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Multidecadal changes in home range characteristics of grey seals in a context of environmental changes and population growth in the Northwest Atlantic

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ABSTRACT: Most marine ecosystems are experiencing increasing cumulative impacts from climate change, fishing, shipping and land-based pollution. The resulting ecosystem responses are challenging to monitor. Studying the space use of top marine predators may provide insight into how these ecosystems react to these impacts. However, natural populations are composed of unique individuals that differ in many ways, including how they use space. Here, we used data from a multidecadal biotelemetry research program on grey seals in the Northwest Atlantic to investigate temporal changes in space use in the context of environmental changes and increasing population size. We quantified temporal changes in monthly home range size, shape and distribution of grey seals in the Gulf of St. Lawrence between 1992 and 2022, while also quantifying interindividual differences. We found that the monthly home ranges of grey seals have increased in size and shifted in distribution over the last 3 decades, indicating that the seals appear to have expanded their space use. We detected individual differences in mean home range characteristics and their level of variability, suggesting that individual identity plays a role in the large-scale space use of grey seals. We also found negative correlations between the mean and level of variability in both home range size and shape, hinting at the potential presence of different tactics within the population. This study highlights how top marine predators can modify their behaviour to adapt to environmental changes and illustrates the importance of considering interindividual differences when exploring population space use patterns.

KEY WORDS: Spatial ecology · Pinniped · Marine mammal · Temporal change · Individual heterogeneity

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1. INTRODUCTION

Understanding how organisms adapt to their environment has been a fundamental endeavour in ecology. As many ecosystems are now facing a period of rapid environmental changes due to human activity and/or climate change, it has become increasingly important to measure how organisms respond to these changes. Because of the speed of these changes, the initial response often consists of behavioural changes (Sih et al. 2011, Tuomainen & Candolin 2011). Behavioural responses can be beneficial or maladaptive, depending on whether they increase or decrease fitness. Species, populations and even individuals can also have varying degrees of behavioural plasticity in how they can adapt to changes in environmental conditions. By studying how organisms respond to these changes, we can gain a deeper understanding of ecosystem health and how resilient they are to changes (Jessup et al. 2004, Moore 2008, Boersma 2008). This knowledge can ultimately help make informed decisions about how to protect, preserve and manage wild species (Lescroël et al. 2016, Hazen et al. 2019).

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Worldwide, most marine ecosystems are experiencing increasing cumulative impacts from climate change, fishing, shipping and land-based pollution (Halpern et al. 2019). These ecosystems are complex and highly dynamic and they can respond to environmental changes at comparable or even faster rates than terrestrial systems (Poloczanska et al. 2013, Antão et al. 2020). Monitoring marine ecosystems can, however, be challenging due to their vast spatial extent and 3-dimensional nature, as most ecological processes occur underwater and are therefore not easily observable. It can thus be difficult to document environmental changes, identify important ecological processes and predict the response of marine ecosystems over time (Poloczanska et al. 2016).

Wide-ranging generalist marine predators integrate information from the whole food chain and can respond to ecosystem changes (Moore 2008, Boersma 2008). They can react to changes in prey communities (Horn & Whitcombe 2015) as well as climatic and environmental conditions (Weise & Harvey 2008, Sydeman et al. 2015, Fleming et al. 2016). They also play a key role in ecosystem structure and function (Estes et al. 2016). As such, top marine predators may act as indicators of ecosystem responses (Hazen et al. 2019), and studying their variations through time may bring key insights into how ecosystems are faring (Adame et al. 2020). Examining the movement metrics of these predators, such as foraging trip duration and distance (Wilcox et al. 2018), or space use metrics, such as timing of migration (Moore 2008) and home range size (Schofield et al. 2010), could reveal changes in spatial distribution, habitat use or foraging behaviour in responses to changes in the ecosystems. For example, foraging trips of male California sea lions *Zalophus californianus* more than doubled in distance and tripled in duration during a year of anomalously high sea temperature and low productivity compared to the previous year (Weise et al. 2006). Identifying definitive explanations for why these changes occurred may be challenging, as top marine predators' responses can be complex and integrate multiple environmental changes (Wolf & Mangel 2008, Warlick et al. 2023).

Natural populations are composed of unique individuals that differ in many ways. This often results in behavioural, morphological and life history variation within a population. While part of this variation can be attributed to ontogeny and sex, a large amount of interindividual variation exists within these groups, which can have important effects on the dynamics of an ecosystem (Bolnick et al. 2003, 2011). Intra- and interspecific interactions, such as competition and predation risk, as well as abiotic factors, such as environmental conditions, can be perceived differently by individuals. Consistent differences in the perception of external factors, in combination with individuals' past experiences, internal state and genotype, can drive individual differences in movement (Shaw 2020). These differences can, in turn, lead to individual variation in foraging search performance, habitat preference, home range utilization patterns and space use tactics (Austin et al. 2004, Lai et al. 2017, Bastille-Rousseau & Wittemyer 2019) that can ultimately affect the population, community and ecosystem (Spiegel et al. 2017, Shaw 2020).

The Northwest Atlantic ecosystem (see Fig. 1A) has been changing rapidly over the last decades (Bernier et al. 2023). Among the changes have been drastic shifts in the biotic communities. In the 1980s, the ecosystem was dominated by long-lived piscivorous groundfish including the Atlantic cod *Gadhus morhua*, which was considered a keystone species and one of the largest sources of piscivory in the system (Savenkoff et al. 2007, Bundy et al. 2009). During the 1990s, many commercial groundfish stocks such as redfish *Sebastes* spp. and white hake *Urophycis tenuis* suffered serious declines (Bundy et al. 2009). Most notable was the Atlantic cod stock, which collapsed due to overfishing and unfavourable environmental conditions (Lilly et al. 2013). Since then, fish communities have switched from being dominated by long-lived piscivorous groundfish to the dominance of small-bodied forage species such as short-lived pelagic fish and invertebrates (Bundy et al. 2009). Despite a decade-long fishing moratorium, the stock has shown little to no signs of recovery, mainly due to the high natural mortality of large adult cod (Shelton et al. 2006). Fisheries-induced evolution (Hutchings 2005, Swain 2011) and grey seal predation (Chouinard et al. 2005) have been suggested as explanations for this increased mortality. Conversely, some marine mammal populations, mainly grey seals *Halichoerus grypus* and harp seals *Pagophilus groeanlidicus*, have increased over the last decades (Hammill et al. 2021, 2023). As a result, marine mammals, including seals, have replaced cod as the top predators in this ecosystem since the 1990s (Bundy et al. 2009).

Grey seals are medium-sized pinnipeds found in the Northwest Atlantic, primarily along the continental shelf from the Atlantic coast of Canada to the northeast USA (Lavigueur & Hammill 1993), where they form a single population (Wood et al. 2011). They were abundant prior to the mid-1800s, but their numbers have since been reduced due to high levels of harvesting (Hammill et al. 2023). Historical estimates of abundance are not available, but during the early 1960s, the estimated abundance was believed to be at an historical low, at around 5000–10 000 animals (Hammill et al. 2023). During the 1960s, however, the population started growing exponentially at a mean rate of 1.095 (9.5% increase yr^{-1}) until the mid-1990s (Hammill et al. 2023). Population growth rate, i.e. proportional change in population size, then started decreasing, and population growth, i.e. the actual change in the number of individuals in the population, started decreasing in the 2010s (Hammill et al. 2023). In 2021, the grey seal population was estimated at more than 360 000 individuals in the Northwest Atlantic and was still growing (Hammill et al. 2023). The increase in population size is thought to be due to a combination of decreased predation, decreased competition for food, increased protection measures and changes in environmental conditions (Bowen 2011). For example, the collapse of cod stocks in the Northwest Atlantic removed a significant predator from the system and may have released predation pressure on important prey such as sand lance *Ammodytes* spp., increasing their availability to grey seals (Bundy et al. 2009, DFO 2011, Swain et al. 2015).

