 years: Future habitat suitability under global warming

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## Abstract

The Arctic is a global warming 'hot-spot' that is experiencing rapid increases in air and ocean temperatures and concomitant decreases in sea ice cover. These environmental changes are having major consequences on Arctic ecosystems. All Arctic endemic marine mammals are highly dependent on ice-associated ecosystems for at least part of their life cycle and thus are sensitive to the changes occurring in their habitats. Understanding the biological consequences of changes in these environments is essential for ecosystem management and conservation. However, our ability to study climate change impacts on Arctic marine mammals is generally limited by the lack of sufficiently long data time series. In this study, we took advantage of a unique dataset on hooded seal (*Cystophora cristata*) movements (and serum samples) that spans more than 30 years in the Northwest Atlantic to (i) investigate foraging (distribution and habitat use) and dietary (trophic level of prey and location) habits over the last three decades and (ii) predict future locations of suitable habitat given a projected global warming scenario. We found that, despite a change in isotopic signatures that might suggest prey changes over the 30-year period, hooded seals from the Northwest Atlantic appeared to target similar oceanographic characteristics throughout the study period. However, over decades, they have moved northward to find food. Somewhat surprisingly, foraging habits differed between seals breeding in the Gulf of St Lawrence vs those breeding at the "Front" (off Newfoundland). Seals from the Gulf favoured colder waters while Front seals favoured warmer waters. We predict that foraging habitats for hooded seals will continue to shift northwards and that Front seals are likely to have the greatest resilience. This study shows how hooded seals are responding to rapid environmental change and provides an indication of future trends for the species—information essential for effective ecosystem management and conservation.

## KEYWORDS

Arctic, climate change, ecological shift, foraging, future projections, hooded seals, ice-associated seal, suitable habitat, time series, warming

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## 1 | INTRODUCTION

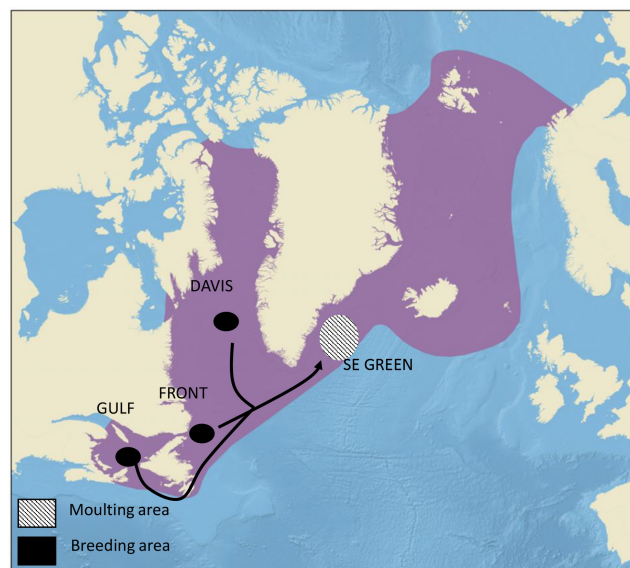
The Arctic has experienced the most rapid warming on the planet, with sea surface temperatures (SSTs) in the region increasing three times faster than anywhere else in the world (Comiso & Hall, 2014). The onset of intense warming has led to changes in sea ice extent and thickness as well as changes in sea ice phenology (ice formation and melting dates) (Kovacs et al., 2011; Laidre et al., 2015) and a deepening of the thermocline (Pachauri et al., 2014). This rapid environmental change has induced changes in ecosystem functioning by affecting marine life from phytoplankton to top predators (Deb & Bailey, 2023; Fossheim et al., 2015; Frainer et al., 2017; Kortsch et al., 2015; Pecuchet et al., 2020). Projected future climate conditions are expected to have cascading effects on Arctic marine habitats and food web structure, which could lead to regional extirpation or even complete extinction of already threatened species (Molnár et al., 2020; Stige et al., 2019). Monitoring the biological consequences of these environmental changes over time is therefore critical to understanding ecosystem dynamics and resilience, and to predicting future trends in the Arctic.

Because of their position at the top of marine food webs, and their close association with sea ice, pagophilic seals are considered good bio-indicators of Arctic ecosystem health (Hazen et al., 2019; Moore, 2008). These seals use sea ice as a haul-out platform for giving birth, lactation, moulting, resting and also for aquatic predator avoidance (Heide-Jørgensen & Laidre, 2004; Laidre et al., 2008; Stirling, 1997). Decreases in sea ice are therefore expected to result in reduced reproductive success, changes in their annual energy budgets (e.g. increased travelling distances between foraging and breeding areas) and decreased survivorship (e.g. Stenson et al., 2020). Sea ice declines will likely also impact the population dynamics of ice-associated seals by affecting their foraging efficiency and movement patterns linked to changes in the abundance and distribution of their prey, which may force these marine predators to either adjust their movements to these new prey distribution patterns or to change their diet (Gilg et al., 2012; Kovacs et al., 2011; Laidre et al., 2008, 2015). Long-lived species are unlikely to exhibit evolutionary responses at rates matching climate change. But distributional shifts and various expressions of behavioural, foraging and dietary plasticity are likely to be among the first observable responses to climate-induced changes in Arctic ecosystems (Gilg et al., 2012; Hoffmann & Sgro, 2011; Shuert et al., 2022).

Estimating behavioural, foraging and dietary plasticity responses of animals in response to environmental changes requires access to long-term movement datasets, ideally complemented by long-term sources of dietary information such as stomach contents (or at least animal tissues that can provide indirect information about prey consumed). However, time series long enough to assess such responses are rare, particularly in the marine realm (Hamilton et al., 2019; Laidre et al., 2015; Post et al., 2009). Hooded seals (*Cystophora cristata*) are one of the few ice-associated top

predators in the Arctic, for which studies of spatial ecology and diet have been carried out for multiple decades, and as such are an excellent model for exploring the long-term effects of environmental change on Arctic marine ecosystems. They are deep-diving, broad-ranging animals that are distributed throughout waters in the North Atlantic Arctic. They are highly dependent on drifting pack ice for pupping during breeding (March), and moulting (July) (Folkow & Blix, 1995; Hammill & Stenson, 2006). Declining sea ice and changes in water stratification may pose a serious threat to hooded seals (Andersen et al., 2009; Andersen, Skern-Mauritzen, et al., 2013; Andersen, Wiersma, et al., 2013; Bajzak et al., 2009; Folkow et al., 1996; Folkow & Blix, 1995; Hammill & Stenson, 2006; Kovacs, 2016; Vacquie-Garcia et al., 2017). Outside the breeding and moulting seasons, hooded seals spend most of the year foraging at sea, feeding on a wide variety of prey including pelagic fish (polar/arctic cod *Boreogadus saida*, capelin *Mallotus villosus*), demersal fish (redfish *Sebastes* spp., Greenland halibut *Reinhardtius hippoglossoides*) and squid (*Gonatus fabricii*) (Haug et al., 2007; Tucker et al., 2009).

Hooded seals are divided into two management stocks, one that breeds in the Northwest Atlantic and the other that breeds in the Greenland Sea (ICES, 2019), although the only available genetics study considered them to be one panmictic population (Coltman et al., 2007). Hooded seals from the Northwest Atlantic stock congregate for breeding off the north coast of Newfoundland (an area known as the FRONT), in the Gulf of St Lawrence (GULF) and in the Davis Strait (DAVIS), before migrating to southeast Greenland (SE GREEN) to moult (Figure 1). Subsequently, they spread through the Northwest Atlantic, including areas west of Greenland for the summer and autumn before returning to their respective breeding areas



**FIGURE 1** Hooded seal distribution map adapted from the North Atlantic Marine Commission website (<https://nammco.no/hooded-seal>). Breeding and moulting areas for the Northwest Atlantic hooded seal stock are shown with black and hatched areas, respectively, within the overall hooded seal range (in purple).

the following year (Bajzak et al., 2009). Previous studies of their foraging behaviour and dietary preferences have provided only snapshots of their foraging ecology (Andersen et al., 2009; Andersen, Skern-Mauritzen, et al., 2013; Andersen, Wiersma, et al., 2013; Bajzak et al., 2009; Hammill & Stenson, 2006; Haug et al., 2007; Tucker et al., 2009). However, the long-term patterns displayed in Northwest Atlantic hooded seals behaviour over the past few decades of dramatic change in the Arctic have never been analysed.

This study takes advantage of a unique ~30-year time series (1992–2019) of movement and serum sample collections for Northwest Atlantic hooded seals to investigate (i) if and how rapid environmental changes in the Arctic have impacted their foraging and dietary habits over time and (ii) how these parameters may change in the future given a probable environmental forecast scenario. To do this, we first investigated temporal patterns of hooded seal foraging habits (foraging distribution [spatial location of foraging habitats] and habitat use [oceanographic characteristics of these habitats]) as well as dietary habits (trophic level of prey and their habitat location) over the past 30 years. We then combined these results with a predictive climate model's output (CIMP6, i.e. Coupled Model Intercomparison Project Phase 6; Copernicus Climate Change Service Climate Data Store, 2021) to project the future location of suitable hooded seal foraging habitat. Considering the large environmental changes that have occurred in the North Atlantic over the past decades, especially the reduction of sea ice, we expect a distributional shift of areas suitable for foraging and perhaps also a change in the oceanographic characteristics of these habitats over time.

## 2 | MATERIALS AND METHODS

### 2.1 | Movement data collection

This study uses all available movement data obtained from biotelemetry/biologging instruments for adult hooded seals in the Northwest Atlantic stock (movement data provided—Vacquie-Garcia et al., 2023a, see “Data Availability Statement” section). This involves tracking data for 92 individuals, spanning a period from 1992 to 2019. Tagging was conducted during the breeding season (pupping—March) in the GULF and at the FRONT and during the moulting season (July) off SE GREEN (See Table S1 for a summary of satellite tag deployments, including deployment area and season, track duration and sex and mass of the tagged seals).

Tagging procedures were consistent across the different fields' seasons (see previously published articles described in Table S1 for more details). First, seals were captured with a V-shaped pole-net on the ice, they were then weighed and immobilized using tiletamine hydrochloride and zolazepam hydrochloride (Telazol; A.H. Robins Company, Richmond, VA, USA) administered intramuscularly (1 mg/100 kg). Finally, tags (Sea Mammal Research Unit, St. Andrews, Scotland) were glued to the head or upper neck of the seal using a quick-setting epoxy glue before the seals were released.

