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Linking morbillivirus exposure to individual habitat use of common bottlenose dolphins *(Tursiops truncatus)* between geographically different sites

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Abstract

1. Dolphin morbillivirus (DMV) is a virulent pathogen that causes high mortality outbreaks in delphinids globally and is spread via contact among individuals. Broadly ranging nearshore and open-ocean delphinids are likely reservoir populations that transmit DMV to estuarine populations.
2. We assessed the seroprevalence of DMV antibodies and determined habitat use of common bottlenose dolphins, *Tursiops truncatus truncatus*, from two estuarine sites, Barataria Bay and Mississippi Sound, in the northern Gulf of Mexico. We predicted that risk to DMV exposure in estuarine dolphins is driven by spatial overlap in habitat use with reservoir populations.
3. Serum was collected from live-captured dolphins and tested for DMV antibodies. Habitat use of sampled individuals was determined by analyzing satellite-tracked movements and stable isotope values.
4. DMV seroprevalences were high among dolphins at Barataria Bay (37%) and Mississippi Sound (44%), but varied differently within sites. Ranging patterns of Barataria Bay dolphins were categorized into two groups: Interior and Island-associated. DMV seroprevalences were absent in Interior dolphins (0%) but high in Island-associated dolphins (45%). Ranging patterns of Mississippi Sound dolphins were categorized into three groups: Interior, Island-east, and Island-west. DMV seroprevalences were detected across Mississippi Sound (Interior: 60%; Island-east: 20%; Island-west:43%). At both sites, dolphins in habitats with greater marine influence had enriched $\delta^{13}C$ values, and Barataria Bay dolphins with positive DMV titers had carbon isotope values indicative of marine habitats. Positive titers for DMV antibodies was more common in the lower versus upper parts of Barataria Bay but evenly distributed across Mississippi Sound.
5. A dolphin's risk of exposure to DMV is influenced by how individual ranging patterns interact with environmental geography. Barataria Bay's partially enclosed geography

likely limits the nearshore or open-ocean delphinids that carry DMV from interacting with dolphins that use interior, estuarine habitats, decreasing their exposure to DMV. Mississippi Sound's relatively open geography allows for greater spatial overlap and mixing among estuarine, nearshore, and/or open-ocean cetaceans. The spread of DMV, and likely other diseases, is affected by the combination of individual movements, habitat use, and the environment.

Keywords: movement ecology, stable isotope analysis, satellite-linked telemetry, Barataria Bay, Mississippi Sound, spatial overlap, individual habitat specialization, pathogen, disease

1 | Introduction

Disease-causing pathogens can strongly affect population dynamics and species distributions (Berger *et al.* 1998; Krkošek *et al.* 2007), leading to population declines and subsequent trophic cascades (Timm *et al.* 2009; Buck & Ripple 2017). In extreme cases, pathogens have led to mass die-offs, extirpations, and extinctions (Thorne & Williams 1988; Aguilar & Raga 1993; Cunningham & Daszak 1998). Viruses are common pathogens that can cause these extreme events, including *morbilliviruses* such as measles, canine distemper, phocine distemper, and cetacean morbillivirus that infect a wide range of mammals (Harder & Osterhaus 1997; Van Bressem *et al.* 2014; Jo, Osterhaus & Ludlow 2018). *Morbillivirus* outbreaks have caused increased mortality and mass dies offs in both terrestrial and aquatic mammals (Lipscomb *et al.* 1994; Timm *et al.* 2009; Kemper *et al.* 2016; Jo, Osterhaus & Ludlow 2018).

Cetacean morbillivirus, and specifically the dolphin morbillivirus strain (DMV), is a virulent pathogen responsible for several large mortality events in delphinids (Van Bressem *et al.* 2014; Jo, Osterhaus & Ludlow 2018). The first detected DMV-associated unusual mortality event (UME) occurred in common bottlenose dolphins (*Tursiops truncatus truncatus*) in the western North Atlantic Ocean during the late 1980s, when an estimated 10 – 50% of coastal dolphins died (Lipscomb *et al.* 1994). DMV-associated UMEs have since been observed globally, including in the Mediterranean Sea (Domingo *et al.* 1990; Keck *et al.* 2010), Gulf of Mexico (Lipscomb *et al.* 1996), Indian Ocean (Stephens *et al.* 2014), and Southern Ocean (Kemper *et al.* 2016). DMV is transmissible among individuals (Van Bressem *et al.* 2014; Jo, Osterhaus & Ludlow 2018), and social marine mammals that form groups and interact with multiple populations are thus particularly prone to exposure and spreading of DMV (Duignan *et al.* 1995; Van Bressem *et al.* 2001). Common bottlenose dolphins and many other small delphinids that are affected by DMV (Lipscomb *et al.* 1994; Jo, Osterhaus & Ludlow 2018), are highly social, forming fission-fusion groups in which individuals from different populations come into contact with each other (Connor, Wells & Read 2000; Balmer *et al.* 2018) and increase the opportunities to spread disease among and within populations (Duignan *et al.* 1996; Félix, Van Bressem & Van Waerebeek 2019).