The deployment of satellite-linked time–depth recorders (hereafter referred to as satellite transmitters or tags) on grey seals has provided an opportunity to study haulout behaviour, movements and diving behaviour of individual seals over a period of many months. Here, we used data from a multidecadal tagging program on grey seals to investigate temporal changes in space use within a context of major environmental changes and increasing population size. We specifically aimed to quantify temporal changes in home range area, shape and distribution of grey seals in the Gulf of St. Lawrence (GSL) between 1992 and 2022. We also quantified the level of interindividual differences in each of these home range characteristics. Based on the ecosystemic changes described above, we assumed that the beginning of our time series corresponds to a period of higher resource availability and lower intraspecific competition due to lower population size and that intraspecific competition for resources should increase across time with the changes in prey availability and increased population size. We thus hypothesized that seals would exhibit temporal changes in their home range area, shape and distribution. We expected that seals in the 1990s and 2000s used few ‘optimal’ habitats, i.e. high-quality habitats maximizing their fitness (Rosenzweig 1981), located near a central haulout site to limit the energetic cost of travelling (Orians & Pearson 1979). As population size increases, we expect seal density to increase and resource availability to decrease near main haulout sites (Birt et al. 1987, Elliott et al. 2009), resulting in the use of more distant feeding areas and longer travel times (Lewis et al. 2001, Ballance et al. 2009). As foraging distances increase, individuals have an incentive to limit travel costs by alternating between multiple central haulout sites (Chapman et al. 1989, McLaughlin & Montgomerie 1989). We thus expected that seals in the 1990s and 2000s used fewer and more localized feeding and haulout sites compared to seals in the 2010s and 2020s. We predicted that home range would become larger, more linear and extend northward with time as a result of seals using more space, moving more and using previously unused or seldom used areas.

2. MATERIALS AND METHODS

2.1. Data collection and processing

A total of 124 grey seals were captured in the GSL and equipped with satellite transmitters at 6 deployment sites in the north, south and center of the GSL (Fig. 1A) between 1992 and 2022 (Table 1). For a detailed description of animal handling, see Harvey et al. (2008). The transmitters were a mix of SDR-T16s, Mk10s and SPLASH10s from Wildlife Computers (n = 69) and satellite relay data loggers from Sea Mammal Research Unit (n = 54).

We extracted Argos locations from all transmitters. Argos locations tend to be error prone and, as is typically the case in marine mammal telemetry studies, most of our locations fall into the less precise quality classes (A and B; CLS 2016). To quality control our locations, we applied a continuous-time state–space model to each seal track with the ‘fit_ssm()’ function from the R package ‘aniMotum’ (Jonsen et al. 2023). The function first applies a pre-filter to identify and reject outliers. The pre-filter removes duplicate observations and keeps only one observation when multiple observations occur within 60 s of each other. It then uses the ‘sda()’ function of the R package ‘trip’ (Sumner 2011) to identify outlier locations, which uses a combination of speed, angle and distance tests to identify and exclude locations that are biologically unrealistic (Freitas et al. 2008). We used a maximum travel rate of 5 m s^{-1} to identify unrealistic locations, meaning that we removed locations that required swimming speeds of $>5 \text{ m s}^{-1}$ unless they were within 5 km of the previous position. We used angles of 15° and 25° with lengths of 2500 and 5000 m to identify implausible location ‘spikes’, meaning that we

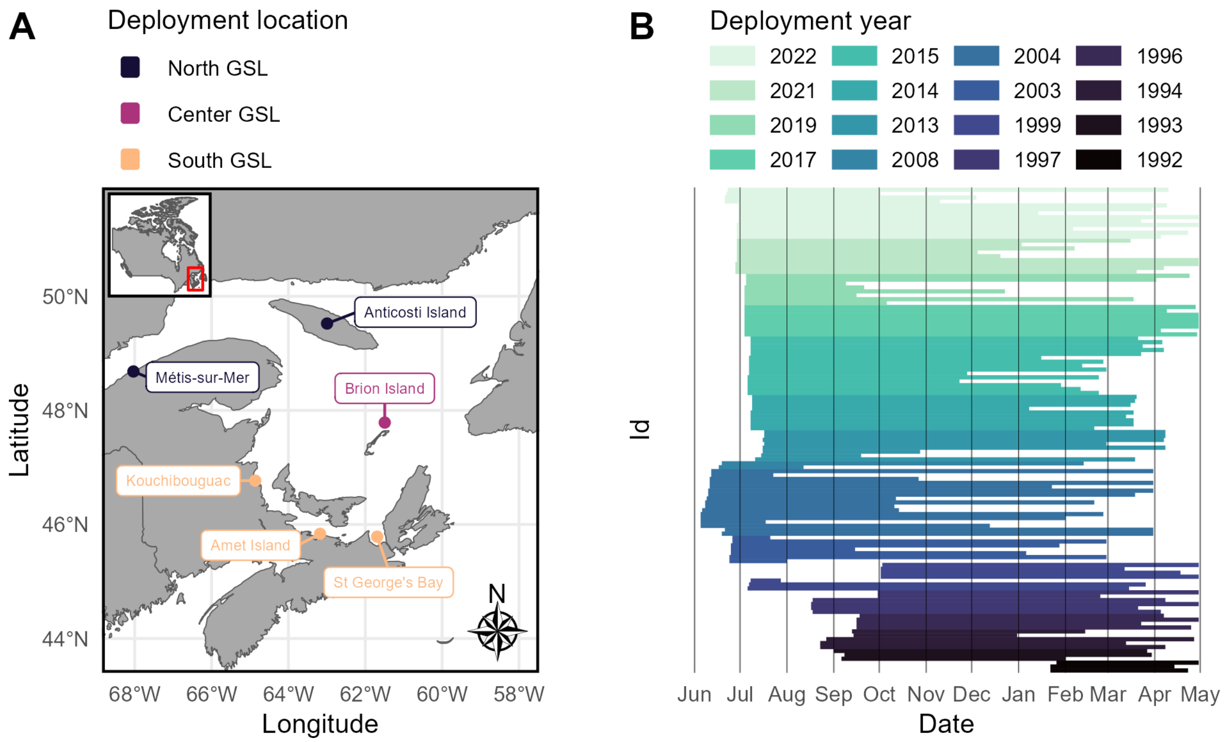

Fig. 1. (A) Deployment sites of grey seals receiving satellite tags in the north, center and south of the Gulf of St. Lawrence (GSL). (B) Temporal coverage of each satellite tag ordered by the year of deployment

removed positions with angles of <15° and distance from a previous position of >2500 m as well as positions with angles of <25° and distance from a previous position of >5000 m. Then, a correlated random walk model was applied to the observed locations that have passed the pre-filter to estimate the 'true' locations and uncertainty around each coordinate while accounting for error-prone observations. We refer to these locations as fitted locations.

2.2. Home ranges

2.2.1. Estimation

Satellite transmitters were not always deployed at the same time of year and did not collect data over the same duration or period (Fig. 1B). To cope with the variability in deployment duration and data availability, we calculated monthly home ranges. We then assessed changes in monthly home range characteristics between 1992 and 2022. We estimated monthly 95% home ranges for each individual using dynamic Brownian bridge movement models (DBBMMs; Kranstauber et al. 2012). This type of model calculates the probability that an animal was present in an area, i.e. the utilization distribution (UD), during the period of interest using point locations along its trajectory, modelling the animal's movement according to Brownian motion. One of the advantages of DBBMMs is they allow the inclusion of uncertainty around the

Table 1. Deployment of 124 satellite transmitters on grey seals in the north, south and center of the Gulf of St. Lawrence (GSL) between 1992 and 2022

Deployment		Adult		Juvenile		Total
Year	Location	M	F	F	M	
1992	South GSL	3				3
1993	North GSL		3			3
1994	North GSL	1		3	1	5
1996	South GSL		2		2	4
1997	South GSL	1	2	2	1	6
1999	South GSL	3	2	2		7
2003	South GSL	3	1	3		7
2004	North GSL	1	1			2
2004	South GSL	5	3	1	6	15
2008	South GSL	2				2
2013	South GSL	3	3	1	1	8
2014	Center GSL		2	5	2	9
2015	Center GSL	4	3	4	4	15
2017	Center GSL	2	1	2	3	8
2019	Center GSL	4	1	1	2	8
2021	Center GSL	1	2	3	3	9
2022	Center GSL	1	6	1	1	9
2022	South GSL	3	1			4

locations in the calculation of the UD, which can be included in the calculation of the home ranges. To do this, we assumed that the standard errors of the x and y coordinates of each fitted location represented semi-minor (x.se) and semi-major (y.se) axes of an error ellipse. We then calculated the radius of a circle with an area equivalent to the area of the ellipse described by these 2 error measurements using the following equation: $\varepsilon_{\text{radius}} = \sqrt{x.\text{se} \times y.\text{se}}$. We used the radius value as the error measure for the location. Home ranges were calculated with the R package 'move' (Kranstauber et al. 2023) using a window size of 7, a margin of 3 and a raster resolution of 1000 m. An individual required a minimum of 9 d in a month where at least one location was observed for its monthly home range to be estimated. Months with less than 9 d of data were excluded from the analyses.

