

Movements and foraging habitats of great shearwaters *Puffinus gravis* in the Gulf of Maine

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ABSTRACT: In the western North Atlantic, great shearwaters *Puffinus gravis* are among the most abundant seabirds during summer months, yet little is known about their movement ecology and habitat requirements in this ecosystem. We deployed platform terminal transmitters on shearwaters captured in the Gulf of Maine and used a Bayesian switching state–space model to describe bird movements, behavior, foraging areas, migration timing, and how such habitat use and movements might be related to age. From July to November, great shearwaters traveled an average of 515 km per week and spent most of their time foraging around the rim of the gulf, primarily using shallower waters (<100 m), where bathymetry was more steeply sloped. A generalized additive model fit to these foraging locations data revealed correlations between foraging habitat use and depth, chlorophyll *a* and sea surface temperature, but not slope. Interestingly, these relationships were not consistent across birds from different tagging sites, suggesting a flexible foraging strategy based on local habitat conditions and high mobility. Movements associated with the shearwaters' southern migration began in August and continued through much of September, with birds leaving the study area via a pathway south of Nova Scotia, Canada. Nape plumage analysis showed most of the captured birds in the Gulf of Maine were young birds; 89% were <3 yr old. These results suggest that modeling shearwater location information using state–space models can be useful in identifying discrete, high-use habitat patches as part of efforts to reduce fishery bycatch.

KEY WORDS: Great shearwater · Gulf of Maine · Foraging areas · Movements · Age composition · Habitat use · State–space models

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INTRODUCTION

Technological advances in wireless telemetry have greatly improved our ability to examine the interaction of free-ranging seabirds and the marine environment at relevant spatial and temporal scales (González-Solís & Shaffer 2009). Detailed observa-

tion of the movement of individual animals offers the potential to understand spatial population processes as the ultimate consequence of individual behavior, physiological constraints and fine-scale environmental influences (Patterson et al. 2008). Across short time scales, the extreme mobility of seabirds allows them to rapidly respond to variations in the spatial

availability of food resources. In contrast, over the long term, seabirds operate at a life-cycle scale and respond to seasonal changes within potential foraging areas (Shaffer et al. 2006), differences in long-distance migrations among juvenile, immature and adult birds (Peron & Gremillet 2013), and implications from nesting success or failure (Weimerskirch et al. 2014). Consequently, both ephemeral events and lasting trends in the marine environment can have concurrent influences on seabird movements and habitat use patterns.

Tracking movements of individual birds and characterizing their relationships to the marine environment can provide early signals of changing environmental conditions and opportunities for mitigating the rapidly increasing spatial threats facing seabird populations. For example, tracking of individual birds has been used to elucidate the impact of recent southern hemisphere wind field changes on foraging patterns (e.g. wandering albatrosses *Diomedea exulans*; Weimerskirch et al. 2012) and to identify previously unknown distributions of rare and endangered species (Guilford et al. 2012, Jodice et al. 2015). Additionally, numerous authors have used movements of individual birds to identify areas of potential bycatch in commercial fisheries (Torres et al. 2013, Hatch et al. 2016). In this paper, we use satellite tracking of individual great shearwaters *Puffinus gravis* to identify the spatiotemporal dynamics of their habitat use in the Gulf of Maine, the physical and biophysical processes that underlie these patterns, and how age structure potentially impacts habitat use and animal movements.

The great shearwater is a long-lived seabird that breeds in the South Atlantic's Tristan da Cunha Island group. In general, they migrate north across the equator during the austral winter and by June they are widely distributed across the western half of the North Atlantic (Cramp 1977). Their migration reaches a peak northern limit at the Grand Banks and western coast of Greenland in July–August (Brown et al. 1975) before starting a southward migration timed to return adults to nesting areas in September–October for egg laying in November (Cuthbert 2005). Based on better-studied shearwater species (e.g. short-tailed shearwaters *Puffinus tenuirostris*; Bradley et al. 1999), great shearwaters probably do not return to nesting colonies until their 4th year and do not start breeding until their 6th to 7th year of life. Thus, a considerable segment of the population is pre-reproductive.

While there exists a broad understanding of great shearwater movements in their wintering range of

the North Atlantic (Wynne-Edwards 1935, Brown et al. 1975, Cramp 1977), there is a little information pertaining to specific foraging areas, migration timing, and how such distribution might be related to age (Riotte-Lambert & Weimerskirch 2013). For US northwest Atlantic waters, fishery observer data showed that a small area (1%) of the Gulf of Maine accounted for the majority of great shearwater bycatch on their wintering range and that a subset of the gillnet fleet constituted the primary interaction (Hatch et al. 2016). Thus, knowledge of timing and use of specific areas where these shearwaters concentrate, as well as any age-related insight about their composition, would be useful to managers attempting to minimize or mitigate such fisheries interactions. In addition, current knowledge of great shearwater habitat use is needed to understand how climate-induced environmental changes might impact the species or to monitor ecosystem changes as they occur.

MATERIALS AND METHODS

Study site

Fieldwork was conducted within the Gulf of Maine, a large gulf of the Atlantic Ocean on the east coast of North America. The gulf is delineated by Cape Cod at the eastern tip of Massachusetts in the southwest and Cape Sable Island at the southern tip of Nova Scotia in the northeast. In this study, the Gulf of Maine includes the Bay of Fundy, southern Scotian Shelf and Georges Bank. We tagged great shearwaters from 2006 to 2014 at 3 sites in the Gulf of Maine: (1) a Massachusetts site in the southwest Gulf of Maine on Stellwagen Bank and coastal waters east of Cape Cod, Massachusetts (41.48 to 42.52° N, 70.49 to 69.51° W), (2) a Maine site in the northwest Gulf of Maine in coastal waters (43.47 to 44.21° N, 69.40 to 67.19° W) and (3) a New Brunswick site in the northern Gulf of Maine within the Bay of Fundy in waters near Grand Manan Island, New Brunswick (44.47 to 44.87° N, 66.82 to 66.52° W) (Fig. 1).

Data collection

Bird capture, transmitter tag deployment, moult and age

We used small vessels to access great shearwaters at known foraging areas. Birds were attracted to

