

SPATIOTEMPORAL CHARACTERIZATION OF NON-BREEDING GREAT SHEARWATERS *ARDENA GRAVIS* WITHIN THEIR WINTERING RANGE

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ABSTRACT

POWERS, K.D., WILEY, D.N., ROBUCK, A.R., OLSON, Z.H., WELCH, L.J., THOMPSON, M.A. & KAUFMAN, L. 2020. Spatiotemporal characterization of non-breeding Great Shearwaters *Ardenna gravis* within their wintering range. *Marine Ornithology* 48: 215–229.

Movements of Great Shearwaters *Ardenna gravis* wintering in the Northwest Atlantic showed age-based spatial and temporal flexibility, with foraging tactics linked to a defined physical preference of their primary prey. From 2013 to 2018, we tracked 58 Great Shearwaters during their wintering season using platform terminal transmitters deployed in the same area of the southwest Gulf of Maine. Utilization distributions (UDs) for individual birds were created from convex hulls, which were then combined for spatial and temporal analyses. Of the 95% kernel UD, 55% were contained within the Gulf of Maine and the remainder extended to the Scotian Shelf off Nova Scotia and the Grand Banks off Newfoundland. Analysis of fecal DNA from tagged birds and others captured with them indicated that Northern sand lance *Ammodytes dubius* were the primary prey while in the Gulf of Maine. This relationship was supported by the overlap of UD and sand lance habitat. The spatial occurrence of sand lance from bottomfish trawl survey data demonstrated that these fish preferred shallow water (< 100 m deep) with substrates consisting of high sand content (> 50%) and grain sizes ranging from 0.35–2.00 mm in diameter. These same properties were associated and spatially aligned with the collective 25% kernel UD of Great Shearwaters. Necropsy of bycaught Great Shearwaters from an area that overlapped in space and time with tagged individuals and sand lance habitat demonstrated that most birds (89%) were young (0–2 years), based on gonadal development, molt score, and/or bursa of Fabricius. Coupling demographic information from necropsies with spatial habits and movement timing of tagged birds suggests this region serves as a winter “nursery” for Great Shearwaters.

Key words: Great Shearwaters, utilization distribution, wintering range, satellite tracking, fecal DNA analysis, sand lance, bycatch necropsies

INTRODUCTION

The distribution of marine vertebrates is the product of a hierarchical structure of processes driven at multiple spatiotemporal scales (Mannocci *et al.* 2017). Many of these driving processes are in flux due to human-induced or climatically mediated stress, resulting in changes in faunal distribution and abundance (Nye *et al.* 2009, Moore *et al.* 2018). In seabirds, shifting environmental conditions are implicated in precipitous declines across taxa and ecoregions (Croxall *et al.* 2012, Paleczny *et al.* 2015, Dias *et al.* 2019). Characterizing current distribution patterns of seabirds is critical to identifying and managing seabird and ecosystem responses to current and predicted environmental changes (González-Solís & Shaffer 2009, Paleczny *et al.* 2015), and there is a paucity of data for juvenile seabirds in particular (Hazen *et al.* 2012). However, in order to be rigorous tools for ecosystem management, descriptions of seabird distributions must be augmented with explanations of the physical and biological processes that contribute to the dynamic nature of such patterns (Fauchald *et al.* 2000, Fauchald 2009, Tremblay *et al.* 2009).

Seabirds may forage across vast coastal and pelagic areas during breeding phases (Weimerskirch *et al.* 1993, Weimerskirch *et al.* 1994, Jouventin *et al.* 1994), and many undertake trans-equatorial

migrations between non-breeding and breeding locations (Schaffer *et al.* 2006, González-Solís *et al.* 2007, Hedd *et al.* 2012). Great Shearwaters *Ardenna gravis* breed on islands in the South Atlantic and spend their wintering season in the North Atlantic, arriving in the western half in May. They return to the Southern Hemisphere passing down the east-central Atlantic starting in September (Brown 1986). Juveniles and sub-adults arrive in the western North Atlantic later (July) and are thought to return south in November, after breeding adults (Brown 1986, Powers *et al.* 2017). The boreal summer distribution of Great Shearwaters off the northeastern United States and Atlantic Canada has been examined in part by a series of loosely connected and spatially overlapping studies using shipboard and aerial observations (Powers 1983, Brown 1986, Winship *et al.* 2018, Wong *et al.* 2018, Carvalho & Davoren 2019). These studies indicate foraging flexibility of wintering shearwaters based on biophysical drivers. For example, Great Shearwaters exhibited inter-annual variability and dietary partitioning with Sooty Shearwaters *A. grisea* as prey availability shifted within the Bay of Fundy (Ronconi *et al.* 2010). Great Shearwater movements within the Gulf of Maine, more recently characterized with satellite tracking data (Powers *et al.* 2017), showed that birds preferred to forage in shallower waters (< 100 m), primarily over sloped rims fringing deeper central basins. However, this analysis of foraging habitat showed inconsistent relationships in terms

of depth, chlorophyll *a*, and sea surface temperature between Georges Bank/the southern Gulf of Maine and the Bay of Fundy (Powers *et al.* 2017). The breeding biology of two closely related shearwaters, Short-tailed Shearwater *A. tenuirostris* and Cory's Shearwater *Calonectris borealis* (Bradley *et al.* 1999, Campioni *et al.* 2020), indicates that age-specific demographics may also play an important role in Great Shearwater movement ecology in the Gulf of Maine, which is postulated as a wintering area for mostly non-breeding birds (Huettmann & Diamond 2000, Powers *et al.* 2017, Ronconi *et al.* 2018).

Platform terminal transmitters (PTTs) provide geographical information that is tracked by Argos, an international satellite system. Using this information, researchers can describe foraging and wintering ranges, migration corridors, and seasonal movements of seabirds (e.g., Pinet *et al.* 2011, Jodice *et al.* 2015). Such information allows mapping of the broad-scale distribution of a population, which is often related to oceanographic variables. Spatial data can also provide insight into fine-scale distribution, which is mostly influenced by prey distribution (Schneider & Piatt 1986, Fauchald *et al.* 2000, Davoren *et al.* 2003, Suryan *et al.* 2016). However, exploration into the role of prey in seabird distributions requires further examination of seabird diet in tandem with tracking data.

Here, we report results of Argos data from PTTs placed on 58 Great Shearwaters that were captured in the southwestern Gulf of Maine over six years (2013–2018). We used these results to characterize the spatial and temporal extent of a defined portion of their wintering range in the Northwest Atlantic over a timeframe that can accommodate cycles of seasonal and inter-annual variability. We explored differences in utilization distributions (UDs), estimating range sizes and interactions with other individuals on an annual basis. We derived behavioral traits from the aggregated spatial data to assess revisitation and flight patterns between areas of differing foraging intensity, in order to corroborate if foraging behaviors align with changes in bird density. Temporal shifts in overall distribution over the Northwest Atlantic were examined on a monthly basis to determine the timing of bird movement through the region and the extent of movement between and within areas in the study region. Characteristics of key foraging areas and the distributions of preferred prey were compared with information on prey selection, which was determined by fecal DNA analysis. Age demographics were determined from primary molt scores and the timing of departure, in comparison with a gonad and bursa analysis of fishery-related bycaught birds. We suggest that primarily young non-breeding Great Shearwaters utilize the southern Gulf of Maine and Georges Bank during their wintering period. This pattern of habitat utilization is associated with the distribution of a key prey

