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Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state–space analysis

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Abstract. In many large pelagic animals, observing behavior is limited to observation by radio or satellite telemetry. In many cases, discriminating different behaviors from telemetry data has been a key, but often elusive, goal. Here we use state–space models (SSMs) to fit a correlated random walk (CRW) model that switches between two unobserved behavioral states (nominally foraging and traveling) to 41 male and 43 female adult grey seal (*Halichoerus grypus*) satellite telemetry tracks. The SSM results reveal markedly different spatial behavior between the sexes, fitting well with sexual size dimorphism and known dietary differences, suggesting that the sexes deal with seasonal prey availability and reproductive costs differently. From these results we were also able to produce behaviorally informed habitat use maps, showing a complex and dynamic network of small, intensely used foraging areas. Our flexible SSM approach clearly demonstrates sex-related behavioral differences, fine scale spatial and temporal foraging patterns, and a clearer picture of grey seal ecology and role in the Scotian Shelf ecosystem.

Key words: animal movement; correlated random walk; foraging; grey seal; Halichoerus grypus; *Nova Scotia, Canada; sex-specific foraging behavior; switching model.*

Introduction

Foraging is central to an animal's life history and ecology. Appropriately synchronizing foraging effort with reproductive costs, seasonal cycles, and environmental variability can mean the difference between success or failure of individuals or whole populations. For most pelagic animals, behaviors at sea are nearly impossible to observe directly. Instead, biologists have been attaching increasingly sophisticated electronic tags that record or transmit location, physiological, and environmental parameters. Satellite telemetry and other forms of tracking have filled vast gaps in our knowledge of ecology and natural history of many marine species (e.g., Stewart et al. 1989, Jouventin and Weimerskirch 1990, McConnell et al. 1992, Prince et al. 1992, LeBoeuf et al. 2000, Shaffer et al. 2006). The extent of ranging by species such as northern elephant seals (*Mirounga angustirostris*), Wandering Albatross (*Diomedea exulans*), or Sooty Shearwaters (*Puffinus griseus*) was far beyond expectation. Tagging studies today are growing in number as tags become smaller and more reliable. Thousands of animal tracks have been logged around the world.

Methods for analyzing tracking data, however, have not kept pace with the rapid improvement of tag technology. There have been some advances, perhaps the most significant is the idea of treating animal tracks as correlated random walks (CRW; Kareiva and Shigesada 1983, Marsh and Jones 1988, Turchin 1998, Okubo and Gross 2002). The idea of using CRWs to understand animal movement is quite old, but fitting CRW models to data proved difficult (see Turchin 1998, Okubo and Gross 2002).

Within the past 10 years, state–space models (SSMs) have been increasingly employed to fit CRW models to animal movement data (Anderson-Spreher and Ledolter 1991, Newman 1998, Sibert et al. 2003). The approach differs from other methods because it simultaneously fits two kinds of error: measurement error (how well the location is known) and process noise (how much an animal's movement deviates from the model being fit). Early SSM implementations used analytical or numerical methods to fit models with known dynamical parameters (e.g., equations of motion; Kalman 1960), but non-Gaussian and/or nonlinear problems generally need to be solved numerically using Markov Chain Monte Carlo (MCMC) simulations or particle filters (Gelfand and Smith 1990, Doucet et al. 2001).

In this analysis, we used a state–space approach to analyze the movements of grey seals (*Halichoerus grypus*) in the northwest Atlantic. Grey seals are abundant upper-trophic-level predators inhabiting both sides of the North Atlantic. There is increasing evidence that marine mammals can have significant top-down effects on ecosystem functioning (Bowen 1997). In addition, there have been several attempts to model

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the impact of pinniped predation on commercially important fish stocks (e.g., Overholtz et al. 1991, Punt and Butterworth 1995, Mohn and Bowen 1996, Trzcinski et al. 2006). A significant limitation of these models is our lack of understanding of how foraging is distributed in time and space.

Grey seals are sexually size dimorphic, and employ a capital breeding strategy whereby both sexes use energy stored months before reproduction to fuel the cost of mate acquisition (males) or lactation (females). Differences in body size and breeding strategy between males and females are reflected in significant differences in diet, diving behavior, and blubber accumulation (Iverson et al. 1993, Beck et al. 2003*b*, *c*, 2005, 2007, Lidgard et al. 2005). Although these differences have been clearly demonstrated, it is not clear if they are life history adaptations of each sex, niche separation due to size difference, or some combination of these factors. Diet differences are strongly seasonal (Beck et al. 2007), and sexual segregation also has a strong seasonal component (Breed et al. 2006). Differences are strongest in midwinter just after the January breeding season when males range much farther south and expand their diets to include a broader range of prey than females. In addition, two analyses demonstrate differences in space use between males and females (Austin et al. 2004, Breed et al 2006). However, these studies could not objectively infer the behavioral of individuals at any particular time or place.

To better understand movement and foraging behavior, we fit a modified version of the Jonsen et al. (2005) two-state behavioral switching model to 84 grey seal tracks collected from Argos satellite tags deployed from Sable Island, Nova Scotia, Canada. The parameters of each state (foraging and traveling) depend upon the animal's behavior at any given time. This allowed us to interpret fine scale behavioral information within the tracks. We use the model to test our expectation that foraging tactics in grey seals vary seasonally, either due to life history patterns timed to reproductive effort or in response to annual cycles of prey availability. We also expected males, which have a wider dietary niche, to forage more broadly than females and structure foraging trips differently, particularly in winter consistent with the diet results of Beck et al. (2007) and range differences of Breed et al. (2006).

METHODS

Tag deployment and data collection

Grey seals were captured on Sable Island, Nova Scotia, Canada, a sand island approximately 300 km east of Halifax (44° N, 60° W), and currently the largest grey seal breeding colony in the world (Bowen et al. 2007). Seals were captured during either January (breeding season), May–June (molt), or September–October from 1995 to 2005. After manual capture with hand-held nets, seals were anesthetized and Argos satellite transmitters (SDR, Wildlife Computers, Redman, Washington, USA; ST-18, Telonics, Mesa, Arizona, USA; and SRDL 7000, Sea Mammal Research Unit, St. Andrews, UK) were attached using 5-minute epoxy (Austin et al. 2003). Some instruments were removed when the animals returned to breed, while others were left on until they failed or fell off. In total, we analyzed satellite-location tracks from 84 adult grey seals (41 male and 43 female). Of these, 21 were duty cycled (programmed 1 or 2 days off between each day transmitting).

State–space model

Argos satellite transmitters report locations at irregular time intervals and are often much less precise than published estimates (Vincent et al. 2002, Jonsen et al. 2005). Error in location causes behavioral CRW models to fit poorly and can lead to erroneous interpretation of results, even after outliers have been removed with ad hoc filtering methods (Jonsen et al. 2006). State–space models accommodate this problem with separate equations for observation error and randomness in the animal's behavior. The observation equation relates satellite observed locations to an animal's true unobserved location. This is linked with a stochastic behavioral model, the transition equation, which predicts where the animal will move next.