### 2.2 | Track filtering

Seals were fitted with different types of tags over time, but they all collected and transmitted Argos locations (via the Argos satellite system, Argos user's manual 2007–2016 CLS [<https://www.argos-system.org>]; Fedak et al., 2002). Geographic positions reported by the tags are assigned to location error classes (LC). Locations from tags deployed after mid-1994 were assigned to an LC of Z, B, A, O, 1, 2 or 3, with 3 being the most accurate location (error <250 m) and Z the least accurate (no actual location estimate achieved). Locations from tags deployed before mid-1994 were assigned a LC number from 3 to 0 (Argos user's manual; Service Argos, 1988), with an additional location indicator (LI) ranging from -10 to 0 for locations LC 0. Location Indicators 0/-1 correspond to locations where four or five satellite messages were received (equivalent to LC 0), LI -2/-3 and LI -4/-5 correspond to locations where two or three satellite messages were received (equivalent to LC A and B, respectively) and LI ≤ -6 correspond to rejected locations (equivalent to LC Z). To standardize the datasets, LI was used to convert the pre-mid-1994 locations into the LC system used for post-mid-1994 locations (LC Z, B, A, O, 1, 2 or 3) based on the descriptions above.

Data processing and analyses were performed using the R statistical framework (R Development Core Team, 2024). First, all repeated or invalid/rejected Z locations were removed. Then, we applied a Bayesian switching state-space model to the cleaned Argos locations. This was used to filter trajectories and to provide an estimate of behavioural state along the tracks of the animals by discriminating Areas Restricted Search (ARS)-type behaviours—that is, reduced swimming speed and increased track sinuosity—used as a proxy of the foraging activity (Benhamou & Bovet, 1989; Charnov, 1976), from transiting behaviours where seals maintain a higher swim speed and travel in a more directed manner (see Jonsen et al., 2005, 2013 for details).

We fit the Bayesian switching state-space model under a hierarchical framework (hSSSM) assuming that individuals are ‘samples’ of a population (which allowed us to analyse short/incomplete tracks; Flemming et al., 2010; Jonsen et al., 2003, 2006). hSSSMs contain a process model that predicts the future state (location and behavioural state) of an animal at fixed time intervals given its current state, estimating the movement parameters (including the combined autocorrelation  $\gamma$  in speed and direction) that allow animals to move from one location to another, and an observation model that corrects tracks for irregularities and variable errors in the observed Argos locations (see Jonsen et al., 2005, 2013; Lydersen et al., 2020). Tracks with data gaps >1 day were split into two or more segments, and tracks or track segments, shorter than 4 days or 10 locations were removed from the dataset because short tracks and/or with large gaps can lead to poor model fits (Lesage et al., 2017).

hSSSMs were run using the R package *bsam* via JAGS 4.2 (Just Another Gibbs Sampler, created and maintained by M. Plummer [<https://mcmc-jags.sourceforge.net>]) in seven separate rounds to allow convergence. Movement parameter priors were based on Jonsen et al. (2005, 2013) and Silva et al. (2013). Given the resolution

of the Argos-derived location data, we fitted hSSMs using a time-step of 2 h (e.g. the average time between Argos-derived locations). hSSMs ran two parallel Markov Chain Monte Carlo (MCMC) simulations, each of 180,000 iterations. The first 100,000 samples were discarded as a burn-in, and the 80,000 remaining samples were thinned by retaining 1 in 40 samples to reduce autocorrelation effects. Model parameters and estimates of seal's locations and behaviour states were thus calculated based on a total of 4000 MCMC samples. We visually assessed model convergence and sample autocorrelation.

Locations and behaviour states every 2 h along the tracks of seals were predicted from hSSM outputs. As outputs were comprised of 4000 estimates from the retained MCMC samples at each location (1 [transit] or 2 [ARS-type behaviour]), final behavioural states were calculated as the mean value of MCMC samples at a given location (i.e. continue values ranged from 1 to 2). The same process was applied to the longitude and latitude for each location.

### 2.3 | Track processing

Filtered tracks were associated with three different deployment decades: 1990s (deployments between 1990 and 1999), 2000s (deployments between 2000 and 2009) and 2010s (deployments between 2010 and 2019) (Table S1).

Tracks were then assigned to the different breeding areas (GULF or FRONT, Figures 1 and 2; Table S1). The boundaries of the different breeding areas were estimated from the deployment locations (i.e. first cleaned Argos locations, or second ones when the first ones were judged aberrant) of individuals equipped in the breeding season (Figure 3). For assigning tracks to the different breeding areas, we used (i) the deployment locations for individuals equipped in the breeding season, or (ii) the hSSM locations between March 7th and March 29th for individuals equipped in the moulting season (i.e. the estimated peak pupping period, corresponding to the minimum and maximum deployment date occurring in the breeding season; Hammill & Stenson, 2006). When no hSSM locations

occurred inside the GULF or at the FRONT breeding areas during the estimated pupping period, or when tags fell off or ceased to send data before this time, tracks were assigned to UNCERTAIN or NA breeding areas, respectively (Table S1).

Finally, tracks were split into seasons (post-moulting, post-breeding, see Figure 2). The post-moulting season was defined as the period from deployment, for individuals tagged in the moulting season, until the start of the next breeding season. Although the deployment date during the breeding season happened earlier over time (median date: March 20th in the 1990s, March 17th in the 2000s and March 7th in the 2010s), the start of the breeding season was set as March 17th, the median deployment date in the pupping period, regardless of the year (Figure 2). The post-breeding season was defined as the period (i) from deployment, for individuals tagged in the breeding season or (ii) from March 17th for individuals equipped in the moulting season, through until the tags ceased to transmit data (see Table S2 for details on season, breeding areas and decades).

### 2.4 | Environmental variables

We calculated two static (bathymetry [m] and minimum distance to the shore [km]) and three dynamic environmental variables (i.e. SST [°C], ice concentration [%] and salinity [psu]) at each seal location. Bathymetry was extracted from the 0.01° resolution ETOPO 1 Arc-Minute global relief data set from the National Geophysical Data Center, NOAA47. The minimum distance to the shore was computed from the land coastline (1:10m) shown at [www.natural-earthdata.com](http://www.natural-earthdata.com). Both SST and ice concentration were extracted from the 0.05° daily grid resolution from the Global Ocean OSTIA Sea Surface Temperature and Sea Ice Reprocessed (Good et al., 2020), while salinity was extracted from the 0.083° daily grid resolution from the Global Ocean Physics Reanalysis (<https://doi.org/10.48670/moi-00021>). The salinity product was not available prior to 1993, so 1993 salinity values were assigned to our 1992 location data.

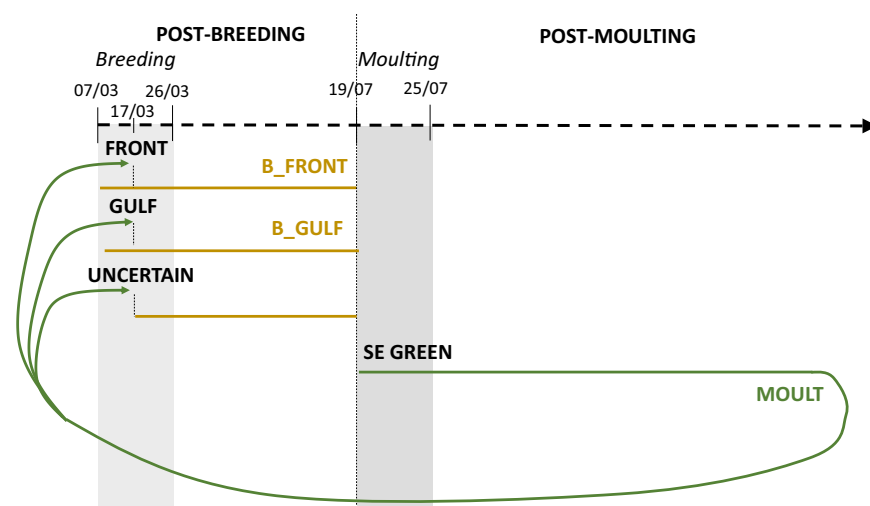
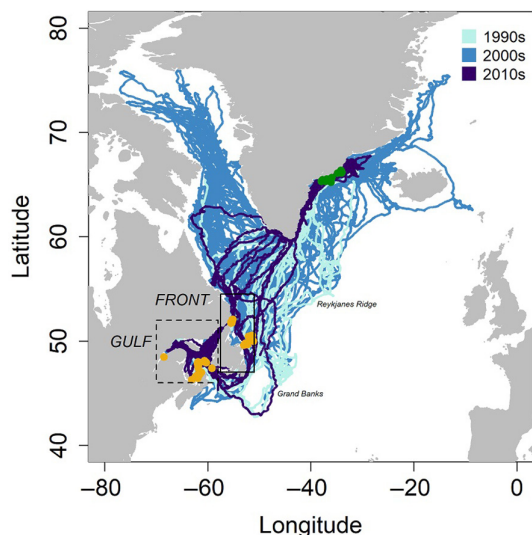


FIGURE 2 Deployment timeline of the Northwest Atlantic hooded seal stock and seal track patterns used in the temporal, distribution and habitat models (B\_FRONT, B\_GULF and MOULT). Breeding and moulting seasons are represented in light and dark grey, respectively. Green lines indicate the post-moulting segments of tracks while orange lines show the post-breeding segments of tracks in their respective breeding areas.



**FIGURE 3** Filtered tracks from 89 hooded seals from the Northwest Atlantic stock instrumented with satellite tags in the North Atlantic area in the 1990s, 2000s and 2010s. Blue lines correspond to 2 h seal locations inferred from the hierarchical switching state-space model (hSSSMs) during the three decades (light blue—1990s, medium blue—2000s and dark blue—2010s). Orange and green dots correspond to the first cleaned Argos locations of seals equipped during the post-breeding and the post-moulting seasons, respectively (see main text for further explanations). The plain and dotted boxes indicate the delimited GULF and FRONT breeding areas. The map was generated from publicly available land coast product available at [www.natural-earthdata.com](http://www.natural-earthdata.com).

## 2.5 | Distribution and habitat use models

### 2.5.1 | Model designs

We assessed potential shifts in foraging distribution over the past 30 years using the tracks from the past three decades (c.f. *distribution model*). To do this, we identified ARS patches along the hSSSM-filtered tracks and used them as a proxy for foraging activity. ARS patches were defined as starting after three or more successive locations with a behavioural state  $>1.75$  (i.e. foraging state according to Jonsen et al., 2007) and ending after three or more consecutive locations with a behavioural state  $\leq 1.75$  (corresponding to either a transiting behaviour ( $<1.25$ ) or uncertain state; Jonsen et al., 2007). We then modelled the changes in longitude and latitude of the identified ARS patch locations by decade in relation to the day of the year (i.e. number of days since January 1st). We included the duration of the ARS patches as a weighted parameter to take into account the longer versus shorter periods of ARS.