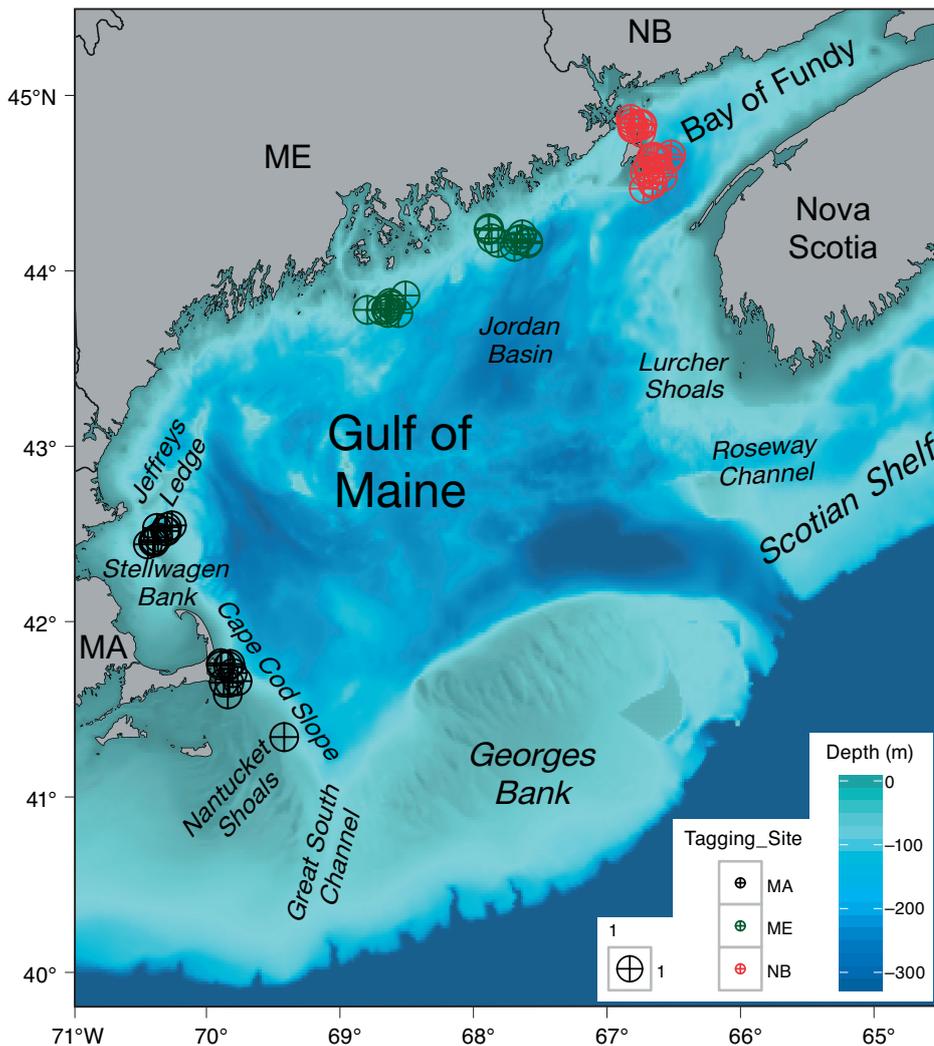


Fig. 1. Locations of satellite tags (PTTs) deployed on great shearwaters at sites in the Gulf of Maine: coastal Massachusetts (MA), Maine (ME) and New Brunswick (NB)

these small vessels using cut fish and squid. Once close enough to the vessel, birds were caught with handled landing nets (Ronconi et al. 2010a). Some birds were caught without bait (Ronconi et al. 2010b).

A total of 66 birds were captured and then fitted with a solar or battery-powered platform terminal transmitter (PTT). PTTs were attached dorsally, central to the body mass of the bird below the nape of the neck and between the wings. Tags were attached using a combination of tape (Tesa tape), glue (Loctite 422), and 4 sub-cutaneous sutures (Prolene suture 4-0, Ethicon) as per MacLeod et al. (2008). PTTs represented less than 3% of body mass for all tagged birds (suggested guidelines for tagging seabirds; Phillips et al. 2003). At the New Brunswick site around Grand Manan Island 24 birds were tagged between 2006 and 2009, 20 birds were tagged from the Maine site in 2010–2012 and 22 birds were tagged in the Massachusetts site off Cape Cod in 2013–2014 (Table 1). Satellite tags used for New Brunswick and Maine birds were Kiwi Sat 202 PTT from SirTrack Wildlife Tra-

Table 1. Details of satellite tag (PTT) deployment by year and tagging site (MA: Coastal Massachusetts; ME: Coastal Maine; NB: Grand Manan Island, New Brunswick). PTT model: (1) Kiwi Sat 202 PTT, SirTrack Wildlife Tracking Solutions, 30 g; (2) Solar PTT-100, Microwave Telemetry, 15 g; (3) NorthStar 9.5, NorthStar Science and Technology, 18 g. Duty cycle: (1) 8 h on, 16 h off; (2) 24 h on

Year	Tag location	No. tags (birds)	Mean tracking duration per bird (d)	Mean no. Argos locations per bird	Mean no. locations per day	Mass (mean \pm SD) per bird (g)	SD bird tag to body mass ratio	PTT model	Duty cycle
2006	NB	6	104	526	5.1	1053 \pm 120	0.003	1	1
2008	NB	9	119	619	5.5	1037 \pm 107	0.003	1	1
2009	NB	9	132	715	5.8	1033 \pm 50	0.001	1	1
2010	ME	8	99	516	5.4	990 \pm 37	0.001	1	1
2011	ME	3	77	461	5.7	985 \pm 29	0.001	1	1
2012	ME	9	101	608	6.1	1032 \pm 58	0.001	1	1
2013	MA	10	60	886	15.1	757 \pm 59	0.002	2	2
2014	MA	11	104	1799	17.3	960 \pm 109	0.002	2	2
2014	MA	1	113	967	8.6	860		3	1

cking Solutions (30 g). Solar PTT-100 tags from Microwave Telemetry (15 g) were used in Massachusetts, except for a single Northstar 9.5 tag from Northstar Science and Technology (18 g). Duty cycles for tags deployed in Massachusetts were 24 h on, except for the Northstar tag, which was set for 8 h on and 16 h off; tags used in Maine and New Brunswick were set at 8 h on and 16 h off. Argos locations were obtained from the time of their release to when the transmitters stopped working.

Moult scores of the primary wing feathers were assigned using the British Trust for Ornithology method (Ginn & Melville 1983). Scores can range from 0 to 50, where 0 indicates all primary feathers are old and 50 indicates that all 10 primaries are new and completely grown. We scored birds at the New Brunswick site in August and early September 2006–2009 ($n = 24$). At the Massachusetts site, moult was scored for birds captured in July 2014 and 2015 ($n = 27$), in September 2014 ($n = 10$) and in October 2015 ($n = 13$). For tagged birds, moult was scored on all birds from the New Brunswick site (2006–2009) and for birds tagged in July 2014 from the Massachusetts site.

Additionally, some birds were aged by nape plumage according to Pyle (2008) into 3 categories: hatch year (HY), second year (SY) and after second year (ASY). HY birds have an entirely brown nape (no white). ASY birds have an entirely white nape (no brown). SY birds have a wide variation of white on the nape, which is always interrupted in the center by brown. Based on photographs, we assigned age by nape plumage for 21 birds tagged in August and September 2006–2009 from New Brunswick, and for 13 birds in July and 13 birds in October 2015 caught at the Massachusetts site, which were not tagged.

Spatiotemporal habitat use environmental variables

To investigate the spatiotemporal habitat use of great shearwaters, we used 4 environmental covariates in our comparisons: depth and slope (proxy for fisheries interactions and underlying hydrology) as static factors, and sea surface temperature (SST) and chlorophyll (proxy for biological productivity) as dynamic factors. Depth indirectly relates to bottom temperature and in a general way sediment types, which delineate stocks of fisheries (Double-day 1981). Constraints of topography and stratification of the water column typically steer currents in the along-isobath direction, except in areas where

steep slopes allow tidal action to mix differing water regimes (e.g. fronts) (Wright 1976, Simpson 1981, Csanady & Magnell 1987). All spatiotemporal habitat use data were collected and analyzed using R (R Core Team 2016). Depth data were obtained from NOAA's ETOPO 1-min data set. Slope was extracted using the terrain function in the raster library (v2.5-2; Hijmans 2016). SST data ($^{\circ}\text{C}$) were obtained from MODIS at a ~ 4 km spatial resolution (monthly averages) (https://podaac.jpl.nasa.gov/dataset/MODIS_AQUA_L3_SST_THERMAL_MONTHLY_4KM_DAYTIME_V2014.0) (Ocean Biology Processing Group 2015). Finally, chlorophyll (chl *a*) data (mg m^{-3}) were acquired from MODIS at a ~ 4 km spatial resolution (monthly averages) (http://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/chlor_a/) (Ocean Biology Processing Group 2014).