Outbreaks of DMV are thought to occur when individuals from exposed populations contact individuals from naïve populations (Raga *et al.* 2008; Morris *et al.* 2015; Jo, Osterhaus & Ludlow 2018). Epidemic modeling showed DMV transmission is likely frequency-dependent (i.e., depends on the number of contacts among individuals) and is transmissible for up to 24 days, during which time individual dolphins could have made extended movements (e.g., > 220 km; Morris *et al.* 2015). Highly social odontocetes that inhabit offshore, open-ocean waters are hypothesized to be DMV maintenance populations and reservoirs of infection (Duignan *et al.* 1995; Duignan *et al.* 1996; Viana *et al.* 2014; Jo, Osterhaus & Ludlow 2018) and are believed to transmit DMV to inshore bottlenose dolphin populations two ways. First, some populations of open-ocean bottlenose dolphins in the western North Atlantic migrate seasonally, ranging several hundred kilometers (reviewed in Hayes *et al.* 2017) and can carry DMV with them (Morris *et al.* 2015). These dolphins spatially overlap and come into contact with naïve dolphins that have limited movements and high site fidelity to localized estuarine habitats and expose them to DMV (Zolman 2002; Balmer *et al.* 2018). Second, other North Atlantic common bottlenose dolphin populations that use both estuarine and nearshore (coastal waters where the shore is visible) habitats but show no evidence of extended, migratory movements (Balmer *et al.* 2018) may be an additional vector for transmitting DMV between open-ocean reservoir species and estuarine dolphin populations in the region (Balmer et al. 2018). Thus, while there are large differences in prevalence between open-ocean, nearshore, and estuarine habitats, the wide-ranging movements of open-ocean dolphins along the eastern U.S.A. coast has historically resulted in no pattern of DMV prevalence (measured with titers that indicate presence of DMV antibodies and previous exposure) along a latitudinal gradient (Duignan *et al.* 1996; Rowles *et al.* 2011; Balmer *et al.* 2018).

DMV occurs across the northern Gulf of Mexico (GoM) (Rowles *et al.* 2011; Fauquier *et al.* 2017), but relationships between ranging patterns and DMV antibodies have been investigated less in the northern GoM compared to other regions even though movement-related transmission of DMV between open-ocean and estuarine dolphins has been hypothesized (Duignan *et al.* 1996; Rowles *et al.* 2011). Some nearshore dolphins in the northern GoM show seasonal movements (Hubard *et al.* 2004; Balmer *et al.* 2008), but the temporal-scale and cues for these seasonal movements remain unclear (Balmer *et al.* 2016; Balmer *et al.* 2018). In addition, several satellite telemetry and photo-identification studies have observed both estuarine populations with high site-fidelity (Mullin *et al.* 2017; Wells *et al.* 2017) and dolphins with extended ranges that use a combination of estuarine and nearshore habitats (Balmer *et al.* 2008; Balmer *et al.* 2016; Wilson *et al.* 2017). Analysis of stranded dolphins has revealed DMV antibody-positive individuals, demonstrating that DMV outbreaks have periodically occurred in the northern GoM during the past several decades (Duignan *et al.* 1996; Lipscomb *et al.* 1996; Fauquier *et al.* 2017). The geographic distribution of antibody-positive individuals can reveal information about how DMV has spread in the GoM, but little is known about the habitat use and movements of DMV antibody-positive dolphins from these previous studies (Duignan *et al.* 1996; Lipscomb *et al.* 1996; Fauquier *et al.* 2017). Furthermore, epidemic simulations suggested that a major DMV outbreak in the northwestern Atlantic during 2013-2014 did not spread into the GoM likely due to low transmission rates (i.e., little contact among populations) or pre-existing immunity in the GoM populations (Morris *et al.* 2015). Thus, examining the prevalence of individuals with DMV antibodies in relation to movement and habitat use across sympatric dolphin populations in the northern GoM could help elucidate the underlying processes and potential drivers for transmission of DMV and other infectious pathogens into estuarine populations.