We also estimated changes in the timing of seal foraging and changes in habitat use over the past 30 years by examining changes in behavioural states by decade in relation to (1) day of the year (c.f. *temporal model*) and (2) oceanographic parameters (i.e. bathymetry, SST, ice concentration, salinity and minimum distance to shore—c.f.

*habitat model*). In these models, the response variable was the behavioural state directly (i.e. continuous values ranging from 1 to 2), which was averaged per day (as was also the case for oceanographic parameters) and logit transformed (after having converted the values from 0 to 1—the higher the logit transformed behavioural state value, the closer the behavioural state to an ARS-type behaviour).

Since the sample sizes in the different decades, seasons and breeding areas (Table S2) differed—and given that animals are located in the northwest part of the North Atlantic region during the breeding season while mostly in the Southeast Greenland during the moulting season, which could bias interpretations with unequal sample sizes—we ran the distribution, temporal and habitat models on three groupings of data. Since the main objective of this study was to investigate changes in foraging habits over the last three decades, the selections were done by seasons and/or breeding areas (Table S2). The first group consisted of data from the GULF breeding area in the post-breeding season (B\_GULF set of models hereafter) in the 1990s, 2000s and 2010s decades. The second group consisted of data from the FRONT breeding area in the post-breeding season in the 1990s and 2000s decades (B\_FRONT set of models hereafter). Finally, the third group consisted of data from the post-moulting season (MOULT set of models hereafter) only in the 2000s (and thus, in contrast with the other set of models, the MOULT model outputs could not be used to study changes over time). We grouped animals from both breeding areas together in the MOULT analyses because of the low sample size in the GULF animals relative to the FRONT ones, and the distribution model was not run for this season (Table S2).

Although some differences have been described between male and female hooded seals in terms of spatial distribution, diving behaviours (e.g. vertical segregation) and diets (Andersen, Skern-Mauritzen, et al., 2013; Bajzak et al., 2009), all hooded seal adults forage in similar habitats at a large scale (Bajzak et al., 2009). Thus, we decided not to consider gender in our models because we sought general patterns within the population over the last three decades; this also kept our model structure simple.

### 2.5.2 | Modelling approach

We used Generalized Additive Mixed Models (GAMMs ‘*gamm*’ function in the R package ‘*mgcv*’; Wood, 2006) to build the distribution, temporal and habitat models assuming Gaussian error distributions in the response variables. Day of the year and/or oceanographic parameters were included as a smooth term (knot value  $k$  was set at 5, 7 and 4 for distribution, temporal and habitat models, respectively—values chosen based on a trade-off between enough degrees of freedom [edf] to fit the data reasonably well but few enough to maintain reasonable computational efficiency). If output edf was equal to 1 for a given parameter, it was switched to a linear term in the rerun model. We included decade (i.e. 1990s, 2000s and 2010s) as a “by” variable (interaction term) in the day of the year and/or oceanographic parameter terms in order to compare patterns over

decades. The distribution, temporal and habitat use models were built as follows:

$$\text{LonARS / LatARS} \sim s(\text{day, by} = \text{Decade}) + \text{Decade}$$

$$\text{LogitBS}_{\text{day}} \sim s(\text{day, by} = \text{Decade}) + \text{Decade}$$

$$\text{LogitBS}_{\text{day}} \sim s(\text{bathymetry, by} = \text{Decade}) + s(\text{SST, by} = \text{Decade}) + s(\text{ice, by} = \text{Decade}) \\ + s(\text{minimum distance to shore, by} = \text{Decade}) + s(\text{salinity, by} = \text{Decade}) + \text{Decade}$$

where LonARS, LatARS and LogitBS<sub>day</sub> refer to the longitude and latitude of the identified ARS patches and the logit-transformed behavioural state averaged per day.

In each model, we included individual ID as a random effect and as a grouping factor in a first-order autoregressive correlation structure (corAR1) to minimize the effects of the hierarchical structure in the data. Collinearity between explanatory variables was checked when needed (when collinearity was  $\geq 0.8$ , only one variable was conserved in the model) and explanatory variables were standardized (i.e. zero mean and unit variance) (Zuur et al., 2009). For each model type, all the combinations of variables were tested and the models were ranked according to Akaike's information criterion (AIC) (Zuur et al., 2009). Models having  $\Delta\text{AIC} < 2$  were considered to be candidate models but when multiple candidate models had a delta AIC less than two, we chose the simplest model. We determined differences between decades using the confidence intervals of the corresponding smooth curves (when the confidence intervals of two curves for different decades were completely separated, the effect of the explanatory variable on the response variable was considered different between these two decades—Zuur et al., 2009). We used diagnostics and temporal autocorrelation assessment plots to validate final models.

## 2.6 | Tissue data collection and dietary habits

Stable isotope analyses are useful in combination with movement data because they provide indirect information on the trophic position and habitat of prey (coastal vs. offshore or pelagic vs. benthic) at a timescale relevant to the tissue turnover rate (Cherel et al., 2008; Kiszka et al., 2010; Meissner et al., 2011; Newsome et al., 2010), and can be compared over time (Heithaus et al., 2013; Lesage et al., 2001; Zhao et al., 2004). Specifically,  $\delta^{13}\text{C}$  is commonly used as an indicator of the feeding area of consumers, as their  $\delta^{13}\text{C}$  ratios a priori reflect those of the primary producers at the base of a specific food chain that varies regionally. The  $\delta^{15}\text{N}$  are used as indicators of the relative trophic level at which an organism has fed (Minagawa & Wada, 1984; Montoya, 2007; Peterson & Fry, 1987) since consumers are enriched in  $^{15}\text{N}$  relative to their food (De Niro & Epstein, 1981; Méndez-Fernandez et al., 2012; Vanderklift & Ponsard, 2003).

In our study, 45 serum samples from Northwest adult hooded seals were used to estimate temporal changes in their dietary habits over time. Samples were collected during the breeding season in the period from 1995 to 2018/2019 in the GULF (Table S3). The

integration time for serum is approximately 1–2 weeks (Lesage et al., 2002), so this analysis provides us with information on the habits of seals in the weeks immediately prior to breeding.

Stable isotope analyses were performed at the Littoral Environment and Societies laboratory (LIENs) at La Rochelle University in France. Since lipids are highly depleted in  $^{13}\text{C}$  relative to other tissue components (De Niro & Epstein, 1978), lipids were extracted from the samples using cyclohexane. Each sample (1 mL) was freeze-dried and then lipid extraction was performed using 4 mL of cyclohexane for 30 min at room temperature; this step was repeated at least two times (up to four times for three samples). The samples were then centrifuged for 10 min at 1000 g at 10°C, and the supernatant containing the lipids was discarded. Finally, the samples were dried overnight and subsamples of  $0.50 \pm 0.004$  mg ( $\pm\text{SE}$ ) of lipid-free powder were placed in tin cups for stable isotope measurements that were performed with a continuous-flow isotope ratio mass spectrometer (Delta V Plus with a Conflo IV interface; Thermo Scientific, Bremen, Germany). The stable isotope ratio for carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) are given in mean  $\pm$  SD ‰ (stable isotope ratio provided, Vacqu e-Garcia et al., 2023b; see "Data Availability Statement" section).

To compare  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios between decades, linear models were used. Since dietary differences have been described between male and female hooded seals (Lesage et al., 2001), effect of gender on the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios was also assessed in the same models. AIC was used to select the best models (keeping the simplest model when  $\Delta\text{AIC}$  was smaller than 2). All samples that were chemically analysed were retained for statistical analysis since lipid extraction appeared successful in all cases (% C to % N ratios  $< 4$ ; Kiszka et al., 2014; Lesage et al., 2010). Ratios of  $\delta^{13}\text{C}$  were corrected for the Suess effect (Teixeira et al., 2022), using the SuessR package, prior to modelling, with 2019 used as our reference year.

## 2.7 | Predicted future suitable foraging habitat in response to global warming

We applied the habitat model with the best support for each model grouping (B\_GULF, B\_FRONT and MOULT [from Section 2.5]) to (i) past oceanographic conditions and (ii) future oceanographic conditions predicted in response to a climate warming scenario, to investigate how suitable seal habitats are expected to change over time. To do so, we constructed a grid with a 25 km  $\times$  25 km resolution encompassing the entire hooded seal distribution range (adapted from the North Atlantic Marine Mammal Commission website map: <https://nammco.no/hooded-seal>). We then extracted oceanographic parameters (see Section 2.4) for each grid cell on the 15th of each month for (i) the years 1993 (representing the 1990s), 2007 (representing the 2000s) and 2018 (representing the 2010s) and (ii) the years 2050 and 2100. We used the INM-CM5-0 model (from the Institute for Numerical Mathematics—50-km precision) of the SSP5-8.5 climate change scenario (Shared Socio-economic Pathways; IPCC, 2022), that is, the CMIP6 'worst case scenario' of the plausible

future climate change projections, to extract SST, ice concentration and salinity for 2050 and 2100 (available from <https://cds.climate.copernicus.eu>; Copernicus Climate Change Service Climate Data Store, 2021). Finally, we predicted daily behavioural states of seals for each geographic cell, month and year, for each habitat model.

Habitat models only provide information on animal preferences within ranges of oceanographic parameters that were actually encountered by the seals, and thus included in the range of each explanatory variable in the habitat models. Consequently, we assigned NA (i.e. uncertain habitat) to predicted daily behavioural states when the cell values of one or more extracted environmental parameters were below or above the corresponding parameter range in the models. Dynamic oceanographic variables were extracted from different available data products in the past (see Section 2.4) and future years (Copernicus, CIMP6). These products have different uncertainties around their estimated oceanographic variables, so we attempted to buffer these differences by artificially increasing the ranges of each dynamic explanatory variable in our habitat models by a  $\pm 5\%$  extra buffer (i.e. we increased/decreased the higher and lower limits in ranges of dynamic variables by 5%).