2.2.2. Characteristics

We calculated the area (in km^2) of the generated monthly home ranges. We quantified their shape with an index of linearity using McGarigal & Marks's (1995) shape index = Perimeter / [$2\sqrt{(\pi \times \text{area})}$]. An index of 1 indicates a perfectly circular home range, while higher values indicate more linear home ranges. Shape index values ranged from ~1 to ~12 (Fig. 2). For the home range distribution, we extracted the coordinates of the centroids of each monthly home range.

2.3. Statistical models

We modelled home range area, shape index and centroid distribution (i.e. coordinates of the centroid) using Bayesian mixed models fitted with the R package 'brms' (Bürkner 2017, 2018). We fitted a model for each home range characteristic, 2 univariate models for area and shape index and a multivariate model for centroid distribution. We used weakly informative priors for all parameters except for model intercepts, for which moderately informative priors were used (further details in the sections below). Continuous population-level effect (fixed effects) variables were centered and scaled to help model fit and intercept interpretation.

Grey seals exhibit sexual and age differences in space use and foraging behaviour (Breed et al. 2006, 2011). To account for these differences, we included a sex and age categorical variable (hereafter referred to as 'sex–age') with 4 levels (adult male, adult female, juvenile male and juvenile female) in all models. Individuals 6 yr old and older were considered adults, while younger individuals were classified as juveniles (Hammill & Gosselin 1995, Harvey et al. 2008). Grey seals in the GSL also exhibit a seasonal life cycle consisting of periods of intense foraging pre- and post-reproduction, prolonged haulout during the reproduction and the molt and reduced foraging effort in the summer (Beck et al. 2003b,c). We thus included a categorical variable in all our models representing the period of the year: pre-breeding foraging effort (October–December), breeding (January), post-breeding foraging effort (February–April) and summer foraging (June–September). Because this foraging pattern is affected by reproduction, it may vary between juveniles and adults and between males and females (Breed et al. 2006). We therefore included an interaction between the sex–age and period variables in our models. We quantified temporal changes in home range area, shape index and coordinates of the centroid using thin plate regression splines on the year of deployment with the 's()' function from the 'mgcv' package (Wood 2003). We included an interaction between the year of deployment spline and the period of the year. This resulted in 4 different splines being produced per model: one for each period of the year; i.e. summer, pre-breeding, breeding and post-breeding. This allowed us to diagnose temporal changes independently for each period of the year.

During our study period (1992–2023), telemetry technology developed rapidly, and modern satellite transmitters usually produce more frequent and pre-

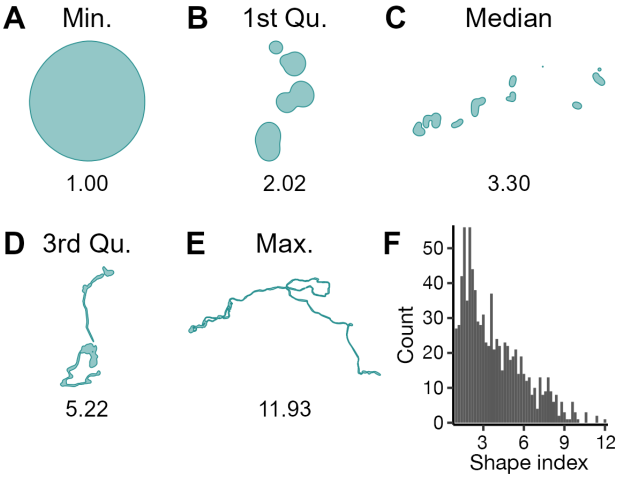

Fig. 2. Range and distribution of shape index. The following quantiles are represented for illustration purposes: (A) 0%, (B) 25%, (C) 50%, (D) 75% and (E) 100%. (F) Distribution of the values of the shape index estimated for all monthly home ranges of grey seals in the Gulf of St. Lawrence between 1992 and 2022

cise locations. The deployment location also changed from the north of the Gulf in the 1990s to the south of the Gulf in the early 2000s and mainly in the center of the Gulf since 2014 following changes in grey seal distribution and access to animals. We thus included different control variables in our model to ensure that the temporal changes in home ranges reflect a biological process and not a consequence of the methodology. For home range area, we included the mean error of the locations used to estimate the home range, as higher error on the locations leads to more uncertainty in the estimation of the UD and larger home ranges. For the shape index model, we included the number of locations used to calculate the home range, as more locations could result in a more detailed and linear home range leading to a higher shape index. For the coordinates of the home range centroid, we included the deployment location as a categorical control variable (i.e. north, south or center of the Gulf).

Inter- and intraindividual variation in home range attributes were investigated using double hierarchical generalized linear models (DHGLMs). These models consist of 2 parts: the mean model, which models the variation and differences in the means of the response variable, and the dispersion model, which focuses on modelling the residual variation (Lee & Nelder 2006, Cleasby et al. 2015). The term 'double' refers to the fact that these models allow for fixed and random effects on both the mean and the dispersion part of the model (Lee & Nelder 2006, Cleasby et al. 2015). We fitted a random intercept of individual identity on both the mean and dispersion models. We could then estimate interindividual differences (i.e. individual differences in trait values) and intra-individual variation (i.e. individuals' level of variability or dispersion) (Cleasby et al. 2015). We then calculated the agreement repeatability, adjusted repeatability and coefficient of variation of the between-individual differences and within-individual variation (Nakagawa & Schielzeth 2010). We included a correlation term between the mean and dispersion models' random intercepts of individual identity to quantify associations between individual's mean trait value and their level of variability (Hertel et al. 2020, O'Dea et al. 2022). We also included a random intercept for year of deployment on both the mean and dispersion models to account for interannual variability not explained by multidecadal trends.

2.3.1. Area

For area, we fitted a univariate DHGLM using a lognormal distribution. Monthly home range area (mean model) was modelled as a function of log-transformed mean location error, period of the year, individual's sex–age class, the interaction between period of the year and sex–age class and thin plate regression splines on the year of deployment for each the period of the year. Group-level variables consisted of random intercepts of individual identity and year of deployment. Residual variation in monthly home range area (dispersion model) was modelled as a population-level intercept with random intercepts of individual identity and year of deployment. We included a correlation term between the mean and dispersion models' random intercepts of individual identity and year of deployment, respectively.

We used a wide prior centered around similar estimates of home range size found in grey seals on the Scotian shelf (Lidgard et al. 2020) for the population intercept of the mean model. We set the prior distribution as a normal distribution with a mean of 7.7 and a standard deviation of 0.7 on the link scale. For the effect of log-transformed mean location error, we set a normal prior distribution with a mean of 0.5 and a standard deviation of 0.5. For the correlation matrix, we set a prior Lewandowski-Kurowicka-Joe (LKJ) distribution with a scalar parameter of 1 resulting in a uniform density across the correlation matrix. The rest of the priors were weakly informative distributions in the form of normal distributions centered around 0 with standard deviations of 0.7 for population-level effects and 1 for group-level and smooths terms. Model equations, brms formulas, prior distributions, convergence diagnostics, trace plots and R code for all analyses, tables and figures are presented in Supplement 1 at www.int-res.com/articles/suppl/m755p133_supp/ (for all Supplements). The results of a simulation study assessing the capacity of the statistical approach to tease apart inter- and intraindividual differences in home range characteristics, while accurately estimating the effects of population level variables, considering the data available, are presented in Supplement 2.