Here, we combined multiple types of datasets from several studies of northern GoM common bottlenose dolphins (hereafter dolphins) to define DMV antibody prevalence and relate that prevalence to specific movement patterns and habitat use. We compared the prevalence of DMV antibodies across various dolphin ranging groups based on telemetry data and corroborated habitat use at each site with stable isotope ratios. Stable isotope ratios in dolphin tissues can complement telemetry data by corroborating habitat use patterns for comparison to DMV prevalence. Stable carbon isotope values of dissolved inorganic carbon (DIC) become enriched from marine to freshwater habitats and can provide information on habitat use (Fry 2002; Wissel, Gaçe & Fry 2005). Stable nitrogen isotope values provide information on trophic level of a consumer, with enriched values indicative of feeding at higher trophic levels (Post 2002; Cloyed & Eason 2017). We predicted that dolphins using lower estuarine habitats and adjacent, nearshore habitats of both regions would have enriched stable carbon isotope ratios reflective of marine habitats and higher DMV seroprevalences because these individuals are more likely to interact with reservoir populations. In contrast, we predicted that dolphins primarily using freshwater-influenced estuarine habitats would have depleted stable carbon isotope values indicative of estuarine habitats, where they would be less likely to interact with reservoir populations and have lower DMV seroprevalences. Because exposure to DMV is likely independent of specific diets and trophic level, we predicted that nitrogen isotope values would vary little with DMV antibodies. The combination of telemetry and stable isotope analyses can better define complex interactions between movement and habitat use (Speed *et al.* 2012), but the two techniques have not been combined to describe patterns of disease prevalence (but see Bridge *et al.* 2014).

2 | Material and Methods

2.1 | Study sites

Barataria Bay, Louisiana (BAR) is a partially enclosed estuary in southeast Louisiana bordered by the Mississippi River to the north and east, Bayou Lafourche to the west, and separated from the GoM at its southern end by barrier islands (Figure 1). BAR has more estuarine habitat to the north and more marine habitat to the south, where the only access to the

GoM and nearshore and open-ocean habitats is from the south via relatively narrow passes between barrier islands (Figure 1). Smooth cordgrass (*Spartina alterniflora)* marshes and non-vegetated bottoms are the dominant habitat types in BAR but oyster shell *(Crassostrea virginica)* deposits are also common. The BAR study site is defined as the nearshore waters surrounding Grand Isle, Grand Terre Islands, and lower Caminada Bay and the estuarine habitats in upper Caminada Bay, Bassa Bassa Bay, West Champagne Bay, and Barataria Bay proper (Figure 1).

Mississippi Sound (MSS) is a large, open embayment formed by the Alabama and Mississippi coastlines to the north and a series of barrier islands to the south, which include (east to west) Dauphin, Petit Bois, Horn, West and East Ship, and Cat Islands (Figure 1). MSS has estuarine habitats along the coast at its northern margin and more marine habitats surrounding the barrier islands at its southern border, with access to the GoM and nearshore and open-ocean habitats via broad passes between the barrier islands as well as at the eastern and western ends of the sound. *Spartina alterniflora* marshes, oyster shell deposits, sea grass beds, and shallow, non-vegetated bottoms are the primary habitats in MSS (Moncreiff 2007). The MSS study site includes the waters adjacent to Pascagoula, MS and surrounding Dauphin, Petit Bois, and Horn Islands (Figure 1).

2.2 | Dolphin sampling

Dolphins were temporarily captured, biological samples collected, and satellite-linked tags attached by a team of experienced researchers as part of health assessments in both study sites during 2011, 2013, and 2018 in BAR and 2013 and 2018 in MSS. Capture-release methodologies for small cetacean health assessments have been previously detailed (Schwacke *et al.* 2014). Briefly, dolphins were captured with a 365 m by 7 m deep seine net. The number of dolphins targeted per capture set depended primarily on water depth (shallow or deep), visually estimated age (adult, subadult, calf), and overall group composition. For shallow-water sets (depth ≤ 1.5 m), we captured up to 5 dolphins aged > 2 years old. For deep-water sets (depth > 1.5 m), we captured 1 – 2 adult or sub-adult dolphins (no mother-calf pairs).

Dolphins underwent a full health assessment by veterinarians whenever possible (detailed in Schwacke *et al.* 2014). Veterinarians determined sex by evaluating the genital slits. Samples were either collected while the dolphin was in the water, on a 3 m long floating mat, or on a specially designed processing vessel (R/V *Megamouth*, a 9.1 m Munson "Packman" monohull;

William E. Munson Company, Burlington, WA, USA). Prior to release, dolphins were freeze-branded to provide long-term identification. The protocols for health assessments were designed with dolphin welfare and human safety being the utmost considerations to ensure all animals were handled safely by the capture team, and samples were collected efficiently to ensure all animals were released as soon as possible.

2.3 | Dolphin morbillivirus (DMV)

We collected blood from the ventral fluke vasculature using a 19g x 19.05 mm butterfly catheter. For serum samples, we spun blood in the field (E8 Fixed-Speed Centrifuge, LW Scientific, Lawrenceville, GA, USA), approximately 30 – 45 minutes post-collection to allow clot formation. Serum samples for DMV testing were stored in a liquid nitrogen (N_2) dry shipper at approximately -190 °C in the field and in a -80 °C freezer at the National Institute of Standards and Technology (NIST) Specimen Bank (Charleston, SC, USA). Serum was shipped to the Marine Mammal Diagnostic Service for DMV serology (Athens Veterinary Diagnostic Laboratory, University of Georgia, Athens, GA, USA). We measured DMV titers against the Belfast strain of DMV, using the virus neutralization test (Saliki & Lehenbauer 2001). We performed two-fold dilutions of serum (25 μL) in 96-well microtiter plates with Dulbecco's minimum essential medium. An equal volume of virus (25 μL) containing approximately 100 $TCID_{50}$ was added to each well and plates were incubated at 35.5 °C for 1 hr. Vero Dog Slam cells (1.5×10^4 cells in 150 μL) were added to each well, and the plates incubated at 35.5°C in 5% CO_2 for 3 days, after which they were examined for cytopathic effects. We defined the antibody titer as the highest dilution of serum that neutralized cytopathic effects and considered titers as positive for DMV antibodies if $\geq$ 1:16 (Rowles *et al.* 2011).