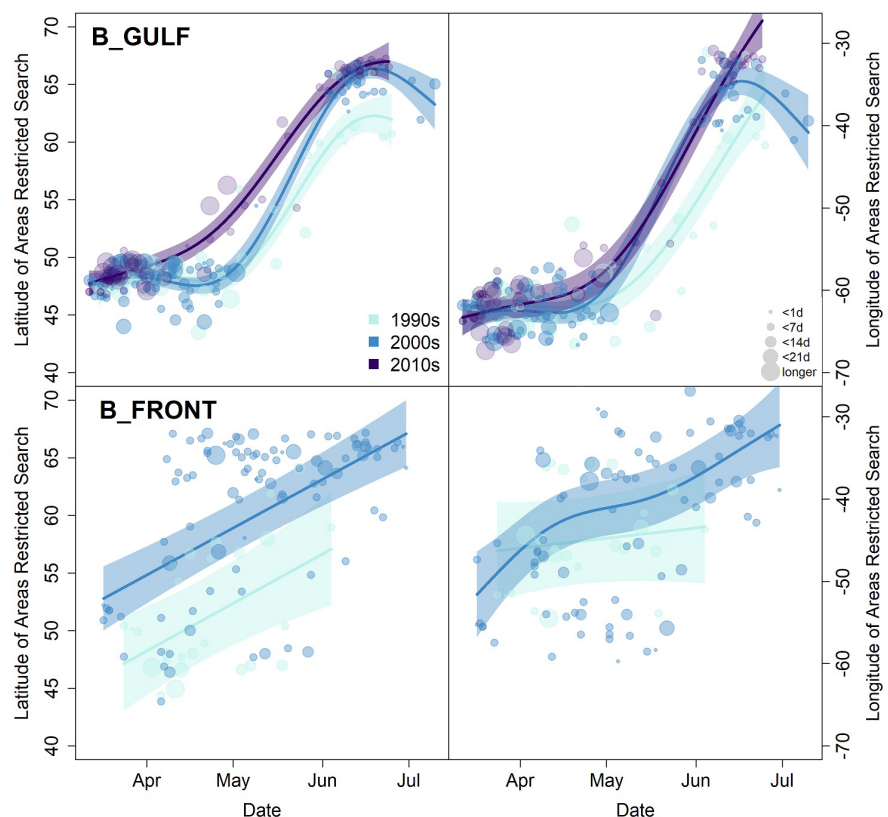
### 3 | RESULTS

A total of 191,019 raw locations from the 92 tagged seals were obtained, with deployments lasting from 6 to 354 days (average  $136 \pm 10$  days,  $\pm$ SE, Table S1). The track cleaning and selection process resulted in the loss of 14.5% of locations and all of the data from

3 of the 92 seals. The hSSSMs run on the remaining data provided two behavioural states for which the posterior marginal distributions of the movement parameter  $\gamma$  (combined autocorrelation in speed and direction) did not overlap during transiting-type behaviour (behavioural state 1—95% CI:  $0.71 \pm 0.05$  to  $0.75 \pm 0.04$ ) and during ARS-type behaviour (behavioural state 2—95% CI:  $0.0003 \pm 0.0001$  to  $0.03 \pm 0.01$ ). The hSSSMs model outputs provided 142,412 predicted locations and behavioural states for the 89 remaining seals at 2 h intervals (Figure 3; Table S2).

#### 3.1 | Distribution shifts

A total of 199 ARS patches were identified along the tracks of GULF seals (mean duration  $8.4 \pm 0.64$  days to  $3.35 \pm 0.30$  per individual) and 120 along the tracks of FRONT seals (mean duration  $5.9 \pm 0.58$  days to  $3.44 \pm 0.36$  per individual, see Table S2). Both B\_GULF and B\_FRONT distribution models showed that ARS patches were located along northeastward migratory paths during the post-breeding season, with a tighter correlation between the spatial occurrence of ARS patches and time of the season for the B\_GULF than the B\_FRONT models (Figure 4). The B\_GULF and B\_FRONT distribution models suggested that seals migrated northward earlier in the latest studied decade (2000s for FRONT animals and 2010s for GULF animals) than in the 1990s. For GULF animals, north migration also occurred earlier in the 2000s than in the 1990s in the month of June (Figure 4; Table 1). In addition, the ARS patches were located significantly further north and east (for GULF seals only; Figure 4;



**FIGURE 4** Temporal variation in latitude and longitude of the Areas Restricted Search (ARS, interpreted as potential foraging spots) identified along the hierarchical switching state-space model (hSSSMs) filtered Northwest Atlantic seal tracks for the B\_GULF and the B\_FRONT distribution models over the different decades (light blue—1990s, medium blue—2000s and dark blue—2010s). Dots of different sizes represent the ARS, weighted by duration in days. Solid lines and shaded areas represent the fitted estimates and their respective confidence intervals, as calculated from the variance-covariance matrices of the random effects of the fitted models.



**TABLE 1** Summary outputs of the B\_GULF and the B\_FRONT distribution models, estimating the temporal variations in latitude and longitude of Northwest Atlantic hooded seals Areas Restricted Search (ARS) over the different decades sampled.

Response	Model	Estimate	t-Value	p-Value	edf	F	p-Value	Phi-value	Adjusted R <sup>2</sup>	
Latitude of ARS	B_GULF	Intercept	51.86	150.97	<.005	3.85	108.7	<.005	0.24	.95
		2000s	1.25	2.92	<.005	3.96	509.0	<.005		
		2010s	2.72	6.12	<.005	3.66	395.4	<.005		
	B_FRONT	Intercept	35.69	7.82	<.005	-	-	-	0.64	.46
		2000s	6.76	1.30	.20	-	-	-		
		day:2000s	-0.002	-0.04	.97	-	-	-		
Longitude of ARS	B_GULF	Intercept	-56.35	-77.22	<.005	3.21	65.0	<.005	0.20	.91
		2000s	1.87	2.06	.04	3.91	280.1	<.005		
		2010s	3.22	3.40	<.005	3.32	272.7	<.005		
	B_FRONT	Intercept	-44.58	-16.11	<.005	1	0.60	.44	0.57	.18
		2000s	3.85	1.21	.23	2.92	16.16	<.005		

Table 1) as decades went by. The pattern observed for GULF seals seems to be accentuated in June–July between the 1990s and the more recent decades (Figure 4).

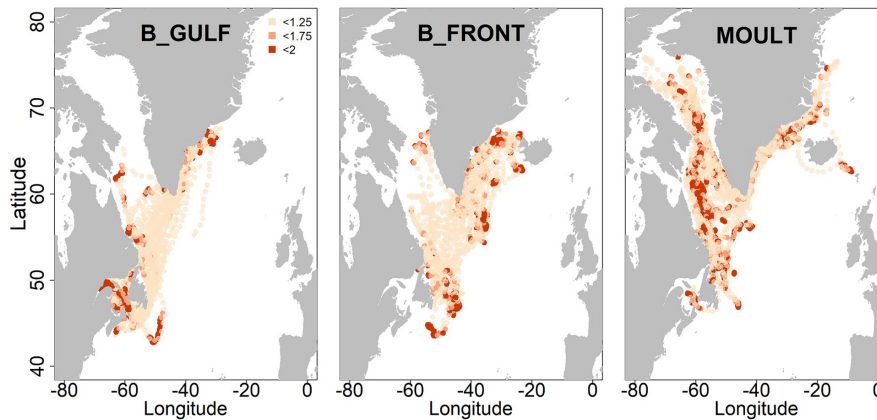
### 3.2 | Habitat use

Daily behavioural states of the seals ranged from 1 to 2 (Figure 5). Daily mean values for bathymetry ranged from 1 to 4174 m ( $920 \pm 9$  m). Mean daily SST ranged from  $-1.9$  to  $14.0^\circ\text{C}$  ( $1.8 \pm 0.1^\circ\text{C}$ ) and ice concentration ranged from 0% to 100% ( $11\% \pm 0.2\%$ ). Mean daily salinity ranged from 18.5 to 35.7 psu ( $32.7 \pm 0.1$  psu) and minimum distance to the shore ranged from 1 to 837 km ( $161 \pm 1$  km) along the tracks in all years sampled.

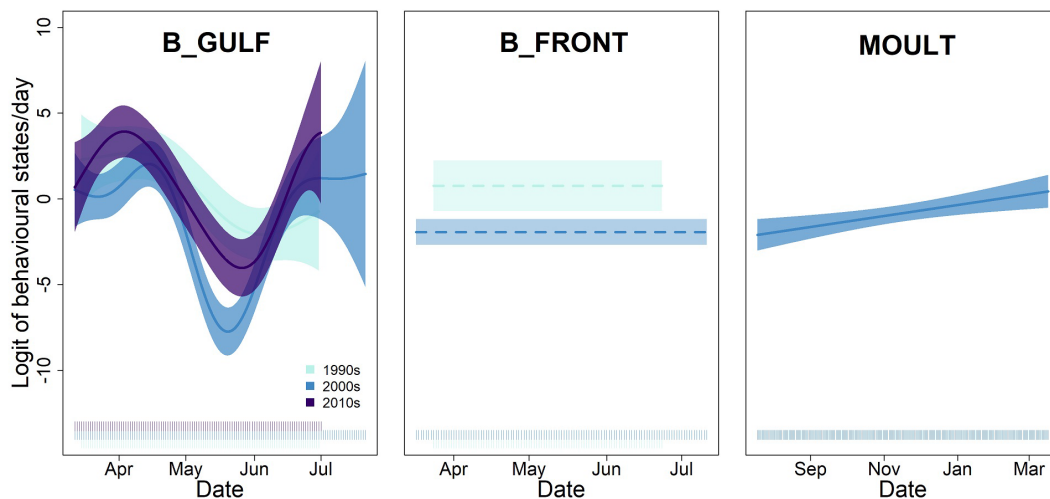
The B\_GULF temporal model showed that GULF seals spent significantly more time in ARS-type behaviour in March/mid-April (post-breeding) and in June–July (pre-moulting) than in April/May (Figure 6; Table 2) in all three decades (the curves overlap despite higher behavioural state values in the 2010s than in the 2000s, Figure 6). Seals performed the most ARS-type behaviour in the GULF and SE GREEN (Figure 5). Ice concentration, salinity, bathymetry and SST all affected the behavioural state values of the seals significantly in the B\_GULF habitat model (Table 3; Figure 7, minimum distance to the shore was excluded as it was collinear with bathymetry). ARS-type behaviour increased significantly with ice concentration and decreased with salinity, bathymetry (first increasing up to 1000 m and then decreasing) and SST (Figure 7). Trends remained similar between decades for all four oceanographic parameters, even though time spent in ARS-type behaviour seemed to increase in the 2010s compared to the 2000s in some cases.