Data analysis

Location and behavior estimation

We fitted the Bayesian switching state–space model (SSSM) described by Jonsen et al. (2005) to all observed Argos location data to estimate spatial locations at fixed intervals of time using the R package *bsam* (v0.43-1; Jonsen et al. 2005). Location classes in the set {3, 2, 1, 0, A, B} were used from the 'observed' data. 'Estimated' locations for each bird were derived with the single animal first-difference correlated random walk with switching (DCRWS) model. Within this modeling framework, we set the number of samples during adaptation and update to 30 000, the number of samples to generate after convergence to 10 000 and the amount of thinning to 10 samples. The model was run with a 3-h time-step. Thus, all estimated locations were normalized in time to 3 h spent in the vicinity of that location on that date.

After fitting the DCRWS model to each individual, we then determined behavioral state at each estimated location using mean estimates of parameter *b* obtained from the DCRWS model, which ranged from 1.0 to 2.0. Similar to Jonsen et al. (2007), we delineated 2 behavioral modes by adopting cut-offs at 1.25 and 1.75. Foraging animals typically exhibit some form of area-restricted search (ARS) with large turning angles and relatively slow travel rates, whereas transiting animals show a lack of turning angles with high travel rates (Jonsen et al. 2007). Therefore, mean estimates below 1.25 were considered transiting and estimates above 1.75 were foraging.

Given the differences in duty cycles with tags used in this study, a separate evaluation (see the Supplement at www.int-res.com/articles/suppl/m574p211_supp.pdf) of SSSM fitted tracks was made using 6 birds with on/off duty cycles that showed a wide range of movement and differing sequences of behavior. We visually compared track fits of 3, 6, 9 and 12 h time-steps for each bird. No issues were found with track fits when using a 3-h time-step. In most cases, a 3-h time-step minimized track overruns often seen with larger time intervals while birds were in the study area. Moreover, the 3-h time-steps of modeled tracks from duty-cycled tags appeared qualitatively similar to modeled tracks from continuously transmitting tags.

Spatiotemporal analysis

Distribution patterns

To investigate general distribution patterns with respect to broad-scale bathymetric and oceanographic conditions, we overlaid estimated locations with a subset of bathymetric and oceanographic polygons based on latitude/longitude coordinates derived from the Bedford Institute of Oceanography (BIO) for the Gulf of Maine, Georges Bank and southern Scotian Shelf (Petrie et al. 1996). These polygons or subareas defined the boundaries of the study area while also providing a set of geographic and hydrographic units to analyze our results. The coastal boundaries of some of these polygons were not contiguous with the coastline; when estimated locations fell between the shoreline and coastal boundary of such subareas, that location was assigned to the adjacent polygon. We tallied all estimated locations by subarea initially to understand spatiotemporal associations with major bathymetric and oceanographic features of the study area.

Movements and migration

We mapped movements of birds across the study area using monthly plots of all estimated locations (July–November) and denoted locations by tagging site: Massachusetts (MA), Maine (ME) or New Brunswick (NB).

Migratory movements were then determined using a 2-step process defined by birds that left the study area in time for possible breeding activity in the southern hemisphere. First, we identified individual

birds that were south of the equator before 1 October. We chose 1 October as our cut-off because great shearwaters start to arrive at the breeding colonies in late September and egg-laying begins in early November (Cuthbert 2005). We then created a kernel density plot using only locations with 'transit' behavior from those early-migrant individuals while they were in the study area. We also noted the timeline for this activity and related any potential implications or associations found with the moult and age information.

Use and behavior using discrete biophysical regions

We combined the individual BIO subareas into biophysical regions based on depth and slope (static parameters) to characterize usage by behavior (transit or ARS) within the study area. Regions were broadly defined by either depth (shallow or deep) and/or slope (e.g. rising or falling edges of banks and shelf break versus lack of slope or uniform depth) within the Gulf of Maine and Georges Bank. Thermal fronts often exist where slopes are steeper (e.g. Townsend et al. 1987, Ullman & Cornillon 1999, Guida et al. 2013). This process created 4 regions: Rim, Basin, Shelf and Offshore (Fig. 2). The Rim group included the shallower, steep slope subareas that surrounded the deep central Gulf of Maine where the water column is not stratified in winter months. In counter-clockwise fashion from the north, this group included the Bay of Fundy, coastal Maine, Stellwagen Bank, Cape Cod Slope, northern edge of Georges Bank, Browns Bank and Lurcher Shoals. The Basin group included the deep and year-round stratified waters of the central Gulf of Maine. The Shelf group included the shallow and well-mixed waters of Nantucket Shoals, Great South Channel, and central and southern parts of Georges Bank, and was characterized by uniform depths with little slope. And the Offshore group was composed of the deepest waters south and east of Georges Bank at the shelf break. We tallied the number of estimated locations per biophysical region by behavior. Usage was defined by number of locations per region and further separated by behavior (transit or ARS). Depth and slope were also categorized within each region using the estimated locations.

Foraging habitat use

Foraging habitat use of great shearwaters was investigated using a delta lognormal generalized ad-

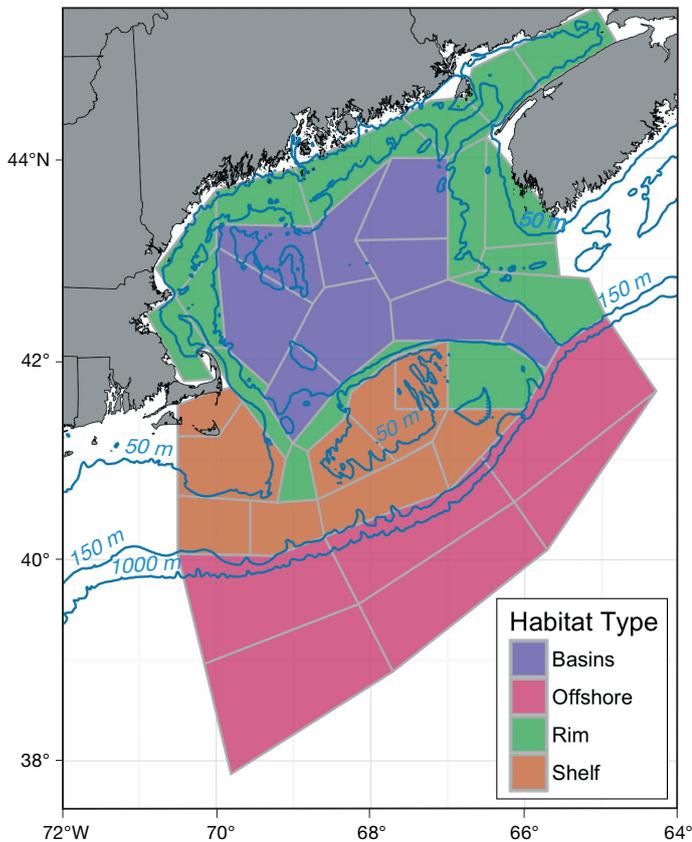


Fig. 2. Habitat types in the Gulf of Maine (Rim, Basin, Shelf and Offshore) depicted on the basis of depth and slope using groups of Bedford Institute of Oceanography polygons (Petrie et al. 1996)

ditive model (GAM) to correlate foraging locations from the DCRWS model to spatiotemporal environmental variables. First, we gridded the BIO study region (Fig. 2), which includes the Gulf of Maine, Georges Bank and southern Scotian Shelf, into $15 \times 15'$ blocks of latitude/longitude. We then overlaid the estimated foraging (ARS behavior) locations on the gridded BIO study region and calculated the monthly total number of estimated foraging locations within each grid cell for each year. We then extracted spatiotemporal environmental variables at the centroid of each grid cell. Depth and slope values were extracted for centroid location. For SST and chlorophyll, we computed a monthly mean estimate for each grid cell for the centroid location using all months birds were in the study area from August 2006 to November 2014.