2.4 | Dolphin tagging, telemetry, and spatial analysis

To measure movements and habitat use, we tagged dolphins with a KiwiSat 202 K2F (Lotek Wireless Inc., Ontario, Canada) or a SPOT-299 (Wildlife Computers, Redmond, WA, USA) satellite-linked transmitter prior to release. Satellite-linked tag data from 2011 and 2013 were previously collected as part of the DWH Natural Resource Damage Assessment (NRDA) and have been previously reported by Mullin *et al.* (2017) and Wells *et al.* (2017). Satellite-linked tag data from 2018 were collected as part of the Consortium for Advanced Research on Marine

Mammal Health Assessment (CARMMHA). Satellite-linked transmitter specifications, programming, and attachment protocols are detailed elsewhere (Balmer *et al.* 2014; Wells *et al.* 2017). The KiwiSat 202 K2F and SPOT-299 tags had a projected battery life of 168 days and 280 days, respectively. To increase transmitter life and provide the highest quality location data, we programmed satellite-linked tags in the Advanced Research and Global Observation Satellite (ARGOS) data collection and location system (Collecte Localisation Satellites 2011) targeting transmission windows with optimal satellite pass durations. The KiwiSat 202 K2F tags were programmed for four, 1-hour transmission windows, and the SPOT-299 tags were programmed for six, 1-hour transmission windows. Tags were attached 38.4 mm from the trailing edge of the dorsal fin and affixed to the lower third of the dorsal fin. We coated tags with Propspeed (Oceanmax, Ltd., Auckland, NZ), excluding the saltwater switches, to reduce biofouling. Telemetry data were received from the ARGOS CLS system and filtered through the Douglas ARGOS-filter algorithm, which evaluates location plausibility using spatial redundancy, ARGOS Location Class (LC), movement through time, and angle of movement across locations (Udevitz *et al.* 2009). ARGOS LC 3, 2, and 1 data were used for subsequent analyses, with estimated errors of < 250 m, 250 – < 500 m, and 500 – 1500 m, respectively.

We used utilization distributions (UD) to provide probabilities of spatial and temporal habitat use (Worton 1989) and determine ranging patterns and short-term site fidelity (Fieberg & Kochanny 2005). Kernel density estimates (KDEs) are a quantitative method to calculate UDs (Citta *et al.* 2018). For both the BAR and MSS study sites, we calculated individual UDs (50% and 95%) for all tagged individuals. Additionally, individuals were grouped into cumulative ranging patterns that were classifications of overall movements within each study site. Cumulative UDs (50% and 95%) were calculated with all locations given equal weight (Citta *et al.* 2018). Although this method biases the cumulative UD towards tags that transmit more frequently and/or for longer durations, it is a conservative approach given we do not know what proportion of the population is represented by tagged individuals (Citta *et al.* 2018).

To calculate UDs, we used a KDE method that included barriers to movement in Geostatistical Analyst and Spatial Analyst Tools (ArcGIS 10.6, ESRI, Redlands, CA, USA) in the Universal Transverse Mercator (UTM) Zone 16 North projection and the World Geodetic System (WGS) 1984 datum. The output grid cell size was 1 km^2 to account for ARGOS LC errors and to allow for fine-scale spatial resolution of the telemetry data (Sprogis *et al.* 2016).

Because bandwidth selection, or the smoothing parameter (h), can strongly affect the KDE distribution (Rayment *et al.* 2009), we used a rule-based ad hoc method (Kie 2013) and Home Range Tools (HRT) for ArcGIS (Rodgers *et al.* 2015) to determine the appropriate bandwidth for KDEs of each individual and cumulative ranging pattern.

2.5 | Stable isotope preparation and analysis

To relate movement to habitat use, we conducted stable isotope analysis on skin samples collected from captured dolphins. Samples from 2011and 2013 were collected as part of the DWH NRDA and have been previously reported by Hohn *et al.* (2017). Briefly, skin samples were collected via biopsy and immediately stored in liquid nitrogen vapor shipper in the field and while transported to a -80°C freezer (Hohn *et al.* 2017). Samples were freeze-dried and lipid extracted with a 2:1 chloroform:methanol mixture for 48 hrs in a Soxhlet extractor (Hohn *et al.* 2017). Cloyed *et al.* (In review) provide details on sample collection and preparation. Briefly, we obtained samples from the dorsal fin of each captured dolphin with an 8 mm coring tool during tag attachment, or from part of a surgical biopsy wedge. Samples were stored at -20° C until processing, at which point all samples were rinsed with ultra-pure (UP) water and lipid extracted using a modified Folch method (Cloyed *et al.* 2020).