We fit a two-state switching CRW model described in Jonsen et al. (2005) to the grey seal data using WinBUGS (*available online*)[5] and R (R Development Core Team 2008). WinBUGS enables Bayesian analysis of statistical models using Markov Chain Monte Carlo (MCMC) estimation methods, typically the Metropolis-Hastings algorithm for our models. Because we use a Bayesian approach, we specified priors for all unknown parameters, using vague priors for most parameters (see Appendix A: Table A1 for priors). An expanded description of the model and its WinBUGS implementation may be found in Appendix A with associated functional model code, instructions, and three sample tracks from our grey seal data set.

Before fitting the model, we constructed an index that related the error of the temporally irregular observations to the regular time steps of the CRW model being fit. The index was created using simple linear interpolation to the regular time steps. This procedure does *not* interpolate, smooth, or otherwise regularize the locations themselves (for full details see Jonsen et al. 2005 and Appendix A). After creating this index, we fit the following CRW model:

$$\mathbf{d}_t \sim \gamma \mathbf{T} \mathbf{d}_{t-1} + N_2(0, \boldsymbol{\Sigma}) \qquad (1)$$

where $\mathbf{d}_{t-1}$ is the distance between locations $\mathbf{x}_{t-1}$ and $\mathbf{x}_{t-2}$, and $\mathbf{d}_t$ is the distance between the locations $\mathbf{x}_t$ and

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[5] ⟨http://www.mrc-bsu.cam.ac.uk/ bugs/winbugs/contents.shtml⟩

$\mathbf{x}_{t-1}$; $\mathbf{d}_t$ and $\mathbf{d}_{t-1}$ are two-element vectors representing differences in latitude and in longitude between consecutive positions on the track $\mathbf{x}$. Since time steps are regular, these are directly related to an animal's speed and thus behavior. Motion is autocorrelated in both direction and speed, where γ is the correlation coefficient ranging from 0 to 1.

$\mathbf{T}$ is a transition matrix that relates the turn angle to the spherical latitude–longitude coordinates of the data and location estimates:

$$\mathbf{T}(\theta) = \begin{pmatrix} \cos\theta & -\sin\theta \\ \sin\theta & \cos\theta \end{pmatrix} \qquad (2)$$

where θ is the mean turn angle. $\mathbf{T}$ relates turn angle to spherical coordinates in a manner similar to converting between polar and Cartesian coordinates. This results in γ correlating both speed and turning angle together, and γ's near 1 are always associated with θ near 0. This property greatly simplifies the construction of the model and has a stabilizing effect when fitting the model.

N_2 represents the randomness in the animal's behavior and is modeled with a bivariate Gaussian distribution with mean 0 and covariance matrix:

$$\boldsymbol{\Sigma} = \begin{pmatrix} \sigma_{\text{lon}}^2 & \rho\sigma_{\text{lon}}\sigma_{\text{lat}} \\ \rho\sigma_{\text{lon}}\sigma_{\text{lat}} & \sigma_{\text{lat}}^2 \end{pmatrix} \qquad (3)$$

where σ_{lon}^2 is the variance in longitude, σ_{lat}^2 is the variance in latitude, and ρ is the correlation coefficient.

The model switched between two behavioral states. The opposing states were represented by two sets of the parameters θ and γ. For each displacement, one set of parameters fit better (deviate less as measured within the Metropolis-Hastings algorithm) than the other depending upon the movement of the animal. The set that fits better at move t was the animal's estimated behavioral state at time t. An additional parameter, α, was estimated to track the probability of switching from one behavioral state to the other (transition probability). Correlation lag was one time step, and time steps were 480 minutes.

At the outset of a model run, γ and θ were split into two groups with nearly identical priors (Appendix A). During model runs, displacements similar to each other naturally aggregated, because individual displacements deviated less from the mean of similar displacements than from the mean of displacements differing greatly. In practice, the resulting parameter estimates of each group of γ and θ were similar across all tracks. One group of parameters tracked migratory-type motion, with displacements forming more or less straight lines aggregating into a group with parameters of θ near 0° and estimates of γ between 0.5 and 1 (henceforth referred to the "traveling" state). More stationary behaviors, such as foraging, produce estimates of $\theta \sim 180°$ and γ's between 0 and 0.6 (henceforth referred to as "foraging"). For the remainder of the paper parameters for the foraging state will be subscripted "for" whereas parameters for the traveling state subscripted "trv" (e.g., γ_{for} vs. γ_{trv}).

To fit the model, two MCMC chains were run for 10 000 iterations, with a burn-in of 7000, sampling all model parameters and each regularized location estimate (which are estimated like parameters). Every fifth point of the 3000 remaining samples was retained for a net of 600 MCMC samples in each chain. From these 600 samples, a mean and variance for each location estimate and model parameter was calculated.

Due to the large size of the data set, computational limitations prevented us from fitting a single hierarchal model as in Jonsen et al. (2006). A hierarchal model would have allowed us to estimate individual parameters for each track as well as population average parameters. In addition, shorter tracks occasionally did not contain enough data to confidently categorize behavior. These tracks, however, could be categorized when combined with other tracks in a single analysis. To use all the data and to provide a limited cross validation, we divided the 84 tracks into 10 independent sets, each containing eight or nine tracks. Groups contained one sex, but satellite tag types were distributed so that each contained three to five of the tag types deployed. Each set was then fit separately.

For this analysis, we were more interested in estimating states for all the data, rather than parameters for individuals. Therefore, for each group of tracks, the model parameters $\boldsymbol{\Sigma}$, α_1, α_2, θ_{for}, θ_{trv}, γ_{for}, and γ_{trv} were estimated for the entire group of eight or nine animals and not for individuals of that group. Only the tag-scaling parameter τ, which uniformly inflated or deflated the precision of each location class to account for variation in tag quality, was estimated individually. Grouping tracks tended to elevate estimates of autocorrelation in the foraging state (γ_{for}, see Appendix A), but had little effect on location or behavioral state estimates.

Since behavioral state was modeled as a binary distribution, each MCMC sample was either fit as the foraging state or travel state, with no middle range. Averaging the binary MCMC samples for inferred behavioral state effectively produced a proportion of MCMC samples fit to the travel state. When this proportion was very low or very high, confidence that the inferred behavioral state was correctly categorized was high. A small number of locations, typically near switches, had proportions that were neither high nor low. Such locations were considered uncertain in their behavioral categorization. Fewer than 10% of locations were uncertain (with proportions between 0.3 and 0.7); these locations were excluded from analyses that compared the characteristics of each behavioral state.