With these data, we then fit the delta-lognormal GAM model using restricted maximum likelihood with the `gam()` function in the `mgcv` library (Wood 2011) using R. Preliminary data exploration and model fitting attempts using count probability distri-

butions (e.g. Poisson, negative binomial) revealed a high proportion of zero values and, consequently, issues of overdispersion and zero-inflation. The delta-lognormal GAM model provided an opportunity to overcome these challenges by using a 2-stage modeling approach (Cragg 1971, Pennington 1983, Potts and Elith 2006). The first stage of the delta-lognormal GAM modeled the presence/absence of estimated foraging (ARS) behavior locations within each grid cell. The second stage of the GAM then focused only on grid cells with present estimated foraging behavior locations and modeled the log-transformed count of estimated ARS behavior locations as foraging intensity in each of those grid cells. For both levels of the model, we included year as a random effect and smooth terms for location (latitude/longitude), depth, slope, SST and $\log_{10}(\text{chl } a)$. Given the different tagging sites and that we wanted to allow for site-specific differences in great shearwater foraging habitat use, we also included tagging site as a parametric factor and as an interaction term with each of the smooth terms [e.g. $s(\text{depth}, \text{by} = \text{'site'})$]. We used thin-plate regression splines for each of the smooth terms and set the flexibility of each smooth term with a basis dimension of each smooth (k) equal to 10. Finally, for model selection we set the 'select' argument to TRUE within the call to the `gam` function. Turning on this 'select' option includes an additional penalty for each smooth term, which acts on the null space of the smooth term and therefore allows smooth terms to be completely removed from the global model (Marra & Wood 2011).

RESULTS

General distribution patterns

The DCRWS model estimated 17 816 locations between July and November from 2006 to 2014 for the 66 tagged great shearwaters. Of those, 75% of the locations occurred within 13 of 40 possible BIO subareas and 50% of the modeled locations were concentrated in just 6 subareas. These highest used subareas were located around Cape Cod, northern Georges Bank, northern Gulf of Maine and Bay of Fundy. In contrast, the remaining 27 subareas with the fewest locations occurred over the basins of the central Gulf of Maine, the shallow waters of central and southern Georges Bank and the deep waters beyond the continental shelf.

Location data were not equally distributed among the 3 capture sites. Sixty-one percent of the esti-

mated locations data were derived from the MA tagged birds (primarily because tags were deployed earlier at this site), 23% from NB and 16% from ME. For MA birds, the mean start transmission date was mid-July (Week 30), the exit date was early October (Week 40) and the mean (\pm SD) residency in the Gulf of Maine was 72.3 ± 38.1 d. ME and NB birds were tagged later, mid-August (Weeks 33–34), and their mean stays were 20.7 ± 17.7 and 24.4 ± 23.6 d, respectively. Mean departure for ME and NB was early September (Weeks 36 and 37, respectively).

Ranges for all birds by tagging site primarily overlapped in the northern and eastern parts of the Gulf of Maine, where the number of locations within individual subareas differed by less than 10% (i.e. SW Bay of Fundy, Jordan Basin and E Gulf of Maine, Lurcher Shoals and Roseway Channel). However, NB birds represented 60% of the estimated locations in the Central Bay of Fundy, and MA birds made up at least 90% of the estimated locations within sub-

areas around Cape Cod (i.e. Cape Cod Slope, Stellwagen Bank, Jeffreys Ledge, Nantucket Shoals), suggesting some fidelity to capture locations after tag deployments.

Movements, migration, moult and age

From July to November, great shearwaters traveled an average of 515 km per week (individual weekly average bird range 365–765 km) while in the study area. We examined their temporal movements during these months using pooled plots of all bird locations by month and tagging site (Fig. 3). Data from July only represented great shearwaters tagged in MA, since ME and NB birds were tagged after that month. Within a week these birds spread across the Cape Cod Slope from Stellwagen Bank south to the Great South Channel. By August, 75% of these birds moved outside of the Cape Cod area, with most

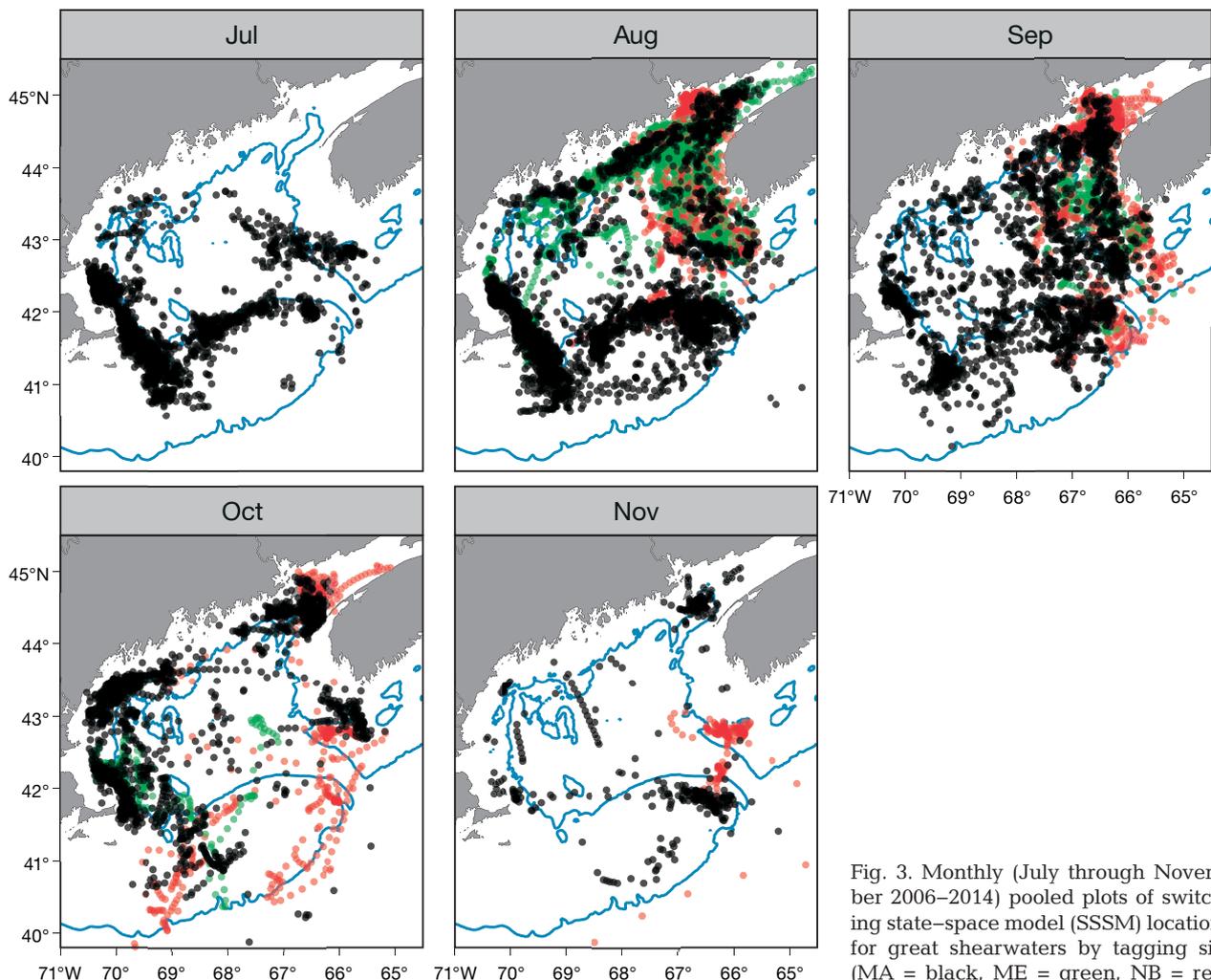


Fig. 3. Monthly (July through November 2006–2014) pooled plots of switching state-space model (SSSM) locations for great shearwaters by tagging site (MA = black, ME = green, NB = red)

going east along the northern edge of Georges Bank. The other 25% remained off MA for 1–2 mo. About half of the birds (12 of 21) that initially left waters around Cape Cod eventually returned to this area for varying amounts of time.