Samples collected as part of NRDA (2011 and 2013) and 2018 samples were prepared similarly. Samples were weighed to ~1 mg and packed into tin capsules. 2011 and 2013 samples were analyzed at IsoForensics (Salt Lake City, UT) and the Stable Isotope Ratio Facility for Environmental Research at the University of Utah. 2018 samples were analyzed at the University of California, Davis Stable Isotope Facility. Isotopic values were expressed using delta notation (δ) in parts per thousand (‰), where $\delta X = (R_{sample} / R_{standard} - 1) \times 1{,}000$, with R_{sample} and $R_{standard}$ representing the molar ratios of C^{13}/C^{12} and N^{15}/N^{14} of the sample and standard reference material, respectively. The reference material was Vienna-Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen. Repeated analysis of in-house reference materials for the 2011 and 2013 samples were 0.02 ‰ for C and 0.04 ‰ for N and for the 2018 samples were 0.08 ‰ for C and 0.07 ‰ for N. The 2011 and 2013 data are publicly available through the NRDA data warehouse (https://www.diver.orr.noaa.gov/). Samples from 2018 were collected as part of CARMMHA and are also available through the NRDA data warehouse (https://www.diver.orr.noaa.gov/).

2.6 | Statistical analysis

We compared the prevalence of positive DMV titers between sites (BAR and MSS) and between dolphin movement patterns within each site. We used a logistic GLM with a quasibinomial distribution and *logit* link to determine differences in the proportions of positive DMV titers between BAR and MSS, age classes (sub-adult [length ≤ 240 cm or age 2 – 10 years] and adult [length ≥ 241cm or age ≥ 10 years]) (Schwacke *et al.* 2009), and sexes at each site. For both sites, habitats at higher latitudes were more estuarine and more marine at lower latitudes. To determine whether dolphins with positive DMV antibody titers had lower latitude ranges (i.e., used more marine habitats), we calculated the mean latitude from all telemetry data for each dolphin. To determine if DMV-positive dolphins had different mean latitudes, we used t-tests separately for each site.

We used hot spot analyses to statistically identify spatial clustering (Queiroz *et al.* 2016). Getis-Ord Gi* (Getis & Ord 1996) is a widely used spatial autocorrelation statistic that provides a z-score and significance (*p*-value) at each location or group of locations. For example, at $p = 0.05$, $z > 2$ indicates hot spots, $z < -2$ indicates cold spots, and $-1 < z < 1$ indicates random spatial processes (Getis & Ord 1996). Tag locations for all cumulative ranging patterns at BAR and MSS study sites were grouped into grid cells of 1 km^2 (Mullin *et al.* 2017), and Getis-Ord Gi* hot spot analyses were performed in ArcGIS 10.6. The distance threshold, which is a measure of how neighboring locations influence a given location, was calculated using the Incremental Spatial Autocorrelation tool and the Global Moran's statistic in ArcGIS 10.6. The distance with the highest *z*-score was used for the distance threshold parameter in the Getis-Ord Gi* hot spot analysis (ESRI 2019). For each cumulative ranging pattern, hot spots were plotted at the $p < 0.01$ and $p < 0.05$ levels to assess differences in spatial clustering. We used Fisher's exact tests (two-sided) to determine differences in the proportions of positive DMV titers among cumulative ranging patterns in both BAR and MSS.

To determine how each isotope type (C or N) varied with mean latitude, collection year, and DMV antibodies, we used general linear models within an Akaike Information Criterion framework (AIC; Burnham, Anderson & Huyvaert 2011). DMV antibody titer was coded as a 0 for negative titer and a 1 for positive titer. Using each isotope (C or N) as a response variable, we constructed a global model that included mean latitude, collection year, and DMV titer as well as interactions among mean latitude and DMV titer, collection year and DMV titer, and collection year and mean latitude. We ran additional null models for each isotope type. The best-fitting models have the lowest AIC values (Burnham, Anderson & Huyvaert 2011). To measure the relative strength of each model, we calculated normalized Akaike weights, *w*, for each model *i*, where $w_i = \frac{e^{-0.5 * \Delta AIC_i}}{\sum_r^R e^{-0.5 * \Delta AIC_i}}$. Akaike weights provides a probability that the given model is the best-fitting of the considered models: values > 0.9 indicate strong model support over others and *w* > 0.1 indicate some model support and should be considered in the analysis (Burnham, Anderson & Huyvaert 2011). All statistical analyses were performed in R (Team 2013).