2.3.2. Shape

For shape, we fitted a univariate DHGLM using a lognormal distribution. Monthly home range shape (mean model) was modelled as a function of number of locations, period of the year, individual's sex–age class, the interaction between period of the year and sex–age class and thin plate regression splines on the year of deployment for each the period of the year. Group-level variables consisted of random intercepts of individual identity and year of deployment. Residual variation in monthly home range shape (dispersion model) was modelled as a population-level intercept with random intercepts of individual identity and year of deployment. We included a correlation term between the mean and dispersion models' random intercepts of individual identity and year of deployment, respectively.

We set the prior distribution for the population intercept of the mean model as a normal distribution with a mean of 2.3 and a standard deviation of 0.7 on the link scale. For the effect of the number of locations, we set a normal prior distribution with a mean of 0.5 and a standard deviation of 0.5. For the correlation matrix, we set a prior LKJ distribution with a scalar parameter of 1 resulting in a uniform density across the correlation matrix. The rest of the priors were weakly informative distributions in the form of normal distributions centered around 0 with standard deviations of 0.7 for population-level effects and 1 for group-level and smooths terms. Model equations, brms formulas, prior distributions, convergence diagnostics and trace plots are presented in Supplement 1.

2.3.3. Distribution

For distribution, we fitted a bivariate DHGLM using Gaussian distributions, with one equation describing the latitude and one equation describing the longitude of the centroids. We also included a first-order autoregressive term (AR1) grouped by individual identity in both equations because the coordinates of the centroid of an individual's monthly home range are in part dependent on the coordinates of the centroid of the previous month. Centroid coordinates (mean models) were each modelled as a function of deployment location, period of the year, individual's sex–age class, the interaction between period of the year and sex–age class and thin plate regression splines on the year of deployment for each the period of the year. Group-level variables consisted of random intercepts for individual identity and year of deployment. Residual variation in centroid coordinates (dispersion model) was modelled as a population-level intercept with random intercepts of individual identity and year of deployment. We included a correlation term between the mean and dispersion models' random intercepts of individual identity and year of deployment, respectively.

We set the prior distributions for the population intercepts of the mean models as wide priors centered around the middle of the GSL using normal distributions with means of 45.5 and −62 with standard deviations of 5 for latitude and longitude, respectively. For the autoregressive term, we set a normal prior distribution with a mean of 0.5 and a standard deviation of 0.5. For the correlation matrix, we set a prior LKJ distribution with a scalar parameter of 1 resulting in a uniform density across the correlation matrix. The rest of the priors were weakly informative distributions in the form of normal distributions centered around 0 with standard deviations of 10 for population-level effects and 1 for group-level and smooths terms. Model equations, brms formulas, prior distributions, convergence diagnostics and trace plots are presented in Supplement 1.

3. RESULTS

3.1. Methodological considerations

As anticipated, the mean error of the locations used to estimate the home range had a positive effect on home range area (Table 2). The number of locations used to calculate the home range also had a positive effect on the shape index, meaning that a larger number of locations resulted in a more linear home range (Table 2). Finally, deployment location influenced centroid latitude and longitude. Individuals tagged in the north had more northern centroids compared to individuals tagged in the center or the south. Individuals tagged in the center of the Gulf (which is also the most easterly deployment location; Fig. 1A) had more eastern centroids compared to individuals tagged in the southern or northern Gulf (Table 2).

3.2. Ontological and seasonal effects

We found differences in monthly home range areas across sex–age classes (Table 2, Fig. 3A). Adult males generally had larger home range areas than adult females, and this difference was particularly important during the post-breeding period. There was less difference in home range area between juvenile males and females. They only differed in the summer months, with juvenile females having smaller home range than juvenile males. Juveniles had similar home range areas to adults during the summer, pre-breeding and breeding periods but had intermediate home range areas between those of adult males and females during the post-breeding months. We also found different seasonal patterns between sex–age classes. Both juvenile and adult females had their smallest monthly home ranges in summer. They expanded their home range during the pre-breeding period and maintained

Table 2. Parameter estimates of 3 Bayesian mixed models describing area (in km^2), shape index and centroid coordinates (latitude and longitude) of 95% monthly home range of grey seals in the Gulf of St. Lawrence (GSL) between 1992 and 2022. Estimates are the mean estimate of the posterior distributions and are accompanied by their 95% credibility intervals. Intercept and intercept sigma represent the intercepts for the mean and dispersion models, respectively

