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Seasonal variation in environmental and behavioural drivers of annual-cycle habitat selection in a nearshore seabird

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Abstract

Aim: Conservation of highly mobile species often requires identifying locations or time periods of elevated vulnerability. Since both extrinsic habitat conditions and intrinsic behavioural and energetic requirements contribute to habitat use at the landscape scale, identifying spatial or temporal foci for conservation intervention requires understanding how habitat needs and distributions vary across the annual cycle. Nearshore marine birds inhabit highly dynamic systems and have widely varying habitat needs among breeding, moult and non-breeding seasons, making them a useful case study for testing the relative contributions of individual resource requirements and environmental conditions in driving annual variation in distribution patterns.

Location: Northern Gulf of Mexico (USA).

Methods: We tracked Brown Pelicans using bird-borne GPS transmitters and used a combination of Hidden Markov Models and multivariate selectivity analysis to compare the characteristics of preferred resident habitats used throughout the annual cycle.

Results: Habitat selection was driven by dynamic oceanographic variables during all stages of the annual cycle. Key habitat characteristics varied between seasons, with particularly strong selection on high productivity, low temperature and low salinity during the breeding and post-breeding moult periods. The post-breeding moult also corresponded to a time of limited availability of preferred habitats, resulting in extensive overlap between breeding populations from different administrative planning areas.

Main conclusions: By incorporating seasonal variation in individual behaviour and resource requirements into our habitat models, we were able to identify the post-breeding moult as a period of high selectivity and restricted availability of preferred habitats for Brown Pelicans. Locations meeting preferred habitat criteria during the post-breeding period, particularly estuarine habitats with high productivity and low salinity, would therefore be high-value targets for management and restoration. Our analysis demonstrates the importance of accounting for both intrinsic and extrinsic temporal variation in evaluating habitat selection.

KEYWORDS
Brown pelican, GPS telemetry, Hidden Markov Model, molt, productivity, salinity

1 | INTRODUCTION

A frequent goal in wildlife conservation is to identify locations or time periods in which management actions are likely to have the greatest positive effect (Radeloff et al., 2013). For mobile organisms, achieving this objective requires first understanding how both extrinsic habitat conditions and intrinsic habitat requirements vary across space and time (Marra, Cohen, Loss, Rutter, & Tonra, 2015). Individuals require different habitat components for activities that vary within or among different stages of the annual cycle, including obtaining food, sheltering from predators, thermoregulating, raising young and moving or migrating among habitat patches (Börger, Dalziel, & Fryxell, 2008; Morrison, Marcot, & Mannan, 2012). Temporal changes in environmental conditions, habitat features and individual resource requirements drive habitat selection on daily (e.g., commuting vs. resting), seasonal (e.g., breeding vs. non-breeding) and annual or even decadal scales (Garthe & Hüppop, 2004). Thus, designing effective conservation strategies requires not only incorporating background variation in biotic and abiotic habitat features, but also understanding how temporal variation in individual resource requirements contributes to observed patterns of occupancy and distribution (Small-Lorenz, Culp, Ryder, Will, & Marra, 2013).

Opportunities to conduct an individual-based analysis of habitat requirements have vastly improved due to miniaturization and refinement of animal-borne tracking devices (Hebblewhite & Haydon, 2010). To date, however, many habitat assessments derived from individual tracking data have considered each location as an independent occupancy record, rather than considering that observed locations are samples of continuous movement processes that vary with underlying behaviour (Tremblay et al., 2009). To better understand the behavioural processes that generate observed locations, advanced computational approaches such as state-space models (Jonsen, Myers, & James, 2007) and Hidden Markov Models (Patterson, Basson, Bravington, & Gunn, 2009) have been developed to detect the underlying patterns represented by a series of locations. Rather than treating each location in isolation, these modelling frameworks interpret locations as steps in a continuous movement process, allowing for the detection of changes in behaviour based on shifts in these latent movement processes. From a conservation standpoint, incorporating dynamic behavioural processes into habitat selection analysis is an important refinement of resource selection models, as it allows the identification of locations or time periods at which either environmental conditions or individual behaviour may result in increased vulnerability (e.g., Cureton & Deaton, 2012).

Marine birds provide a particularly interesting case study for assessing effects of temporal variation in individual resource requirements on habitat selection. Seabirds have widely varying habitat requirements between the breeding season, when birds are central-place foragers breeding on land (often offshore islands) and foraging at sea close to the colony site, and the non-breeding season, when birds range widely throughout marine habitats (Weimerskirch

& Wilson, 2000). Within each stage of the breeding cycle, habitat use also depends on individual characteristics and condition (Bearhop et al., 2006), phenology (Catry, Ramos, LeCorre, & Phillips, 2009), colony size and location (Lamb, Satgé, & Jodice, 2017; Lewis, Sherratt, Hamer, & Wanless, 2001), and environmental features (Tew Kai et al., 2009). These factors all contribute to variation in individual energy requirements, resulting in differences in foraging strategies and habitat preferences (Daunt, Afanasyev, Silk, & Wanless, 2006; Phillips, Bearhop, McGill, & Dawson, 2009). Moreover, since marine environments are highly dynamic, habitat features present at any given location may vary widely in space and time. Nearshore habitats contain a particularly high diversity of landscape features, including estuaries, river plumes and upwellings, which support varying prey species assemblages (Becker & Beissinger, 2003), and are structured by different oceanographic and anthropogenic processes than large marine ecosystems (Gray, 1997). Among marine birds, factors driving habitat selection differ between pelagic seabirds, which inhabit offshore marine environments, and nearshore seabirds that utilize coastal systems (Thaxter et al., 2012). Many of the same underlying individual, colony-based and environmental factors that influence habitat choice in pelagic species also affect nearshore seabirds (e.g., Erwin, 1977; Suryan, Irons, & Benson, 2000); however, since most studies of habitat selection in marine birds have focused on pelagic species, the importance of nearshore habitat features to seabirds remains poorly understood.

One of the most visible nearshore seabirds in the neotropics and subtropics is the Brown Pelican (*Pelecanus occidentalis*), typically found within 20 km of the nearest shoreline (Shields, 2014). Although currently abundant, the species was reduced to near extinction by DDT exposure during the mid-twentieth century (McNease, Richard, & Joanen, 1992) and continues to experience high mortality rates during oil spills (USFWS, 2011), making it an important target of regional monitoring and mitigation efforts (Jodice, Adams, Lamb, Satgé, & Gleason, 2019). Despite this conservation interest, limited information is available on habitat requirements of Brown Pelicans outside of terrestrial breeding sites. The majority of the eastern subspecies *P. o. carolinensis* of Brown Pelicans breeds in the northern Gulf of Mexico (GOM), where their breeding habitat occurs within three administrative planning areas (BOEM, 2012). However, since boundaries of planning areas are based on offshore geomorphology rather than species ecology, it is unclear whether they represent appropriate units for management of mobile marine species. Indeed, data from band recoveries suggest that Brown Pelicans may move widely during non-breeding (Schreiber & Mock, 1988; Stefan, 2008), meaning that current administrative boundaries may not encompass year-round habitat needs for breeding pelicans. Previous studies of fine-scale habitat use and movement patterns of Brown Pelicans in the GOM (King et al., 2013; Walter, Leberg, Dindo, & Karubian, 2014) have been limited to pelicans captured in a small portion of the central planning area. An integrated understanding of year-round movements of the species throughout the GOM would allow for more detailed analyses of spatial patterns, including identifying locations or time periods of critical habitat, quantifying vulnerability

to stressors and evaluating whether current administrative boundaries effectively encompass the habitat needs of breeding populations within those regions.

Based on 3 years of tracking data from Brown Pelicans breeding in the northern GOM, we characterized year-round habitat preferences. To ensure that locations used to determine habitat preferences accurately reflected areas where individuals were interacting with marine habitat features, we filtered points based on modelled behavioural states, retaining only points that represented resident behaviour. We then evaluated habitat selection across a suite of environmental variables. Our results provide a baseline understanding of how nearshore habitat features influence patterns of use and occurrence in marine birds, and how seasonal variation in individual behaviours and resource requirements drives habitat selection on an annual scale.

2 | METHODS

2.1 | Study area

From 2013 to 2015, we collected data on breeding adult and nestling pelicans as part of a region-wide study from six colonies in the northern GOM between 83° and 98° W and 27° and 31°N (Figure 1). All colony sites were within the same marine ecoregion (Spalding et al., 2007), although local environmental conditions and breeding population size varied among sites (Lamb et al., 2017). Individuals of both sexes were captured at all colonies, although sex ratios varied between sites since sex could not be determined prior to capture and therefore could not be included in the experimental design (Table 1).