3 | Results

3.1 | Dolphin sampling

DMV antibodies, satellite telemetry, and stable isotope data were analyzed from 41 dolphins in BAR during 2011, 2013, and 2018 (♀ = 16 ♂ = 25) and 32 dolphins in MSS during 2013 and 2018 (♀ = 16 ♂ = 19; Figures 2 and 3). Capture locations in BAR were primarily on the bay-side of Grand Isle and Grand Terre Islands and extended northward into the Barataria Basin in all years. Capture locations in MSS differed between sampling years, targeting the waters surrounding Pascagoula and adjacent barrier islands (Horn and Petit Bois) in 2013 and the waters surrounding Dauphin Island in 2018. For all years combined, tags transmitted for 124 ± 67 days (mean ± S.D.) and 172 ± 53 days in BAR and MSS, respectively.

3.2 | Dolphin morbillivirus antibody prevalence

The prevalence of dolphin morbillivirus (DMV) antibody titers was 37% (N = 15/41; 95% CI = 23% – 52%) for all individuals sampled in BAR and 44% (14/32; 28% – 61%) for all individuals sampled in MSS. Majority of the positive titers ($\geq$ 1:16) in BAR suggested intermediate to high antibody serum concentration in many individuals, whereas majority of the positive titers in MSS suggested low to intermediate antibody serum concentration (Figure S1). There were no differences in DMV antibody prevalence between BAR and MSS ($t_{1, 66}$ = 0.723, *p* = 0.469), subadult and adult individuals ($t_{1, 66}$ = -0.229, *p* = 0.820; Table 1), and sexes ($t_{1, 66}$ = 0.774, *p* = 0.442; Table 1). Dolphins with DMV antibodies were associated with a lower mean latitude in BAR (Figure 4; $t_{36.2} = 2.06$, $p = 0.047$), but not in MSS, where dolphins with DMV antibodies tended to be more common at higher mean latitudes (Figure 4; $t_{27} = -1.46$, $p = 0.16$).

3.3 | Ranging patterns and relationships to dolphin morbillivirus

In BAR, individual UDs ranged between 0.3 km^2 – 18 km^2 (50%) and 0.3 km^2 – 77 km^2 (95%) and extended northward to Little Lake, southward to the nearshore habitats from Port Fourchon, and to the east of the Grand Terre Islands (Table 2; Figure 2). Two cumulative ranging patterns emerged from the BAR satellite telemetry data and individuals were classified post-hoc into Interior (N = 8, ♀ = 4, ♂ = 4; West Champagne Bay and Bassa Bassa Bay northward) and Island-associated ranging patterns (N = 33, ♀ = 12, ♂ = 21; Caminada Bay, southern Barataria Bay, and estuarine habitats from Port Fourchon eastward past the Grand Terre Islands) (Figure 2A, C). Hot spot analyses identified differences in spatial clustering between Interior and Island-associated ranging patterns (Figure 2B, D).

In MSS, individual UDs ranged from 5.0 km^2 – 37 km^2 (50%) and 5.8 km^2 – 130 km^2 (95%) and included the estuarine habitats from Ocean Springs, MS eastward into Mobile Bay and the sound/nearshore habitats from Ship Island east to and including Dauphin Island (Table 2; Figure 3). Three cumulative ranging patterns emerged from the MSS satellite telemetry data and individuals were classified post-hoc: Island-west (N = 7, ♀ = 4, ♂ = 3; Ship Island, Horn Island, Petit Bois Island, and western Dauphin Island) (Figure 3A, B), Island-east (N = 10, ♀ = 4, ♂ = 6; Dauphin Island) (Figure 3C, D), and Interior (N = 15, ♀ = 5, ♂ = 10; estuarine and sound waters from Ocean Springs east to Mobile Bay) (Figure 3E, F). Hot spot analyses identified differences in spatial clustering ($p < 0.05$ and $p < 0.01$) between cumulative ranging patterns, with Interior animals in the estuarine and sound waters off Pascagoula, Island-east animals clustered at the western and eastern ends of Dauphin Island, and Island-west animals clustered in the waters between Horn and Petit Bois Islands (Figure 3B, D, F).

There were site-specific differences in DMV antibody prevalence between ranging patterns. In BAR, there was a distinct difference in DMV antibody prevalence between Interior and Island-associated ranging patterns ($p = 0.018$); none of the Interior BAR dolphins had positive DMV titers but nearly 50% of the Island-associated dolphins were positive (Table 2). In MSS, there were no differences in antibody prevalence between Interior, Island-east, and Island-west ranging patterns ($p = 0.163$; Table 2).