No objective general validation methods are available for our SSMs (Jonsen et al. 2006). Thus we opted to assess the results of our model by comparing them against independent data. We used bathymetry data for

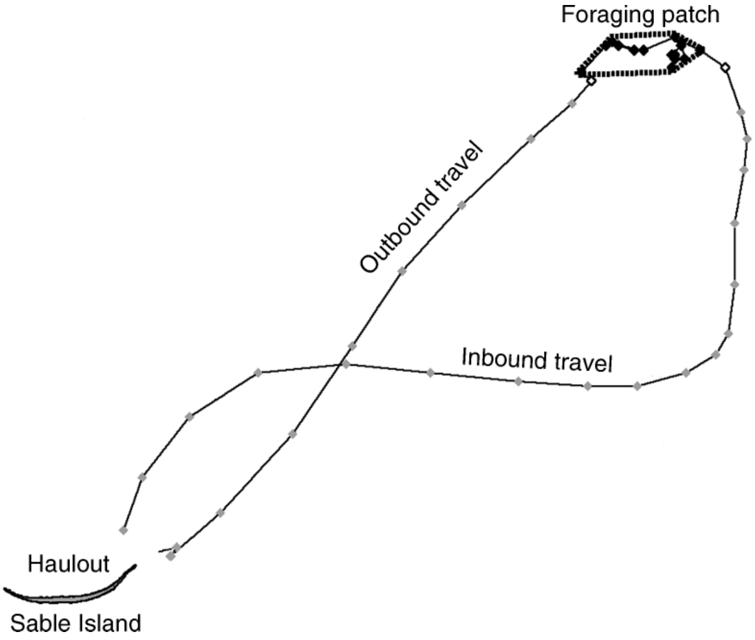

FIG. 1. Typical grey seal (*Halichoerus grypus*) foraging trip showing outbound travel segment, foraging patch, and inbound travel segment. Segments were discriminated using behavioral state estimates from the state–space model (SSM). Gray diamonds are traveling locations, black diamonds are foraging, and open diamonds are uncertain. In this case, the trip began and ended on Sable Island, Nova Scotia, Canada. Haulout locations are not plotted as they are not included as part of the trip. The dotted polygon shows the minimum convex polygon of the foraging patch from which patch areas were calculated.

this purpose, and formulated a series of mixed-effects models to compare bathymetry data (Sandwell and Smith 1992; 3-km spatial resolution) with location estimates and predict whether water depth affected behavioral state.

Testing behavioral hypotheses

We used mixed-effects models to investigate the relationship between SSM estimated behavioral state and a wide range of environmental and demographic covariates.

After state–space modeling, we stratified the resulting state estimates of location and behavior by sex and, based on the results of Breed et al. (2006), into three seasons (winter, January–April; summer, June–August; fall, September–December). We used these categories to construct a series of mixed-effects models to investigate demographic, environmental, and seasonal parameters affecting behavior.

Our first series of mixed-effects models assessed relationships between the response variable of SSM inferred behavioral state and depth, sex, and season (fixed effects) and included seal identity as a random effect. Since inferred behavioral state ranged from 0 to 1, we initially fit the data directly to the 0–1 range using a beta distribution and logit link. However, the beta model was difficult to fit so we logit transformed behavioral state and fit the same model assuming a normal distribution.

The model assumed an AR(1) autocorrelation structure. The full model, including all main effects and two-way interaction terms was as follows:

$$\begin{aligned}\ln\left(\frac{\text{state}_t}{1-\text{state}_t}\right) \sim\ & \beta_0+\beta_1 G+\beta_2 s_t+\beta_3 d_t+\beta_4 G' s_t \\ & +\beta_5 G' d_t+\beta_6 s' d_t \\ & +\phi \ln\left(\frac{\text{state}_{t-1}}{1-\text{state}_{t-1}}\right)+\nu_{\text{seal}} \qquad (4)\end{aligned}$$

where state_t is SSM-inferred behavioral state at time t, G the demographic group (males or females), s_t the season at time t, d_t the water depth at time t, ϕ is the AR(1) autocorrelation coefficient, ν_{seal} the random effect of the ith seal, the prime symbol "′" indicates interaction terms, and β's are the model estimated explanatory coefficients for each fixed effect. Before logit transforming SSM behavioral state, we added 0.001 to behavioral state values of 0, and subtracted that amount from values of 1. Locations within 5 km of shoreline were excluded from the analysis in order to exclude haulout and locations in shallow inshore water. We used AIC scores to select the best model from all possible combinations of main effects and interaction terms.

We had independent TDR data for 14 tracks, all from September–October 2001. We fit a linear mixed-effects model of the same form as Eq. 4 with logit transformed behavioral state as the response variable to investigate the relationship between dive parameters and behavioral state. We assigned dives to the temporally closest SSM

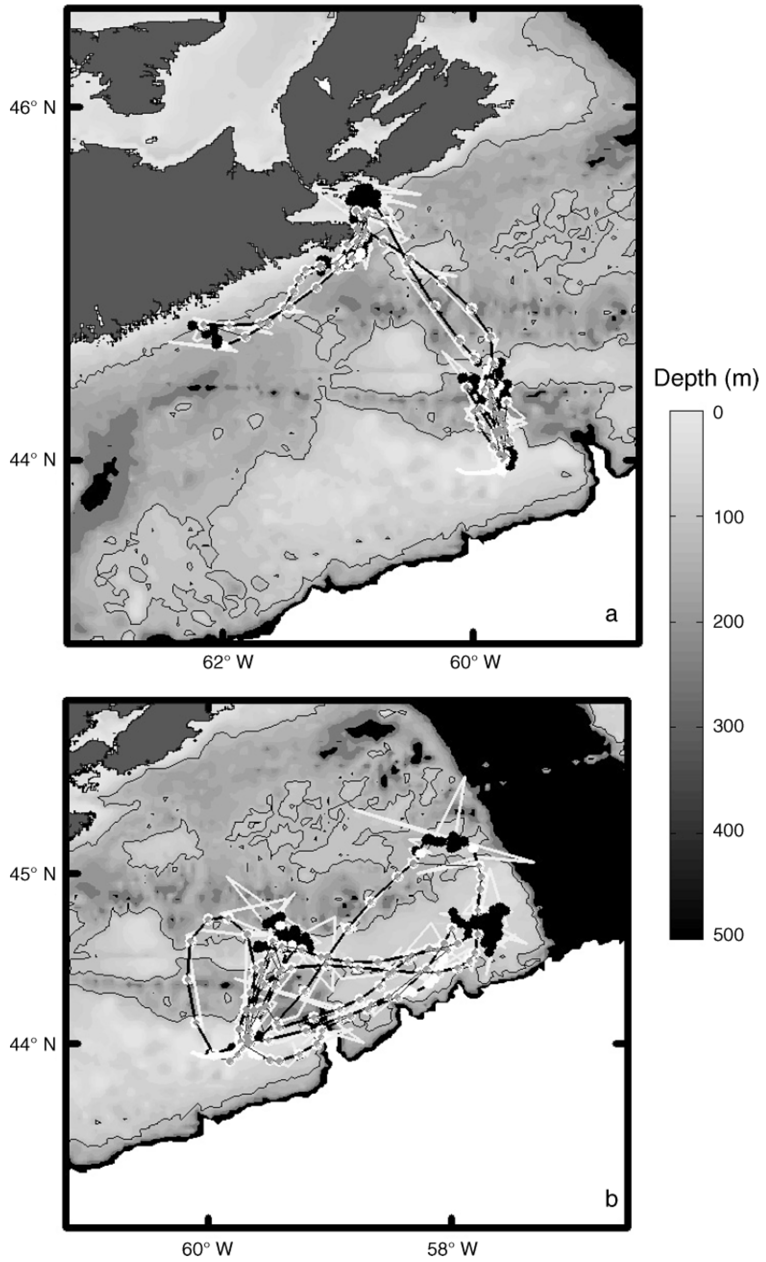

FIG. 2. Example SSM fits for (a) male and (b) female grey seal tracks. Foraging locations are black circles, and travel locations are open white circles; the light gray line indicates the raw Argos track. Solid white points indicate locations of uncertain behavioral classification (with Markov chain Monte Carlo [MCMC] traveling : foraging proportions from 0.3 to 0.7). Since grey seals are shelf animals, only depths shallower than 500 m (black) are contoured. The black line is the 100-m contour; Sable Island (44° N, 60° W) is highlighted in white.