2.2 | Pelican locations

To track movement patterns of adult pelicans, we used 65 g solar GPS Platform Terminal and Cellular Terminal transmitters (GeoTrak Inc; NorthStar Science and Technology) with a backpack-style Teflon ribbon harness attachment (Dunstan, 1972). To elevate the transmitters and prevent feathers from covering the solar panels and antenna, we mounted each device on a 6 mm thick neoprene pad that also extended 6 mm beyond the perimeter of the transmitter in all directions. Transmitters were programmed to collect 12 fixes/day during breeding (April–August; every 90 min from 1030 to 0130 GMT), 10 fixes/day during pre- and post-breeding (September–October and February–March; every 90 min from 0700 to 0100 GMT) and 8 fixes/day during winter (November–January; every 120 min from 0700 to 0100 GMT). We obtained an average error estimate for GPS points from transmitters at known locations (N = 220) of 4.03 ± 2.79 m.

Over 3 years, we fitted 85 individual pelicans with GPS transmitters, 67 of which recorded sufficient data for subsequent analysis (i.e., transmitted over at least 30 days; Table 1). Adults were captured at nests using leg nooses in either the late incubation or early chick-rearing stage of breeding. All captured adults were weighed, measured, banded and sampled for blood and feathers. We also calculated adult body condition index (BCI) as the residual of the linear relationship between culmen length and mass (Eggert, Jodice, & O'Reilly, 2010). Since morphology is not always sufficient to determine sex in Brown Pelicans, adults were later sexed via PCR using DNA obtained from blood samples (Itoh et al., 2001). Total handling time from capture to release averaged 19 min (±6.5 min standard deviation). To avoid subsequent influence of disturbance on observed movement patterns, we avoided entering or trapping in areas of the colony where we had already captured nesting pelicans. Since individual characteristics (e.g., sex, size, physical condition) may influence pelican foraging movements during breeding (Walter et al., 2014), we used nested ANOVAs to determine whether individual characteristics of tracked adults differed systematically among planning areas or between colonies within each planning area. Unless otherwise specified, all statistical manipulation of spatial data was conducted using the "adehabitat" family of packages (Calenge, 2006) in R 3.2.3 (R Core Team, 2014).

For each individual, we removed all locations between when the individual was first released and when it returned to its nest site (typically 2–4 hr after release). We manually identified and removed outliers using a speed cut-off of 65 km/hr between successive points, which is the maximum travel speed recorded for Brown Pelicans (Schnell & Hellack, 1978). Cleaned locations for each individual were then interpolated to regular 90-min intervals. Since location data were not collected overnight, we chose not to interpolate tracks between successive days, and we differentiated each day as a separate trajectory by cutting tracks between each set of two successive points separated by a gap of greater than 6 hr.

2.3 | Movement states

To distinguish resident from commuting behaviour, we fit a two-state Hidden Markov Model (HMM; Patterson et al., 2009) to the regularized movement trajectories using the moveHMM R package (Michelot, Langrock, Patterson, & Rexstad, 2015). Hidden Markov Models are a particularly flexible and efficient way of characterizing behavioural states from precise and regularized tracking data (Langrock et al., 2012), and thus, are a good fit for GPS tracking locations. Briefly, the model assumes a priori that observed movement data are driven by underlying movement "states," characterized by a distribution of step lengths (distance between successive points) and turning angles. Each point therefore represents a sample drawn from these underlying distributions and can be assigned to one or the other based on probability. A Markov chain is used to describe the state parameters and classify data according to its most probable state membership.

To reduce spatial autocorrelation and characterize patterns of movement between rather than within days, we fit the model to a reduced data set of one location per day, calculated as the centroid of all locations for that day. We began with the assumption
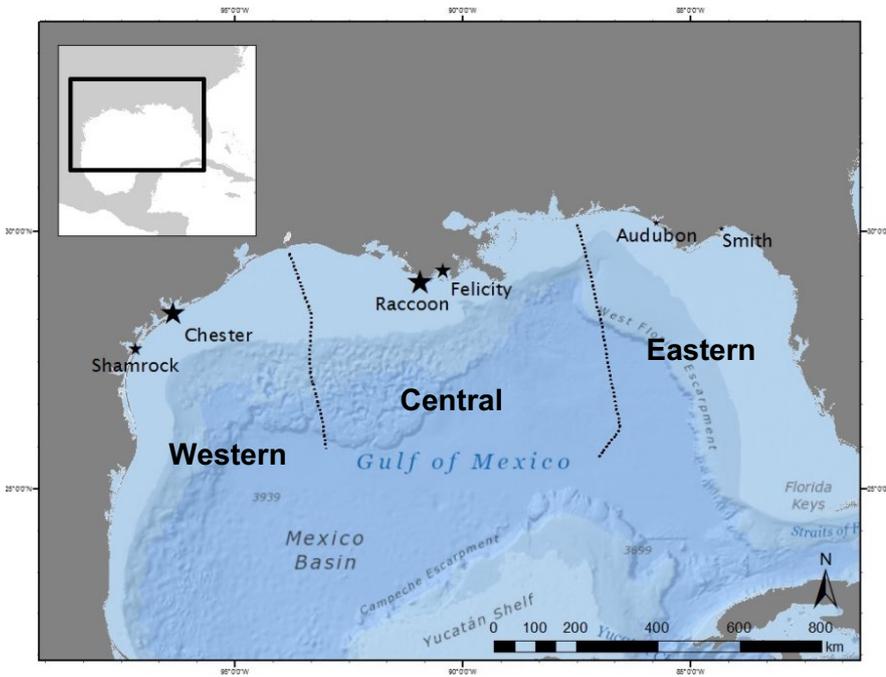
FIGURE 1 Locations of Brown Pelican study colonies in the Gulf of Mexico, 2013–2015 (Albers Equal-Area Conic projection). Sizes of stars represent comparative colony sizes. Grey lines indicate boundaries between administrative planning areas (BOEM)

TABLE 1 Colony characteristics and measurements of tracked adults captured at six Brown Pelican breeding colonies in the northern Gulf of Mexico, 2013–2015

	Eastern		Central		Western	
	Smith	Audubon	Felicity	Raccoon	Shamrock	Chester
Colony size	40	100	1,800	4,300	1,400	3,200
Adults tracked	9	11	12	14	11	10
% male	0.78	0.64	0.50	0.57	0.55	0.30
Mass (g)	3,414 (432)	3,414 (558)	3,448 (369)	3,546 (353)	3,459 (562)	3,070 (508)
Culmen length (mm)	322 (22)	315 (21)	313 (23)	316 (23)	321 (25)	309 (19)
Body condition index[a]	−141 (273)	−241 (205)	77 (195)	121 (263)	−19 (306)	−147 (281)

Note: Measurements are reported as mean values, with standard deviations listed in parentheses.
[a]Body condition Index = residual of linear relationship between culmen length and mass.

that local movement would be characterized by short step lengths and sharp turning angles (State 1) and commuting movement by long step lengths and wide turning angles (State 2). Therefore, initial step lengths were set at 5 (±5) km for State 1 and 10 (±10) km for State 2. Initial turn angles were set at π radians for state 1 and 0 radians for State 2. Angle concentration for each state was initially set at 1. In subsequent analyses, all points along the trajectory for a given day were assigned to the movement state associated with that day.

We further assigned resident locations to one of three stages—breeding, migration or wintering—based on their positions within the annual cycle. We defined the breeding stage as the period during which individuals returned to the colony site at least once every three days (i.e., successive locations at the colony site were separated by no more than 72 hr). We considered the winter stage to begin when an individual arrived at the end of its final period of commuting movements. All movements between the end of the breeding

stage and the beginning of the wintering stage were classified as migratory. Individuals that did not migrate (i.e., whose breeding and wintering ranges overlapped) progressed directly to the wintering stage at the conclusion of breeding.