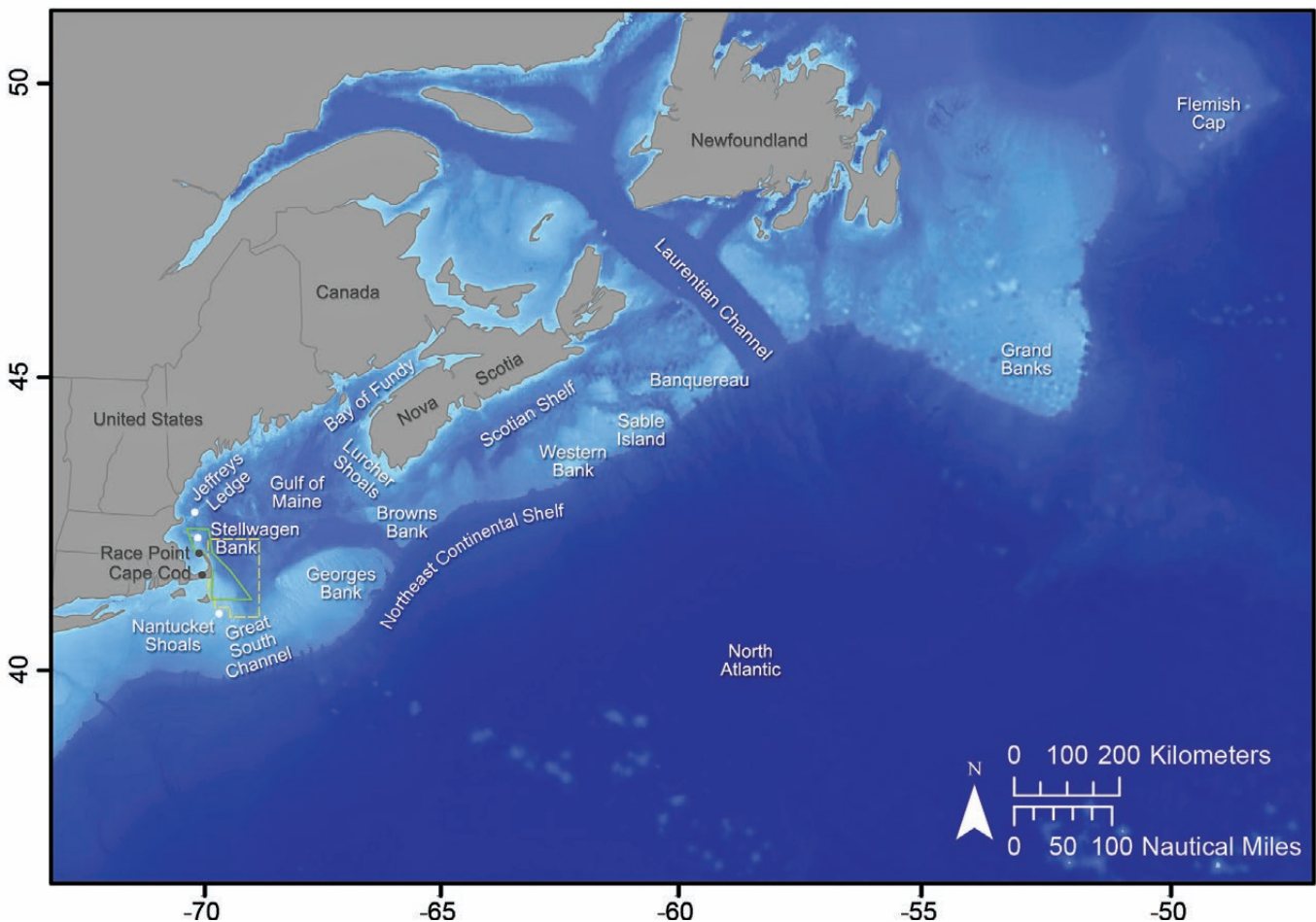


Fig. 1. Map of study area in the northwestern Atlantic Ocean. The shearwater capture area is noted by the green polygon in the southwestern Gulf of Maine. Bycatch specimens were collected in NOAA/NEFOP Statistical Area 521, which is noted by white dashed line east of Cape Cod, Massachusetts, USA.

species that has distinct biological, physical, and geographical habitat preferences.

STUDY AREA AND METHODS

Data collection

We tagged Great Shearwaters from 2013 to 2018 off the coast of Massachusetts in the southwestern Gulf of Maine, from the Stellwagen Bank National Marine Sanctuary to the coastal waters east of Cape Cod (41.3° to 43.0° latitude, -70.5° to -69.5° longitude; Fig. 1). We used small vessels to access birds at known foraging areas and attracted birds to the vessel using cut fish and squid. Once they were close enough to the vessel, birds were caught with handled landing nets.

Over six consecutive years, we placed PTTs on 58 shearwaters (*ca.* 10 yr⁻¹; Table 1). Solar PTT-100 tags (15 g, Microwave Telemetry, 8835 Columbia 100 Parkway, Suites K & L, Columbia, MD 21045, USA) were used with duty cycles of 24 hours on (i.e., continuous). Tags were attached dorsally, central to the body mass of the bird below the nape and between the wings, using four subcutaneous sutures (Prolene suture 4.0 Ethicon) as per MacLeod *et al.* (2008). All tags eventually stopped transmitting, and we expected that they fell off when the Prolene sutures degraded. Tags represented less than 3% of body mass for all tagged birds to minimize effects on flight efficiency (see Phillips *et al.* 2003). Tags were typically deployed in July, except for 2017, when poor weather conditions delayed tagging until early August, and a single bird in September 2016. Body weight and primary molt were scored using the BTO method (Ginn & Melville 1983) for each tagged bird. Sex was identified genetically from blood or feather samples provided (see Acknowledgements).

Data analysis

Range estimation using kernel density

We used the Time Local Convex Hull (T-LoCoH, <http://tlocoh.r-forge.r-project.org>) method (Lyons *et al.* 2013) in R version 3.4.0 (R Development Core Team 2018) to analyze our Argos location dataset. T-LoCoH generalizes the non-parametric UD construction method LoCoH (Getz *et al.* 2007) and integrates time with space in the construction of local hulls through a scaling that relates distance and time to the individual's characteristic velocity (Lyons *et al.* 2013). A hull is defined as a minimum convex polygon constructed around each Argos location point using a set of 'nearest neighbors' (i.e., other Argos location points). Hulls represent space-use; if constructed with time, they are localized in space and time (Lyons *et al.* 2013). The resulting hulls also enable estimation of behavioral metrics describing both 1) movement phase and 2) multiple dimensions of time use, including revisitation and duration (Lyons *et al.* 2013). Space-state models (Jonsen *et al.* 2005, Jonsen *et al.* 2007) provide temporal normality and flight behavior to asynchronous satellite telemetry data, but the incorporation of time into range construction using the T-LoCoH approach expands the concept of UDs beyond a traditional density gradient facilitated via state-space models to spatial models of movement and time (Lyons *et al.* 2013). Location error is problematic with Argos locations using either method with respect to partitions of space or edges of utilization. But, compared to location error introduced via either modeling approach, gaps in temporal resolution have

larger consequences on space and time use as well as behavioral characterizations (Powers *et al.* 2017 supplement). PTTs in this study transmitted continuously, and temporal resolution was limited only by satellite availability.

Argos locations were converted to Universal Transverse Mercator (UTM) projections using Easting (X) and Northing (Y) coordinates based on UTM Zone 19 for this analysis. This Mercator projection preserves angles and direction but distorts distance over multiple zones. So, we confined the analysis to an area bounded by 38° to 50° latitude and -50° to -73° longitude (Fig. 1). Argos location classes in the set {3, 2, 1, 0, A, B} were used for the observed data. T-LoCoH's 's' parameter controls the degree to which the time difference between two locations is factored into the calculation of their physical 'distance', which is used to identify 'nearest neighbors' (Lyons 2014). Nearest-neighbor selection is based on a distance metric (time-scaled distance, TSD) (Lyons *et al.* 2013), and we selected 's' to scale hull creation into 24-hour intervals per Argos location. The effect of time-distance is to separate points that are far away in time even though they may be close in two-dimensional space (Lyons *et al.* 2013). Hulls were created using the adaptive *a*-method, which selects all points whose cumulative distance to a parent point, ordered smallest to largest, is less than or equal to *a*. The *a*-method (vs. *r*-fixed radius method and *k*-nearest neighbor method) produces more robust UDs because this method is the least sensitive to suboptimal choices for its kernel parameter *a* (Getz *et al.* 2007); thus, it provides good results in both dense and sparse areas of use. In this study, UDs were created from density isopleths of hull parent points (i.e., centroid locations) for 95%, 50%, and 25% kernel densities, with the 25% kernel UD representing areas of greatest bird concentration and 95% kernel UD areas of the largest spatial extent. We then determined the amount of overlap or individual interactions within these UDs, both among individuals in the same year and among all individuals during the entire study. Physical covariates (depth and substrate properties) were assigned according to the parent point of each hull (centroid) using available data layers. Substrate properties included sediment sand content (%) and mean grain size (mm) for the United States northeast continental shelf (NOAA/NCCOS unpubl. data).

Correlation of individual range size and PTT duration was determined statistically using Pearson's product moment test. If a correlation was found, we then examined whether assumptions of homogeneity of variance differed in individual tag duration by year and number of tag days by year using Bartlett's test before proceeding to ANOVA. ANOVA (*F*-statistic) was used to determine whether UD groups (by year) or behavioral groups were different, using Tukey's test in post-hoc analyses. We also used the Kruskal-Wallis test to determine whether characteristics (e.g., tag days, range size, body weight, molt scores, sex ratio) of population distributions were identical when we could not assume a normal distribution.

Time-use and behavioral characteristics

Time-use metrics were used as another line of evidence to examine spatial use (Lyons *et al.* 2013). We used an inter-visit gap (IVG) period of 24 h to understand daily movements. IVG is a unit of time that must pass before another occurrence in a hull is considered a separate visit. So, for daily foraging behavior, we did not want two locations that were a day apart to be considered nearest neighbors, even if they were close in space. To explore the relationships among the distribution of hulls in time-use space, we examined duration

(i.e., the number of locations in a hull within the IVG) and equated that to an amount of time a bird spent in a hull on each visit. We expected that birds should spend more of their time each day in areas of higher foraging intensity. We also expected that revisitation, or the number of times a bird revisited the same hull outside of the IVG, would reflect longer periods of daily usage of an area.