Starting in August we examined the movements of birds from all 3 tagging sites. During August, 22% ($n = 6$) of the birds from MA moved to the Bay of Fundy while the remainder stayed near Cape Cod ($n = 10$) or on Georges Bank ($n = 6$). Eighty percent ($n = 16$) of ME birds moved into the Bay of Fundy and 15% ($n = 3$) went south to Cape Cod. A single ME bird remained near coastal ME. Eighty-one percent ($n = 13$) of the ME birds that went into the Bay of Fundy continued east to Lurcher Shoals off the western coast of Nova Scotia. Of the NB birds, 88% ($n = 21$) used the Bay of Fundy and Lurcher Shoals; 8% ($n = 2$) traveled to Georges Bank and 4% ($n = 1$) proceeded southwest along the coast of ME.

Movements associated with the southern migration also began in August and continued through much of September. Thirty birds (45% of 66) flew south of the equator by the end of September and, thus, were designated as early migrants. Nineteen were tagged in NB, 9 in ME and 2 in MA. These birds left the study area via a pathway south of Nova Scotia (Fig. 4) between 14 August and 13 September with a median date of 1 September. They reached the equator between 13 and 30 September, taking an average of 18.7 ± 5.3 days traveling an average of 472 ± 197 km per day. After passing the southern tip of Nova Scotia, they typically headed ENE to the Grand Banks off Newfoundland before heading south towards the equator.

The timing of this migration event was coincident with the end of primary moult (Fig. 5). Primary moult was most variable in early July (Week 28) based on birds examined from MA. Scores reflected birds that were both just starting and finishing moult. Birds from MA examined in mid-July (Week 30) had all completed moult through the 5th primary. By mid-August (week 33), moult scores were close to 50 and varied only in the outermost or last primary (10th) to finish as noted with NB birds. Moult was completed on all birds examined in mid-September (Week 38) and mid-October (Week 43) off MA.

Birds that remained in the Gulf of Maine after 1 October continued to use the Bay of Fundy, Stellwagen Bank and Cape Cod Slope (Fig. 3). Two of these birds tagged in ME reached the equator in October. Another 4 birds representing all tagging sites reached the equator in December. 11% of the birds tagged (5 from MA and 2 from NB) were still in the

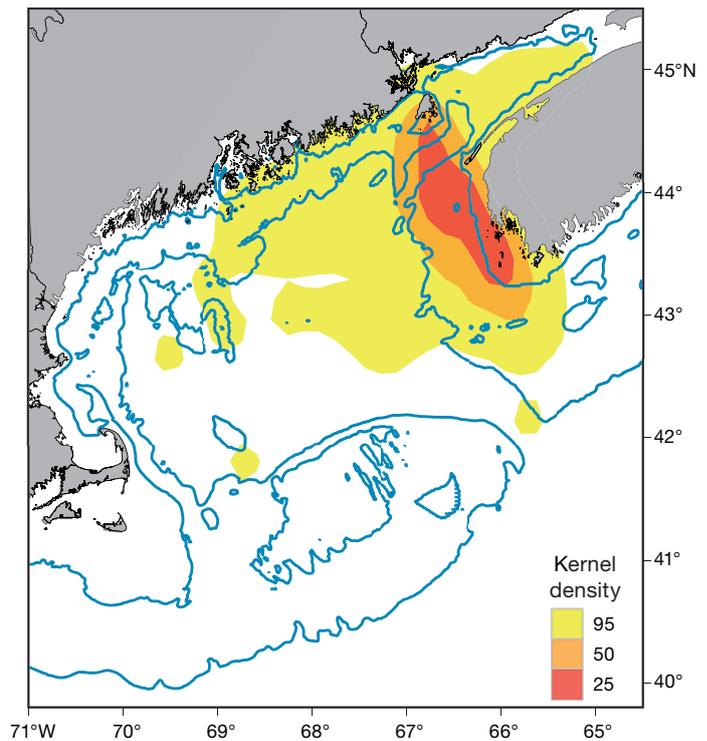


Fig. 4. Migration pathway out of the Gulf of Maine for early migrant great shearwaters (August and September) based on kernel density plots using transit behavior of 30 individuals

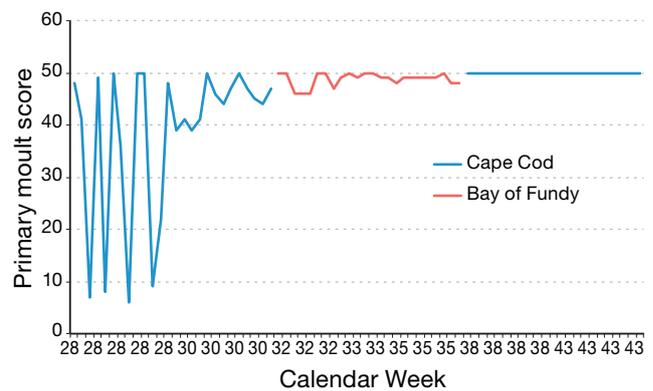


Fig. 5. Individual primary moult scores for great shearwaters from 2 areas (Cape Cod and Bay of Fundy) in the Gulf of Maine by calendar week and location

Gulf of Maine when their tags expired in November.

The age composition of the Gulf of Maine great shearwaters as determined by nape plumage was predominately young (<3 yr old); 89% ($n = 42$) of the birds examined were classified as HY or SY and 11% ($n = 5$) ASY. While SY birds were found in similar proportions in the Bay of Fundy and off Cape Cod (67 and 62%), the Bay of Fundy had more ASY birds

than Cape Cod (19% and 4%). Of the early-migrant individuals tagged in NB that were aged by nape plumage ($n = 16$), 81% ($n = 13$) were SY, 13% ($n = 2$) were HY and 6% ($n = 1$) were ASY. Five late-migrant NB birds (south of the equator after 1 October) classified by nape plumage were HY ($n = 1$), SY ($n = 2$) and ASY ($n = 2$).

Discrete biophysical regions

Our broad-scale habitat use analysis within discrete biophysical regions showed that the most heavily used habitat group was the Rim region, comprising 77% of all locations (Table 2). Of these Rim locations, 97% were classified as foraging (Table 2). The remaining 24% of locations by region used as ranked from most to least were Basin (12%), Shelf (11%) and Offshore (<1%), respectively. Birds spent similar amounts of time in the Basin and Shelf regions (12 and 11%), but used more transit behavior when in the Basin region (11 versus 3%; Table 2). The Offshore region was the least used region (<1%) and had the highest ratio of transit behavior (30%).

Rim and Shelf regions exhibited the shallowest water depth (<100 m) and had the highest ratio of ARS to transit behavior. However, mean slope in Rim (0.41°) was steeper than that in Shelf (0.34°) (Table 2). Birds exhibited more transit behavior in Basin and Offshore regions, where the water was deeper.

Foraging habitat use

Overall, each of the 2 stages of the delta-lognormal GAM explained a relatively large percent of the variability in the datasets. The presence/absence component, modeling the presence/absence of estimated ARS behavior in a grid cell, explained 38% of the deviance. The foraging intensity component, which modeled the log-transformed count of estimated ARS

behavior locations in a grid cell, explained 28% of the deviance.