2.4 | Environmental variables

We measured environmental characteristics of resident locations using seven habitat variables, four of which were fixed for any given point (distance to coastline, distance to river outflow, bathymetry and bottom substrate) and three of which we measured monthly (net primary production, sea surface salinity and sea surface temperature; Table 2). We chose these variables to represent a suite of likely drivers of nearshore habitat variation, particularly the distribution of pelican prey which tends to include Gulf

TABLE 2 Environmental data layers used for habitat analysis

Variable name	Layer name	Data source	Original resolution
Environmental variables			
Distance to coast	World Vector Shoreline, Intermediate Resolution	Global Self-consistent Hierarchical High-Resolution Geography Database, NOAA (Wessel & Smith, 1996)	1:25,000
Distance to river outflow	North American Rivers and Lakes	North American Data Atlas, U.S. Geological Survey ttps://www.sciencebase.gov/catalog/item/4fb55 df0e4b04cb937751e02	1:100,000
Bathymetry	2-min Gridded Global Relief Data, (ETOPO2) v2	NOAA (National Geophysical Data Center, 2006)	0.033°
Bottom substrate	Dominant Bottom Types and Habitats	Gulf of Mexico Data Atlas, NOAA	
Net primary production	Vertically Generated Production Model	Ocean Productivity, Oregon State University (O'Malley, 2012)	0.083°
Sea surface temperature	Sea Surface Temperature, Climatological Mean, 10 m depth	NOAA National Centers for Environmental Information (Boyer et al., 2011)	0.1°
Sea surface salinity	Sea Surface Salinity, Climatological Mean, 10 m depth	NOAA National Centers for Environmental Information (Boyer et al., 2011)	0.1°

TABLE 3 Median values and ranges of habitat characteristics at Brown Pelican resident locations in the Gulf of Mexico, 2013–2015

	Median value	Range	Units
Habitat variable			
Distance to coast	0.4	0 to 134.4	km
Bathymetry	−2.0	9.0 to −81.0	m above sea level
Distance to river outflow	53.7	0.01 to 580.4	km
Substrate	n/a	n/a	Categorical
Net primary production	2,603.4	327.6 to 10,843.2	mg C day^{-1} m^{-3}
Sea surface temperature	25.8	15.1 to 30.1	°C
Sea surface salinity	33.3	22.2 to 37.0	PSU

Menhaden (*Brevoortia tyrannus*) and other schooling fish (e.g., Deegan, 1990). Since limited data are available on fine-scale variation in oceanographic features such as currents and eddies, and since these features have a high degree of short-term variability in coastal areas (Kaltenberg, Emmett, & Benoit-Bird, 2010), we used the distance to physical features that influence the movement of water in coastal areas (coastline, major river outflow) as proxies for these processes. Following the North American Rivers and Lakes map, we defined major rivers as orders 4 and higher in the Horton classification system. Depth and bottom substrate can influence both prey distributions and oceanographic characteristics. Net primary production uses remotely sensed ocean colour and its known relationships to primary production throughout the water column to calculate daily phytoplankton fixation of chlorophyll per unit of ocean surface (see Behrenfeld & Falkowski, 1997 for full details of these calculations). Compared to sea surface chlorophyll concentrations, net primary production provides a more robust index of total oceanographic productivity, which in turn influences the distribution of consumers at

higher trophic levels. Salinity and temperature also influence the distribution of aquatic prey species depending on their osmotic and thermal tolerances. Since some data were reported at finer spatial resolutions than others (Table 2), we standardized all variables to a resolution of 0.1-degree grid squares (approximately 100 km²). Distance values were calculated as the distance from the grid square centroid to the feature of interest. For all other variables, we resampled the data using the mean value for each 0.1-degree grid square.

2.5 | Habitat suitability and distribution

We mapped preferred habitat characteristics in ecological space using a multivariate ordination of all habitat variables using a Hill–Smith principal components analysis (Hill & Smith, 1976), which allows the inclusion of both categorical and continuous variables. For each grid square, we calculated habitat suitability as the squared Mahalanobis distance of that point from optimal location
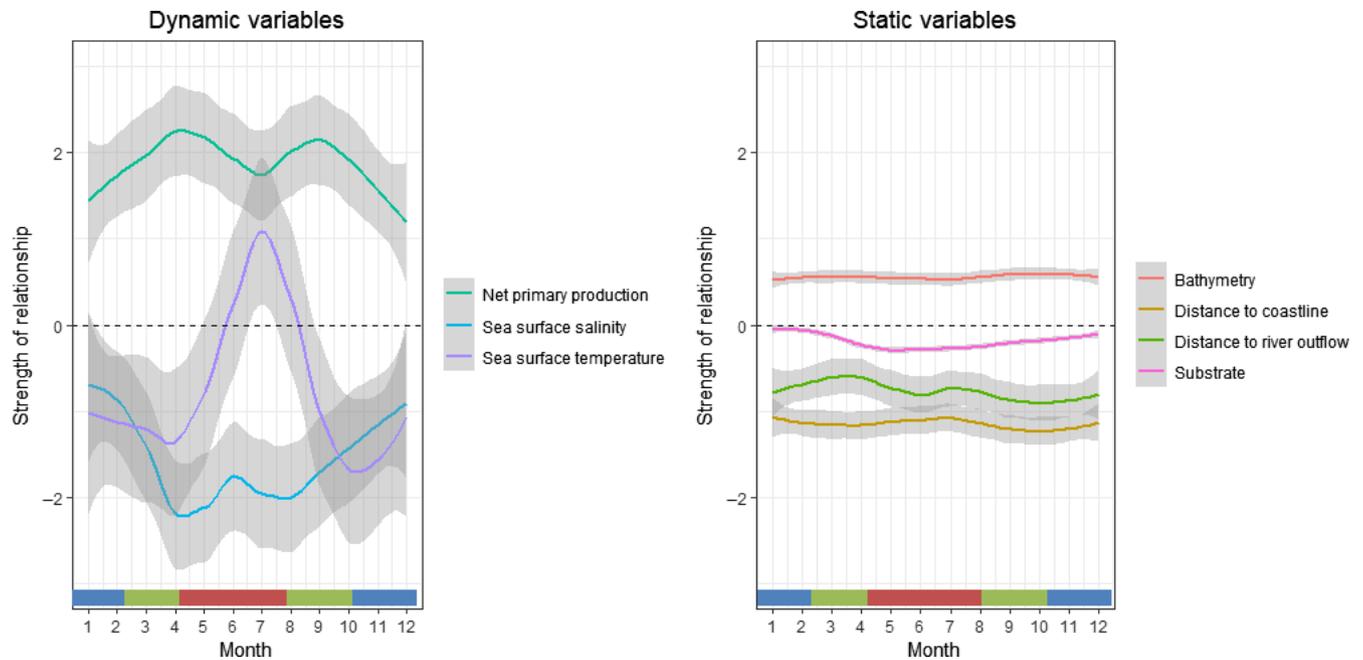
FIGURE 2 Annual patterns of strength and direction of selection by Brown Pelicans on measured dynamic (left) and static (right) habitat variables, Gulf of Mexico, 2013–2015. Strength of selection (positive or negative) is generated from Outlying Mean Index and increases with distance from zero. Lines represent generalized additive model regressions (smoothing parameter = 0.5) of monthly averages for each variable, and grey areas are 95% confidence intervals of regression lines. Coloured bars along the x-axis indicate the approximate timing and duration of breeding (red), wintering (blue) and migratory staging (green) periods

of the species in the multivariate ordination (i.e., higher distances indicate lower habitat suitability; Calenge, Darmon, Basille, Loison, & Jullien, 2008; Clark, Dunn, & Smith, 1993). We projected habitat suitability as the probability of obtaining a higher squared Mahalanobis distance for that cell than the calculated value. Thus, in the final suitability scores, values closer to 1 indicate lower distance from the multivariate optimum location and higher habitat suitability.

To characterize individual responses to the measured habitat variables, we used an Outlying Mean Index (OMI) analysis (Dolédec, Chessel, & Gimaret-Carpentier, 2000). Briefly, OMI is an ordination technique that characterizes available sites based on a set of environmental variables, sets the mean of all conditions at zero in n-dimensional space then determines the axis that describes the maximum amount of marginality (difference from the mean: i.e., similar to residuals) of individual animals or species in ecological space. Thus, the first axis of the OMI is the combination of environmental characteristics that best explains the position of animals across available resources. Similarly, the position of each habitat characteristic on the first axis of the OMI represents that variable's contribution to animal distributions; that is, the strength of selection on that characteristic. Outlying Mean Index does not assume specific resource selection functions and allows differences in individual niche selection to be taken into account when describing the distribution of a group of animals. We conducted OMIs for each month on all individuals and habitat variables for each behavioural state, then averaged the scores of individuals on the first OMI axis to calculate niche location and breadth for

groups within the population. We considered scores between −1 and 1 to represent relatively weak associations, while scores <−1 or >1 represented relatively strong associations. We also examined spatial distribution of breeders from different administrative planning areas (western, central and eastern planning areas for the Bureau of Ocean Energy Management; BOEM) that contained differing levels of oil and gas activity in marine waters. We calculated 95% kernel density estimates for all individuals from each breeding area using the "ks" package (Duong, 2015) with a plugin bandwidth estimator (Gitzen, Millspaugh, & Kernohan, 2006; Wand & Jones, 1994). We then used an Albers Equal-area Conic Projection to calculate the areas included within each planning area's 95% kernel contour and to estimate the intersection areas between kernels from different planning areas.