location (always within 4 hours; totaling between 1 and 50 dives), and assigned the behavioral state at the nearest SSM location to each dive. We then used maximum depth, mean dive depth, dive duration, dive shape, and bottom time as explanatory variables. We did not use interaction terms because the dive parameters were not independent. Seal id was included as the random effect. Locations with no dives within 4 hours or within 5 km of shore were excluded.

Trip analysis

After locations and behavioral state were estimated with the SSM, we divided trips into segments based on behavior. Trips were identified as at least 1 day more than 5 km from any shoreline. Each trip was then divided into segments containing foraging locations and traveling locations. We defined any area of at least three consecutive foraging locations as a foraging patch, and then measured the area of foraging patches using a minimum convex polygon method. Most trips contained a clear outbound segment, one foraging patch, and an inbound segment (Fig. 1). However, about one-third of trips were more complex, containing multiple foraging areas or no foraging locations at all. In addition, some trips contained no travel locations as animals began foraging immediately after entering the sea.

Once trips and trip segments were identified, we measured a range of trip properties, and examined how they differ through the year and between sexes. We chose seven properties: proportion of trips with no foraging locations, proportion of trips with no traveling locations, proportion of locations inferred as foraging for each trip, trip length, area of the first foraging patch, distance to first foraging patch from haulout, and patch residence at the first foraging patch. Trip attributes were transformed before model fitting; proportions were logit-transformed and distances and areas were log-transformed. After transformation, trip properties were modeled as the response variable in the following mixed-effects model to compare how these properties varied between the sexes and among seasons:

$$\mathrm{trip}_t \sim \beta_0 + \beta_1 G + \beta_2 s + \beta_3 G' s + \phi \ln(\mathrm{trip}_{t-1}) + \nu_{\mathrm{seal}} \tag{5}$$

where "trip" is one of the transformed trip properties, G is sex, s the season, ϕ the autocorrelation to the previous trip, and ν_{seal} is the random effect of individual. All mixed-effects analyses were conducted using the "mixed" procedure in SAS (Version 9.1.3; SAS Institute 2008).

RESULTS

Model performance

The model detected two behavioral states in all tracks. Inspections of posterior distributions, autocorrelation plots, and MCMC traces indicated MCMC runs converged and model fits were consistent across the data set (see Appendix A for diagnostic results). Foraging moves were slow (averaging 0.4–1.3 km/h), often reversals of previous moves, while travel moves were faster (averaging 2.3–3.1 km/h) and almost always added to the previous move to continue in the same direction. Differences between the two behavioral states were highly significant ($P < 10^{-16}$ for most individuals; see Appendix A: Tables A2 and A3 and Figs. A2, A5, and A6). Results from two representative tracks are shown in Fig. 2.

Spatial behavior and bathymetry

A striking pattern of foraging locations over shallow banks is apparent. By contrast, most locations over deep canyons were inferred as travel (Figs. 3 and 4). Mixed-effects model results indicate depth was a predictor of SSM behavioral state, although sex and season also strongly predicted behavioral state (Table 1).

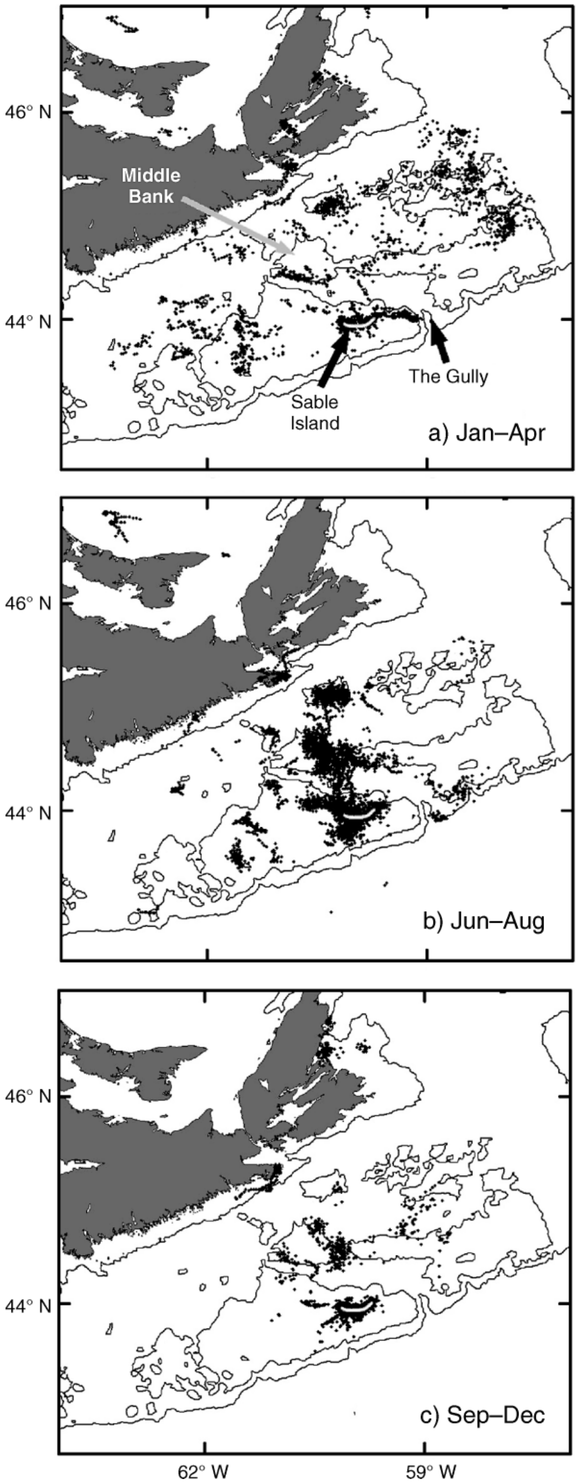

FIG. 3. Inferred foraging locations for all females grouped by season (a–c, black points); 18 individuals are represented in panel (a), 12 in panel (b), and 34 in panel (c). In panel (d), all modeled locations for the 43 tracked females are plotted for the entire year, with inferred travel shown as gray points and uncertain locations as open diamonds. The 100-m and 400-m isobaths are drawn, and Sable Island (44° N, 60° W) is shown as a light gray crescent. A color version is available in Appendix B: Fig. B4.