Estimation of directional movement of shearwaters was based on a behavioral metric: eccentricity (Lyons *et al.* 2013). Eccentricity is measured on the bounding ellipsoid of a hull. The eccentricity of an ellipse varies from 0 for a perfect circle to 1 for a line. Hulls with low eccentricity represent areas of non-directional movement, such as area-restricted searching or foraging, whereas higher values indicate areas where an animal is moving directionally, such as migrating or traversing habitat of low resource value (Lyons *et al.* 2013). The *a*-method reduces the number of neighbors per hull in outlying areas, where hulls become more eccentric (more directional travel), compared to hulls constructed in areas of more equidistant neighbors, which are less eccentric (more area-restricted searching). We also examined temporal patterns of spatial use (latitude and longitude, by month) within the 95%–50%, 50%–25%, and < 25% bands of kernel density by using the aggregate dataset.

Fecal DNA analysis

For food habits analysis, birds were captured in 2017–2018 and temporarily placed into individual pet carriers on mesh netting suspended over an aluminum foil covered floor. Fecal material captured on the foil was collected for each individual and frozen either dry or in ethanol. Fecal samples were transported to a genetics lab and stored at –20°C until processing. Frozen samples were scraped into 2.0-mL tubes using flame-sterilized forceps and frequent glove changes. Genomic DNA was extracted from each sample using a Qiagen (Valencia, California, USA) stool mini-kit following manufacturer protocols, with the following modifications: samples were incubated at 60°C overnight in the first buffer and we added 1 µL of carrier RNA after the second incubation. We employed polymerase chain reaction (PCR) to target a fragment of the mitochondrial 16S gene that is about 110–130 bp long. We used the Chord_16S_F_TagA (forward) and Chord_16S_R_Short (reverse) primers from Deagle *et al.* (2009), standard PCR conditions, and a blocking primer (GrSh-block1: 5'-TGTGGAACCTAAAAATCAACGA-3') that we designed for this study to terminate in a C3 spacer, which would limit predator reads. Previous work demonstrated that this primer set (forward, reverse, and blocking) could reconstruct vertebrate prey items from seal fecal samples collected from the Gulf of Maine, with species-level taxonomic resolution for most items (K. Flanders pers. comm.). Pre-PCR and PCR workflows took place in dedicated labs in separate buildings to minimize the potential for contamination.

Amplicons were cleaned and sent to a genomics facility, where they were indexed and sequenced on 1/8th of a flow cell on an Illumina (San Diego, California, USA) MiSeq using 2×300 bp chemistry (*ca.* two million reads). Forward and reverse reads were assembled in PANDaseq (Masella *et al.* 2012) using the default primer-match threshold. After trimming adapters and primers, *de novo* operational taxonomic units (OTUs) were picked using a threshold of 97% sequence similarity using QIIME2 (Caporaso *et al.* 2010).

OTUs with < 2 reads were trimmed using the “phyloseq” package (McMurdie & Holmes 2013) in R version 3.2.5 (R Development

Core Team 2018). Remaining OTUs above the 1% threshold of Deagle *et al.* (2009) were identified to the lowest possible taxonomic resolution with NCBI Blast+ in the Cloud software accessed through Amazon Web Services Marketplace (Seattle, Washington, USA), which queried OTUs against a server copy of the nucleotide database. Taxonomy was assigned to each OTU based on the lowest expect value (e-value), with a maximum threshold of 1e–20 (see Thomas *et al.* 2014). If multiple database matches shared the same lowest e-value, we selected the match whose species is known to occur in the study area. If the OTU matched best (i.e., lowest e-value) to more than one geographically appropriate species, the OTU was assigned to the lowest taxonomy shared between the matches (e.g., family or genus instead of species). OTUs with identical taxonomy were combined using the “phyloseq” package, and those identified as obviously not prey (e.g., human, shearwater) were removed as contaminants.

Distributions of potential prey

We examined the National Oceanic and Atmospheric Administration’s (NOAA) bottomfish population assessment database for comparisons of potential prey distribution to Great Shearwater distribution (Politis *et al.* 2014). NOAA trawl logs included location (latitude and longitude), depth, and number of fish caught, but we independently assigned substrate properties (sand content and grain size) based on location using our substrate data layers (NOAA/NCCOS unpubl. data). Based on insight gleaned from the fecal analysis, we investigated distributions of Northern sand lance *Ammodytes dubius*, Atlantic mackerel *Scomber scombrus*, and Atlantic herring *Clupea harengus*. Mackerel feed throughout the water column, so bottomfish surveys may be inconclusive in mackerel stock assessments. Atlantic menhaden *Brevoortia tyrannus* is a mid-water fish, so it was not represented in these bottom trawl surveys. While sand lance is not specifically targeted in trawl surveys, it is caught as bycatch and is included in trawl survey datasets. We examined spring (April–May) and fall (October–November) logs of trawls from 2013 to 2017 covering the northeastern US continental shelf (east of –73°) including Georges Bank. These surveys did not include the Scotian Shelf in Canada. We identified all trawl stations as spatial points to define the scope of bottom trawl sampling, and we characterized bathymetry, substrate, surface temperatures, and bottom temperatures at locations where targeted fish were caught. Sampling of fish was uniform across the northeastern US continental shelf for each spring and fall survey (Politis *et al.* 2014), so we summed the locations of fish caught over the entire period.

Age analysis using bycatch birds

Data from bycaught individuals was used to examine age and sex demographics in the southwestern Gulf of Maine. Bycaught shearwaters were obtained from the US NOAA Northeast Fisheries Observer Program (NEFOP) in the Gulf of Maine (Northeast Statistical Area 521 in Appendix A of NEFSC FSB 2016) and from scientific longline surveys around Gough Island in the Tristan da Cunha archipelago in the South Atlantic. Individuals were frozen upon collection and necropsied as part of a larger study following the methods of van Franeker (2004). Morphometric data were collected on live birds captured in the southwestern Gulf of Maine (see Fig. 1) in July 2019 for comparison to bycaught specimens.

Within this study, we relied upon gonad development, molt score, and the presence/size of the bursa of Fabricius to gauge sex and likely age. Based on visual assessment of gonad color and quantitative measurement of gonad size, gonad development was scored as one of four classes: hatch year, immature, sub-adult/non-breeder, or breeding bird. As noted in previous studies incorporating necropsy data, the sub-adult category (Class 3) includes both immature birds close to maturity and non-breeding adults, since gonadal development of these two stages is very similar (Cortes *et al.* 2018, Hector *et al.* 1986). Molt score was examined following BTO methods, and each specimen was assigned a score from 0 to 50. Bursa presence and size was also noted when possible because these can be used as non-plumage-based evidence to estimate the age of procellariiform seabirds (Broughton 1994) instead of the nape plumage characteristics noted by Pyle (2008). The bursa begins to enlarge shortly after hatching and reaches its maximum size in four to six months (Broughton 1994). Involution is typically complete by the end of a bird's first year of life, and the bursa is absent in adult birds (Glick 1983, Mase & Oishi 1991). Vestigial bursas have internal walls that cannot be visibly differentiated from the cloacal wall (Broughton 1994).

Gonad development, molt score, and bursa presence/size were assessed together for each bird to assign a likely age class: young or mature. Collected measurements were compared between Cape Cod (Northwest Atlantic as assumed non-breeders) and Gough Island (South Atlantic as suspected or confirmed breeders). The Wilcoxon test was used to compare parameter means as we could not assume that the measurements were normally distributed.

RESULTS

PTTs provided an average of 19.1 Argos locations per day per tag. These were used to create TSD hulls for individual Great Shearwaters with an IVG of 24 hours. A total of 73 302 convex hulls were determined for 4 477.5 days (Table 1).

Annual ranges, expressed in TSD units, were calculated per bird (Table 1). The 50% kernel UD in any year typically represented 21.8% of an individual's 95% kernel UD. The number of range intersections among individual birds in any year increased proportionately with range size: 32.3% in the 25% kernel UD and 62.3% in the 50% kernel UD, relative to total intersections within the 95% kernel UD. But, the area of intersection was disproportionately larger in the 95% kernel UD, and 83.6% of the overlap occurred outside of the 50% kernel UD (Table 1).