3 | RESULTS

3.1 | Pelican locations

After cleaning and interpolating all collected locations (N = ca. 180,000), we obtained a total of 169,990 GPS locations from 77 individual Brown Pelicans (mean per individual = 2,237 ± 1688; range per individual = 34–7,371 points; 30–614 days). Sex ratios of captured adults varied among planning areas, but did not differ significantly between the two colonies within each planning area (Fisher's exact test; eastern: p = .64; central: p = 1; western: p = .39). Body size of captured adults also did not differ significantly among or within
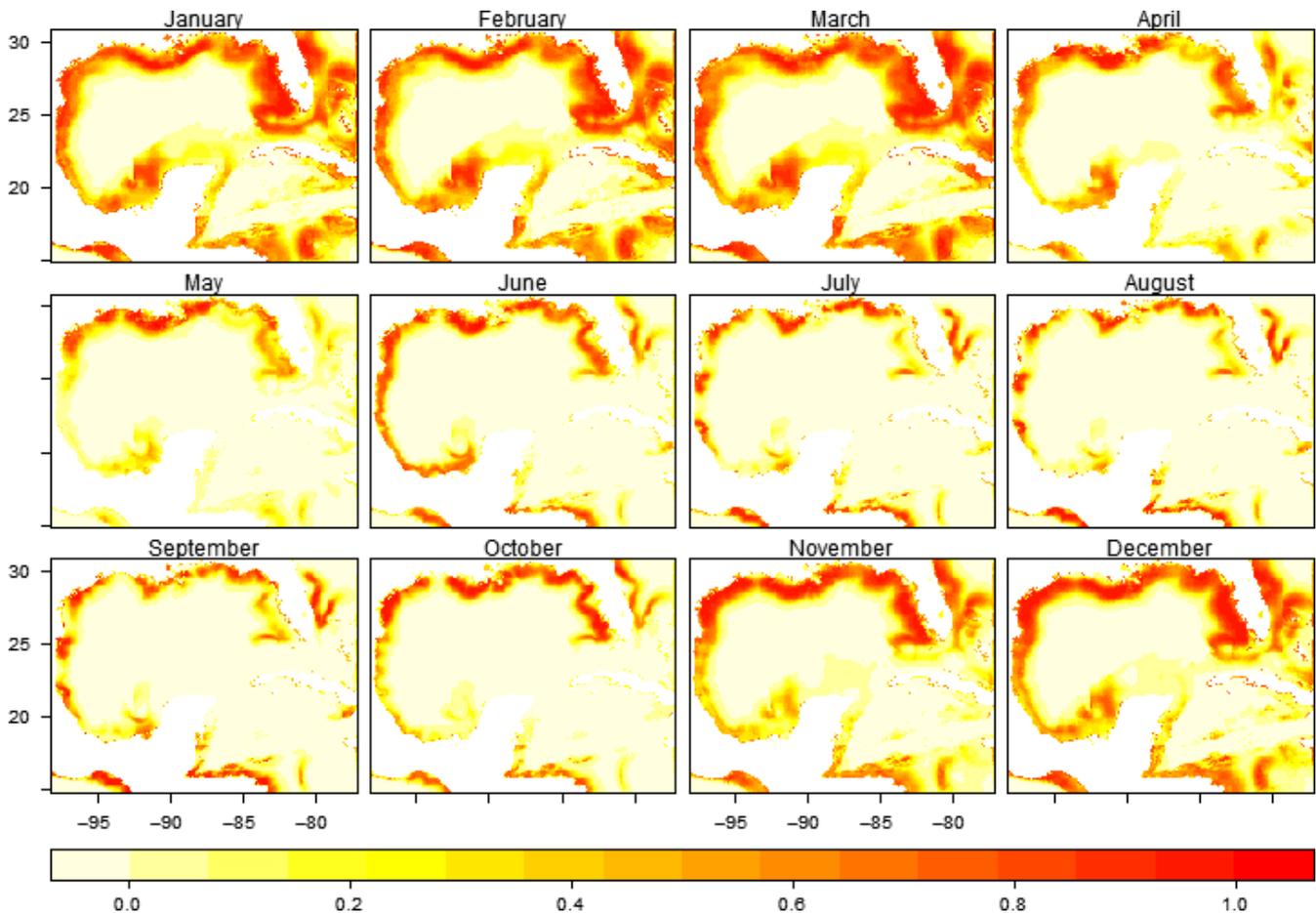
FIGURE 3 Suitability scores of available habitat for Brown Pelicans in the Gulf of Mexico based on Mahalanobis distances, 2013–2015 (Albers Equal-Area Conic projection). Darker colours indicate higher suitability

planning areas (nested ANOVA; mass – F_3 = 1.51, p_{among} = 0.35, p_{within} = 0.61; culmen – F_2 = 0.17, p_{among} = .85, p_{within} = .83) BCI – F_2 = 6.18, p_{among} = .09, p_{within} = .59).

3.2 | Movement states

The HMM converged on two distinct movement states. State 1 (resident) had a mean step length of 3.24 (±3.57) km and mean turning angle of −3.11 (±0.59) radians. State 2 (transient) had a mean step length of 26.95 (±30.44) km and a mean turning angle of 0.04 (±0.30) radians (Appendix S1 in Supporting Information, Figure S1.1). Individuals were more likely to remain in their current state than transition to the other (transition probabilities, resident → resident: 0.94; transient → transient: 0.90). Both resident and transient points occurred throughout the GOM and within each individual trajectory (Figure S1.1).

Overall, 61.5% of bird-days were classified as resident and 38.5% as transient (Appendix S1 in Supporting Information, Figure S1.2). The proportion of time individuals spent in each state did not differ significantly by sex (ANOVA, $F_{1,76}$ = 2.12, p = .15). Between breeding areas, individuals tagged in the eastern planning area spent relatively more time in the resident state (μ = 0.73 ± 0.04) than did individuals

tagged in the central (μ = 0.53 ± 0.03) or western (μ = 0.65 ± 0.05) planning areas (ANOVA, $F_{2,74}$ = 6.61, p = .002). Both states were observed year-round; however, resident behaviour was relatively more common between December and March and between May and August, while transient behaviour was the more frequently observed state during the remaining months (Figure S1.2).

3.3 | Habitat suitability and distribution

Resident locations were concentrated in shallow nearshore waters (Table 3). The habitat variables most strongly associated with resident locations year-round were net primary production (positive) and sea surface salinity (negative) (Figure 2). Sea surface temperature was negatively associated with residency during non-breeding, but the association diminished to near zero during the breeding season. Compared to dynamic variables, fixed factors were less strongly associated and less variable in their relationship to pelican habitat use and did not vary during the year. Bathymetry had a positive relationship with residency (i.e., pelicans were more likely to occupy shallower waters), while distance to coastline and distance to river outflow were both negatively associated with use by pelicans (i.e., pelicans preferentially occupied habitats closer to coastlines and

river mouths). Overall, areas of highest habitat suitability year-round were located in the northern Gulf, particularly the central and western planning areas (Figure 3). During summer, the total area of preferred habitat was narrowly restricted to coastal areas of the northern Gulf; however, during the fall and winter, suitable habitat characteristics also occurred from the nearshore region out to ca. 600-km offshore.

3.4 | Seasonal habitat associations

The average values of dynamic habitat characteristics in occupied habitats were generally similar between the breeding and staging periods, but differed significantly during winter (Figure 4). In general, pelicans utilized lower-productivity, higher-salinity and lower-temperature waters during winter compared to either breeding or migration. Selection for high productivity and low salinity relative to mean values peaked during breeding and migration periods, while selection for low temperatures was highest during winter (Figure 2).

3.5 | Regional variation and overlap

Patterns of association with dynamic habitat variables varied between planning areas (Figure 5), while static habitat associations were consistent across planning areas. Pelicans breeding in the central planning area of the Gulf exhibited the highest degree of variation in environmental characteristics of selected habitat and were more strongly associated with waters characterized by high productivity and low salinity during summer (breeding) than during winter (non-breeding). Pelicans from the western and eastern planning areas selected habitat with a lower degree of seasonal variation in environmental characteristics, although pelicans from all planning areas associated more strongly with sea surface temperature during breeding than during non-breeding.