	Area		Shape		Centroid			
	Estimate	(95% CI)	Estimate	(95% CI)	Latitude Estimate	(95% CI)	Longitude Estimate	(95% CI)
Population-level effects								
Intercept	7.39	(7.13 to 7.64)	1.38	(1.24 to 1.53)	46.50	(46.04 to 46.93)	−61.21	(−61.70 to −60.70)
Location error	0.75	(0.62 to 0.87)	–		–		–	
Number of locations	–		0.44	(0.38 to 0.49)	–		–	
North GSL	–		–		1.60	(0.71 to 2.49)	−1.99	(−3.09 to −0.86)
South GSL	–		–		−0.71	(−1.07 to −0.33)	−2.53	(−3.14 to −1.90)
Post-breeding	−0.15	(−0.43 to 0.13)	−0.06	(−0.22 to 0.11)	0.11	(−0.21 to 0.43)	−0.30	(−0.64 to 0.04)
Pre-breeding	−0.09	(−0.36 to 0.17)	−0.29	(−0.44 to −0.14)	1.00	(0.67 to 1.37)	−0.35	(−0.62 to −0.08)
Summer	−0.57	(−0.84 to −0.30)	−0.50	(−0.66 to −0.34)	1.24	(0.86 to 1.65)	−0.48	(−0.85 to −0.12)
Adult M	0.33	(0.00 to 0.66)	−0.11	(−0.30 to 0.08)	0.30	(−0.23 to 0.87)	0.40	(−0.26 to 1.05)
Juvenile F	0.37	(0.03 to 0.72)	−0.04	(−0.24 to 0.16)	1.06	(0.56 to 1.61)	−0.38	(−0.94 to 0.17)
Juvenile M	0.30	(−0.04 to 0.65)	−0.17	(−0.37 to 0.03)	0.90	(0.37 to 1.47)	−0.01	(−0.63 to 0.63)
Post-breeding: adult M	0.54	(0.17 to 0.91)	0.28	(0.06 to 0.49)	−0.40	(−0.91 to 0.12)	1.34	(0.81 to 1.87)
Pre-breeding: adult M	−0.13	(−0.48 to 0.22)	0.15	(−0.05 to 0.35)	−0.07	(−0.57 to 0.38)	−0.15	(−0.65 to 0.36)
Summer: adult M	0.21	(−0.15 to 0.57)	0.35	(0.14 to 0.57)	−0.19	(−0.72 to 0.30)	−0.45	(−1.06 to 0.18)
Post-breeding: juvenile F	−0.01	(−0.40 to 0.39)	0.04	(−0.19 to 0.28)	−0.27	(−0.71 to 0.18)	0.90	(0.43 to 1.40)
Pre-breeding: juvenile F	−0.12	(−0.49 to 0.24)	0.12	(−0.09 to 0.33)	−0.93	(−1.41 to −0.49)	0.29	(−0.11 to 0.70)
Summer: juvenile F	−0.17	(−0.55 to 0.21)	0.14	(−0.08 to 0.36)	−1.09	(−1.62 to −0.60)	0.31	(−0.21 to 0.82)
Post-breeding: juvenile M	0.06	(−0.34 to 0.46)	0.28	(0.05 to 0.52)	−0.71	(−1.29 to −0.14)	0.46	(−0.08 to 1.03)
Pre-breeding: juvenile M	−0.15	(−0.52 to 0.22)	0.28	(0.07 to 0.50)	−0.70	(−1.19 to −0.23)	0.06	(−0.37 to 0.50)
Summer: juvenile M	0.35	(−0.03 to 0.72)	0.48	(0.26 to 0.70)	−0.96	(−1.49 to −0.44)	−0.02	(−0.59 to 0.54)
Intercept sigma	−0.47	(−0.62 to −0.32)	−1.14	(−1.31 to −0.98)	−0.44	(−0.64 to −0.23)	−0.01	(−0.24 to 0.23)
Year: breeding	0.45	(−0.90 to 1.69)	0.14	(−0.66 to 1.09)	2.31	(−0.83 to 6.89)	−1.72	(−4.49 to 2.46)
Year: post-breeding	0.22	(−1.10 to 1.51)	0.07	(−0.83 to 0.83)	−0.95	(−8.62 to 5.31)	−2.99	(−8.08 to 0.72)
Year: pre-breeding	0.80	(−0.49 to 1.80)	0.07	(−0.66 to 1.02)	3.55	(−0.22 to 10.10)	−0.89	(−4.16 to 2.15)
Year: summer	0.03	(−1.32 to 1.41)	0.02	(−1.08 to 0.85)	−1.67	(−8.34 to 1.43)	−0.65	(−4.71 to 2.49)
Smooth terms								
Year(Breeding)	0.67	(0.04 to 1.79)	0.25	(0.01 to 0.94)	0.81	(0.05 to 1.96)	0.53	(0.02 to 1.75)
Year(Post-breeding)	0.63	(0.10 to 1.51)	0.23	(0.01 to 0.76)	1.92	(0.22 to 3.66)	0.75	(0.04 to 1.99)
Year(Pre-breeding)	0.37	(0.01 to 1.25)	0.25	(0.01 to 0.86)	0.92	(0.05 to 2.29)	0.52	(0.02 to 1.63)
Year(Summer)	1.27	(0.33 to 2.66)	0.37	(0.01 to 1.57)	0.70	(0.02 to 2.10)	0.62	(0.03 to 1.70)
Group-level effects								
~ID (No. of levels: 124)								
sd(Intercept)	0.29	(0.22 to 0.37)	0.14	(0.10 to 0.18)	0.05	(0.00 to 0.14)	0.08	(0.00 to 0.24)
sd(sigma_Intercept)	0.30	(0.23 to 0.39)	0.24	(0.15 to 0.33)	0.64	(0.52 to 0.77)	0.55	(0.45 to 0.67)
cor(Intercept,sigma_Intercept)	−0.73	(−0.96 to −0.40)	−0.55	(−0.94 to −0.08)	0.10	(−0.91 to 0.95)	0.22	(−0.86 to 0.97)
~Year (No. of levels: 16)								
sd(Intercept)	0.13	(0.01 to 0.30)	0.06	(0.00 to 0.14)	0.12	(0.00 to 0.35)	0.23	(0.01 to 0.62)
sd(sigma_Intercept)	0.24	(0.12 to 0.41)	0.28	(0.15 to 0.45)	0.28	(0.04 to 0.56)	0.38	(0.20 to 0.63)
cor(Intercept,sigma_Intercept)	0.25	(−0.66 to 0.94)	0.06	(−0.82 to 0.89)	0.08	(−0.91 to 0.95)	0.18	(−0.86 to 0.95)

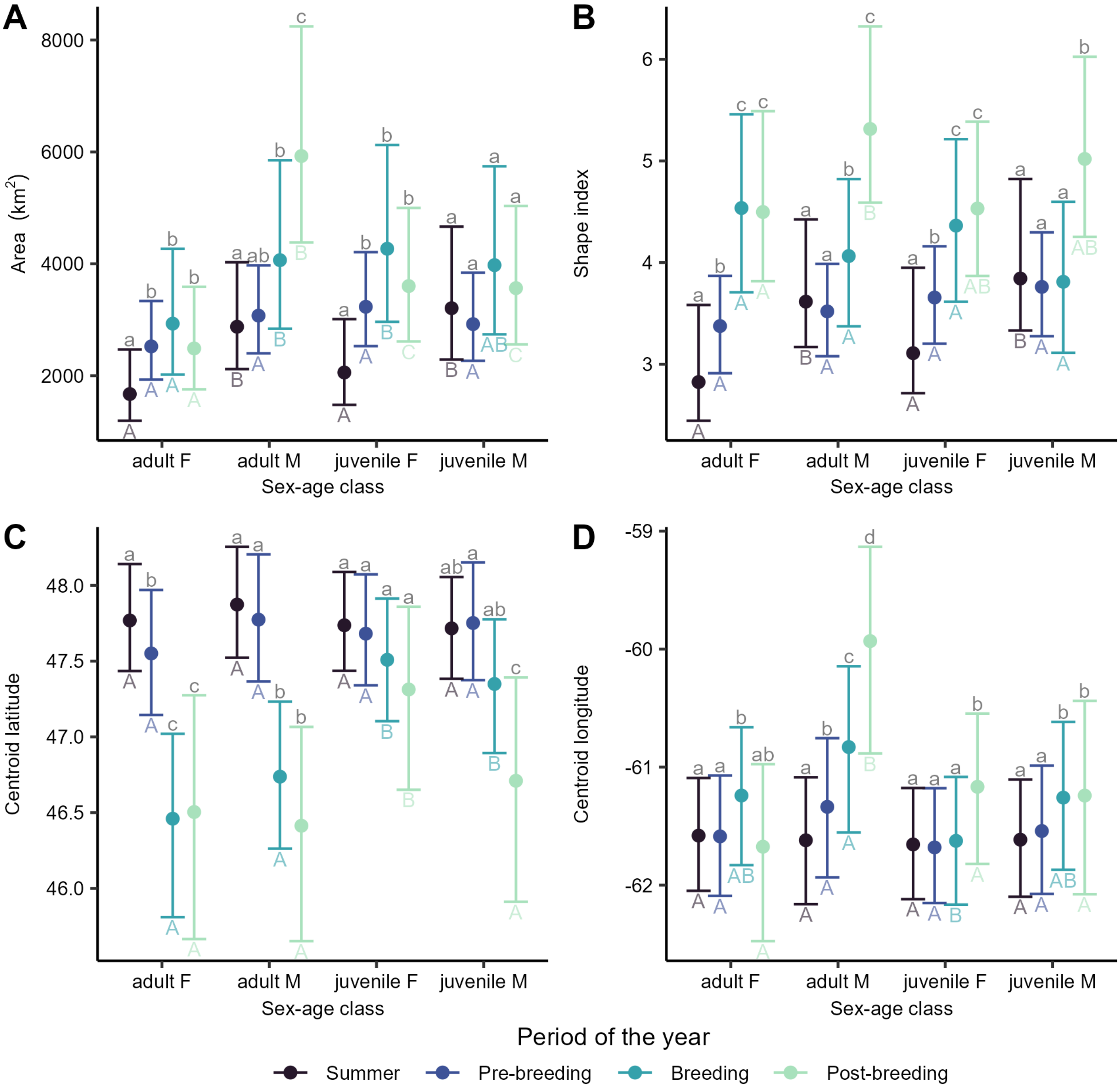

Fig. 3. Ontological and seasonal variation in monthly home range (A) area, (B) shape index, (C) centroid latitude and (D) centroid longitude as a function of sex–age classes of grey seals. Dots represent the predicted values of the response from the models when other population-level numerical variables are fixed at their mean value and categorical values are fixed at their reference value (deployment location of Brion Island). Error bars: lower and upper bounds of the 95% credibility interval of the response. Letters indicate statistically different groups: lowercase letters above bars: differences between periods of the year within each sex–age class (Table S1); uppercase letters below bars: differences between sex–age classes within each period of the year (Table S2)

larger home ranges during the breeding and post-breeding periods. Adult males had similar home range sizes during the summer and pre-breeding months followed by an increase in home range size during the breeding period. In contrast with other sex–age classes, adult males displayed another increase in home range area in the post-breeding months. Juvenile males showed no clear seasonal variation in home range area.