The B\_FRONT temporal model showed no effect of season on the behavioural state in the 1990s or the 2000s (even though time spent in ARS-type behaviour was higher in the 2000s, Table 2; Figure 6), which suggests that FRONT seals have not changed their ARS behaviour patterns during the post-breeding season and over decades. The seals spent more time in ARS-type behaviour on the shelves of the Grand Banks, along Reykjanes Ridge and in pelagic waters south-east of Greenland (Figure 5). The B\_FRONT habitat model showed that time spent in ARS-type behaviour increased significantly with ice concentration, SST and minimum distance to the shore (small decrease of behavioural state up to 200 km away from the coast and then it increased, with maximum time spent in ARS-type behaviour at long distances from the coast), and decreased with bathymetry (salinity was not significant, Table 3; Figure 8). Trends between behavioural states and oceanographic parameters were similar between decades, even though there was a greater tendency to be in ARS-type behaviour overall in the 1990s compared to the 2000s [some relationships were non-significant at a 5% threshold in the 1990s (Figure 8)].

The MOULT temporal model showed a linear increase in behavioural state (i.e. more ARS-type behaviours) post-moult (Table 2; Figure 6), with animals increasing their ARS activity gradually towards Feb/March (before breeding) in the Labrador Sea and Davis Strait (Figure 5). Seal behavioural states from the MOULT habitat model increased significantly with ice concentration and minimum



**FIGURE 5** Daily average behavioural states of Northwest Atlantic hooded seals breeding in the GULF, in the FRONT and moulting in the SE GREEN, as used in the B\_GULF, B\_FRONT and MOULT temporal and habitat models, respectively—the two first panels involve the post-breeding season while the third panel involve the post-moulting season only. Light to dark colours represent the mean daily behavioural states from  $<1.25$  (i.e. transiting) to  $>1.75$  (i.e. foraging). The maps were generated from publicly available land coast products available at [www.naturalearthdata.com](http://www.naturalearthdata.com).



**FIGURE 6** Temporal variation in Northwest Atlantic hooded seal daily behavioural state (logit converted) obtained from the B\_GULF, the B\_FRONT and the MOULT temporal models over different decades. The higher the logit transformed behavioural state value, the closer the behavioural state to foraging. Lines and shaded areas represent the fitted estimates and their respective confidence intervals, as calculated from the variance-covariance matrices of the random effects of the fitted models. Solid lines indicate significant relationship (at a 5% threshold) while dashed lines indicate non-significance. Different shades of blue indicate different decades (light blue—1990s, medium blue—2000s and dark blue—2010s).

distance to the shore and decreased with bathymetry and salinity (SST was not significant, Table 3; Figure S1).

### 3.3 | Dietary habits

Females and males sampled in the GULF had Suess-corrected  $\delta^{13}\text{C}$  values of  $-18.05 \pm 0.22\text{‰}$  and  $-18.04 \pm 0.15\text{‰}$ , respectively, in the 1990s and  $-18.24 \pm 0.21\text{‰}$  and  $-18.10 \pm 0.23\text{‰}$  in the 2010s.  $\delta^{15}\text{N}$  ratio were  $17.33 \pm 0.41\text{‰}$  and  $18.24 \pm 0.44\text{‰}$  for females and males, respectively, in the 1990s and  $16.18 \pm 0.42\text{‰}$  and  $17.41 \pm 0.22\text{‰}$  in the 2010s. The  $\delta^{13}\text{C}$  values decreased significantly from the 1990s to the 2010s

(estimate 2010's =  $-0.16$ ,  $t$ -value =  $2.48$  and  $p$ -value =  $.02$ , Figure 9) for both sexes (sex had no impact on the Suess-corrected  $\delta^{13}\text{C}$  ratios). Both male and female hooded seals showed significantly lower  $\delta^{15}\text{N}$  values in the 2010s compared to the 1990s (estimate 2010's =  $-1.07$ ,  $t$ -value =  $-8.85$  and  $p$ -value  $< .005$ ), with higher values for males than females (estimate Males =  $1.07$ ,  $t$ -value =  $7.38$  and  $p$ -value  $< .005$ , Figure 9).

### 3.4 | Predicted future suitable foraging habitats

The best habitat models (B\_GULF and B\_FRONT) were used to predict past and future foraging habitats across the entire hooded seal

**TABLE 2** Summary outputs of the B\_GULF, B\_FRONT and MOULT temporal models, investigating the temporal variation of daily behavioural states of the Northwest Atlantic hooded seals over the different decades sampled.

Model	Estimate	t-Value	p-Value	edf	F	p-Value	Phi-value	Adjusted R <sup>2</sup>
B_GULF	Intercept	1.25	.21	3.21	7.04	<.005	0.88	.37
	2000s	-3.71	<.005	5.54	19.54	<.005		
	2010s	-0.36	.72	4.80	10.44	<.005		
B_FRONT	Intercept	1.01	.31	-	-	-	0.89	.06
	2000s	-3.21	<.005	-	-	-		
MOULT	Intercept	-3.88	<.005	-	-	-	0.88	.03
	day	3.11	<.005	-	-	-		

range. As temporal resolution of raw locations differed between decades (more numerous in the 2000s and 2010s than in the 1990s), so did their location accuracy, and ultimately the resulting accuracy of behavioural state estimation (based on these initial locations). This difference in estimate accuracy between decades means that the probability of identifying ARS-type behaviours might be higher in the later decades than in the earlier ones. Consequently, comparisons of absolute values of behavioural states between decades might not be entirely reliable. However, comparisons of relative trends from the temporal and habitat models between decades would.

With this in mind, we did not detect any significant change in relative trends in habitat use over a decade for the B\_GULF and the B\_FRONT habitat models (Figures 7 and 8). Thus, data from all decades were combined in each of these models to build global habitat models (without any new model selection), and we then used the output to predict past and future suitable foraging habitats (Figures S2 and S3). The adjusted-R<sup>2</sup> of the best MOULT habitat model was too low (.01—Table 3) to be relevant for prediction, so we did not pursue analyses further for this season.

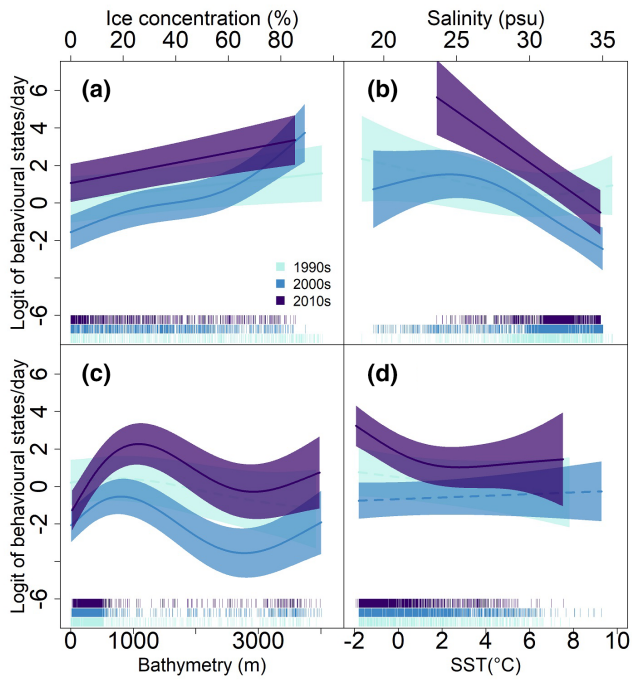
Spatial predictions from the B\_GULF global habitat model showed that habitats where ARS-type behaviour was expected to occur decreased over time (from the 1990s to 2100) for all months of the post-breeding season, while uncertain habitats expanded (Figures 10 and 11a). Northwest and Northeast Greenland remain suitable for this type of behaviour in the future, but the areas where animals exhibited the highest value of predicted ARS-type behaviour in the past three decades (GULF in March–April and SE GREEN in June–July) become unfavourable by 2050 (Figure 10). Habitats of high value for ARS-type behaviour predicted by the B\_FRONT global habitat model also decreased over time (Figures 11b and 12), with future favourable habitats also being located primarily in Northeast and Northwest Greenland. However, in contrast to the spatial predictions from the B\_GULF global habitat model, areas where seals breeding at the FRONT exhibited the highest value of predicted ARS-type behaviour in the past 30 years (over the shelves of the Grand Banks, in Reykjanes Ridge and SE GREEN) in April, May and June–July, remain favourable in 2050 and beyond to 2100 to some extent (Figure 12).

## 4 | DISCUSSION

The Arctic is a global climate 'hot-spot' that has already experienced sharp increases in air and SSTs and decreases in sea ice cover. This is expected to continue, and a seasonally ice-free Arctic is projected before the end of this century (Overland et al., 2010; Wang & Overland, 2009). These changes pose significant challenges to Arctic ecosystems, with potential declines in suitable habitats for ice-associated species (Overland, 2020; Overland et al., 2019; Peng et al., 2020; Ribeiro et al., 2021), as well as shifts in spatial distribution, in community composition and ecosystem structure and functioning (Grimm et al., 2013). In this study, we show that environmental changes have already resulted in hooded seals shifting the

TABLE 3 Summary outputs of the B\_GULF, B\_FRONT and MOULT habitat models, investigating the relationship between oceanographic parameters and daily behavioural states of Northwest Atlantic hooded seals over the different decades sampled.