Observed use areas of pelicans from the western, central and eastern planning areas overlapped spatially throughout the Gulf (Figure 6). Breeders from central Gulf colonies occupied shared habitat in 41% of their locations, western Gulf breeders in 36% and eastern Gulf breeders in 15%. Habitats occupied by both central and western breeders accounted for 94% of total shared habitat. Breeders from all three planning areas overlapped in the central Gulf, with areas of overlap concentrated around the Mississippi Delta (Figure 6, inset).

4 | DISCUSSION

Our study provides insights into the habitat associations of an abundant and highly visible nearshore seabird, the Brown Pelican, with fine-scale environmental characteristics in the northern GOM. We documented strong associations between pelicans and several
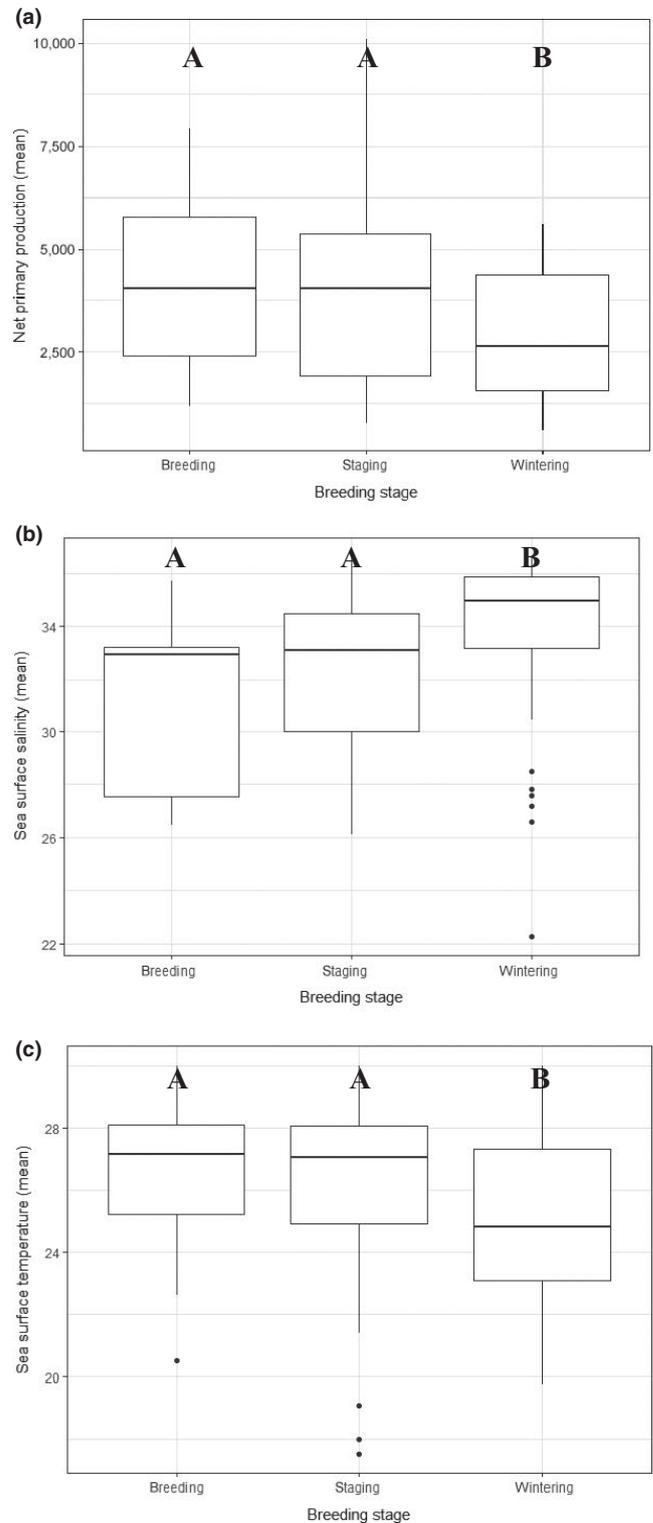
FIGURE 4 Distribution of seasonal average values for net primary production (a), sea surface salinity (b) and sea surface temperature (c) in areas used by Brown Pelicans during breeding, migratory staging and wintering in the Gulf of Mexico, 2013–2015. Central lines within boxes represent median values, dots represent outliers and letters in each subfigure denote significant ($p < .05$) between-group differences
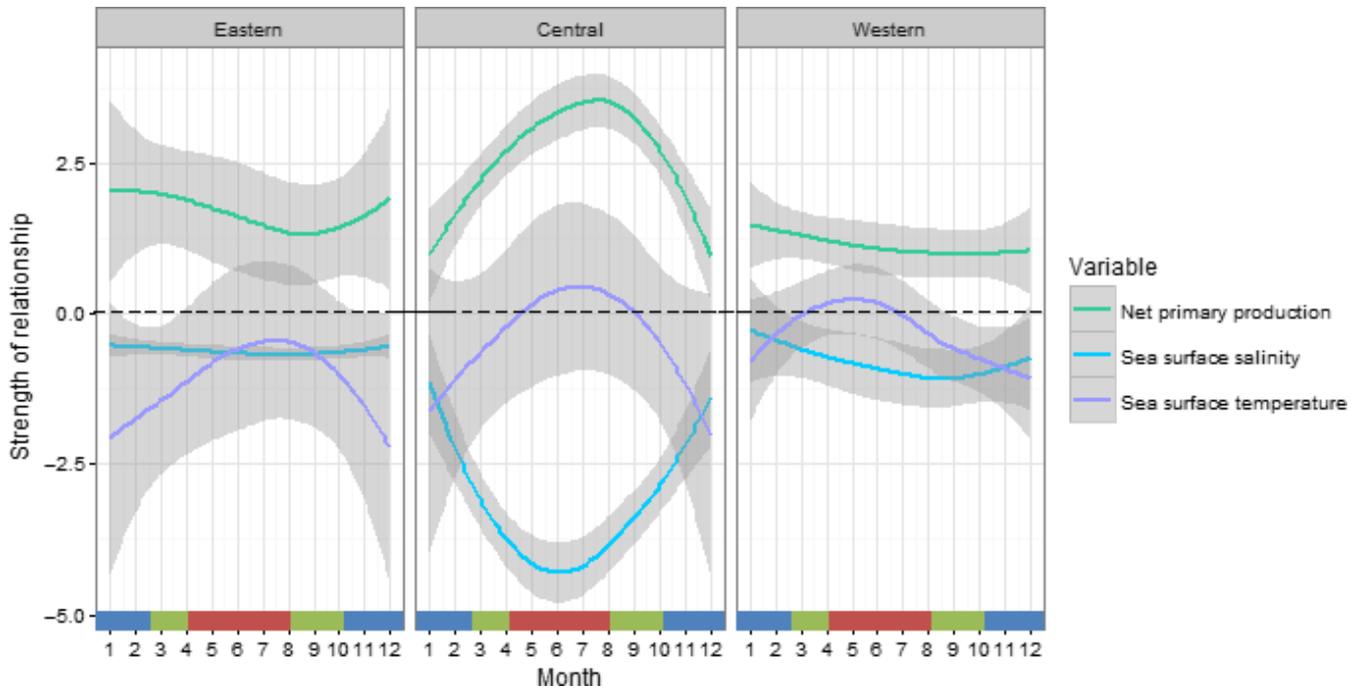
FIGURE 5 Annual patterns of strength and direction of selection by Brown Pelicans on seasonally varying habitat variables by breeding region, Gulf of Mexico, 2013–2015. Strength of selection (positive or negative) is generated from Outlying Mean Index and increases with distance from zero. Lines represent generalized additive model regressions (smoothing parameter = 1.3) of monthly averages for each variable, and grey areas are 95% confidence intervals of regression lines. Coloured bars along the x-axis indicate the approximate timing and duration of breeding (red), wintering (blue) and migratory staging (green) periods

dynamic habitat features, particularly primary production and salinity. These associations peaked during the early chick-rearing and moult stages of the annual cycle, suggesting that highly productive low-salinity habitats (i.e., estuaries) are particularly crucial during energy-intensive periods.