We found limited differences in home range shape indices between sex–age classes within periods of the year. All sex–age classes had similar home range shapes during each period of the year except during the summer months, when both adult and juvenile females had more circular home ranges than adult and juvenile males (Fig. 3B). There was, however, substantial seasonal variation within each sex–age class, and the seasonal pattern differed between the classes (Table 2, Fig. 3B). Home ranges of adult and juvenile females were generally more circular during summer, more linear during pre-breeding and most linear during the breeding and post-breeding periods. Adult males tended to have more circular home ranges during the summer and pre-breeding periods, followed by more linear home ranges during the breeding period and an abrupt increase in home range linearity during the post-breeding months. Juvenile males had home ranges of similar shapes during the summer, pre-breeding and breeding periods followed by abruptly more linear home ranges during the post-breeding months.

We detected differences in the distribution of home ranges across sex—age classes and periods of the year (Table 2, Fig. 3C,D). Home range centroids of all sex—age classes overlapped during the summer and pre-breeding periods. All sex—age classes tended to move towards the south during the breeding and post-breeding periods, but the movement was stronger for adults than juveniles (Fig. 3C). Home range centroids of adult males were located farthest to the west during the summer months, shifted eastward during pre-breeding, moved eastward again for breeding and were farthest to the east during the post-breeding months. During the post-breeding months, adult males' home ranges were located farthest to the east of any other sex—age class. Adult females' home ranges were located more to the east during breeding compared to summer and pre-breeding months. There was more population-level variation in centroid longitude during the post-breeding period, but home ranges were not located more to the east or west compared to other periods of the year. Juvenile females had home range centroids located more to the east in the post-breeding months compared to the other periods of the year. Juvenile males' home ranges were located more to the west during the summer and pre-breeding periods and were more eastward during the breeding and post-breeding periods (Fig. 3D). Post hoc comparisons for differences between periods of the year within sex—age classes (Table S1) and between sex—age classes within periods of the year (Table S2) are available in Supplement 3.

3.3. Temporal changes (1992–2022)

We identified multidecadal temporal changes in monthly home range characteristics (Table 2). Home ranges increased considerably in area in all periods of the year across the 30 yr study period (Fig. 4A). Mean model predictions for the area of the monthly home range of an adult female at the beginning of the study period in 1992 were 914, 1460, 1334 and 1293 km^2 for the summer, pre-breeding, breeding and post-breeding periods, respectively. For the 2022 deployments, the mean predictions for an adult female were 3168, 3594, 3651 and 3595 km^2 for the same periods of the year. We did not detect changes in home range shape over the years (Fig. 4B). Instead, most of the observed variation was due to methodological considerations, i.e. the effect of the number of locations used to estimate the home range, and seasonal variation, i.e. the interactive effect of sex—age class and period of the year. We found some temporal changes in the distribution of home range centroids from 1992 to 2022. We detected no clear change in north—south coordinates (latitude) of the centroids over the past 3 decades, but centroids were located increasingly to the west (longitude) during breeding and post-breeding (Figs. 4C,D & 5).

3.4. Individual differences

We found consistent interindividual differences in average monthly home range area and shape index. The greatest magnitude of differences relative to the population mean was for the shape index (see coefficient of variation of the mean model, CV_m, in Table 3). Repeatability estimates (Rp_m; mean and 95% credibility intervals) were 0.101 (0.053–0.161) and 0.078 (0.040–0.128) for area and shape index, respectively (Table 3). Adjusted repeatability estimates (Rp adj_m) were 0.220 (0.096–0.374) and 0.459 (0.224–0.682) for area and shape, respectively (Table 3). We found no interindividual differences in the average latitude and longitude of monthly home range centroids, meaning individuals did not consistently differ from each other in their distribution once population-level effects were considered (Table 3). Individuals displayed differences in their levels of variability for all home range characteristics. The magnitude of these differences was most pronounced in the shape index, followed by centroid latitude, area and centroid longitude (see CV_v in Table 3). These differences were most consistent for both coordinates of the centroids and less for the area and shape index (see Rp_v in Table 3). There were negative correlations between the random intercepts of individual identity of the mean and dispersion models for area (−0.73 [−0.96 to −0.40]) and shape index (−0.55 [−0.94 to −0.08]) (Table 2). Individuals with larger and more linear home ranges were thus less variable in their monthly home range areas and shape indices. As there were no individual differences in the mean latitude and longitude centroids, there were also no correlations between individuals' mean trait values and their

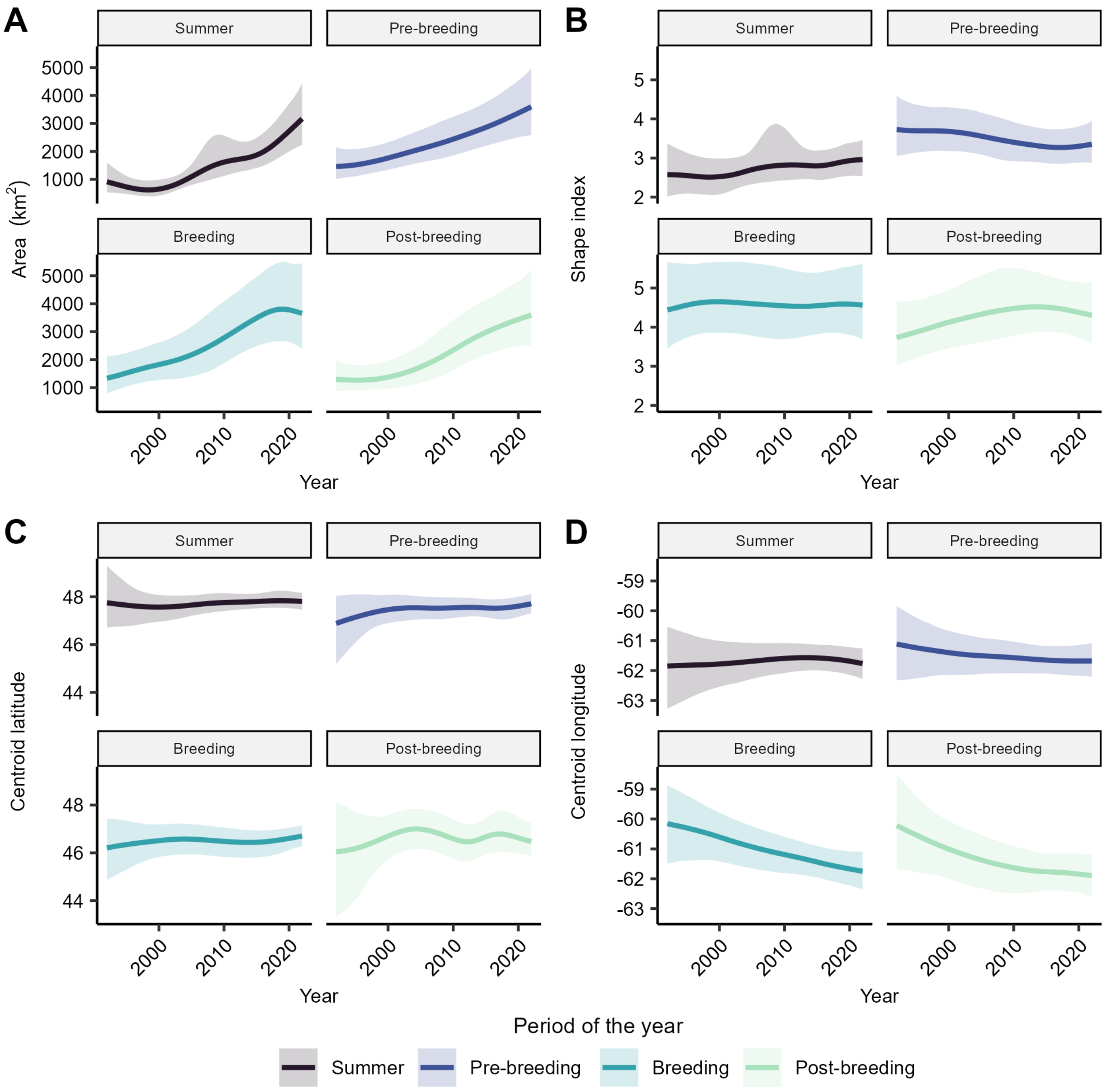

Fig. 4. Temporal change in monthly home range (A) area, (B) shape index, (C) centroid latitude and (D) centroid longitude as a function of the year of deployment for grey seals. Lines: predicted values of the response from the models when other population-level numerical variables are fixed at their mean value and categorical values are fixed at their reference value (adult female from Brion Island); shading: lower and upper bounds of the 95% credibility interval of the response

level of variability for these traits (latitude: 0.10 [−0.91 to 0.95]; longitude: 0.22 [−0.86 to 0.97]).