Model	Estimate	t-Value	p-Value	edf	F	p-Value	Phi-value	Adjusted R <sup>2</sup>
B_GULF	Intercept	0.42	.47	2.25	2.82	.12	0.90	.28
	2000s	-2.08	<.005	2.96	17.47	<.005		
	2010s	0.30	.69	2.96	23.98	<.005		
	-	-	-	1.20	0.93	.29		
	-	-	-	1	0.34	.56		
	-	-	-	2.49	10.90	<.005		
	-	-	-	1	4.13	.04		
	-	-	-	2.78	23.85	<.005		
	-	-	-	1	20.82	<.005		
	-	-	-	2.13	2.69	.10		
B_FRONT	Intercept	-2.18	<.005	2.55	6.62	.0056	0.87	.27
	BATHY	-1.39	<.005	1	0.01	.91		
	ICE	0.98	<.005	2.90	16.10	<.005		
	1990s	2.7	<.005	1	0.28	.59		
	BATHY:1990s	0.89	<.005	-	-	-		
	ICE:1990s	-0.54	.09	-	-	-		
	Intercept	-0.88	<.005	1.80	3.10	.03	0.89	.01
	COAST	0.60	<.005	2.77	46.05	<.005		
	-	-	-	2.73	8.89	<.005		
	-	-	-	-	-	-		

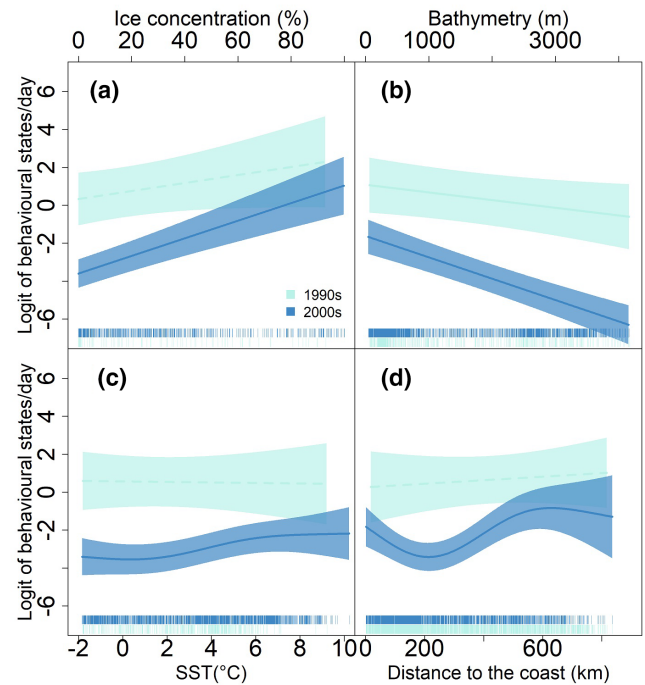


**FIGURE 7** Effect of Ice concentration (a), salinity (b), bathymetry (c) and sea surface temperature [SST, (d)] on the daily behavioural states (logit transformed) of the Northwest Atlantic hooded seals for the B\_GULF habitat model. The higher the logit transformed behavioural state value, the closer the behavioural state to foraging. Lines and shaded areas represent the fitted estimates and their respective confidence intervals, as calculated from the variance-covariance matrices of the random effects of the fitted model. Solid lines indicate significant relationship (at a 5% threshold) while dashed lines indicate non-significance. Different shades of blue indicate different decades (light blue—1990s, medium blue—2000s, and dark blue—2010s).

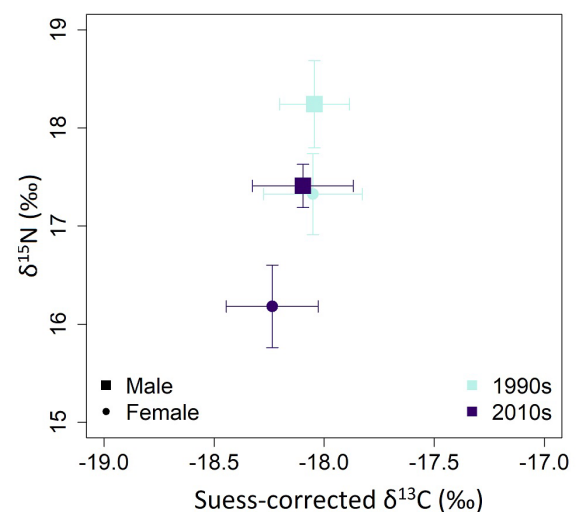
areas in which they search for food northward in recent decades and that they have shifted the phenology of their migration as well. We predict that this will continue if hooded seals maintain their habitat preferences.

#### 4.1 | Foraging and dietary habit changes in the past 30 years

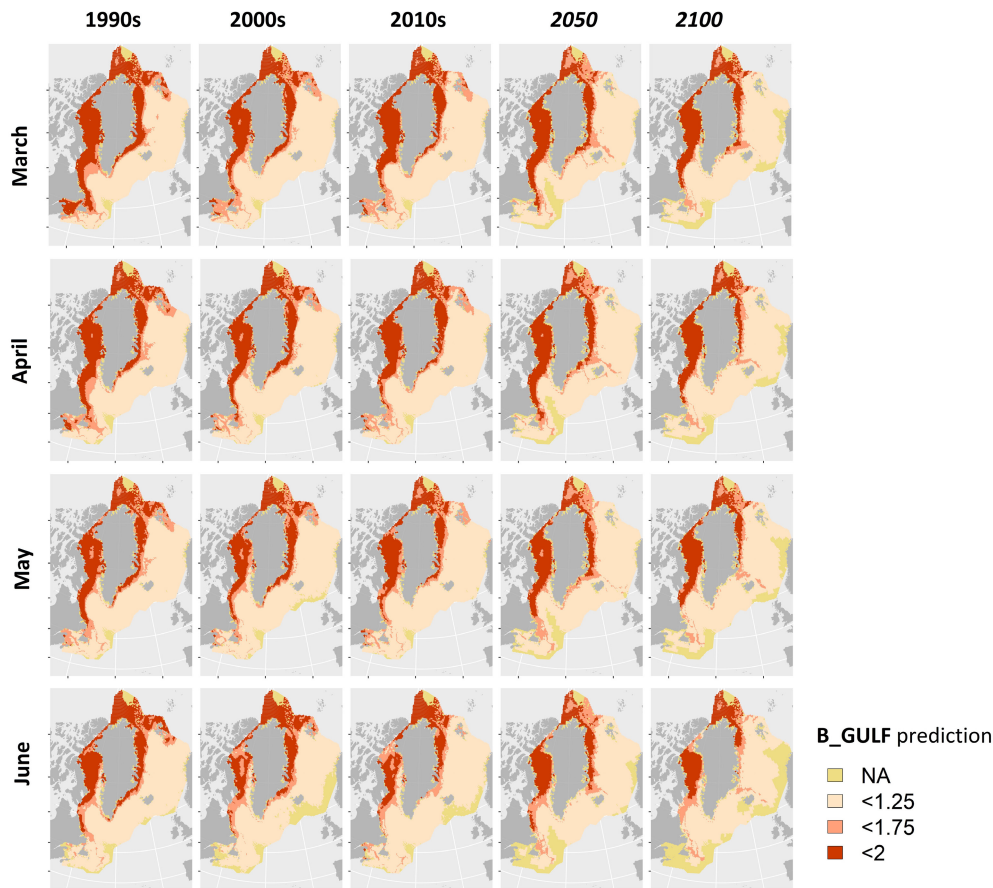
In this study, high behavioural state values (high proportion of time in an ARS-type behaviour) and ARS patches were used as foraging indicators (e.g. seals were likely searching for prey). However, high foraging efficiency in an area could in reality result in less time spent feeding (Florko et al., 2023). It is also important to keep in mind that the characteristics of ARS-type behaviour (i.e. decrease in swimming speed and increase in sinuosity), may also characterize other types of behaviours not necessarily linked to foraging, such as haul-out behaviour. Haul-out time was not systematically recorded in the 1990s tags (Table S1), so this information could not be processed further in the filtration and analysis processes. Some locations classified as ARS-type behaviour by the hSSSM could thus in reality be



**FIGURE 8** Effect of Ice concentration (a), bathymetry (b), sea surface temperature [SST, (c)] and distance to the coast (d) on the daily behavioural states (logit transformed) of the Northwest Atlantic hooded seals for the B\_FRONT habitat model. The higher the logit transformed behavioural state value, the closer the behavioural state to foraging. Lines and shaded areas represent the fitted estimates and their respective confidence intervals, as calculated from the variance-covariance matrices of the random effects of the fitted model. Solid lines indicate significant relationship (at a 5% threshold) while dashed lines indicate non-significance. Different shades of blue indicate different decades (light blue—1990s, medium blue—2000s).



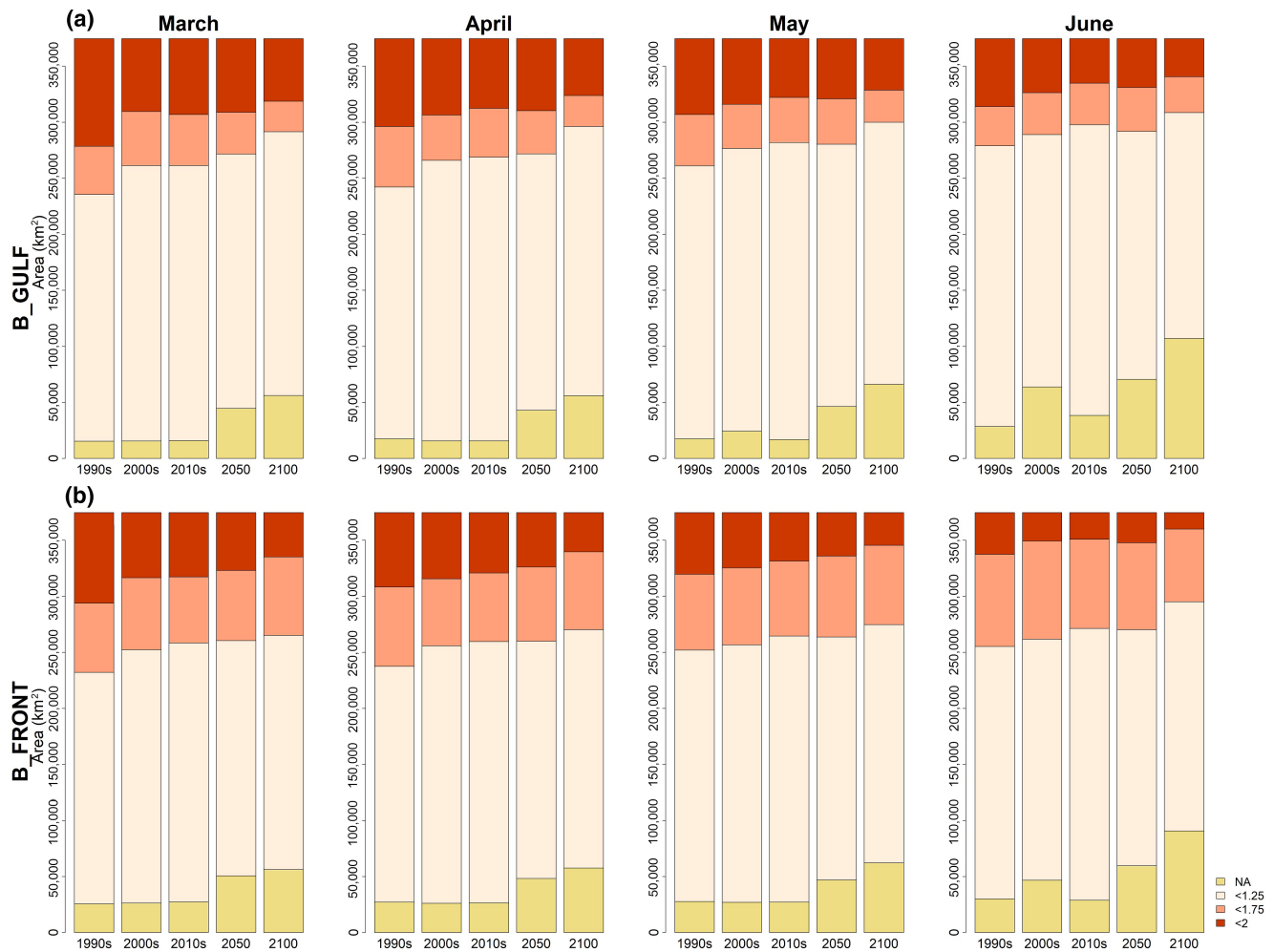
**FIGURE 9** Stable isotope ratio (mean  $\pm$  SD) for nitrogen ( $\delta^{15}\text{N}$ ) and Suess-corrected carbone ( $\delta^{13}\text{C}$ ) in 45 Northwest Atlantic hooded seals serum samples sampled in the Gulf of St Lawrence (GULF) during the breeding season in the 1990s (light blue) and in the 2010s (dark blue) for males (squares) and females (circles).