Although extensive work has described the environmental factors driving at-sea habitat use by seabirds in pelagic waters (e.g., Haney, 1985; Pinaud & Weimerskirch, 2005; Tew Kai et al., 2009), relatively little is known about the factors driving marine habitat use in nearshore seabirds. For the most part, prior studies of habitat preferences in nearshore-foraging species have been conducted in northern temperate waters (e.g., Becker & Beissinger, 2003; Day, Nigro, & Prichard, 2000; McLeay et al., 2010; Yen, Sydeman, Bograd, & Hyrenbach, 2006). Similar to results from these systems, we found that marine productivity was the most significant driver of habitat selection of Brown Pelicans in the GOM. Also, in concordance with previous results (Becker & Beissinger, 2003; Day et al., 2000), we found that the influence of sea surface temperature on at-sea distribution was significant but highly variable over time. In a departure from previous assessments of habitat use of nearshore seabirds, which generally found little effect of salinity on habitat use, we found that salinity strongly influenced habitat use for Brown Pelicans. Although the effects of salinity have not been extensively documented on this species or other coastal seabirds, recent studies (e.g., Zamon, Phillips, & Guy, 2014) have suggested that river plumes can be important nearshore-foraging habitat for seabirds, concentrating prey in a manner analogous to oceanic fronts in pelagic

systems. While distance to river outflow was only weakly related to pelican habitat suitability in this study, pelicans were often located in relatively large estuarine complexes and therefore may ultimately be responding to salinity gradients that exist even at comparatively greater distances from river mouths.

Since the scale of movement that we observed was relatively small (on the order of tens of kilometres per day, rather than hundreds of kilometres as is commonly observed in pelagic seabirds), we chose environmental variables likely to relate to the distribution of prey rather than those that might facilitate long-distance movement (e.g., prevailing winds) or visual identification of foraging areas (e.g., ocean colour). The influence of salinity in particular is correlated with the abundance and distribution of prey items. Brown Pelicans in the GOM forage primarily on Gulf Menhaden (Lamb et al., 2017), which concentrate during the spring and summer in low-salinity estuarine environments (Deegan, 1990). Both summer and winter distribution of preferred pelican habitat corresponded closely with Gulf Menhaden distributions, indicating that pelicans select habitat principally as a function of prey concentrations. We did not find that the spatially fixed metrics we tested (distance to coastline, distance to river outflow, bathymetry or bottom substrate) had a strong influence on habitat suitability. Previous studies (e.g., Suryan, Santora, & Sydeman, 2012) have suggested that such metrics tend to provide a more consistent predictor of the distribution of seabirds than seasonally varying environmental characteristics. The lack of a strong relationship of pelican distributions to static marine features may result from the short timescale of this study, or may be a feature of the
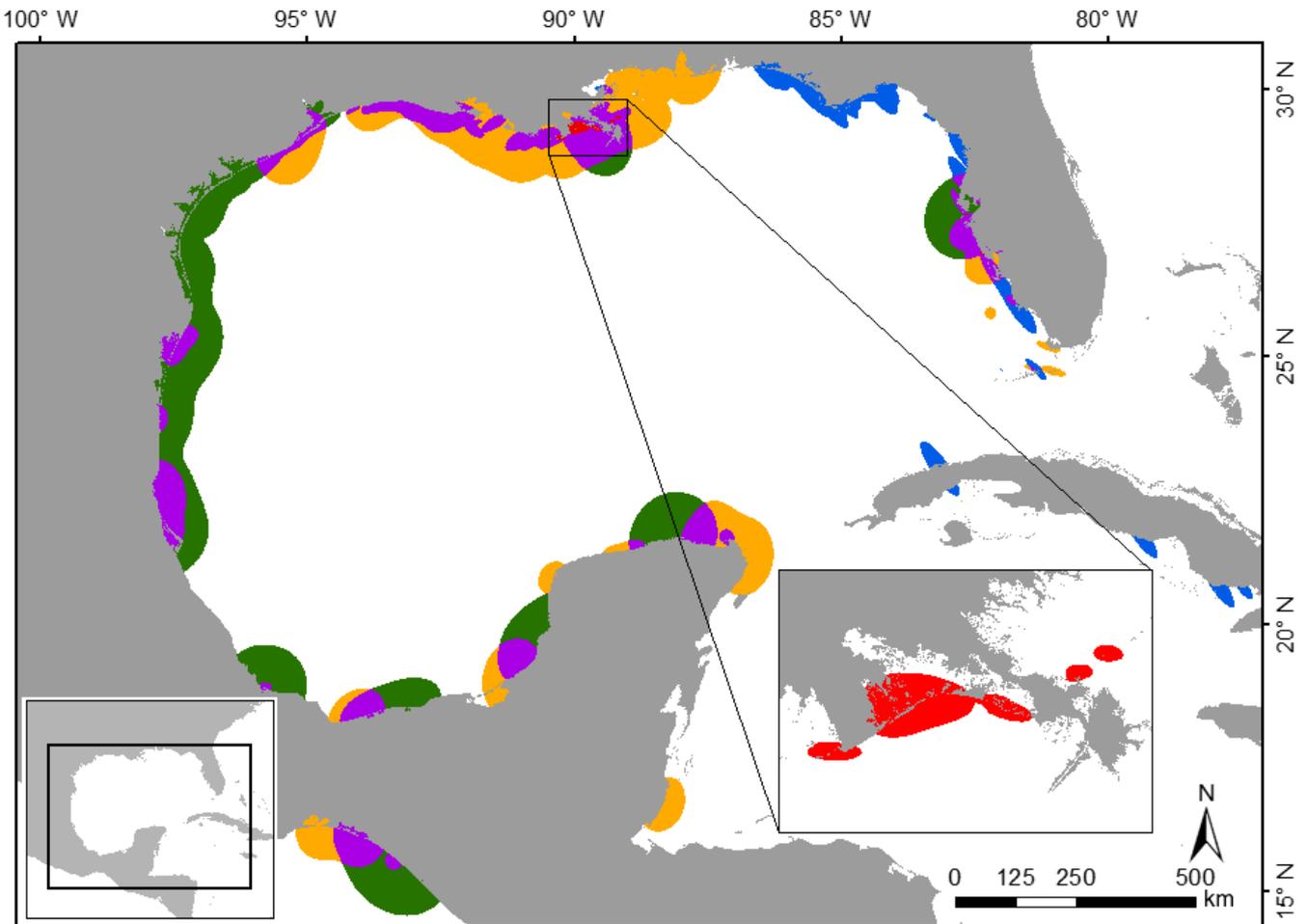
FIGURE 6 Annual 95% kernel density estimates for locations of Brown Pelicans originally captured at breeding colonies in the eastern (blue), central (orange), and western (green) planning areas, 2013–2015 (Albers Equal-Area Conic projection). Areas used by breeders from two or more planning areas are shaded in purple, and areas used by breeders from all planning areas are shaded in red. The inset map shows only the area of overlap between breeders from all three planning areas

GOM which is dominated by silt and sand and has a highly dynamic coastal geography and bathymetry relative to rocky shores in more northern regions where most other studies have occurred (Britton & Morton, 2014).

Another possible explanation for the lack of a strong relationship of pelican habitat suitability to static features may relate to the scale at which we conducted our analysis. The spatial scale of the environmental data available (10 km^2) and the temporal resolution of the GPS data collected (90-min intervals) did not allow us to distinguish fine-scale foraging areas from commuting or resting habitat. Thus, we focused on mesoscale movement patterns and habitat selection on a monthly timescale. The fact that seasonally varying parameters were more strongly related to habitat selection than physical oceanographic features is consistent with previous observations that mesoscale habitat use is likely to be driven by primary productivity, while physical features become more important at the micro (<10 km) scale (Becker & Beissinger, 2003). Habitat selection likely also occurs at finer temporal scales than those described by this study (Kristan, 2006) and may vary with daily or weekly changes in estuarine dynamics that alter distribution and concentrations of prey.

4.1 | Seasonal variation

We found that pelicans showed a particular preference for high-productivity, low-salinity habitats during the energetically demanding breeding and post-breeding moult periods. Correspondingly, the availability of suitable habitat was much lower during the summer (May–July) and early fall (August–September), which are peak times for chick rearing and post-breeding dispersal respectively, than during the remainder of the year. Moreover, the habitats that contained these preferred features tended to be located in areas of high anthropogenic activity. Preferred foraging areas included highly productive coastal estuaries, which were often located near shipping hubs and ports in the comparatively cooler waters of the northern Gulf. During moult, breeding pelicans from throughout the northern Gulf used habitats in and around the Mississippi Delta (Figure 6, inset), which is also a hot spot for shipping, oil extraction and concentrations of agricultural and industrial contaminants from throughout central North America. The early chick-rearing and moult periods therefore may represent hot moments (McClain et al., 2003), in which a confluence of habitat requirements and availability

may increase exposure to risk factors for breeding Brown Pelicans; however, further analysis is required to assess the potential extent and consequences of this elevated exposure. Although our study focuses on Brown Pelicans, the variation in both habitat features and annual-cycle energetic needs that drive pelican occupancy is likely to be experienced by a suite of nearshore waterbird species, which also rely on prey-rich nearshore habitats and experience increased energy demands during chick-rearing and moult.