Depth was a significant predictor regarding presence/absence of great shearwater foraging for all sites (MA, ME and NB) in the Gulf of Maine (Fig. 6A). Birds preferred shallower waters. But depth was a highly significant predictor ($p < 0.001$) of foraging intensity only for MA birds, particularly in waters <200 m deep, where variance of the predictor response was least (Fig. 7A). These locations would be in shallower waters from Stellwagen Bank south along the Cape Cod Slope to Nantucket Shoals and east across the northern edge of Georges Bank, which are all areas within the Rim biophysical region (Fig. 2).

Slope was not a significant predictor regarding presence/absence or foraging intensity of great shearwaters in the Gulf of Maine (Figs. 6B & 7B).

SST was a highly significant predictor ($p < 0.001$) of presence/absence for foraging birds for all sites (MA, ME and NB) (Fig. 6C). MA birds showed a preference for warmer waters ($\geq 18^\circ\text{C}$). ME birds showed a particular preference for colder water (< 13°C) and NB birds favored water temperatures between 13 and 20°C . SST was also a highly significant predictor ($p < 0.001$) of foraging intensity for all sites (Fig. 7C). MA birds continued their preference for warmer water ($\geq 18^\circ\text{C}$), which was generally associated with areas south of 42°N latitude. Frequency of locations with foraging intensity diminished considerably when SST was $>20^\circ\text{C}$. Maximum observed SST reached 26°C off the continental shelf south and east of Georges Bank. Foraging intensity for ME birds was bimodal with one peak between 11 and 14°C and another at $>18^\circ\text{C}$. NB birds also showed a bimodal response but the peaks were found in colder waters (i.e. $<11^\circ\text{C}$ and between 14 and 18°C). The areas with colder water (< 18°C) were only found in the northern Gulf of Maine and the Bay of Fundy. The foraging intensity response of ME birds to the warmer SST can be attributed to some individuals

Table 2. Breakdown of great shearwater activity and behavior (area-restricted search [ARS] or transit) by biophysical region using locations determined by the switching state-space model (SSSM) within each biophysical region including depth and slope with 95% confidence intervals (CI)

Biophysical region	No. locations	Total use (%)	No. ARS	No. transit	ARS (%)	Transit (%)	Depth (m)		Slope ($^\circ$)	
							Mean \pm SD	CI	Mean \pm SD	CI
Rim	11745	76.7	11361	384	96.7	3.3	93.3 \pm 92.5	92.4–94.1	0.412 \pm 0.603	0.401–0.423
Basins	1860	12.1	1663	197	89.4	10.6	198.4 \pm 42.8	196.4–200.3	0.430 \pm 0.647	0.400–0.460
Shelf	1644	10.7	1589	55	96.7	3.3	47.9 \pm 19.3	47.0–48.8	0.330 \pm 0.451	0.308–0.352
Offshore	70	0.5	49	21	70.0	30.0	1410.9 \pm 1170.3	1131.8–1689.9	0.484 \pm 0.779	0.298–0.670

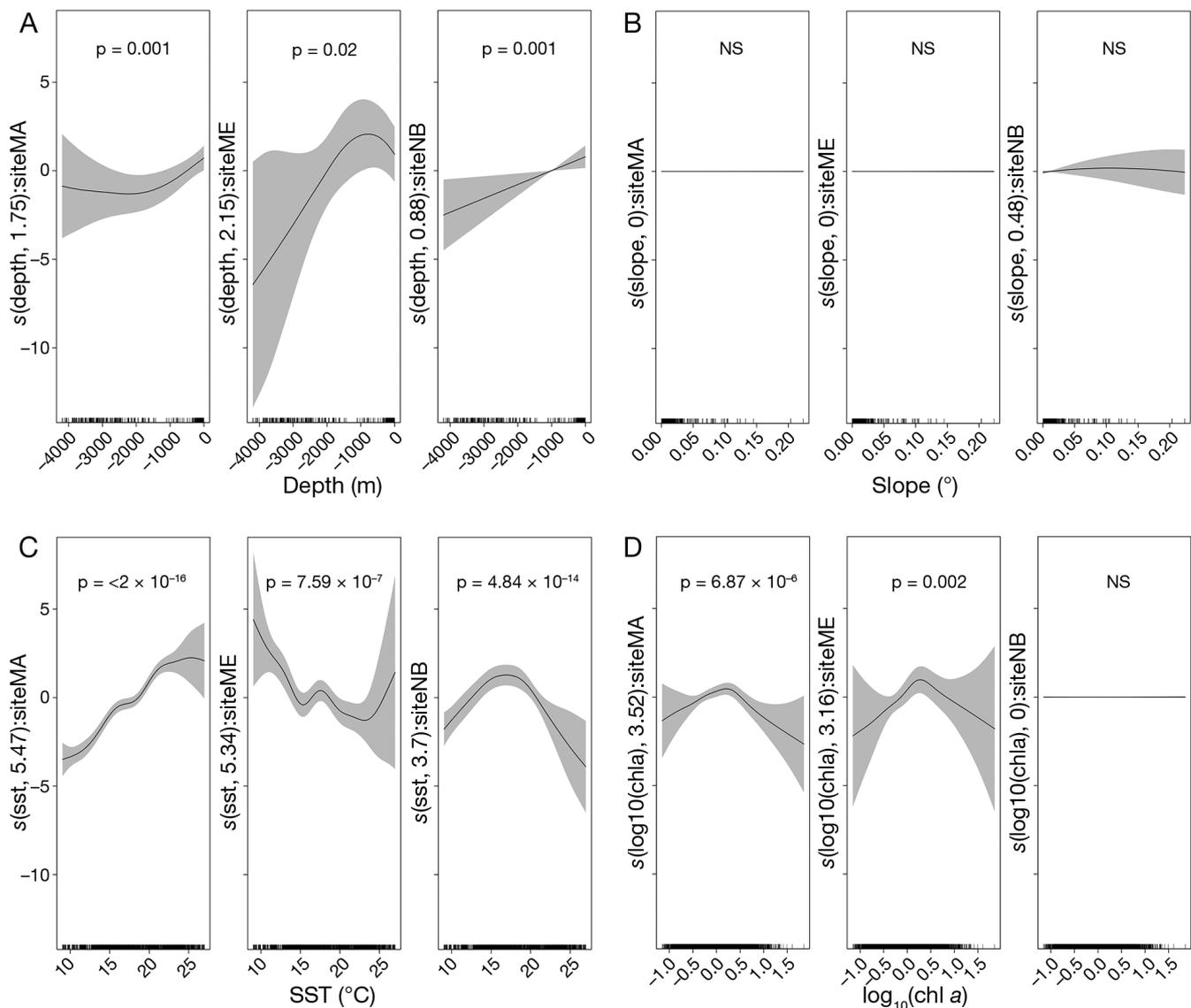


Fig. 6. Generalized additive model smooth terms fitted to presence/absence great shearwater foraging data within the Gulf of Maine. Within each panel (A–D) there are 3 plots, one for each smooth term against the predictor variable for the 3 different tagging sites (MA: Massachusetts; ME: Maine; NB: New Brunswick). (A) Depth; (B) slope; (C) sea surface temperature (SST); and (D) log chlorophyll *a* concentration (chl *a*). Significance of the smooth terms is displayed within each of the plots, where NS indicates a non-significant smooth term. x-axis labels depict the values of the predictor variable; y-axis labels are read as: s(predictor variable, estimated degrees of freedom):site; shaded area represents variation in the smooth estimate (± 2 SE); and rug plots show observations included in the model fitted datasets

that moved into the southwest parts of the Gulf of Maine during October ($<43^\circ$ N latitude; Fig. 3).