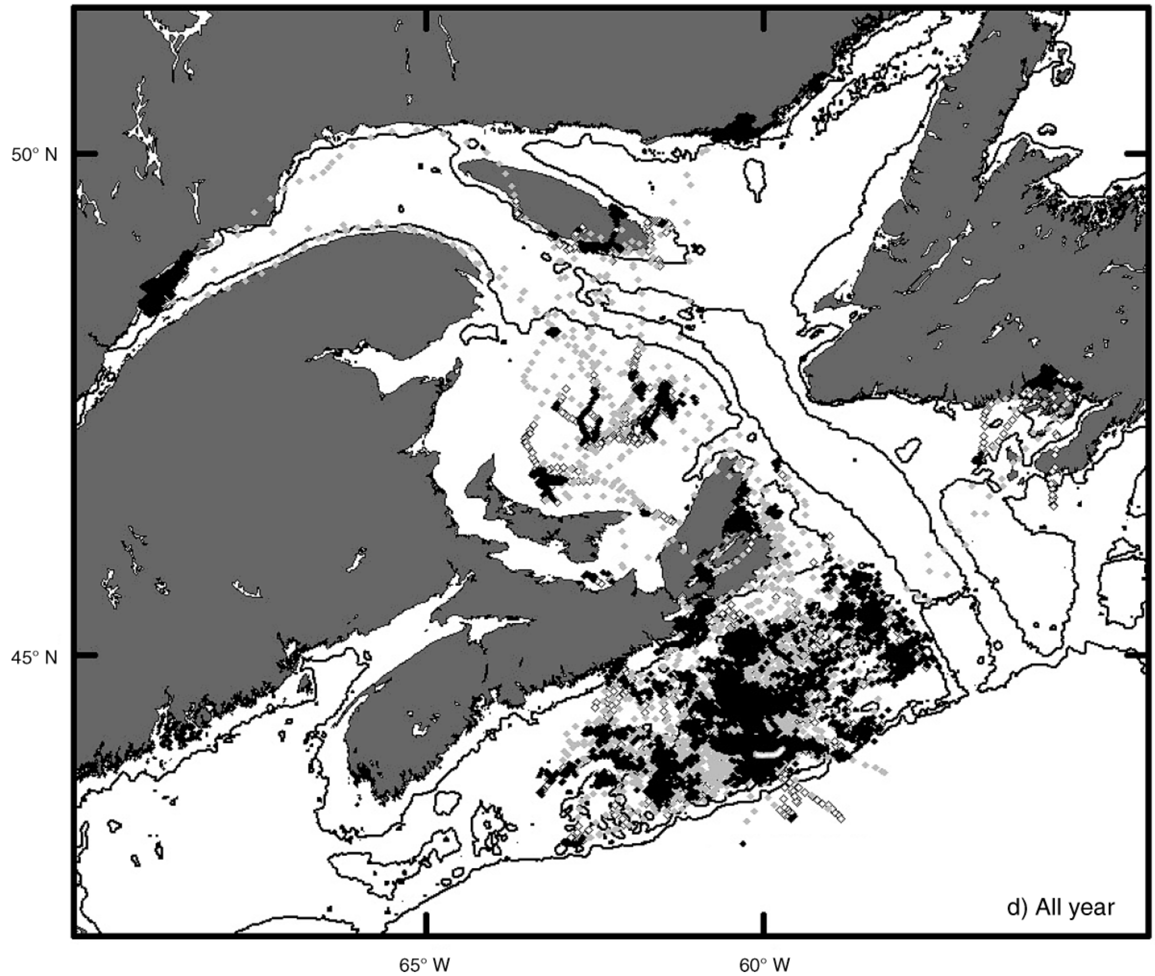

Fig. 3. Continued.

Mixed-effects results associated shallower water with a higher likelihood of being in the foraging state; foraging locations occurred in water that averaged 20–30 m shallower than traveling locations in females, 5–15 m shallower in males. Seasonal and sex effects were also strong, with males tending to forage in deeper areas than females (averaging 5–10 m deeper, depending upon season), and both sexes foraged in deeper water in winter and shallower water in summer (Figs. 5 and 6). Taking maps and mixed-effects results together, spatial behavior was strongly influenced by bathymetry and foraging effort focused in shallower areas of the shelf. This general pattern, however, is dynamic and differs markedly between the sexes and through the year.

Effect of sex and season on foraging behavior

The distribution of foraging locations suggests at-sea spatial behavior might differ between sexes and among seasons (Figs. 3 and 4). As noted, mixed-effects models indicate sex and season and sex × season strongly influenced the probability of being in the foraging state ($P < 0.0001$ for all three effects; Table 1, Fig. 5). Males were less likely to be in the foraging state than females, but the degree to which this was true varied with season. In winter, both sexes were less likely to be in the foraging state than other times of the year.

Many aspects of trip structure differed between the sexes and through the year (Table 2). Sex significantly affected the ratio of foraging locations : total locations in a given trip, as well as patch distance and patch area. Female trips contained more foraging locations (mean 15–30% more) and females foraged at closer (mean 30–80 km closer), smaller patches (mean 60–100 km^2 smaller) than males. Season significantly affected trip length, patch area, and patch residence; both sexes made longer trips and spent more time foraging on larger patches in the fall compared to other seasons (but see Table 2 for specific details). There were no significant sex-by-season interactions in trip characteristics.

Spatial behavior and diving

Although we expected to find a relationship between diving and SSM inferred behavioral state, mixed-effects models indicated that no dive shape parameters significantly predicted SSM behavioral state. Plots of TDR data vs. bathymetry and SSM behavioral state indicate travel segments between foraging and haulout sites align well with breaks in the dive data (see Appendix B: Figs. B1, B2, and B3), but dive shape or type was not informative for predicting spatial behavior. We note, however, that our TDR data may not be representative of dive data generally because they were collected in early fall when most animals remain close to shore, make very shallow dives, and rarely make longer translocations that would be inferred as traveling.

Discussion

The state–space approach for modeling movement from satellite telemetry data has revealed a number of important aspects of the biology, habitat preference and behavior of this marine species. Without the ability to simultaneously account for observation error and process noise inherent in the complex and error prone Argos data, we could not have fit a behavioral switching model and so clearly demonstrated the heterogeneous and seasonal nature of favored foraging areas, differences between male and female foraging behavior, or change in depth of preferred habitat over the course of the year.