4. DISCUSSION

In this study, we used data from a long-term biotelemetry research program to investigate temporal changes in home range characteristics of a top marine predator in the GSL. We found significant ontological, sexual and seasonal variation in home range area, shape and distribution. We also found that home ranges have increased in size and shifted in distribution over the last 3 decades. Additionally, we detected individual differences in home range characteristics.

4.1. Ontological and seasonal effects

We found home ranges of similar size to those of grey seals equipped with satellite transmitters on the Scotian shelf for corresponding seasons and years of

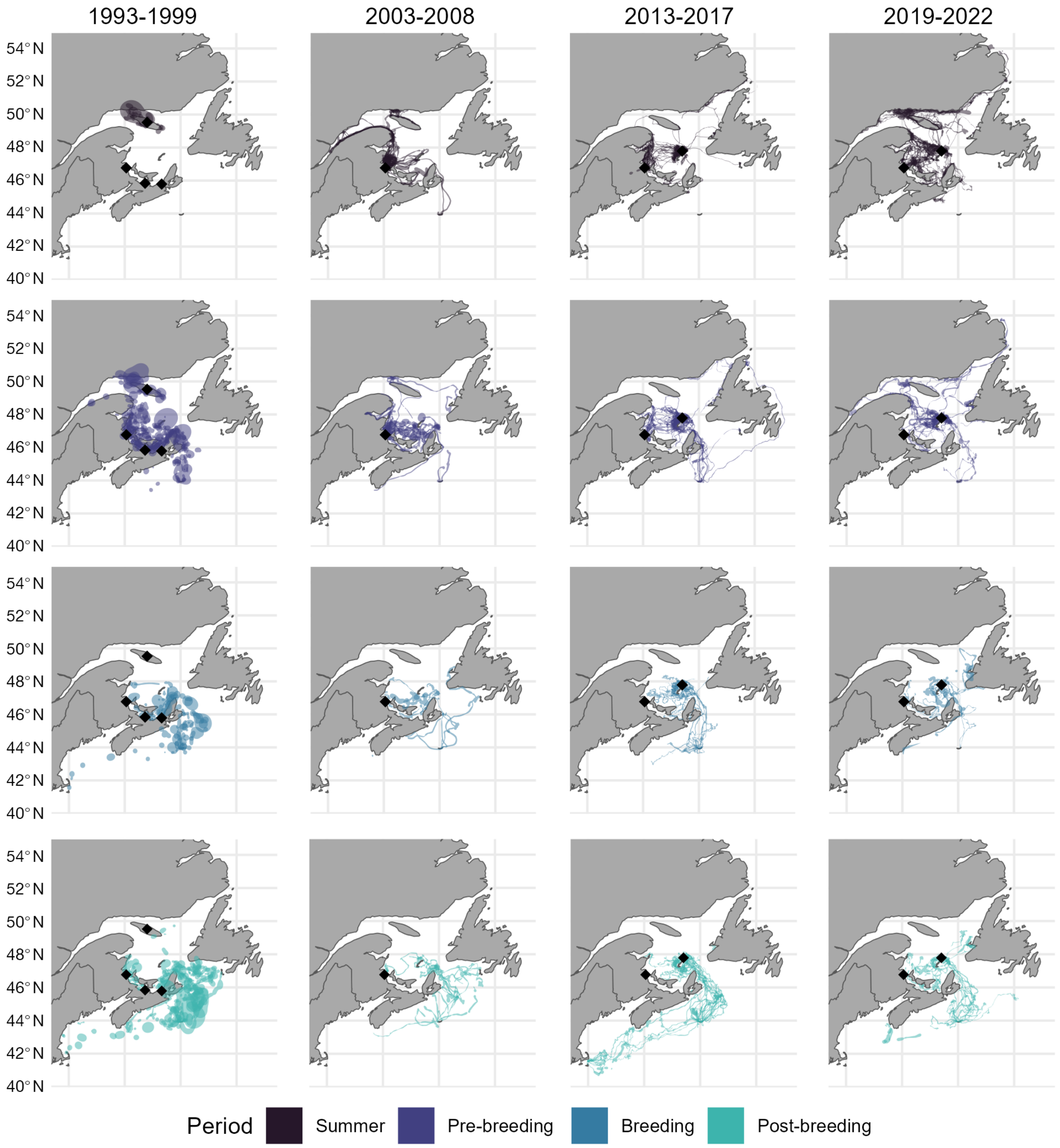

Fig. 5. Monthly home ranges of grey seals in the Gulf of St. Lawrence. Overlapping individual home ranges are represented by period of the year and years of deployment. Black points: deployment sites for each period of years

deployment (Lidgard et al. 2020). In both systems, adult males had larger home ranges than adult females throughout the year (Austin et al. 2004, Lidgard et al. 2020). This may be because males are generally larger than females, with adult males being about 1.5 times larger than adult females (Beck et al. 2003a), and space use can increase with body size (Jetz et al. 2004).

We found that home ranges were the smallest and most circular in summer for females. Their home ranges became larger and more linear in the pre-breeding months, corresponding to increased foraging trip duration, distance travelled and distance from shore previously found in the fall compared to summer for grey seals in the Gulf (Harvey et al. 2011). Contrary to females, there was no increase in home range size or linearity in the pre-breeding months compared to summer for males. They instead exhibited their smallest and most circular home ranges

Table 3. Interindividual differences in mean and within-individual variability of 95% monthly home range area (in km^2), shape index and centroid coordinates (latitude and longitude) of grey seals in the Gulf of St. Lawrence (GSL) between 1992 and 2022. Estimates are the mean estimate of the posterior distributions and are accompanied by their 95% credibility intervals (95% CI). Rp: repeatability; Rp adj: adjusted repeatability (fixed effect variance removed from denominator); CV: coefficient of variation