4.2 | Annual-cycle movements and spatial population structure

In addition to biophysical habitat associations, we examined specific habitat use by pelicans captured while breeding in colonies in three planning areas of the northern Gulf: the eastern (Florida panhandle), central (Alabama, Mississippi and Louisiana coasts) and western planning areas. We observed a distinct separation between birds from eastern Gulf colonies and those in the central and western planning areas. While year-round habitat overlaps between breeders from central and western colonies totalled 30%–40%, eastern breeders shared only 15% of their total habitat area. Moreover, while central and western Gulf breeders extensively used the same set of non-breeding areas in the southern Gulf along the east coast of Mexico and throughout the Yucatan Peninsula, eastern Gulf breeders typically migrated southward to the Florida Keys and Cuba. We did not observe overlap between the eastern breeding population and either the central or western groups in southern Gulf wintering habitat. The only area in which breeders from all three planning areas overlapped was in the Mississippi Delta, in the central Gulf. The apparent separation between the eastern breeding colonies and the rest of the northern Gulf population is particularly interesting in the light of the fact that translocations from eastern colonies were used to re-establish the central Gulf breeding population following DDT-related extirpation (McNease, Joanen, Richard, Shepard, & Nesbitt, 1984).

To date, studies of Brown Pelican non-breeding movements have been limited to information on band recoveries, typically from birds banded as juveniles (Schreiber & Mock, 1988; Stefan, 2008) and tracking data from individuals captured during non-breeding (King et al., 2013; Poli, 2015). This has limited the possibility of linking non-breeding birds to breeding colonies outside the breeding season. Our study incorporates individual data on year-round movements of pelicans from known breeding locations. Measuring overlap between breeding populations in different planning areas of the GOM used for large-scale marine spatial planning helps to refine current understanding of the distribution of environmental risk among management units and to better identify which segments of the overall breeding population are affected by spatially explicit threats in the marine environment. Moreover, our results highlight the wide-ranging movements of marine vertebrates, which regularly travel between administrative planning areas across the northern GOM. For these species, an integrated approach to risk assessment and restoration activities may be needed in order to effectively manage the regional population.

DATA AVAILABILITY STATEMENT

The data used in this study are available on Movebank (movebank.org, Movebank Study ID 296027617) and are published in the Movebank Data Repository with https://doi.org/10.5441/001/1.7856r086.

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REFERENCES

Bearhop, S., Phillips, R. A., McGill, R., Cherel, Y., Dawson, D. A., & Croxall, J. P. (2006). Stable isotopes indicate sex-specific and long-term individual foraging specialization in diving seabirds. *Marine Ecology Progress Series*, *311*, 157–164.

Becker, B. H., & Beissinger, S. R. (2003). Scale-dependent habitat selection by a nearshore seabird, the Marbled Murrelet, in a highly dynamic upwelling system. *Marine Ecology Progress Series*, *256*, 243–255. https://doi.org/10.3354/meps256243

Behrenfeld, M. J., & Falkowski, P. G. (1997). Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography*, *42*, 1–20. https://doi.org/10.4319/lo.1997.42.1.0001

BOEM (2012). *Gulf of Mexico NAD 27 Federal Outer Continental Shelf (OCS) Administrative Boundaries*. Retrieved from https://www.boem.gov/uploadedFiles/BOEM/Oil_and_Gas_Energy_Program/Mapping_and_Data/Administrative_Boundaries/Gulf_Plan.pdf

Börger, L., Dalziel, B. D., & Fryxell, J. M. (2008). Are there general mechanisms of animal home range behavior? A review and prospects for future research. *Ecology Letters*, *11*, 637–650.

Boyer, T. P., Biddle, M., Hamilton, M., Mishonov, A. V., Paver, C. R., Seidov, D., & Zweng, M. (2011). Gulf of Mexico regional climatology. NOAA/NODC. https://doi.org/10.7289/V5C53HSW

Britton, J. C., & Morton, B. (2014). *Shore ecology of the Gulf of Mexico.* Austin, TX: University of Texas Press.

Calenge, C. (2006). The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Calenge, C., Darmon, G., Basille, M., Loison, A., & Jullien, J. M. (2008). The factorial decomposition of the Mahalanobis distances in habitat selection studies. *Ecology*, 89, 555–566. https://doi.org/10.1890/06-1750.1

Catry, T., Ramos, J. A., LeCorre, M., & Phillips, R. A. (2009). Movements, at-sea distribution and behavior of a tropical pelagic seabird: The wedge-tailed shearwater in the western Indian Ocean. *Marine Ecology Progress Series*, 391, 231–242.

Clark, J. D., Dunn, J. E., & Smith, K. G. (1993). A multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management*, 57, 519–526. https://doi.org/10.2307/3809276

Cureton, J. C., & Deaton, R. (2012). Hot moments and hot spots: Identifying factors explaining temporal and spatial variation in turtle road mortality. *The Journal of Wildlife Management*, 76, 1047–1052. https://doi.org/10.1002/jwmg.320

Daunt, F., Afanasyev, V., Silk, J. D. R., & Wanless, S. (2006). Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behavioral Ecology and Sociobiology*, 59, 381–388. https://doi.org/10.1007/s00265-005-0061-4

Day, R. H., Nigro, D. A., & Prichard, A. K. (2000). At-sea habitat use by the Kittlitz's Murrelet Brachyramphus brevirostris in nearshore waters of Prince William Sound, Alaska. *Marine Ornithology*, 28, 105–114.

Deegan, L. A. (1990). Effects of estuarine environmental conditions on population dynamics of young-of-the-year gulf menhaden. *Marine Ecology Progress Series*, 68, 195–205. https://doi.org/10.3354/meps068195

Dolédec, S., Chessel, D., & Gimaret-Carpentier, C. (2000). Niche separation in community analysis: A new method. *Ecology*, 81, 2914–2927. https://doi.org/10.1890/0012-9658(2000)081[2914:NSICAA]2.0.CO;2

Dunstan, T. C. (1972). A harness for radio-tagging raptorial birds. *Inland Bird Banding News*, 44, 4–8.

Duong, T. (2015). *Ks: Kernel Smoothing.* R package version 1.10.1.

Eggert, L. M. F., Jodice, P. G. R., & O'Reilly, K. M. (2010). Stress response of Brown Pelican nestlings to ectoparasite infestation. *General and Comparative Endocrinology*, 166, 33–38. https://doi.org/10.1016/j.ygcen.2009.08.009

Erwin, R. M. (1977). Foraging and breeding adaptations to different food regimes in three seabirds: The common tern, *Sterna hirundo*, royal tern, Sterna maxima, and black skimmer, Rynchops Niger. *Ecology*, 58, 389–397. https://doi.org/10.2307/1935613

Garthe, S., & Hüppop, O. (2004). Scaling possible adverse effects of marine wind farms on seabirds: Developing and applying a vulnerability index. *Journal of Applied Ecology*, 41, 724–734. https://doi.org/10.1111/j.0021-8901.2004.00918.x

Gitzen, R. A., Millspaugh, J. J., & Kernohan, B. J. (2006). Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *Journal of Wildlife Management*, 70, 1334–1344. https://doi.org/10.2193/0022-541X(2006)70[1334:BSFFAO]2.0.CO;2

Gray, J. S. (1997). Marine biodiversity: Patterns, threats and conservation needs. *Biodiversity and Conservation*, 6, 153–175.

Haney, J. C. (1985). Wintering phalaropes off the southeastern United States: Application of remote sensing imagery to seabird habitat analysis at oceanic fronts. *Journal of Field Ornithology*, 56, 321–333.

Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology.

Philosophical Transactions of the Royal Society of London B, 365, 2303–2312. https://doi.org/10.1098/rstb.2010.0087

Hill, M. O., & Smith, A. J. E. (1976). Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon*, 25, 249–255. https://doi.org/10.2307/1219449

Itoh, Y., Suzuki, M., Ogawa, A., Munechika, I., Murata, K., & Mizuno, S. (2001). Identification of the sex of a wide range of Carinatae birds by PCR using primer sets selected from chicken EE0.6 and Its related sequences. *Journal of Heredity*, 92, 315–321. https://doi.org/10.1093/jhered/92.4.315

Jodice, P. G. R., Adams, E. M., Lamb, J. S., Satgé, Y., & Gleason, J. S. (2019). Strategic Bird Monitoring Guidelines: Seabirds. In Wilson et al (eds.). *Strategic avian monitoring plan for the Northern Gulf of Mexico, Gulf of Mexico avian monitoring network. Mississippi agricultural and forestry experiment station research bulletin* (pp. 133–172). Starkville, MS: Mississippi State University.