Habitat use and behavior

Our large sample of long tracks (2–11 months each) allowed us to draw population-level inferences about behavior and habitat use. To interpret our results biologically, we assume animals that remain in any small area for extended periods are likely in favorable habitat. This assumption is a central tenant of optimal foraging theory (Stephens and Krebs 1986, Zollner and Lima 1999) and has been observed in the behavior of numerous species (e.g., Lima 1983, Munger 1984, Alonso et al. 1995), including large mammals similar to grey seals (e.g., Senft et al. 1987, Mori and Boyd 2004). Applying that assumption to inferred foraging locations, our results indicate favorable habitat was heterogeneously distributed, and comprised a patchwork of intensely used areas separated by large gaps of unfavorable, often deeper, habitat. These results also indicate that the edges of favorable areas, such as Middle Bank, can be sharp. By contrast, the most widely used methods for analyzing telemetry data use some form of kernel density estimator (e.g., Worton 1989). Kernel density methods treat all telemetry points equally and cannot use behavior as information about habitat suitability (though some can use habitat data to adjust kernel shape, e.g., Matthiopoulos 2003). In addition kernel densities tend to smear the data by placing a bivariate normal or other probability distribution over each location, distorting any sharp edges into gentle

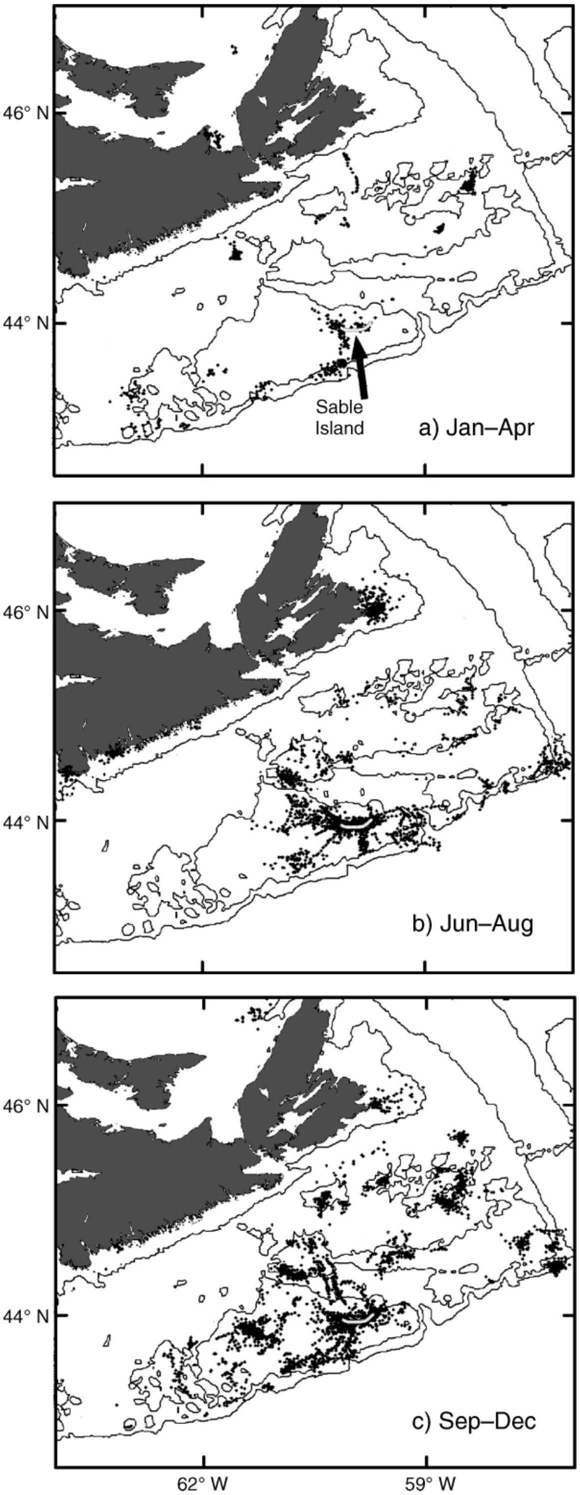

FIG. 4. Male foraging locations; 16 individuals are represented in panel (a), 11 in panel (b), and 30 in panel (c). In panel (d), all modeled locations for the 41 males are plotted for the entire year. See the Fig. 3 legend for an explanation of shading in the figure. A color version is available in Appendix B: Fig. B5.

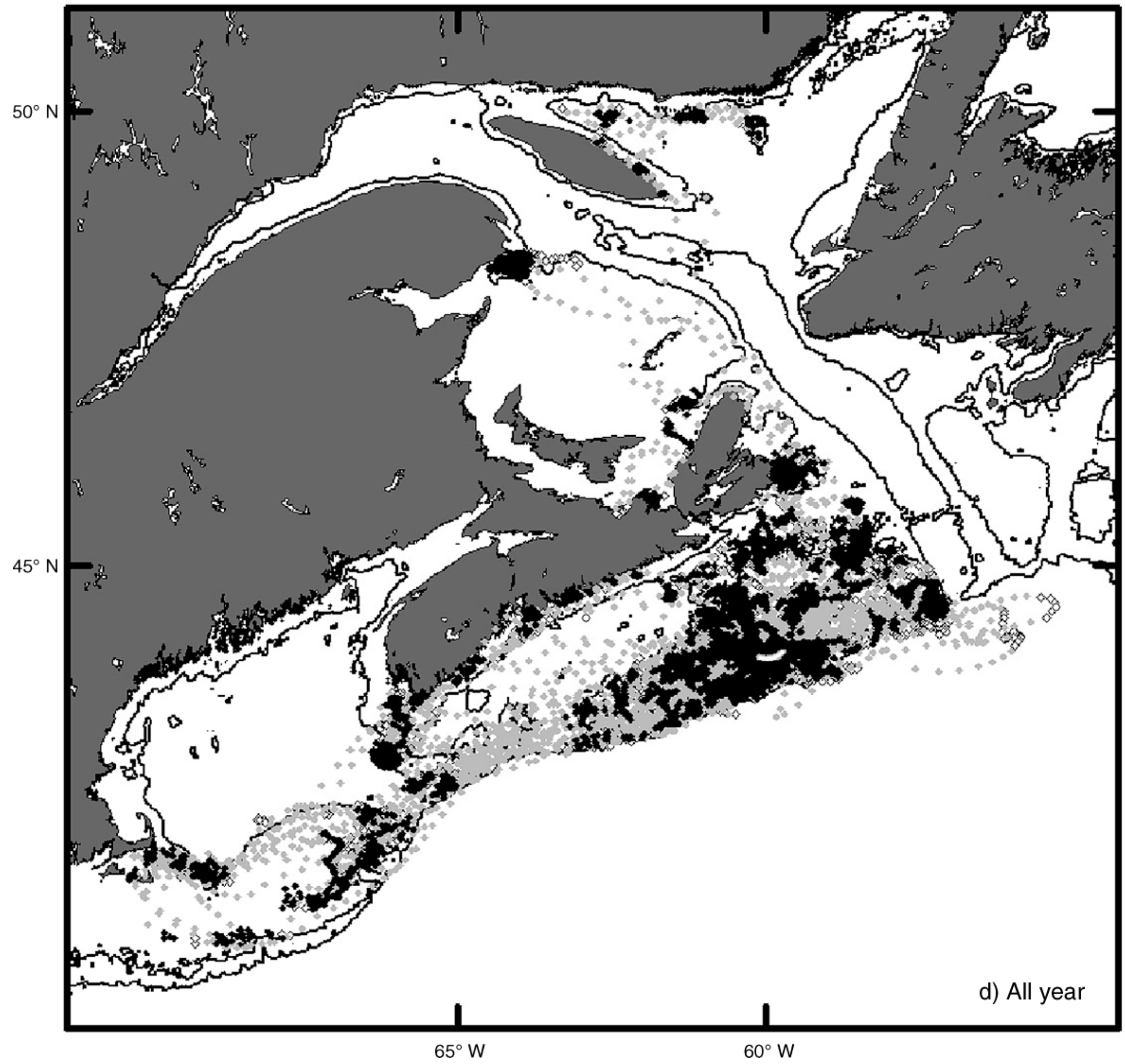

FIG. 4. CONTINUED.

gradients, regardless of whether those edges are real or an artifact of the data.