Chlorophyll was a significant predictor of foraging presence/absence for birds tagged in MA and ME, but not NB (Fig. 6D). Foraging intensity at the MA and ME sites was greatest where chlorophyll concentrations ranged from 1–2 mg m^{-3} . Such concentrations were ubiquitous throughout the Gulf of Maine, but higher concentrations ($>2 \text{ mg m}^{-3}$) were typically found in the Bay of Fundy. Thus the lack of signifi-

cance of chlorophyll as a predictor for NB birds is masked by the wider availability of chlorophyll throughout the region, as foraging was always present in waters with concentrations $>1 \text{ mg m}^{-3}$. Chlorophyll was a significant predictor ($p < 0.02$) of foraging intensity for birds from all sites (Fig. 7D). The positive response to chlorophyll for MA birds was limited to areas with lower concentrations (1–1.5 mg m^{-3}), but the response of ME increased with higher concentrations. However the foraging intensity of NB

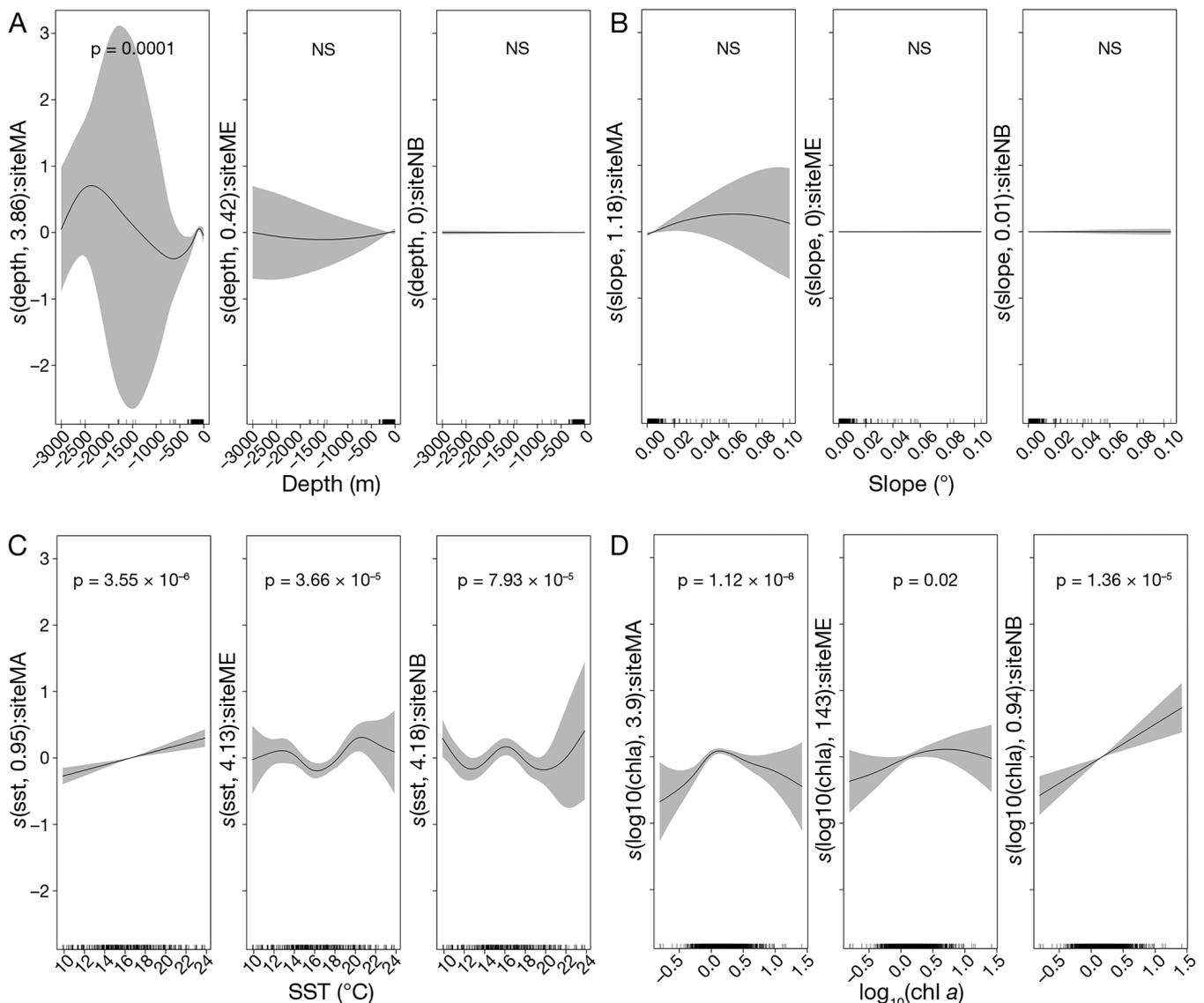


Fig. 7. Generalized additive model smooth terms fitted to $\log(\text{count of foraging locations})$ great shearwater foraging data within the Gulf of Maine. Within each panel (A–D) there are 3 plots: one for each smooth term against the predictor variable for the 3 different tagging sites (MA: Massachusetts; ME: Maine; NB: New Brunswick). (A) Depth; (B) slope; (C) sea surface temperature (SST); and (D) log chlorophyll *a* concentration (chl *a*). Significance of the smooth terms is displayed within each of the plots, where NS indicates a non-significant smooth term. x-axis labels depict the values of the predictor variable; y-axis labels are read as: $s(\text{predictor variable, estimated degrees of freedom})\text{:site}$; shaded area represents variation in the smooth estimate (± 2 SE); and rug plots show observations included in the model fitted datasets

birds increased progressively with higher concentrations of chlorophyll, although the frequency of foraging locations diminished as concentrations exceeded 2 mg m^{-3} .

DISCUSSION

This study provides unique details on the movement and habitat use of great shearwaters within the

Gulf of Maine. It is the first study in this area where such movements were based on tracking of individual pelagic seabirds rather than summaries of at-sea surveys (Brown et al. 1975, Powers 1983). We tagged birds at 3 distinct geographical sites within the Gulf of Maine. Given the use of these particular tagging sites, we could have introduced some bias into the location data with birds having a tendency to remain in the vicinity of where they were captured. However, across tagging sites, great shearwaters were

highly mobile, typically traveling hundreds of kilometers per week. Additionally, this site fidelity might also have resulted from birds aggregating in those areas because of the ecological factors that define them, rather than birds simply staying in the area in which they were captured. Short-tailed shearwaters in the southeastern Bering Sea fed in discrete locations long enough (several weeks) to reflect regional differences in prey availability (Baduini et al. 2006), and these shearwater flocks showed little movement among sampled locations for periods up to several weeks. While Baduini et al. (2006) used the term 'flocks' to describe short-tailed shearwaters, we found no indication of flocking behavior as individual great shearwaters did not remain in coherent groups (i.e. flocks) after tagging. Instead, they moved about independent of each other while probably intermingling in loosely formed assemblages with other birds in the same areas.

The characterization of nape plumage at 2 different sites (Cape Cod and Grand Manan Island) and at different times (months and years) suggests that great shearwaters in the Gulf of Maine are typically young, comprising predominately HY and SY birds. Earlier studies noted the presence of many great shearwaters in the northwest Atlantic after September, which implicated them as non-breeders or young birds (e.g. Rowan 1952, Powers & Brown 1987), and assessment of stranded great shearwaters also identified high proportions of juveniles along the eastern coast of the USA (Haman et al. 2013). The present study further supports the determination that the vast majority of great shearwaters in the Gulf of Maine from July to November are young, pre-reproductive birds. Spatial segregation by age class has been identified in other seabirds. For example, wandering albatrosses *Diomedea exulans* adjusted their foraging strategy to meet the requirements of successive life stages as their foraging skills and ability to cover greater distances improved (Weimerskirch et al. 2014). Age-specific habitat selection patterns have been observed in or discussed with regards to other seabirds (Cooper et al. 1991, Gutowsky et al. 2014).