Comparing range size by year, we found a positive correlation between tag days and the estimated 95% kernel UD ($P = 3.578 \times 10^{-6}$, $R^2 = 0.552$). As a result we examined, but found no difference in, both the length of individual tag duration (variance) by year (Bartlett's $K^2 = 2.1842$, $df = 5$, $P = 0.8231$) and the number of tag days (sampling effort) by year ($F = 1.0712$, $df = 5$ and 52, $P = 0.3871$). However, the 95% kernel UD size by year was significantly different ($F = 3.162$, $df = 5$ and 52, $P = 0.0144$) between 2013 and 2015 (Tukey's test, $P = 0.028$) and between 2015 and 2018 (Tukey's test, $P = 0.035$; Table 1). Plotting 95% kernel UDs by year (Fig. 2) showed that most individuals in 2013 and 2018 stayed within the Gulf of Maine, as opposed to 2015, when

TABLE 1
Annual breakdown of platform terminal transmitter (PTT) metrics related to sampling effort, kernel density range estimates as scaled by time-scaled distance (TSD), individual range intersections, and morphological measurements for Great Shearwaters ($n = 58$) tagged in 2013–2018

Statistic	Density	2013	2014	2015	2016	2017	2018
Total tags (PTT)		10	11	10	10	9	8
Mean tag duration (day)		59.2	85.1	96.2	69.3	79.7	72.1
Total tag days		591.8	936.4	962.0	693.3	717.6	576.4
Total convex hulls		10878	14037	12981	13079	11889	10438
Mean range by density (TSD*1e-6)	0.25	2319	6160	8655	2806	1251	2212
	0.50	9144	11256	21399	13222	11777	6879
	0.95	33457	74914	98053	48388	49160	31434
Mean tag intersections by density	0.25	13	25	17	23	19	7
	0.50	31	35	37	32	27	15
	0.95	45	55	45	44	36	28
Mean intersection area by density (TSD*1e-6)	0.25	325	982	1275	950	774	617
	0.50	594	2990	2845	1842	1545	886
	0.95	3742	17685	21935	8417	8863	4939
Mean body weight per bird (g)		754	940	874	859	716	734
Mean primary molt score (0–50)			45.6	35.8	48.9	48.9	47.6
Range primary molt score			41–50	6–50	45–50	44–50	41–50
Gender (M/F)				5/4	4/6	2/6	5/3
Tagging date (dd-mmm)		12-Jul	20-Jul	09-Jul	12-Jul	04-Aug	9-Jul

the UD of half of the individuals extended east to the Scotian Shelf and north to the Grand Banks. The breadth of the 95% kernel UD in 2018 was also underrepresented, as two individuals (ID numbers: 112710 and 112717), within three weeks of capture, moved east of the study area ($< -50^\circ$ longitude): one to the Flemish Cap ($47^\circ, -44^\circ$) and the other to the mid-Atlantic Ridge ($41^\circ, -30.5^\circ$). Thus, the overall wintering range of Great Shearwaters extends east of Atlantic Canada (-50° longitude) and beyond the longitudinal boundary used in this study.

In the context of UD size, we rearranged metrics by individual to derive a table showing birds that primarily used the Gulf of Maine compared to those that also extended to the Scotian Shelf or the Grand Banks (Table 2). In this configuration, there was a significant difference in tag days per range group (Kruskal-Wallis $\chi^2 = 7.3174$, $df = 2$, $P = 0.02577$), so we could not statistically compare UD sizes. Birds restricted to the Gulf of Maine had the smallest 95% kernel UD compared to those that also used the Scotian Shelf (median

20250 vs. 87000 TSD* $1e-6$) or the Grand Banks (median 115500 TSD* $1e-6$). Body weight was significantly different among these range groups (Kruskal-Wallis $\chi^2 = 8.671$, $df = 2$, $P = 0.0131$) and increased with larger UDs (Table 2). Primary molt score was not statistically different between groups (Kruskal-Wallis $\chi^2 = 3.7689$, $df = 2$, $P = 0.1519$). However, all birds in the Grand Banks group were in active molt, whereas most of the Gulf of Maine group were not in molt when tagged. There was no significant difference in sex between these regional groups (Kruskal-Wallis $\chi^2 = 1.1681$, $df = 2$, $P = 0.5576$).

In a spatial context, individual 50% kernel UDs of Great Shearwaters intersected each year along the 100-m isobath east of Cape Cod and south to the Great South Channel. In several years, this area extended north to include the Stellwagen Bank National Marine Sanctuary (2014–2017) or east along the same isobath across northern Georges Bank (2013–2016). Multiple individuals had 50% kernel UDs in the Bay of Fundy in 2014 and 2018, and on

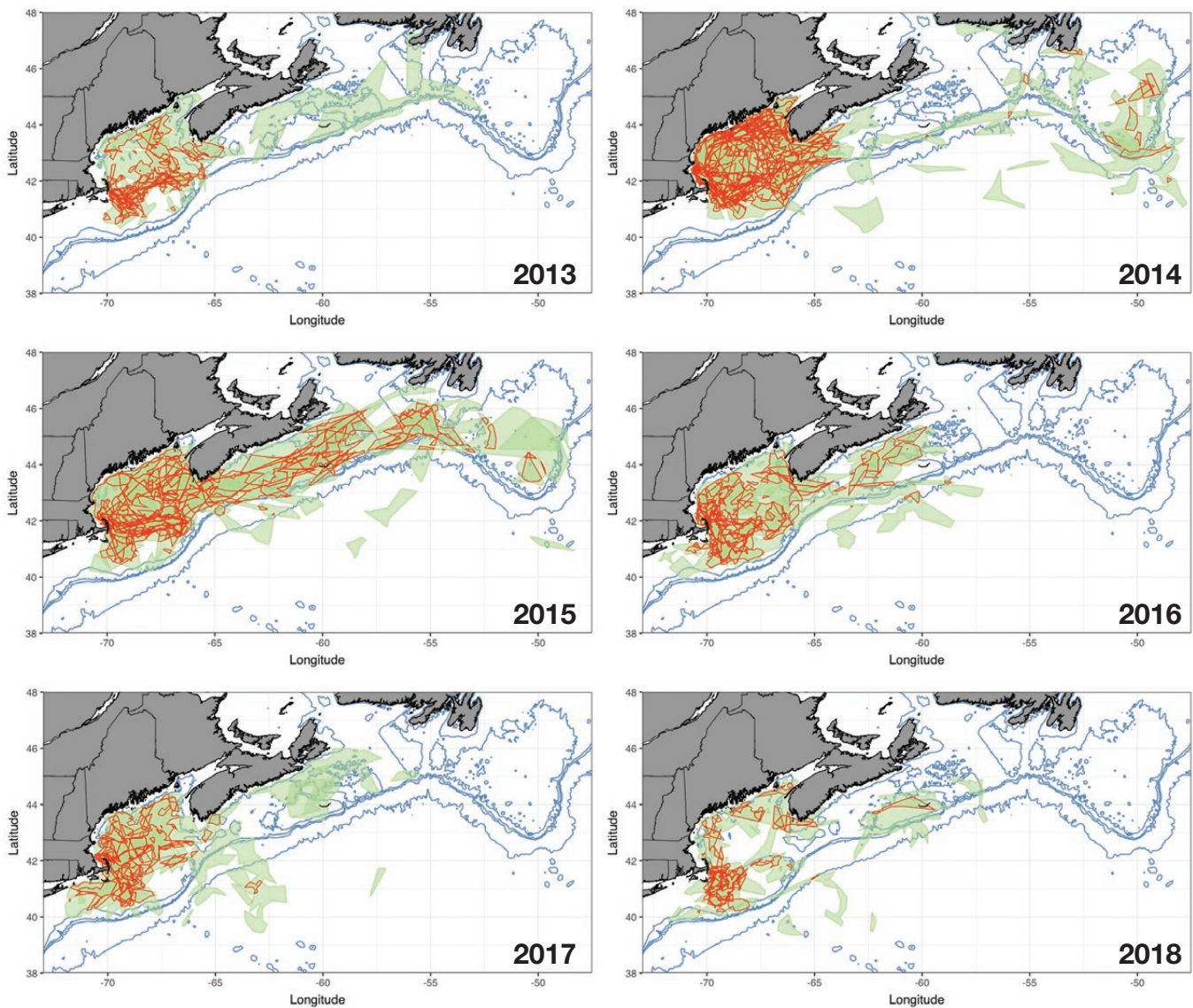


Fig. 2. Plots of Great Shearwater 95% kernel utilization distributions (UDs) derived from convex hulls of individual birds tagged per year (2013–2018). Individual UD are filled in green. Red borders denote intersections of individuals within that year. In 2018, two UD extended east of -45° longitude outside of the study area.

the southern New England shelf west of Nantucket Shoals in 2017. Thus, the majority of 50% kernel UD were in tangential areas across the southwestern Gulf of Maine, but the 25% kernel UD shifted from year to year.