3.3 | Stable isotope values and relationships to DMV

Mean latitude, presence of DMV antibodies, and year best explained patterns of δ^{13}C values in dolphin skin from BAR (Table 3; $F_{4, 36} = 9.93$, $p < 0.001$, $R^2 = 0.47$, $w = 0.59$). δ^{13}C values in BAR decreased with mean latitude (Table 2; Figure 5A) and were marginally higher for DMV antibody-positive individuals (Table 3; Figure 5A). δ^{13}C values were highest in 2011 and similar between 2013 and 2018 (Table 3; Figure 5A). Two other models had $w > 0.1$ (Table S1), and in both cases the most important factor was mean latitude (Table S2). Mean latitude was the only variable included in the best-fitting model for δ^{15}N values (Table 3; $F_{2, 38} = 6.48$, $p < 0.22$, $R^2 = 0.22$, $w = 0.50$), and δ^{15}N values in dolphins from BAR decreased with mean latitude but with a shallower slope compared to the δ^{13}C values (Table 3; Figure 5B). The model that included mean latitude and DMV antibody prevalence had a similar weight as the best-fitting model ($w = 0.45$; Table S3), but DMV titer had little effect on δ^{15}N values (Table S4).

Mean latitude was the only variable included in the best-fitting model for δ^{13}C values (Table 3; $F_{1, 29} = 44.00$, $p < 0.001$, $R^2 = 0.59$, $w = 0.70$), and δ^{13}C values decreased with latitude (Figure 5C). The model that included mean latitude and DMV antibody prevalence had a $w = 0.19$ (Table S5), but DMV titer did not affect δ^{13}C values (Table S6). Mean latitude was included in the best-fitting model for δ^{15}N in dolphin skin from MSS (Table 3; $F_{1, 29} = 0.244$, $p = 0.625$, $R^2 = -0.03$, $w = 0.37$), but the δ^{15}N values did not change with latitude (Table 3; Figure 5D). The null model had a $w = 0.26$ (Table S7), further supporting that δ^{15}N values did not change with latitude in MSS (Table S8).

4 | Discussion

The prevalence of DMV antibodies was relatively high at both study sites in the northern GoM. While the prevalence of DMV antibodies varies broadly among geographic regions (e.g., Gulf of Mexico, western north Atlantic; Rowles *et al.* 2011; Fauquier *et al.* 2017), the prevalence was higher at our study sites relative to most other dolphin capture-release health assessment study sites in the southeastern U.S. (Rowles *et al.* 2011). Although the presence of DMV antibodies is typically thought to be more likely for dolphins in open-ocean waters compared to estuarine waters (Rowles *et al.* 2011; Balmer *et al.* 2018), our data indicate that some estuarine dolphin populations can have a high prevalence of positive DMV titers as well. Dolphins tagged in BAR, for example, are likely members of the Barataria Bay Estuarine System Stock (Waring *et al.* 2007; Wells *et al.* 2017), while dolphins tagged in MSS are likely members of the Mississippi Sound, Lake Borgne, Bay Boudreaux Stock or Mobile Bay Stock (Waring *et al.* 2007; Mullin *et al.* 2017). Overall, the frequency of positive DMV antibody titers in these estuarine animals had 95% confidence intervals that overlapped with those of the Western North Atlantic Northern Migratory Coastal Stock (33%, N = 4/12; 95% CI = 12 - 61%; Rowles *et al.* 2011), a hypothesized DMV carrier stock (Rowles *et al.* 2011). The northern GoM St. Joseph Bay Estuarine System Stock, which is in a partially enclosed embayment with spatial overlap between the estuarine and adjacent nearshore dolphins, had a relatively low prevalence of DMV antibodies that marginally overlapped with the prevalence at BAR but was lower than at MSS (18%, N = 4/22; 6 - 37%; Rowles *et al.* 2011). The prevalence of DMV antibodies at our study sites suggests that DMV may be endemic or have periodic incursions in some GoM estuarine stocks (Duignan *et al.* 1996; Rowles *et al.* 2011), and the lack of differences between adult and subadult dolphins at both sites suggests such incursions have been relatively recent (< 10 years).

The spatial variation in DMV antibody prevalence associated with ranging patterns differed between BAR and MSS. In BAR, a higher prevalence of dolphins with positive DMV antibodies was identified for the Island-associated ranging pattern, surrounding the barrier islands, where dolphins may be more likely to encounter infected dolphins from other populations. In contrast, all dolphins in the Interior ranging group, which more heavily use the interior of BAR, were negative for DMV antibodies. This finding suggests that the enclosed geography of BAR and high degree of site fidelity may decrease the likelihood of DMV exposure from dolphin populations in adjacent, nearshore waters. These results are corroborated by the enriched $\delta^{13}C$ isotope values in DMV positive dolphins, indicating they use marine-influenced habitats in the lower sections of BAR. Prevalence of DMV antibodies in MSS was more similar across ranging patterns as compared to BAR, which may be driven by the relatively open water environment. The overlap between estuarine and nearshore and open-ocean populations is not well understood in MSS, but MSS dolphin abundance is known to fluctuate seasonally (Hubard *et al.* 2004; Mullin *et al.* 2017), with some individuals having extended movements (> 300 km; Balmer *et al.*

2016). It is possible that dolphins from different nearshore and estuarine stocks can more easily interact in MSS, and this mixing drives the even spatial distribution of DMV-antibody positive individuals. Thus, the observed spatial variation within sites was likely influenced by the interaction of enclosed (BAR) and open (MSS) geographies with the narrow habitat use by individual dolphins.