Great shearwaters, presumably young birds or failed breeders, begin their moult in the southern hemisphere as early as January (Watson 1971, Bugoni et al. 2015). We found wide variability in the primary moult of great shearwaters off Cape Cod in July. This suggested that some of the captured birds had started moulting prior to migration, but nape plumage characteristics indicated that they were less than 3 yr old and therefore had not yet attempted breeding. Early southward migration was not limited

to older ASY birds. The majority of early migrants noted from New Brunswick were SY birds but did include both HY and ASY birds. Yet, only juvenile and immature birds (HY and SY) were examined off Cape Cod in September and October after early migrants had left the Gulf of Maine. Thus, it seems that the urge to migrate in time for the nesting season in the southern hemisphere is not limited to breeding birds and the reason for some birds to migrate and for others to remain in the Gulf of Maine is unknown.

During their stay in the Gulf of Maine great shearwaters spent the majority of their time using the Rim habitat of the gulf, where they predominately exhibited ARS foraging behavior. In contrast, birds spent little time over the deeper basins of the gulf or beyond the continental shelf. Additionally, while using these less frequented habitats, birds were more apt to exhibit transiting behavior. In general terms, the Rim habitat used was characterized by shallower depth (<100 m) with steeper topographic slope. Slope-induced mixing of the water column combined with surface and tidal currents act as a nutrient pump where primary productivity is maintained throughout the summer (Townsend et al. 1987). Beyond the southern rim of the gulf, great shearwaters also exhibited foraging behavior over Nantucket Shoals and Georges Bank, areas characterized by shallow water that is well mixed from tidal currents (e.g. Petrie et al. 1996, Guida et al. 2013). Energy transferred to seabirds in Bristol Bay (Bering Sea) varied with depth and hydrographic regime, as higher rates of energy flux were observed in shallower water inside the inner front on the shelf than in stratified water seaward of this front (Schneider et al. 1987).

Foraging habitat use patterns related to environmental predictors revealed both global and local characteristics of great shearwaters, and these relationships were strongest for the dynamic variables SST and chlorophyll concentration. For example, SST was a significant predictor of both foraging presence and intensity for birds captured across all tagging sites in the Gulf of Maine. However, there was evidence of site-specific habitat preferences. Birds tagged in ME and NB preferred colder surface temperatures (11 to 18°C), which aligns with foraging areas of great shearwaters on the Patagonian Shelf within the Sub-tropical Frontal Zone (10 to 16°C) (Ronconi et al. 2010c). In contrast, birds tagged at the MA site in waters off Cape Cod and on Georges Bank preferred warmer surface temperatures (18 to 20°C), but foraging activity was absent in the warmest water found on the outer edge of the continental shelf and further offshore. Chlorophyll concentration

was also a significant predictor of foraging presence and intensity in the Gulf of Maine, but higher concentrations did not necessarily increase the intensity of foraging. The mere presence of chlorophyll is indicative of biological activity, but site-specific conditions may dictate how that productivity can be elevated further up the food chain. Static environmental variables appeared to be less important for determining the presence/absence or intensity of foraging great shearwaters across the Gulf of Maine. Across all 3 tagging sites, depth showed a significant relationship with the presence of foraging in shallower water, but was only related to a significant increase in foraging intensity for birds from MA. Slope had no significant relationship with the presence or intensity of foraging for birds in the Gulf of Maine.

Specific combinations of oceanographic and environmental conditions within each area may allow for different mechanisms facilitating prey availability to shearwaters. For example, the lower Bay of Fundy has high productivity from strong tidal currents that interact with steep bathymetric gradients. This combination enhances vertical mixing and concentrates prey near the surface for marine birds and mammals, particularly during flood tides (Brown et al. 1979, Brown & Gaskin 1988, Huettmann et al. 2005, Johnston et al. 2005a,b, Thorne & Read 2013). Shearwaters in this region prey on herring, krill and squid near localized tidal fronts (Brown et al. 1981, Ronconi et al. 2010b), which allows them to feed in water that might otherwise have been considered too deep for foraging.

The foraging response of great shearwaters in shallow waters around Cape Cod and Georges Bank may be aligned with the availability of forage fish, which are tolerant of these warmer waters. The distribution of sand lance *Ammodytes* sp. (Azarovitz & Grosslein 1987) is coincident with the foraging range of great shearwaters in the southern Gulf of Maine. Sand lance occur in waters <100 m deep and feed on copepods in school formation between midwater and the surface before burrowing themselves into clean sandy sediments when not schooling (Meyer et al. 1979). Since the early 1970s, sand lance abundance has increased in the Gulf of Maine, particularly on Stellwagen Bank and the Cape Cod Slope (Meyer et al. 1979). Sand lance was found to be a preferred prey of great shearwaters in waters <100 m to the east of Cape Cod and in the Great South Channel (Powers & Backus 1987). Brown et al. (1981) noted that great shearwaters preferred sand lance to euphausiids when both were available off Brier Island, Nova Scotia. Sand lance was also found to be

a common prey item taken by Atlantic bluefin tuna *Thunnus thynnus* in the Great South Channel (Chase 2002). Payne et al. (1986) noted that humpback whales *Megaptera novaeangliae* followed the bottom profile north of the Great South Channel until they reached dense concentrations of available sand lance. Predators such as whales will drive sand lance close to the ocean's surface as they feed (Hain et al. 1982). Great shearwaters are shallow feeders, typically pursuit divers within 2 m of the ocean surface, but can go as deep as 18 m (Ronconi et al. 2010c). Thus, these birds may take advantage of other local predators to make this preferred prey more available to them (Obst & Hunt 1990, Anderwald et al. 2011).

Overall, the site-specific importance of environmental variables measured might be indicative of a more flexible foraging strategy based on high mobility. Given their ability to transit across large areas, such mobility might allow the birds to exploit diverse habitats as oceanographic conditions change and foraging areas move spatially or temporally. Such flexibility is also shown by great shearwaters during their stay in the southern hemisphere. Breeding great shearwaters on Inaccessible Island can forage as far as 4000 km away from the colony in a wide range of oceanographic conditions (Ronconi et al. 2010c). This adaptability can be contrasted with less mobile seabirds such as alcids, which are impacted by long-term climate changes at local scales during the breeding season (e.g. Gjerdrum et al. 2003). Tufted puffins *Fratercula cirrhata* advanced their breeding phenology over time to align with changing periods of maximum food availability for chick hatching as SST trends increased over decades, but there was no such relationship between hatch date and SST in any given year (Gjerdrum et al. 2003).

Seabirds are more threatened than any other group of birds, and pelagic seabirds such as great shearwaters are more at risk than coastal seabirds (Croxall et al. 2012). Among the myriad threats facing pelagic seabirds, bycatch is a primary concern (e.g. Anderson et al. 2011), along with the potential impacts of environmental changes. Within the Gulf of Maine, previous work suggests that great shearwaters constitute a significant proportion of seabird bycatch (Hatch et al. 2016). When these findings are combined with our analysis on great shearwater age and habitat use patterns, it seems likely that a large proportion of these bycatch individuals may be young and pre-breeding individuals. The consequence of this potential age-targeted bycatch of younger birds could manifest into a long-term loss in shearwater recruitment if age or inexperience does play a role in

rates of capture from fixed gear throughout their range. In turn, conservation actions that target by-catch reduction efforts may have the greatest impact on conserving great shearwater populations, and our results suggest that modeling location information using state–space models may guide managers in identifying these discrete, high-use habitat patches.

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