Jonsen, I. D., Myers, R. A., & James, M. C. (2007). Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series*, 337, 255–264. https://doi.org/10.3354/meps337255

Kaltenberg, A. M., Emmett, R. L., & Benoit-Bird, K. J. (2010). Timing of forage fish seasonal appearance in the Columbia River plume and link to ocean conditions. *Marine Ecology Progress Series*, 419, 171–184. https://doi.org/10.3354/meps08848

King, D. T., Goatcher, B. L., Fischer, J. W., Stanton, J., Lacour, J. M., Lemmons, S. C., & Wang, G. (2013). Home ranges and habitat use of Brown Pelicans (*Pelecanus occidentalis*) in the Northern Gulf of Mexico. *Waterbirds*, 36, 494–500.

Kristan, W. B. (2006). Sources and expectations for hierarchical structure in bird-habitat associations. *Condor*, 108, 5–12. https://doi.org/10.1093/condor/108.1.5

Lamb, J. S., Satgé, Y. G., & Jodice, P. G. R. (2017). Influence of density-dependent competition on foraging and migratory behavior of a subtropical colonial seabird. *Ecology and Evolution*, 7, 6469–6481. https://doi.org/10.1002/ece3.3216

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., & Morales, J. M. (2012). Flexible and practical modeling of animal telemetry data: Hidden Markov models and extensions. *Ecology*, 93, 2336–2342. https://doi.org/10.1890/11-2241.1

Lewis, S., Sherratt, T. N., Hamer, K. C., & Wanless, S. (2001). Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, 412, 816–819. https://doi.org/10.1038/35090566

Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, 11, 20150552. https://doi.org/10.1098/rsbl.2015.0552

McClain, M. E., Boyer, E. W., Dent, C. L., Gergel, S. E., Grimm, N. B., Groffman, P. M., ... Pinay, G. (2003). Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems*, 6, 301–312. https://doi.org/10.1007/s10021-003-0161-9

McLeay, L. J., Page, B., Goldsworthy, S. D., Paton, D. C., Teixeira, C., Burch, P., & Ward, T. (2010). Foraging behavior and habitat use of a short-ranging seabird, the crested tern. *Marine Ecology Progress Series*, 411, 271–283.

McNease, L., Richard, D., & Joanen, T. (1992). Reintroduction and colony expansion of the Brown Pelican in Louisiana. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies*, 46, 223–229.

McNease, L. M., Joanen, T., Richard, D., Shepard, J., & Nesbitt, S. A. (1984). The brown pelican restocking program in Louisiana. *Proceedings of the Annual Conference of the Southeast Association of Fisheries and Wildlife Agencies*, 38, 165–173.

Michelot, T., Langrock, R., Patterson, T., & Rexstad, E. (2015). *moveHMM: Animal Movement Modelling using Hidden Markov Models.* R package version 1.1.

Morrison, M. L., Marcot, B., & Mannan, W. (2012). *Wildlife-habitat relationships: Concepts and applications*. Madison, WI: University of Wisconsin Press.

National Geophysical Data Center (2006). *2-minute Gridded Global Relief Data (ETOPO2) v2. National Geophysical Data Center, NOAA*. https://doi.org/10.7289/V5J1012Q

O'Malley, R. (2012). *Ocean Productivity Home Page*. Retrieved from http://www.science.oregonstate.edu/ocean.productivity/index.php

Patterson, T. A., Basson, M., Bravington, M. V., & Gunn, J. S. (2009). Classifying movement behavior in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology*, 78, 1113–1123.

Phillips, R. A., Bearhop, S., McGill, R. A. R., & Dawson, D. A. (2009). Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabird species during the non-breeding period. *Oecologia*, 160, 785–806.

Pinaud, D., & Weimerskirch, H. (2005). Scale-dependent habitat use in a long-ranging central place predator. *Journal of Animal Ecology*, 74, 852–863. https://doi.org/10.1111/j.1365-2656.2005.00984.x

Poli, C. (2015). *Variability in movement patterns and habitat use of two species of Pelecaniformes*. Thesis. Clemson, SC: Clemson University.

R Core Team, (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Radeloff, V. C., Beaudry, F., Brooks, T. M., Butsic, V., Dubinin, M., Kuemmerle, T., & Pidgeon, A. M. (2013). Hot moments for biodiversity conservation. *Conservation Letters*, 6, 58–65. https://doi.org/10.1111/j.1755-263X.2012.00290.x

Schnell, G. D., & Hellack, J. J. (1978). Flight speeds of Brown Pelicans, Chimney Swifts, and other birds. *Bird-banding*, 49, 108–112. https://doi.org/10.2307/4512338

Schreiber, R. W., & Mock, P. J. (1988). Eastern Brown Pelicans: What does 60 years of banding tell us? *Journal of Field Ornithology*, 59, 171–182.

Shields, M. (2014). In A. Poole (Ed.), *Brown Pelican (*Pelecanus occidentalis*), the birds of North America Online*. Ithaca, NY: Cornell Lab of Ornithology. Retrieved from http://bna.birds.cornell.edu/bna/species/609

Small-Lorenz, S. L., Culp, L. A., Ryder, T. B., Will, T. C., & Marra, P. P. (2013). A blind spot in climate change vulnerability assessments. *Nature Climate Change*, 3, 91. https://doi.org/10.1038/nclimate1810

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., ... Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience*, 57, 573–583. https://doi.org/10.1641/B570707

Stefan, S. (2008). *An analysis of recovery patterns in Brown Pelicans (*Pelecanus occidentalis*) and Royal Terns (*Sterna maxima*) banded in South Carolina*. MS Thesis. (p. 55). Charleston, SC: The College of Charleston.

Suryan, R. M., Irons, D. B., & Benson, J. (2000). Prey switching and variable foraging strategies of black-legged kittiwakes and the effect on reproductive success. *Condor*, 102, 374–378. https://doi.org/10.1093/condor/102.2.374

Suryan, R. M., Santora, J. A., & Sydeman, W. J. (2012). New approach for using remotely sensed chlorophyll a to identify seabird hotspots. *Marine Ecology Progress Series*, 451, 213–225. https://doi.org/10.3354/meps09597

Tew Kai, E., Rossi, V., Soudre, J., Weirmerskirch, H., Lopez, C., Hernandez-Garcia, E., ... Garcon, V. (2009). Top marine predators track Lagrangian coherent structures. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 8245–8250.

Thaxter, C. B., Lascelles, B., Sugar, K., Cook, A. S. C. P., Roos, S., Bolton, M., ... Burton, N. H. K. (2012). Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biological Conservation*, 156, 53–61. https://doi.org/10.1016/j.biocon.2011.12.009

Tremblay, Y., Bertrand, S., Henry, R. W., Kappes, M. A., Costa, D. P., & Shaffer, S. A. (2009). Analytical approaches to investigating seabird–environment interactions: A review. *Marine Ecology Progress Series*, 391, 153–163. https://doi.org/10.3354/meps08146

USFWS. (2011). *NRDAR Bird Impact Data Reports*. Retrieved from http://www.fws.gov/home/dhoilspill/collectionreports.html

Walter, S. T., Leberg, P. L., Dindo, J. J., & Karubian, J. K. (2014). Factors influencing Brown Pelican (*Pelecanus occidentalis*) foraging movement patterns during the breeding season. *Canadian Journal of Zoology*, 92, 885–891.

Wand, M. P., & Jones, M. C. (1994). Multivariate plugin bandwidth selection. *Computational Statistics*, 9, 97–116.

Weimerskirch, H., & Wilson, R. P. (2000). Oceanic respite for wandering albatrosses. *Nature*, 406, 955–956. https://doi.org/10.1038/35023068

Wessel, P., & Smith, W. H. F. (1996). A global self-consistent, hierarchical, high-resolution shoreline database. *Journal of Geophysical Research*, 101, 8741–8743. https://doi.org/10.1029/96JB00104

Yen, P. P. W., Sydeman, W. J., Bograd, S. J., & Hyrenbach, K. D. (2006). Spring-time distributions of migratory marine birds in the southern California Current: Oceanic eddy associations and coastal habitat hotspots over 17 years. *Deep Sea Research Part II: Topical Studies in Oceanography*, 5, 399–418. https://doi.org/10.1016/j.dsr2.2006.01.013

Zamon, J. E., Phillips, E. M., & Guy, T. J. (2014). Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. *Deep Sea Research Part II: Topical Studies in Oceanography*, 107, 85–95. https://doi.org/10.1016/j.dsr2.2013.03.031

BIOSKETCH

The research team focuses on distribution patterns, habitat associations and threats to marine birds in the South Atlantic Bight, Caribbean, and Gulf of Mexico (www.atlanticseabirds.org).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.