The UD of all individuals tagged in 2013–2018 were collectively plotted to show individual boundaries with aggregated 95%, 50%, and 25% kernel density isopleths (Fig. 3). Isolated from an annual perspective, 25% kernel UD became contiguous within the southwestern Gulf of Maine, along with separate isolated pockets in the northern Gulf of Maine (including Bay of Fundy and the northeastern corner of the Scotian Shelf (Banquereau)). The centralized 25% kernel UD within the Gulf of Maine were connected by the 50% kernel UD, which also encapsulated those 25% kernel UD on the Scotian Shelf (Fig. 3).

In the aggregate view, more hulls from between the annual 25%–50% kernel density isopleths collapsed into a single 25% kernel UD, and the overall number of hulls between the aggregate 50%–95% isopleths were disproportionately reduced. A comparison of behavioral characteristics by density groups (Table 3) showed

significant differences in revisitation ($F = 3347$, $df = 2$ and $71\ 623$, $P < 2.2e-16$), duration ($F = 622$, $df = 2$ and $71\ 623$, $P < 2.2e-16$), and eccentricity ($F = 497$, $df = 2$ and $71\ 623$, $P < 2.2e-16$) (Table 3).

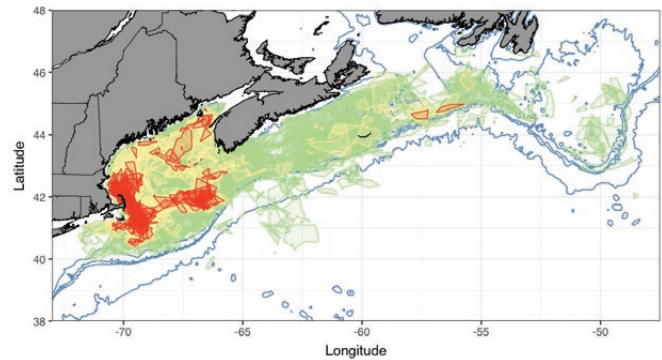


Fig. 3. Aggregate plot of all individual utilization distributions of Great Shearwaters ($n = 58$) from 2013 to 2018 with kernel density groupings based on entire convex hull dataset: < 25% (red), 25%–50% (yellow), and 50%–95% (green). Shading is caused by overlapping ranges of differing density.

TABLE 2
Platform terminal transmitter metrics related to sampling effort, area of 95% kernel utilization distribution (UD) as scaled by time-scaled distance (TSD), and morphological measurements by inclusive regions of the continental shelf in the Northwest Atlantic for Great Shearwaters ($n = 58$) tagged in 2013–2018 (median, 1st–3rd quartiles)

Measurement	Gulf of Maine	Scotian Shelf	Grand Banks
Total individuals	32	14	12
Tag days	59.2 (29.9–97.2)	85.1 (98.0–119.7)	96.2 (46.8–188.3)
Area of 95% kernel UD (TSD*1e–6)	20250 (6395–38150)	87000 (60525–112250)	115500 (61075–138500)
Body weight (g)	758 (699–853)	858 (793–885)	898 (826–943)
Primary molt score	50 (45–50)	49 (46–50)	46 (43–48)
Total male	10	4	2
Total female	9	6	4

TABLE 3
Physical properties and behavioral characteristics of convex hull locations for Great Shearwaters ($n = 58$) tracked in 2013–2018, as summarized by three density groupings with median, 1st–3rd quartiles of each group. Substrate properties represent locations within only the Gulf of Maine and on the western Scotian Shelf.

Measurement	< 25%	25%–50%	50%–95%
Convex hulls ¹	41637	17007	12982
Depth (m) ²	64 (43–103)	108 (57–171)	102 (65–174)
Eccentricity (0–1) ³	0.82 (0.71–0.90)	0.85 (0.74–0.93)	0.87 (0.76–0.94)
Revisitation ⁴	5 (2–8)	3 (2–5)	2 (1–4)
Duration ⁵	16.8 (10.9–27.0)	14.0 (9.7–22.0)	15.0 (10.0–22.0)
Sand content of sediment (%) ⁶	61.9 (45.7–77.4)	37.1 (13.8–75.0)	44.5 (28.9–82.2)
Mean grain size of sediment (mm) ⁷	0.577 (0.206–0.961)	0.202 (0.044–0.531)	0.287 (0.084–0.457)

¹ Hulls are minimum convex polygons constructed around each location point (Argos) from a set of nearest neighbors (other locations).
² Water depth determined at the centroid of each convex hull.
³ Eccentricity is the degree of elongation of each individual hull and indicates directionality of movement.
⁴ Revisitation is the number of daily visits to the same hull.
⁵ Duration is the number of locations counted at each hull when it was visited.
⁶ Sand content is percent amount of sand in the sediment per hull.
⁷ Mean grain size is the predicted diameter of sediment grain structure.

Revisitation significantly increased from 2 to 5 visits per hull as kernel density decreased (i.e., 95%–25% density), indicating that birds went back to the same hulls on more different days in the < 25% kernel band. Regarding revisitation, each of the density bands was statistically different (Tukey's test, $P = 0.00$). As expected, duration was significantly higher in the collective < 25% kernel density band, indicating that birds stayed in those hulls for longer periods during each daily visit: 16.8 locations hull⁻¹ vs. 14–15 locations hull⁻¹ when kernel density was 25%–95% (Table 3). Outside of the < 25% kernel density band, there was no significant difference in duration between the 25%–50% or the 50%–95% kernel density groups (Tukey's test, $P = 0.775$). Once outside of the primary foraging areas, birds did not linger but instead moved to other areas. Regarding eccentricity, the < 25%

density group was significantly different from both the 25%–50% group (Tukey's test, $P = 0.004$) and the 50%–95% group (Tukey's test, $P = 0.0002$). Hull shapes were rounder, indicating substantially more “area-restricted search” behavior within the 25% kernel density isopleth, where eccentricity was 0.82 vs. 0.85–0.87 outside of it (Table 3). Thus, calculated behavioral traits that were measured corroborated more intense foraging activity within the aggregated 25% kernel UD.

Physical characteristics of the aggregate kernel density groups also showed significant differences in depth ($F = 3.024$, $df = 2$ and 71623, $P < 2.2e-16$), sand content in the substrate ($F = 1550$, $df = 2$ and 54653, $P < 2.2e-16$), and mean grain size of sediment ($F = 1597$, $df = 2$ and 54653, $P < 2.2e-16$). None of the density groups overlapped (Tukey's test, $P = 0.00$). The < 25% kernel density band had the shallowest depths (median 64 m), highest sand content (median 62%), and coarsest grain size (median 0.578 mm). Hulls in the 50% and 95% kernel density groups were in deeper water (> 100 m), where the substrate had lower sand content (< 45%) and finer grain sizes (< 0.287 mm) (Table 3). There was no single surficial sediment data layer for the entire study area, so we used a single sediment layer for only the Gulf of Maine, Georges Bank, and the western Scotian Shelf including the Bay of Fundy (NOAA/NCCOS unpubl. data; Table 3). A separate sediment layer (Fader *et al.* 1982) was used for hulls located on the eastern Scotian Shelf (Browns Bank and Lurcher Shoals north to Laurentian Channel). Almost half of the Scotian Shelf hulls (44% or 3892 of 8927) were located over gravel sediment with > 50% sand and an average depth of 67 m. Seventy percent of these locations with sandier substrates occurred around Sable Island, Banquereau, Western Bank, and Browns Bank (see Fig. 1).

Since birds were tagged near Cape Cod, all individual movements across all years emanated from the same general area starting in July, except for 2017 when birds were tagged in early August (Fig. 4). Birds in the < 25% density group consistently stayed in the same general area centered at 42°, –70° (southwest Gulf of