In grey seals, the seasonal change of inferred foraging locations is striking. Winter foraging trips were longer and required more travel time to more distant foraging locations. Winter foraging locations were more scattered and depth of foraging locations deeper than other seasons. Deeper dives require more ascent and descent time, leaving less stored body oxygen for bottom foraging than shallower dives, and are thus less efficient (Houston and Carbone 1992, Mori 1999, Thompson and Fedak 2001). Diving animals should go only as deep as they need to successfully forage. Being benthic foragers, moving to deeper habitat during winter suggests shallower more accessible areas used is summer and fall are less favorable in winter. This, and the scattered nature of foraging locations during winter, suggests prey are less predictable, occur in deeper water, and require more effort to acquire than in summer or fall. In the western Atlantic, many fish species migrate to deeper water during the winter and to shallow banks during the summer and fall to remain in warmer water (Perry and Smith 1994, Swain et al. 1998), and it is likely predators, including seals, track this migration.

In summer and fall, foraging locations occur in more focused patterns, especially over Middle Bank. From May through August, both sexes, but especially females, remain inshore near haulout sites, and spend a larger proportion of their time ashore. Foraging trips are much shorter, and many trips require little or no travel to reach foraging areas. Despite the reduction in foraging effort, both sexes gain body mass (Beck et al. 2003*a*), suggesting prey may be more accessible during this period. Finally, the intense use of Middle Bank and

TABLE 1. Mixed-effects model results showing the effect of sex, season, and water depth on state–space models (SSM) inferred behavioral state of grey seals (*Halichoerus grypus*).

Model	AIC	sn	sx	dpth	sn × sx	sn × dpth	sx × dpth
sn + sx + dpth + sn × sx	120 363.3	****	****	***	*		
sn + sx + dpth + sn × sx + sx × dpth	120 375.5	****	****	***	*		ns
sn + sx + dpth + sn × sx + sn × dpth	120 378.7	****	****	***	*	*	
sn + sx + dpth	120 384.7	****	****	***			
sn + sx + dpth + sn × sx + sn × dpth + sx × dpth	120 388.4	****	****	***	*	*	ns
sn + sx + dpth + sx × dpth	120 396.7	****	****	***			ns

Notes: All possible models were tested; the six best are shown here. Effects are abbreviated as follows: sn, season; sx, sex; dpth, depth. Columns to the right of the AIC show the type III P value of each term of the model. The model in boldface type is the best fitting using AIC, and tables of pairwise comparisons from this model for the effect of each season and sex are available in Appendix B: Tables B1 and B2.

* $P < 0.05$; *** $P < 0.001$; **** $P < 0.0001$; ns, $P > 0.05$.

surrounding areas while other equally accessible areas are left practically unexploited suggests a highly predictable prey resource over this bank in the fall. Fatty acid analysis show that females heavily rely on Atlantic sandlance (*Ammodytes dubius*) during this period. Given the suitability of Middle Bank for sandlance (Frank 1996, Beck et al. 2007), it is likely in abundant, predictable supply, and has been for some time, since our telemetry data spans 10 years and females exploited the bank through the period.

Males had significantly fewer inferred foraging locations and traveled more than females. This was especially true in winter, and given the much lower rates of inferred foraging and more numerous travel-only trips by males in winter, males probably found this season difficult. Prey aggregations were probably less predictable, required more searching or longer migration to more favorable habitat near the southwestern tip of the Scotian Shelf and on Georges Bank. Both sexes foraged in deeper water during winter, suggesting prey were generally deeper, but this change affected males more than females.

Sexual differences in foraging were likely due to size dimorphism. Male grey seals are about 50% heavier than females and must consume more food to maintain and gain mass. Males, but not females, have a negative body energy balance over the winter (Beck et al. 2003*a*). Earlier work suggested that winter negative energy balance was the result of evolved life history, and that males delay blubber accumulation to avoid negative fitness consequences of long term blubber storage, while females immediately store blubber to support pregnancy (Beck et al. 2003*a*, *b*, *c*). Life history may play a role, but our behavioral analysis suggests that the winter foraging environment is harsh and larger animals have a harder time meeting their energy needs than smaller ones.

Although females focus foraging effort to a greater degree than males, a few small shelf areas receive a disproportionate amount of foraging effort regardless of sex. Given the large grey seal population in eastern North America, we might expect to find ecosystem effects in high use areas. Unfortunately, few fish community surveys are conducted in the fall when foraging activity by grey seals appears to be most focused. With that lack of data, it is difficult to suggest which species would be affected and by how much. Our overall impression is that spatial behavior changes with annual cycles of prey abundance. To help explain changes in movement of grey seals, future work should examine how prey distributions change seasonally.

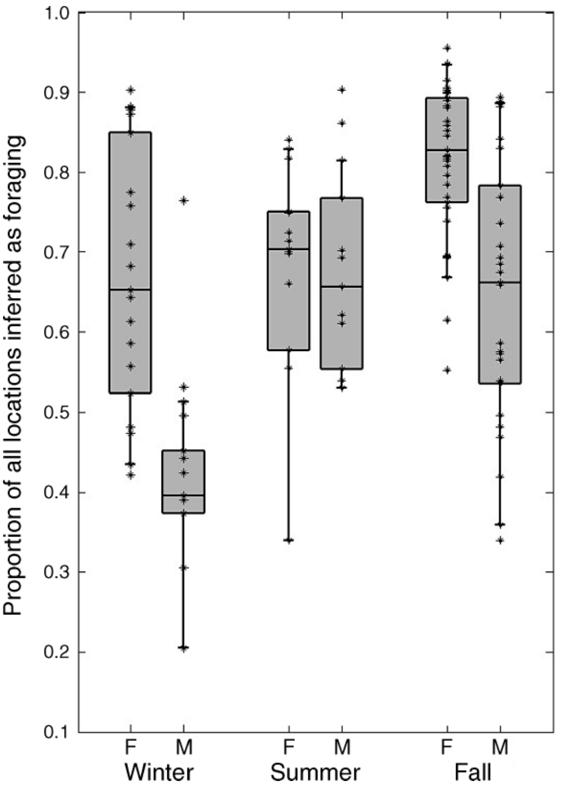

FIG. 5. Fraction of SSM locations inferred as foraging. Stars indicate the median proportion of locations inferred as foraging for each individual for the respective sex and season; the boxes show interquartile range; and whiskers the 10th and 90th percentiles. Horizontal lines in the boxes represent the mean. Locations with uncertain behavioral classification or within 5 km of shore were not included. The mixed-effects model results shown in Tables 1 and 2 indicate that sex and season strongly influence behavioral state. Abbreviations: F, female; M, male.