**FIGURE 10** Suitable habitat for the Northwest Atlantic hooded seals based on predicted daily behavioural states obtained from the B\_GULF habitat model for March, April, May and June in the 1990s, 2000s, 2010s and for the future in 2050 and 2100. Colours represent areas where seals will likely display foraging based on the local oceanographic parameters, dark red representing foraging (i.e. predicted daily behavioural state  $>1.75$ , i.e. suitable habitat), while areas where they are unlikely to display foraging are represented in light pink (representing transiting i.e. predicted daily behavioural state  $<1.25$ , i.e. unsuitable habitat). Geographic cells in yellow represent predictions outside the model ranges (assigned to NA). Predictions for 2050 and 2100 are based on predicted oceanographic parameters from the CMIP6 SSP5-8.5 scenario (<https://cds.climate.copernicus.eu>).

haul-out behaviour. Based on available haul-out information ( $N=19$ ; Table S1), we found that the hooded seals hauled-out primarily in June ( $30.0\% \pm 5.6\%$  of their time vs.  $<15\% \pm 2.3\%$  for the other months— $N=19$ ). This month was also the month with the highest proportion of locations identified as being ARS-type behaviours by the hSSSM—which were, in reality, haul-outs ( $45.6\% \pm 8.3\%$  of locations with a behavioural state  $>1.75$  corresponding to haul-out periods in June vs.  $<22.2\% \pm 4.7\%$  for the other months). To confirm that haul-out periods did not significantly bias outputs from our models, we compared the results of the B\_GULF and B\_FRONT habitat models that included June data with models that excluded them. There were no significant differences (Figures S4 and S5). Therefore, we conclude that the habitat models were reliable for inferring foraging area preferences. To summarize, ARS-type behaviours and ARS patches were interpreted as foraging activity in this study, but it is necessary to keep in mind the possibility for false positives and false negatives in model outputs (i.e. foraging activity could occur in areas not associated with ARS-type behaviours, and haul-out behaviours could be confused for ARS behaviours, especially in June).

After breeding, seals from the GULF remained in the general area to forage during March–April. Subsequently, they crossed the Davis Strait rapidly and resumed foraging off SE GREEN until they moulted. In these two foraging areas, seals targeted consistent oceanographic conditions over time despite the large environmental changes that occurred (Heide Jørgensen et al., 2022; Long et al., 2016). They consistently preferred shallow waters (around 1000m) targeting shelf edges, with low SSTs and low salinity across all three decades, similar to what has been documented in previous studies (Andersen, Wiersma, et al., 2013); some of these areas were characterized by high ice concentrations. However, their migration has shifted earlier in the year across the study period and foraging locations have shifted northward especially in the period from April to June–July and eastward in the period from May to June–July, with the strongest northward and eastward shift in June–July. These changes in distribution suggest that hooded seals may track specific prey that exhibits strong preferences for specific oceanographic conditions (Morley et al., 2018; Peck & Pinnegar, 2018). While animals spend a lot of time in areas with little or no ice ( $55.0\% \pm 2.4\%$  of their time in

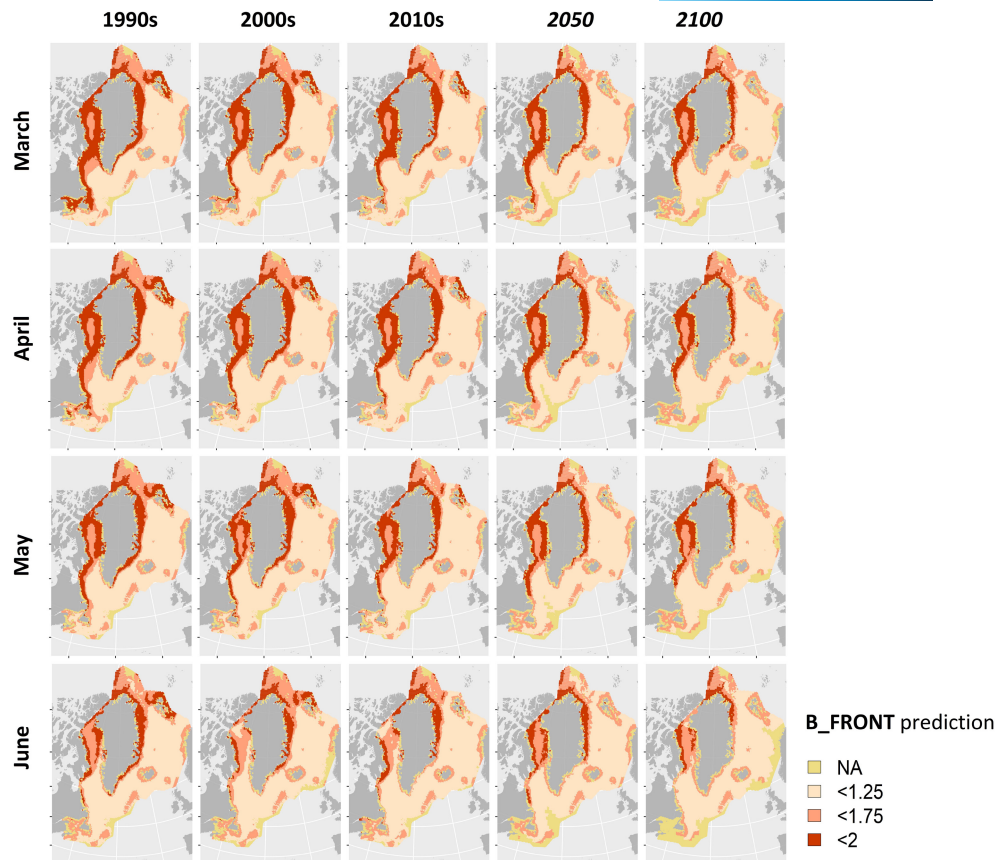


**FIGURE 11** Areas of suitable foraging habitats for Northwest Atlantic hooded seals over decades based on the B\_GULF (a) and B\_FRONT (b) habitat models.

ice-free areas, and see Andersen, Wiersma, et al., 2013), our habitat model suggests that high ice concentrations were still highly favourable foraging locations. The preference for these high ice cover areas might be in part due to access to sea ice resting platforms for hauling out. However, some key hooded seal prey species are known to be ice-associated, and time in ice-covered habitats could increase foraging efficiency (decrease search and transit time) (David et al., 2016). As migrating animals will travel to specific locations at given times of year for life cycle events, it is also possible that these time-locations nexus condition preference for sea ice to forage at specific times of the year where they seasonally are. After foraging in the post-breeding and pre-moulting periods, hooded seals begin hauling out in June (with  $30.0\% \pm 5.6\%$  of their time hauling out in that month) and July. Thus, the observed decadal distributional shift in June–July likely results, at least partly, from the search for reliable drifting sea ice platforms for moulting, which are found further northeast over the last three decades, along the southeast coast of Greenland.

The oceanographic characteristics of the foraging areas selected by GULF seals (i.e. GULF and SE GREEN areas) are consistent with Arctic refugia (Haug et al., 2007; Lesage et al., 2001), where benthic

or demersal prey, such as polar/arctic cod, redfish and Greenland halibut are available (Bowering, 1982; Lesage et al., 2001; Savenkoff et al., 2007). However, dietary habits of the seals foraging in the GULF just before breeding changed significantly between 1995 and 2018/2019, as indicated by stable isotope analyses. Suess-corrected  $\delta^{13}\text{C}$  ratios decreased during this period (similarly for both sexes). This suggests that while males and females generally remained in similar areas for foraging, the seals likely foraged on prey originating from further offshore in the 2010s compared to the 1990s (Hobson, 1999). The  $\delta^{15}\text{N}$  ratios also revealed a significant decrease from the 1990s to the 2010s, which might suggest that hooded seals shifted over decades to feed on prey at lower trophic levels or on smaller individuals of traditional prey species having lower  $\delta^{15}\text{N}$  ratios (Chouvelon et al., 2011). Climate change in marine systems is triggering a redistribution of organisms with a global northward shift in subarctic regions, and generalist predators such as hooded seals (Grose et al., 2020) could shift to newly available species (Campagna et al., 2020; Poloczanska et al., 2013; Sunday et al., 2012), even though their preference for consistent oceanographic conditions rather than geographical areas suggests otherwise at this time.



**FIGURE 12** Suitable habitat of the Northwest Atlantic hooded seals based on predicted daily behavioural states obtained from the B\_FRONT habitat model for March, April, May, and June in the 1990s, 2000s, 2010s and for the future in 2050 and 2100. Colours represent areas where seals will likely display foraging mode based on the local oceanographic parameters, dark red representing foraging (i.e. predicted daily behavioural state  $>1.75$ , i.e. suitable habitat), while areas where they are unlikely to display, foraging mode are represented in light pink (representing transiting, i.e. predicted daily behavioural state  $<1.25$ , i.e. unsuitable habitat). Geographic cells in yellow represent predictions outside the model ranges (assigned NA). Predictions for 2050 and 2100 are based on predicted oceanographic parameters from the CMIP6 SSP5-8.5 scenario (<https://cds.climate.copernicus.eu>).