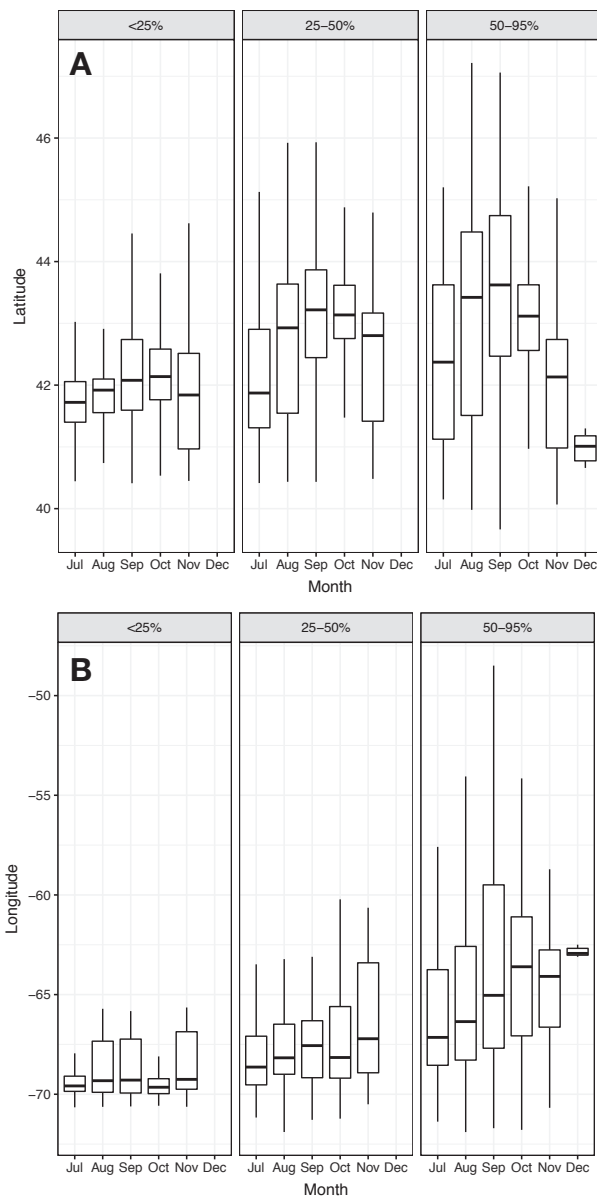


Fig. 4. Histograms of monthly (Jul–Nov) average latitude (A) and longitude (B) by kernel density groups (< 25%, 25%–50%, 50%–95%) from 2013 to 2018. All birds were tagged off Cape Cod in July, except for 2017 when one was tagged in early August. Most birds (32 of 58) remained the Gulf of Maine during their tag lifespan.

TABLE 4
Number of samples (count) and frequency of occurrence (FOO) of prey groups representing food habits of Great Shearwaters. Data were derived from metagenomic analysis of 35 successfully sequenced fecal samples collected in waters off Massachusetts, USA.

Prey group	Common name	Count	FOO
<i>Ammodytes</i> spp.	Sand lance	25	71.4%
<i>Brevoortia tyrannus</i>	Atlantic menhaden	17	48.6%
<i>Scomber scombrus</i>	Atlantic mackerel	11	31.4%
<i>Leucoraja erinacea</i>	Little skate	7	20.0%
<i>Peprilus triacanthus</i>	Atlantic butterfish	3	8.6%
<i>Clupea harengus</i>	Atlantic herring	2	5.7%
<i>Squalus acanthias</i>	Spiny dogfish	2	5.7%
<i>Morone saxatilis</i>	Striped bass	1	2.9%
<i>Merluccius bilinearis</i>	White hake	1	2.9%
Pleuronectiformes	Flatfishes (flounders)	1	2.9%
<i>Tautoglabrus adspersus</i>	Cunner	1	2.9%

Maine) from July through November. Birds in the 25%–50% and 50%–95% density groups showed northward progressions from July through September, a pattern that then shifted southward from October through December (Fig. 4A). Their monthly longitudinal progression was increasingly eastward while in the study area (Fig. 4B). The majority of the 25%–50% group was contained within the Gulf of Maine, with some reaching the Bay of Fundy to the north in September while staying west of Nova Scotia ($< -65^\circ$ longitude) through October. In November there was considerable movement east of Nova Scotia ($> -65^\circ$ longitude) as tagged birds left the study area (Fig. 4B). The 50%–95% group showed the largest latitudinal and longitudinal expansions over time. The northernmost points reached 48° in August to September, after which the birds progressively moved southward to 41° by December (Fig. 4A, also Fig. 2 for years 2014 and 2015). By September most of this group was east of Nova Scotia ($> -65^\circ$), extending to the Grand Banks ($< -55^\circ$) (Fig. 4B). In 2018, individuals (ID number: 112710 and 112717) moved east of the Grand Banks to -30° in August. The eastward trend continued into December while average latitude was decreasing southward. Thus, eastward movement out of the study area occurred over a wide latitudinal band (40° to 47°) and was most pronounced in the outer parts of their collective UD (50%–95% kernel density) after September. Of the 58 birds in this study, 18 were tracked south of the Equator, 3 by the end of September and the remaining 15 in November and December. Only two of the birds tracked south of the Equator visited the Tristan da Cunha archipelago and neither stayed more than a single day before returning to the Patagonian Shelf.

Fecal DNA analysis

Prey sequences were successfully obtained for 35 of the 47 fecal samples. Samples were collected in August and September 2017 and in July and November 2018. Average prey diversity was 2.11 ± 0.28 (mean \pm 1 SE, min = 1, max = 7). Most samples (71.4%) contained sand lance; the next most frequent prey item was menhaden (48.6%, Table 4). Only 14.3% (5 of 35) of samples lacked sand lance or menhaden. Mackerel, Atlantic butterfish *Peprilus triacanthus*, and herring were also identified in Great Shearwater diets at lower frequencies. Sand lance, menhaden, and mackerel were consumed in both years sampled (2017 and 2018).

In the remaining six prey groups, it is unclear whether shearwaters were taking juvenile fish directly (which might explain the occurrence of striped bass *Morone saxatilis*, white hake *Merluccius bilinearis*, cunner *Tautoglabrus adspersus*, and a pleuronectiform flatfish) or whether birds were scavenging chum or bait from fishing vessels (which might explain the occurrence of little skate *Leucoraja erinacea* and spiny dogfish *Squalus acanthias*). Alternatively, primary prey may have contained bait or chum that we detected indirectly (Sheppard *et al.* 2005).

Depth, substrate, and prey distribution

Foraging in 25% kernel UDs was linked to shallow depths and substrates with high sand content of coarser grain sizes (Table 3). During the 2013–2017 period, 88 of 2319 trawls conducted by NOAA's National Marine Fisheries Service (NMFS) captured sand lance, while 67% of trawls with sand lance were over the aggregate 25% kernel UD of Great Shearwaters (Fig. 5). The physical properties of these sand lance locations were similar to those hulls in the shearwater 25% kernel UD having a mean depth of 61.6 m

(± 48.5 m) with 71.1% ($\pm 22.7\%$) sand content of relatively coarse grain size (median 0.685 mm). In addition, 89% (78 of 88) of the NMFS trawls with sand lance also occurred within the 100-m isobath. Of these 88 sand lance locations for which we could extract sand content and grain size information, we found that 64% (56 of 88) were found over substrates with $> 50\%$ sand and grain sizes in the range of 0.35–2.00 mm. This range of grain sizes encompasses coarse to very coarse sand (Krumbein & Sloss 1963; Fig. 5). Of the Great Shearwater locations in the 25% kernel UD, 63% (26 355 of 41 637) were within the 100-m isobath with $> 50\%$ sand content; 49% (20 562) were also coincident within this inclusive range of sediment grain sizes.

Mackerel were caught at 688 locations on the northeastern US continental shelf, with greatest abundance near Race Point off Cape Cod, eastward along the 100-m isobath to northern Georges Bank. Among trawls with mackerel, 38% (259 of 688) occurred within the shearwater 25% kernel UD, and the fish were caught at an average depth of 111.1 ± 68.2 m over substrate with $51.4\% \pm 30.1\%$ sand content and a median grain size of 0.238 mm. Herring were caught in 1225 locations, with highest abundance over western Nantucket Shoals, northern Georges Bank, and in Cape Cod Bay north to Jeffreys Ledge. Among trawls with herring, 36% (447 of 1225) occurred within the shearwater 25% kernel UD, and the fish were caught at an average depth of 125.7 ± 72.1 m over substrate with $44.6\% \pm 29.0\%$ sand content and a median grain size of 0.174 mm.

Age analysis using bycatch

Necropsies were performed on Great Shearwaters caught as bycatch near Gough Island in the Tristan da Cunha archipelago and near Cape Cod. South Atlantic specimens were landed in April 2018 ($n = 23$, 16 male and 7 female), December 2012 ($n = 1$, male), and October 2018 ($n = 1$, female). Northwest Atlantic specimens were landed in August 2017 ($n = 71$, 27 male and 44 female).

The median gonad area in males was 8 mm² for Northwest Atlantic birds and 32 mm² for South Atlantic birds. In females, median gonad area was 33 mm² for Northwest Atlantic birds and 100 mm² for South Atlantic birds. Gonad size was significantly different in both sexes between regions (males: $W = 429$, $P = 1.248\text{e-}06$; females: $W = 327$, $P = 0.000136$). A truth table was developed to sort age categories and determine maturity (Table 5). All birds from the South Atlantic were mature, but only two males and six females from the Northwest Atlantic region were mature. We then compared gonad size of young vs. mature birds for both sexes between the Northwest Atlantic and the South Atlantic groups. In terms of gonad size, young birds from the Northwest Atlantic were significantly different (smaller) from the South Atlantic birds (males: $W = 424$, $P = 4.411\text{e-}06$; females: $W = 301$, $P = 1.648\text{e-}05$), whereas there was no significant difference for mature birds (males: $W = 5$, $P = 0.1404$; females: $W = 26$, $P = 0.8461$). Thus, 11% (8 of 71) of the Northwest Atlantic bycatch specimens were sub-adults or adults who may have been possible breeders, while 89% (63 of 71) were juvenile or immature individuals considered to be pre-breeders.