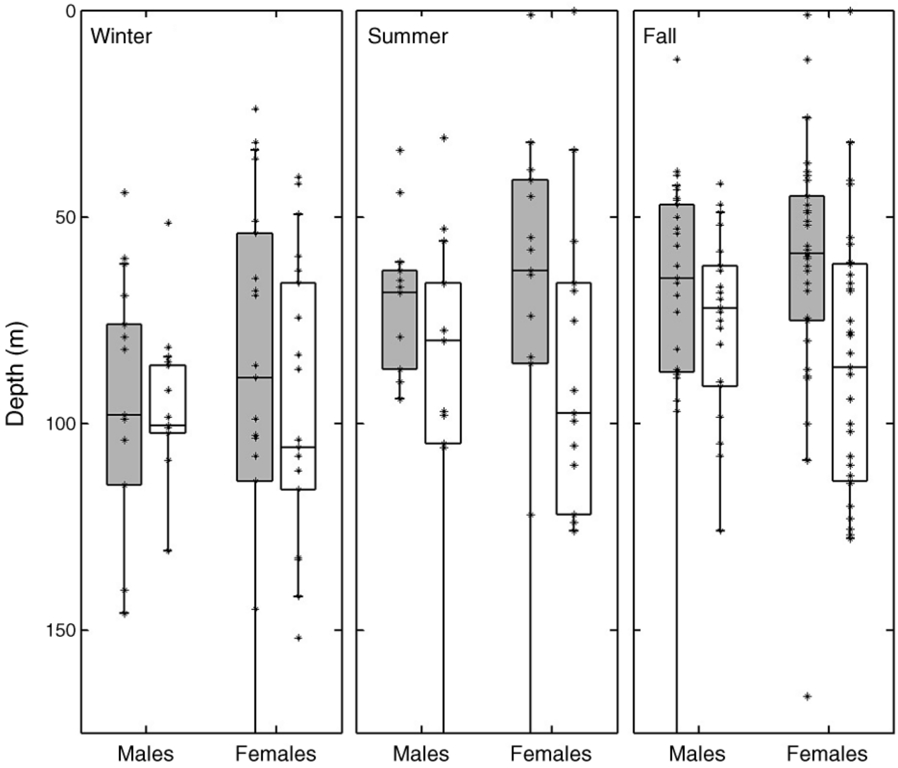

FIG. 6. Depth of the water column from bathymetry data at SSM modeled points inferred as foraging (gray bars) or travel (white bars). The sample was further grouped by sex and season to show differences in depth at foraging and travel locations as well as depth changes through the year. Stars indicate the median depth used by each individual for each behavioral state; the boxes show interquartile range; horizontal lines in boxes are means; and whiskers the 10th and 90th percentiles.

Model efficacy and conclusions

Animals draw upon a continuum of behaviors with differences too subtle to resolve with Argos data and the current approach. However, even with only two behavioral states, this model yielded new insights. The ability to fit more than two states is as much a limitation of the data as it is the SSM approach. Another state, haulout, should easily be discriminated from foraging using a state–space switching model. It is not, however, because the signal-to-noise ratio is too high in Argos data to separate the perfectly stationary haulout behavior from near stationary foraging behavior. GPS tags with the resolution to observe such subtle differences are becoming increasingly available, and SSMs will be able to objectively discriminate finer scale behaviors from such data.

TABLE 2. Grey seal foraging trip characteristics by season and sex and the strength of sex and season effects on each characteristic according to the mixed-effects model described in Eq. 5.

	Winter		Summer		Fall		Model effect		
Trip character	Male	Female	Male	Female	Male	Female	sx	sn	sx × sn
No. trips (individuals)	50 (16)	49 (15)	70 (14)	40 (13)	131 (32)	133 (30)			
Trips with patches (%)	68	98	81	85	82	91			
Trips without travel (%)	14	10	11	18	9	28			
Trip length (d)	10.5 ± 8.5	7.1 ± 5.7	9.4 ± 7.7	5.4 ± 11.6	12.7 ± 11.9	10.5 ± 11.4	0.083	0.003	0.306
Forging ratio†	0.33 ± 0.28	0.61 ± 0.22	0.48 ± 0.29	0.62 ± 0.28	0.49 ± 0.31	0.67 ± 0.29	<0.0001	0.071	0.819
Patch area (km^2)	259 ± 324	201 ± 285	315 ± 530	200 ± 246	385 ± 720	307 ± 488	0.003	0.006	0.734
Patch distance (km)	180 ± 209	82 ± 65	69 ± 50	62 ± 56	81 ± 54	49 ± 45	<0.0001	0.181	0.599
Patch residence (d)	3.26 ± 2.82	5.36 ± 4.49	4.63 ± 5.03	4.92 ± 5.38	5.49 ± 5.83	6.74 ± 7.32	0.690	0.003	0.410

Note: For the last five characteristics, values are mean ± SD. See Table 1 for key to model effects.

† Foraging ratio is the portion of foraging trip spent in the foraging state.

SSM methods hold great promise for analyzing and understanding animal telemetry data. Earlier analyses of this dataset produced an impression of a species that foraged broadly on the shelf (Austin et al. 2004, Breed et al. 2006). In contrast, the current analysis suggests grey seals focus foraging efforts on a tiny fraction of the total shelf area. While grey seals may be found across the entire shelf, many deeper areas are not suitable habitat and animals travel through them on their way to predictable and productive foraging patches. These results have implications for understanding the effects of grey seal predation on fish populations and potential conflict with fisheries, currently an important ecological and political issue.

With nearly 40 years of sustained population growth at over 12% annually, Northwest Atlantic grey seals can hardly be regarded as a conservation concern (Bowen et al. 2007). However, for many marine species at risk, satellite telemetry has been a primary method of observation (e.g., James et al. 2005*a*, *b*). Using this or similar state–space approaches to study such species could greatly improve our understanding of their ecology and aid conservation and management efforts worldwide.

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APPENDIX A

Details and diagnostics of WinBUGS Markov chain Monte Carlo model fitting procedure (*Ecological Archives* E090-228-A1).

APPENDIX B

Additional tables and figures: detailed mixed-effects models results, plots of TDR data vs. SSM results, and color versions of Figs. 3 and 4 (*Ecological Archives* E090-228-A2).

SUPPLEMENT

A compressed package of scripts, functions, sample data, and instructions required to implement the state–space model described in the text (*Ecological Archives* E090-228-S1).