Estimate	Area Mean (95% CI)	Shape Mean (95% CI)	Centroid Latitude Mean (95% CI)	Centroid Longitude Mean (95% CI)
Mean model				
Rp_{m}	0.101 (0.053 to 0.161)	0.078 (0.040 to 0.128)	0.001 (0.000 to 0.006)	0.001 (0.000 to 0.007)
Rp adj_{m}	0.220 (0.096 to 0.374)	0.459 (0.224 to 0.682)	0.003 (0.000 to 0.018)	0.002 (0.000 to 0.012)
CV_{m}	0.037 (0.028 to 0.047)	0.109 (0.078 to 0.143)	0.001 (0.000 to 0.003)	−0.001 (−0.004 to 0.000)
Dispersion model				
Rp_{v}	0.068 (0.034 to 0.113)	0.034 (0.010 to 0.072)	0.154 (0.092 to 0.222)	0.074 (0.043 to 0.114)
CV_{v}	1.361 (0.888 to 1.940)	4.181 (2.310 to 6.471)	2.061 (1.229 to 3.078)	0.787 (0.448 to 1.223)

during both the summer and pre-breeding periods. In the Gulf, summer appears to be a period of localized and overlapping space use for all sex–age classes, as there were no clear differences in monthly home range area, shape or distribution. During this period, grey seals in the Gulf foraged closer to haulout sites and stayed closer to shore (Harvey et al. 2011). Their foraging trips were also shorter and they travelled less distance overall (Harvey et al. 2011). There are several possible explanations for this pattern of apparent reduction in foraging effort during summer (Breed et al. 2006, 2009). One explanation is that it might be linked to resource availability. Summer may be a period of high prey availability, leading to reduced intraspecific competition, reduced foraging effort and lower spatial segregation. On the Scotian shelf, for example, seals keep gaining body mass during the summer (Beck et al. 2003a) despite apparent reduced foraging effort (Breed et al. 2006, 2009). Males, however, might require more space to fulfill their dietary and energetic needs (Jetz et al. 2004) due to their larger size and broader range of prey species (Beck et al. 2007) and not be able to reduce their space use as much as females in the summer despite high resource availability. Alternatively, individuals might choose to reduce their food intake to avoid carrying more fat than necessary in the warm summer months. Blubber represents stored energy reserves that will be important during the breeding period but also alters buoyancy and affects the diving behaviour of grey seals (Beck et al. 2000), which might affect their foraging ability and predator escape capacity and prove more energetically costly than useful when energetic reserves are not necessary, especially for females. On the Scotian shelf, they start increasing their body fat percentage and total body energy at a slower rate post-moult (June–October) and accelerate in the pre-breeding months (October–January) (Beck et al. 2003a). Males, on the other hand, increase their total body energy and body fat percentage rapidly in the months following the end of the molt and slow down in the pre-breeding months (Beck et al. 2003a). This reflects the pattern of home ranges being larger and more linear for males compared to females in the summer but similar for both sexes during the pre-breeding period. Individuals might also reduce their at-sea activity during the summer months in response to increased predation risks. White shark *Carcharodon carcharias* presence in the GSL increases during the summer months (Franks et al. 2021, Bowlby et al. 2022) and an increase in shark occurrence is associated with reduced offshore foraging and limited at-sea activity in grey seals (Moxley et al. 2020). Again, this effect could be important for females, as they increased their space use in the fall, a period when predators gradually leave the Gulf (Franks et al. 2021). Thus, one may expect that male grey seals may be more available to predation by sharks during the summer period.

The difference in home range area between adult males and females was most important during the post-breeding months. Grey seals are capital breeders, relying on stored energy for reproduction (Iverson et al. 1993), making breeding energetically costly for both males and females (Beck et al. 2003a, Lidgard et al. 2005). The post-breeding months are a critical period of energy recovery for females, as the timing of embryo implantation seems to be linked with body condition (Boyd 1984), but not so critical for males who continue losing body energy and fat in favour of lean mass (Beck et al. 2003a). This is also the period with the greatest differences in diet composition between males and females, with females targeting few, specific high-calorie species and males consuming a greater quantity and diversity of low-energy prey (Beck et al. 2007). This is reflected in their space use, with males having larger, more linear home ranges than females. At this time, we also observed the largest spatial separation between home range centroids of adult males and females. A similar pattern was found in Scotian shelf grey seals, with males travelling more, spending a lower proportion of their time foraging and being spatially segregated from females (Breed et al. 2006, 2009).

4.2. Temporal changes

Over the past decades, the GSL has undergone important changes in species composition. In the early 1990s, overfishing and exceptionally cold water conditions led to the collapse of several groundfish species, such as Atlantic cod and American plaice *Hippoglossoides platessoides*, which remain at historical lows (Bernier et al. 2018). Meanwhile, the northwest Atlantic grey seal population grew considerably, increasing from ~90 000 seals in 1990 to >360 000 in 2021 (Rossi et al. 2021). Grey seals appear to have responded to these environmental changes and/or their population increase by expanding their space use. Although grey seals are not considered social foragers, there is evidence of intraspecific competition during foraging (Lidgard et al. 2012), resulting in young of the year being excluded to deeper offshore waters in periods of lower resources availability (Harvey et al. 2008, Breed et al. 2013). The increase in home range area found in this study could indicate an increase in intraspecific competition due to population growth and/or changes in the abundance of resources. Larger home ranges can indicate an increase in energy expenditure for individuals, particularly the smaller juveniles, which could provide a mechanism for the reduced population growth in recent years (Rossi et al. 2021).

The last few decades were also a period of environmental changes in the Gulf, characterized by reduced winter sea ice cover (Bernier et al. 2018, Galbraith et al. 2022). Grey seals in the GSL historically used sea ice as a breeding platform. With the decline in sea ice cover, they have shifted to breeding sites on small and isolated islands (Hammill et al. 2017). As the seal population increased, these breeding colonies have also been expanding. In the Gulf, they are located, on average, more to the west than historical breeding sites (e.g. Sable Island). This shift in breeding site location is coherent with the shift we observed in the distribution of monthly home ranges to the west during the breeding and post-breeding periods. Reduced sea ice cover in the GSL could also open up foraging habitats that were previously inaccessible during the winter and spring months.

4.3. Individual differences

We found individual differences in average monthly home range size and shape as well as individual differences in the level of variability of home range size, shape and distribution. A previous study in the Scotian shelf ecosystem found that individual identity explained a good proportion of the variance found in grey seal movements at a fine scale (Lidgard et al. 2020). Our results suggest that individual identity may also play a role in the space use of grey seals at a larger scale (see also Austin et al. 2004). We also found negative correlations between individual average home range size and linearity and their level of variability, meaning that individuals with larger or more linear monthly home ranges were more predictable.

In this study, individual differences in space use could potentially indicate the presence of different tactics within the population. These differences occurred even within sex–age classes and deployments, echoing the fact that grey seals of the same age and same sex can exhibit interindividual variation in space use and foraging behaviour (Russell et al. 2014). One explanation for this pattern could be the presence of generalist and specialist feeding tactics in the population resulting in different space use patterns. Populations composed of both generalist and specialist individuals have indeed been observed in seabirds and marine mammals (Tinker et al. 2012, Catry et al. 2014, Kernaléguen et al. 2016, McHuron et al. 2016, Riverón et al. 2021, Franco-Trecu et al. 2022). Individuals may display a range of alternative movement and foraging tactics, from mobile individuals occupying larger home ranges, exhibiting higher movement and having lower site fidelity to resident individuals with smaller home ranges, lower movement and higher site fidelity. Similar variable behavioural patterns have been observed in fishes and terrestrial mammals (Harrison et al. 2015, Lai et al. 2017, Villegas-Ríos et al. 2017, Webber et al. 2020, Eldøy et al. 2021).

5. CONCLUSIONS

We found temporal changes in home range characteristics of grey seals in the context of multidecadal environmental change and population growth in the GSL. Home ranges increased in size over time in all periods of the year, hinting at overall poorer foraging conditions, perhaps because of increased competition, and providing a possible mechanism for the slowing of population growth in recent years. Future studies should look at the links between home range characteristics and foraging patterns to confirm that these changes are driven by foraging behaviour. Grey seals also shifted the distribution of their breeding and post-breeding home ranges over the course of the study period, possibly in response to reduced sea ice cover and associated changes in whelping areas. Further studies should examine foraging behaviour, diet, morphometrics and/or demography to reveal a more complete picture of the mechanism regulating grey seals' responses to these ecosystemic changes.

Finally, even after considering methodological, ontological and seasonal variation, we found interindividual differences in space use among individuals of the same population. This re-enforces the recent literature suggesting that we should consider individual-level differences when looking at species or population tendencies in space use (Spiegel et al. 2017). Further studies should determine how these individual differences in space use are correlated to each other and if it is possible to identify spatial tactics or syndromes within the population. If we use top marine predators as ecosystem sentinels, it may be important to consider these individual differences. Different spatial tactics or syndromes could, for example, reveal different changes in the ecosystem (Hertel et al. 2020).

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