We analyzed 53 of the 71 Northwest Atlantic birds and all 25 South Atlantic individuals for bursas. For the Northwest Atlantic specimens, bursas were identified in 13 males and 24 females and deemed absent (involved) in 7 males and 9 females. Bursas were not found in any South Atlantic individuals, as they were all mature. Thus, of those

birds examined for bursa, 70% of the pre-breeders from the Northwest Atlantic specimens were juvenile or hatch-year individuals.

We also compared primary molt score and head-bill length (mm) between the regional necropsy samples (Northwest vs. South

Atlantic) and 18 live shearwaters caught in July 2019 within the tagging area. The median primary molt scores among these areas (NwAtl-necropsy, NwAtl-live, SAtl-necropsy) were 50, 46.5, and 0, respectively. The average head-bill lengths for the same areas were 101.4 ± 3.0 mm, 103.5 ± 4.5 mm, and

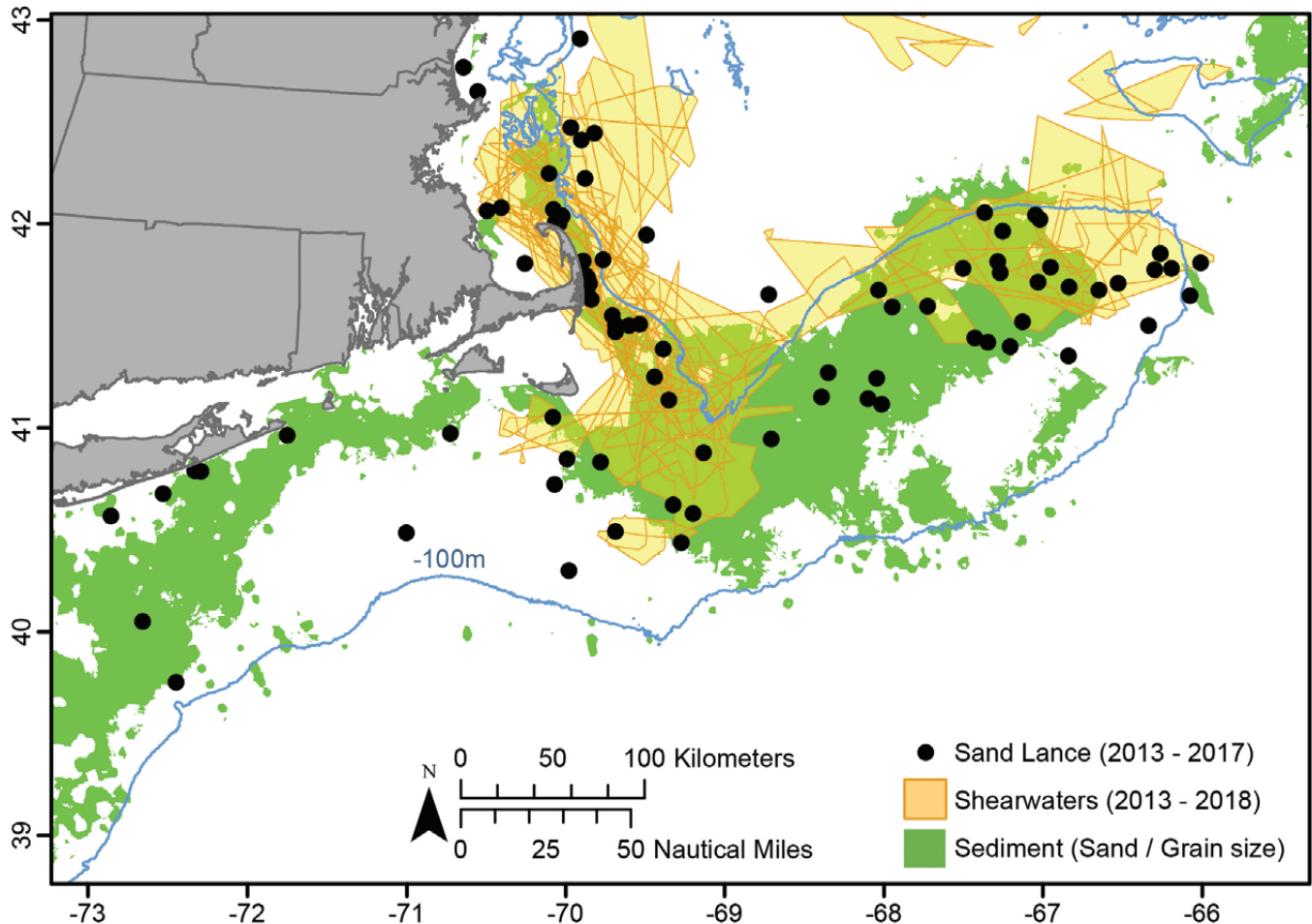


Fig. 5. Plot of aggregate 25% kernel utilization distributions (UDs) of Great Shearwaters, sand lance trawl captures, and substrate properties common to both species in the southwestern Gulf of Maine and Georges Bank. Most sand lance (at least 64%) caught in US NOAA/NMFS bottomfish trawl samples (2013–2017) occurred within the 100 m isobath over sediment with > 50% sand content and grain sizes ranging from 0.35–2.00 mm in diameter. Within the 25% kernel UD, 67% of sand lance captures occurred and 49% of shearwater hull locations intersected with these sediment properties.

TABLE 5
Parameters used to designate “mature” and “young” age categories of necropsied Great Shearwaters

Parameter	Distinguishing features between ages	Notes
Molt score	HY ¹ = 50, non-HY = < 50	HY birds typically complete primary molt before arriving in the southwestern Gulf of Maine; immature and sub-adult individuals complete molt following migration
Gonad class	Classes 1 & 2 = young Classes 3 & 4 = mature	Visual assessment of color and gonad size were used to define gonad class
Gonad size comparison	Within min-max range of suspected post-breeding birds	Birds considered “mature” if gonad area overlapped the range of gonad area observed in suspected post-breeding adult/sub-adult individuals from Gough Island
Bursa presence/size	Present, bulbous = HY	Bursa present in only HY individuals

¹ HY = Hatch year

105.3 ± 2.5 mm, respectively. The necropsied birds from the Northwest Atlantic had the smallest head-bill lengths and had predominantly completed molt, suggesting young individuals. The live birds from the Northwest Atlantic showed a mixture of younger and older birds, with most in active molt and larger head-bill lengths. The necropsied birds from the South Atlantic (April 2018 samples) were all older with the largest head-bill lengths and old primary feathers (molt score = 0).

DISCUSSION

We used individual tracks from 58 Great Shearwaters over a six-year period (2013–2018) to characterize the spatiotemporal utilization of Great Shearwaters over a large portion of their wintering range in the Northwest Atlantic. This study improves our understanding of Great Shearwater use of the Gulf of Maine and Atlantic Canada by providing temporal and behavioral dynamics across the entire region, along with a more comprehensive examination than available previously of how age is integrated into spatial use. In general, Great Shearwaters begin to arrive on Georges Bank in late May (Powers 1983) and are abundant across the southern Gulf of Maine in June and July (Powers *et al.* 2017). They undergo a rapid molt upon arrival, which does not render them flightless (Brown 1986, Brown 1988). Molt scores of birds in this study showed that primary molt was > 90% complete (average score 45.4 of possible 50) in July (Table 1). Molt should have been completed in August, as has been noted in the Bay of Fundy (Powers *et al.* 2017), yet we found a preponderance of completed primary molt in July (20 of 48 scored). This indicated that many of our captures were hatch-year or, less likely, immature pre-breeders that molted in the South Atlantic prior to coming north (Watson 1971, Bugoni *et al.* 2015).

Our molt data were supported by our necropsy data on gonad size, which showed that only 11% had gonad sizes comparable to that of individuals from the Gough Island breeding colony and that 89% were non-adults. The presence of visually prominent bursa indicates that 70% of non-adult birds in the study area may be hatch-year birds. The non-breeding status of the birds was further supported by our tracking data. No birds that we tracked into the South Atlantic for this study spent any significant time near the breeding islands of Tristan da Cunha. As characterized by nape plumage, 89% of Great Shearwaters in the Gulf of Maine were thought to be less than three years of age (Powers *et al.* 2017). However, that methodology was derived from Pyle (2008) and has not been thoroughly vetted in the literature. In addition, birds tagged in the Bay of Fundy by Powers *et al.* (2017) were confirmed as non-breeders (Ronconi *et al.* 2018). An evaluation of mass strandings of Great Shearwaters along the eastern coast of the United States noted that birds stranded in the southeastern US were primarily juveniles while those in the northeast were a mix of adults and juveniles (Haman *et al.* 2013). The breeding population of Great Shearwaters has been estimated at 5–6 million pairs (10–12 million birds) (Ryan 2007) and the global population (inclusive of pre-breeding birds) is thought to be around 16.5 million (Fishpool & Evans 2001), as noted by Ronconi *et al.* (2018). These population estimates indicate that 27%–40% of the world population may be non-breeding. So, if our Gulf of Maine sample consists of 89% non-breeders, it may be an important area used primarily by younger non-breeding birds. Most adult birds may be wintering in areas further north on the Grand Banks, as suggested by Brown (1986).