Another explanation could be that such redistribution of species and change in water mass circulation may have influenced the  $\delta^{15}\text{N}$  baseline (i.e. primary consumers) across the Arctic and subarctic (de la Vega et al., 2023), inducing changes throughout Arctic food webs (Post et al., 2013). In this case,  $\delta^{15}\text{N}$  ratios of primary consumers might have impacted the isotope signatures within hooded seals through a food web cascade, with the seals eating the same prey, which now has different  $\delta^{15}\text{N}$  signatures (Cherel et al., 2008; Hobson, 1999). It is currently not possible to separate these two possibilities. However, it is known that the ecosystem structure in the Gulf of St Lawrence has shifted dramatically over recent decades from one dominated by demersal fish (cod, redfish) to one dominated by small-bodied forage species (capelin, mackerel, *Scomber scombrus*, herring, *Clupea harengus*; Savenkoff et al., 2007). Such changes in community composition, are consistent with a decrease of  $\delta^{15}\text{N}$  in predator tissues and possibly also with a decrease of  $\delta^{13}\text{C}$  between the 1990s and 2010s. This should be investigated further by exploring other trophic markers and/or seal diving behaviour over time. With regard to difference between sexes, the lower  $\delta^{15}\text{N}$  ratios for females compared to males indicate that females likely feed on

prey at lower trophic levels than males, or on smaller organisms of the same species (Chouvelon et al., 2011), consistent with what has been found in the past (Lesage et al., 2001).

Hooded seals breeding at the FRONT also showed constant post-breeding migration patterns through time and selected similar oceanographic features when foraging in the 1990s and 2000s. However, unlike animals breeding in the GULF, FRONT seals foraged in areas along their migratory paths towards SE GREEN, either over the shelves of the Grand Banks, along Reykjanes Ridge or in SE GREEN, with very little spatial overlap with GULF seals. While FRONT seals sometimes selected high ice concentrations and shallow bathymetry to forage, they foraged primarily in areas further offshore with warmer SSTs compared to GULF seals. Foraging in areas characterized by a combination of high ice concentration and high SST seems counterintuitive, but likely results from seals preferring ice-covered areas, but not encountering these conditions often (seals spend  $75\% \pm 4.0\%$  of their time in ice-free areas). It is also important to note that while the habitat models were focused on the post-breeding season, seals could forage in habitats characterized by different oceanographic parameters within the same



season. Consequently, the selection of high ice concentrations and warm SST could also arise from them using two or more different foraging areas. The selection of warm SSTs differs from Andersen, Wiersma, et al.'s (2013) findings for the Northwest Atlantic hooded seal stock, but is similar to previous results for hooded seals from the Greenland Sea stock in the Northeast Atlantic (Vacquie-Garcia et al., 2017).

In combination, the results suggest that GULF and FRONT hooded seals have different foraging habits, with FRONT seals behaving more like hooded seals from the Greenland Sea than GULF seals. Seals breeding at the FRONT select warmer temperatures than GULF seals and may already be foraging more on Atlantic and offshore pelagic prey, such as Atlantic cod, *Gadus morhua*, that are expected to increase in East Greenland (Drinkwater, 2005; Heide Jørgensen et al., 2022). It is noteworthy that the shelves of the Grand Banks and Reykjanes Ridge are also within the distributional range of redfish (Kristinsson & Sigurðsson, 2011; Sigurðsson et al., 2006), so it is likely that redfish are also part of the diet of FRONT seals. Although no tissue samples from FRONT seals were analysed in this study, redfish and Atlantic cod have been identified previously as key prey species for FRONT seals, consistent with this interpretation (Hammill & Stenson, 2000; Tucker et al., 2009). Despite the apparent adaptability of the FRONT seals to foraging in warm waters, they have adjusted their spatial distribution, shifting northward over the decades, similar to the case for GULF seals—finding their normal habitat choices at more northerly locations than in the past.

This is the first time that differences in the timing of foraging activity and habitat use patterns have been demonstrated for hooded seals from the two Northwest Atlantic breeding areas. Such differences could arise from different habitat preferences between animals from the two breeding areas, or simply from geographical differences in prey availability. Seals breeding in the GULF might remain close to their breeding areas to forage post-breeding simply because the area is productive enough to sustain them, while seals breeding at the FRONT target areas beyond their breeding patches, but within their usual range such as the Grand Banks and Reykjanes Ridge. Assessing potential changes in diving behaviour, as well as accessing samples for stable isotope analyses both from potential prey and the seals, would be needed to refine our understanding of foraging choices and the differences between foraging behaviours between animals from the two breeding areas. The common northward shift of the hooded seals' foraging areas, in the post-breeding season is almost certainly a response to climate change. This novel finding for the species is consistent with trends seen for other Arctic marine mammals (e.g. Carlyle et al., 2021; Chambault et al., 2020; Koenigstein, 2020; Kovacs et al., 2011; Shuert et al., 2022).

Post-moulting seals foraged primarily in the Labrador Sea prior to breeding (see also Andersen, Wiersma, et al., 2013). Consistent with the results from the post-breeding season, post-moulting seals favoured foraging areas with high ice concentrations, shallow depths and low salinities, though they selected areas further offshore. This bathymetry pattern has been highlighted previously (Andersen, Wiersma, et al., 2013), but not the importance of ice concentration

in the hooded seals' habitat selection. Since all breeding areas were pooled together in this model, we cannot address potential differences among seals from the different breeding areas. Nevertheless, it is interesting to note that five individuals equipped with tracking devices in SE GREEN overlapped during the breeding season with the Greenland Sea stock's range in Northeastern Greenland.

## 4.2 | Future suitable foraging habitats in response to a predicted climate change scenario

We combined satellite-tracking records from Northwest Atlantic hooded seals during the post-breeding season (March to June) and predictive climate models to compare past and likely future habitats in response to a climate change scenario. We used only one climate model in this study, representing a worst case of plausible future climate change projections, so our predictions should be interpreted accordingly. We predict that GULF and FRONT hooded seal foraging habitats will decline and shift further northwards in 2050 and 2100 compared to the 1990s to 2010s, similar to findings on other polar species (e.g. Chambault et al., 2022; Koenigstein, 2020; Kovacs et al., 2011; Lameris et al., 2021). As conditions at the southern limits of species' current ranges no longer meet their ecological needs, they will either disappear (via increased mortality or reduced reproduction) or migrate to higher latitudes. For species that have high fidelity to specific locations and/or established migratory routes, adjusting migration timing and foraging locations are among the only options available to respond to changing climate (Shuert et al., 2022). It is difficult to predict whether hooded seals possess enough behavioural plasticity to meet climate-induced challenges. However, even if hooded seals are sufficiently adaptable, a reduction in suitable foraging habitats will likely increase both intra- and inter-specific competition for marine resources, as well as the risk of predation (Kovacs et al., 2011; Lameris et al., 2021). Accessibility to foraging areas might also be reduced if breeding or moulting areas do not also shift northwards (Shuert et al., 2022), although such a shift is likely for hooded seals. This has already been observed for harp seals (e.g. Stenson et al., 2020; Stenson & Hammill, 2014). Given that sea ice is forecasted to disappear from current hooded seal breeding and moulting areas in the future in the southern breeding patches in the Northwest Atlantic (e.g. Heide Jørgensen et al., 2022; Long et al., 2016), pup predation risk from polar bears, *Ursus maritimus*, is also likely to increase for Northwest Atlantic hooded seals. Polar bear predation on hooded seals in East Greenland has increased 9.5% per decade since the mid-1990s (McKinney et al., 2013). It is thought that this source of mortality is possibly becoming a major driver of the population trend of Greenland Sea hooded seals (Øigård et al., 2014).

Prey availability (and abundance) for hooded seals is difficult to predict in the future. In this study, we only predicted the behavioural state of the animals (as a proxy of foraging activity) based on spatial variability in the oceanographic parameters within the study area—changes in availability and abundance of prey in the predicted suitable

foraging areas are hence not directly integrated into our analyses. We have shown that suitable foraging habitat for Northwest Atlantic hooded seals is likely to decrease in the future. But the GULF seals' current foraging areas are predicted to disappear by 2050 while the FRONT seals' current foraging areas might persist further into the future. FRONT breeding areas are also expected to remain suitable for breeding longer than those in the GULF (see details sea ice projections <https://www.dkrz.de/en/communication/climate-simulations/cmip6-en/results/sea-ice/mpj-esm-hr>). Given that GULF breeding areas occur at the southern limit of the seasonal pack ice, it is not surprising that they would be impacted first by the reduction of sea ice (Stenson & Hammill, 2014). GULF breeders might hence shift north to join FRONT animals if they have the behavioural flexibility to do so.

## 5 | CONCLUSION

This study identified different foraging habits within the Northwest Atlantic hooded seal stock. GULF seals forage in cold areas whereas FRONT seals select warmer foraging areas. Seals from each breeding area remained consistent in the selection of the oceanographic features they have targeted for foraging over decades. However, to find these conditions, they have had to migrate further north earlier. Unless hooded seals shift their foraging habits dramatically in the future, this northward migration to forage is likely to continue in the context of global warming, with potential increases in both inter- and/or intra-specific competition and increased predation risks. Suitable foraging areas in warm offshore waters are predicted to be more available in the future than cold ones, and the migration of offshore warm foraging areas is likely to be retained longer in the population. Further research is needed, particularly on diving behaviours, dietary habits and the demography of Northwest Atlantic hooded seals. However, our study sheds light on how Arctic ecosystems are responding to rapid change and provides insights into likely future trends for hooded seals breeding in different areas—crucial information for effective ecosystem-based management and conservation.

### AUTHOR CONTRIBUTIONS

**Jade Vacquié-Garcia:** Conceptualization; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Jérôme Spitz:** Conceptualization; methodology; resources; supervision; writing – review and editing. **Mike Hammill:** Resources; writing – review and editing. **Garry B. Stenson:** Resources; writing – review and editing. **Kit M. Kovacs:** Resources; writing – review and editing. **Christian Lydersen:** Resources; writing – review and editing. **Marianna Chimienti:** Methodology; writing – review and editing. **Mathylde Renaud:** Formal analysis; writing – review and editing. **Paula Méndez Fernandez:** Formal analysis; writing – review and editing. **Tiphaine Jeanniard du Dot:** Conceptualization; methodology; resources; supervision; writing – original draft; writing – review and editing.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study (raw movement data and extracted stable isotope ratio) are openly available in, respectively, <https://doi.org/10.21334/npolar.2024.d41ba23a> and <https://doi.org/10.21334/npolar.2024.126bc092>.

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