The 95% kernel UD of birds in this study indicated that Great Shearwaters utilized much of the continental shelf from southern New England across the Scotian Shelf to the Grand Banks after their initial arrival to the southwestern Gulf of Maine and Georges Bank. Nearly half (45%) of the birds moved to Atlantic Canada by August, while the remainder (55%) stayed within the Gulf of Maine until November. Wong *et al.* (2018) noted the highest densities of Great Shearwaters in the Bay of Fundy in early September, which is coincident with the start of southern migration for ‘early’ migrants (Powers *et al.* 2017). The spatial spread over time was generally northward until October and eastward into November. The frequency of birds staying in the Gulf of Maine was consistent from year to year, but the number of birds with ranges that extended to Atlantic Canada varied annually.

It’s not entirely clear why some birds stayed in the Gulf of Maine and others undertook more extensive travelling, but it may be related to age and experience. With increasing maturity, individuals identify new resources across their wintering range. Cory’s Shearwaters do not become familiar with main migratory routes until they reach four years of age, when they broadly use the same routes as older immatures and adults (Campioni *et al.* 2020). Beyond this age their migratory behavior becomes progressively adult-like until time of first breeding (Campioni *et al.* 2020). This observation of older Great Shearwaters expanding their UD on the wintering range is supported by our data showing heavier birds tending to move out of the Gulf of Maine before lighter birds. While age at first breeding is unknown for Great Shearwaters, the related Short-tailed Shearwater breeds at six or seven years old (Bradley *et al.* 1999) and Cory’s Shearwater at nine years (Campioni *et al.* 2020); Great Shearwaters might be similar. The long duration of immaturity in Wandering Albatross *Diomedea exulans* relates to a long period of experiential learning about spatial, behavioral, and resource constraints (Riotte-Lambert & Weimerskirch 2013). The ontogeny of long-distance migratory strategies and related patterns of spatial distribution in young Cory’s Shearwaters progressively changes with age (Campioni *et al.* 2020).

Thus, most Great Shearwaters (55%) stayed within the Gulf of Maine from July to November instead of moving to Atlantic Canada. Individual 50% kernel UD sizes typically represented 22% of a bird’s 95% kernel UD, and 84% of individual range interactions occurred outside of the 50% kernel UD, indicating that foraging occurs over wide areas each year. When we aggregated all individuals across all years into a single dataset, the contrast of utilization reversed, and 82% of the hulls were within the 50% kernel UD. The merge of all tangential 50% kernel UDs from each year created a singular 25% kernel UD, which included 58% of all hulls. Thus, birds were foraging in similar areas each year with significant overlap among years. Behavioral traits in the high-density region supported more intense daily foraging activity as birds remained in hulls for longer periods of time (duration), revisited the same hulls on different days more often (revisitation), and showed more area-restricted search behavior (eccentricity). The aggregate 25% kernel UD also had commonality in its physical characteristics, as it was shallow (median 64 m) with high sand content (median 62%) of coarser grains (median 0.58 mm) than the more peripheral bands of the 50% or 95% kernel UDs.

The physical characteristics of shallow habitat with coarsely grained sand selected by Great Shearwaters was also spatially aligned with that of sand lance, which our fecal samples identified as their main

prey (71% Frequency of Occurrence). The habitat preferences (deeper, with less sand and smaller grains) of mackerel and herring were less aligned with that of shearwaters, and these species were identified as lesser prey in our fecal samples (mackerel 31%, herring 6%). Research trawl data showed that 67% of locations containing sand lance fell within the Great Shearwater 25% kernel UD, while far fewer locations containing mackerel and herring fell within this UD (38% and 36%, respectively). Further, at least 64% of trawls with sand lance occurred in waters where depth was < 100 m, sand content was > 50%, and sediment grains were 0.35–2.00 mm in diameter. This combination of factors was also coincident with 49% of shearwater locations in their 25% kernel UD. This indicates that sand lance and the habitats that support them are key factors in shearwater habitat use. Depth (< 100 m) was a significant predictor for the presence/absence of Great Shearwaters in the Gulf of Maine, and this may be related to their reliance on sand lance as forage (Powers *et al.* 2017).

Shearwater utilization of the eastern Scotian Shelf was also associated with banks having shallow waters and high sand content. Sand lance on the Scotian Shelf occur on most of the major banks, where the bottom consists of sand or fine gravel (Scott 1982), and in the shallower areas of the Grand Banks, particularly in the northeastern and southeastern areas (Winters 1983). Previous assessments of Great Shearwater diets in the southwestern Gulf of Maine noted sand lance as a common food item (Powers & Backus 1987), while euphausiids *Meganyctiphanes norvegica*, herring, mackerel, and short-finned squid *Illex illecebrosus* dominate shearwater diets in the Bay of Fundy (Brown *et al.* 1981, Ronconi *et al.* 2010). Around Newfoundland, spawning aggregations of capelin *Mallotus villosus* and immature short-finned squid attract shearwaters (Brown *et al.* 1981, Davoren *et al.* 2012).

Sand lance distributions are patchy with considerable annual fluctuations in abundance, and larval forms are prey to both herring and mackerel (Staudinger *et al.* 2020). Populations increased 5- to 10-fold in the Gulf of Maine from 1976 to 1981, but abundance subsequently dropped between 1982 and 1987 (Nelson & Ross 1991). 2016 to 2018 were poor years for herring (and likely mackerel), which may have contributed to the high frequency of occurrence of sand lance found in shearwater fecal samples. Age-1 recruitment of herring in the northeastern US has been below average since 2013, and four of the six lowest annual recruitment estimates have occurred since that year (NEFSC 2018b). Since 2005, diets of Atlantic Puffins *Fratercula arctica* and Razorbills *Alca torda* in the Gulf of Maine switched from herring to sand lance due to the decline in herring (Scopel *et al.* 2019). Based on fisheries model results and sensitivity, the mackerel stock in the northeastern US was estimated to be at an all-time low in 2012, having experienced increasing exploitation (overfishing) through the early 2000s to a high in 2010 (NEFSC 2018a). We note that concurrent with obtaining some fecal samples, there was an unusual event of mackerel driving yearling menhaden into the shoreline at Race Point on Cape Cod, Massachusetts in August 2017. Menhaden were taken by shearwaters in both 2017 and 2018, but in 2017 we observed hundreds of Great Shearwaters feeding on beached menhaden along the shoreline. Menhaden nursery grounds in New England have become significant contributors of age-1 fish (Anstead *et al.* 2016). Since 2015, abundance of both adult and juvenile menhaden has increased in the Gulf of Maine (ASMFC 2017). Menhaden and mackerel were previously unknown in diets of Great Shearwaters in the northeastern US, so their importance as prey may be increasing

in this region. The availability of any suitable prey is important, but Great Shearwaters in the southwestern Gulf of Maine in 2013–2018 foraged most intensively over the same habitat used by sand lance.

Latitudinal differences in trophic levels of Great Shearwaters, as measured by stable isotopes (feathers and blood) between populations in Newfoundland, the Bay of Fundy, and southwestern Gulf of Maine, could be attributable to preferences in primary prey (Ronconi *et al.* 2010, Gulka *et al.* 2017, Hong *et al.* 2019). The dietary niche of shearwaters in coastal Newfoundland was found to narrow with increased availability of capelin, and shearwaters were uniquely qualified to forage over broader scales to continuously maintain contact with capelin patches (Gulka *et al.* 2017). Similarly, Great Shearwaters in the southwestern Gulf of Maine and northern Georges Bank showed selectivity for habitats with higher availability of preferred prey (sand lance).

In summary, a combination of PTT tracking and necropsy data indicate that the Gulf of Maine is a key wintering area for young (0–2 years) Great Shearwaters. The characteristics of identified foraging areas and DNA from fecal samples from birds indicate that shallow, sandy-bottomed marine habitat and sand lance are important aspects of their habitat use and survival. Since juveniles represent an important demographic in the viability of any species (Hazen *et al.* 2012), we suggest that management actions in the Gulf of Maine that would impact their preferred habitat and prey should consider Great Shearwaters in their decision-making.

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Disclaimer

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