The combination of small ranges and distinct $\delta^{13}C$ values indicate that habitat use ranged from estuarine to more marine-influenced waters (Wissel, Gaçe & Fry 2005). Dolphin skin has an isotopic retention time of 2 – 4 weeks and thus provides habitat and diet information for several weeks prior to sampling (Browning *et al.* 2014). The agreement of $\delta^{13}C$ (retrospective) and movement (prospective) data demonstrates that dolphin habitat use was similar pre- and post-capture, providing robust evidence that BAR and MSS dolphins are individual habitat specialists, similar to other estuarine dolphins in the northern and eastern GoM (Rossman *et al.* 2015; Wilson *et al.* 2017). It is possible that the differences in $\delta^{13}C$ values for MSS dolphins are driven by year, as most Interior dolphins were captured in 2013 and most Island associated dolphins were captured in 2018. But this was not always the case. Two 2013 dolphins had lower latitudes and isotopically resembled the 2018 dolphins from lower latitudes, and one 2018 dolphin had a higher latitude and resembled the 2013 dolphins with higher latitudes. As such, the north-south habitat gradient across the sound likely drives this pattern in $\delta^{13}C$ values and not differences among years. Although we have relatively low sample sizes pooled among several years, and small groups or individuals could have had a large influence on our results, our movement and habitat use patterns are highly consistent with those of other estuarine dolphins populations; numerous studies using satellite telemetry, photo-identification, and stable isotopes have identified similar structure in estuarine dolphin populations worldwide (Lusseau *et al.* 2006; Balmer *et al.* 2008; Gonzalvo *et al.* 2014; Wilson *et al.* 2017). Thus, many estuarine dolphin populations are likely individual habitat specialists, and the narrow habitat use of these dolphins may limit contact with individuals from other populations. In this way, individual habitat specialization appears to mediate the risk of DMV exposure and patterns of DMV antibody prevalence in estuarine habitats (Balmer *et al.* 2018).

Although trophic status varied with habitat attributes among locations, diet was not a likely driver of DMV prevalence. Dolphins from BAR, but not MSS, that used interior, estuarine habitats likely fed at a lower trophic level than dolphins from marine-influence habitats in the southern portions of the bay. These patterns were weak, though, and habitat use and not differences in trophic level were not related to the presence of likely drove DMV prevalence. Unlike $\delta^{13}C$ values, $\delta^{15}N$ values generally increase from marine to estuarine habitats (Fry 2002), but we did not observe this pattern in BAR dolphins, suggesting dolphins from more estuarine habitats fed at a lower trophic level than dolphins that inhabit more marine habitats (Post 2002). Many fish species (the primary prey of dolphins in the GoM; Berens McCabe *et al.* 2010; Wilson *et al.* 2017) use estuaries as nursery habitats, and fish from upper parts of the estuary are likely smaller and feed at lower trophic levels compared to fish from lower parts of the estuary (Baltz & Jones 2003). In MSS, $\delta^{15}N$ values remained similar from north to south. Dolphins in MSS did not use upper estuarine habitats as exclusively as BAR dolphins in the Interior ranging pattern and MSS dolphins used the open sound waters frequently, whether that included waters off the mainland or surrounding the barrier islands. Accordingly, the similar $\delta^{15}N$ values in dolphins throughout MSS are consistent with these habitats supporting a greater mix of fish from varying trophic levels compared to upper BAR habitats (Baltz & Jones 2003; Schrandt, Powers & Mareska 2015). DMV prevalence did not vary with $\delta^{15}N$ values at either site, supporting the idea that habitat use and not dietary differences drove patterns of DMV prevalence.

Studies that incorporate multiple parameters to better understand the impacts of these cumulative stressors are essential to developing robust management strategies and restoration plans for future anthropogenic impacts. We integrated data from dolphin health assessments with satellite telemetry and stable isotope data to identify at-risk populations and test whether exposure to DMV can depend on individual ranging patterns and habitat geography. Our results corroborate other work that fine-scale movements and habitat use can drive DMV exposure for estuarine dolphins (Balmer *et al.* 2018). We build upon this earlier work by demonstrating how individual range patterns and habitat specialization within two estuarine dolphin populations interact with the geography of their habitats to drive DMV exposure. This habitat-dependent exposure risk is consistent with previous hypotheses (Duignan *et al*. 1996) and epidemic modeling that found DMV spread is driven by the frequency of contacts among individuals, with higher prevalence of DMV antibodies in places where spatial overlap among individuals from differing populations is highest (Morris *et al.* 2015; Balmer *et al.* 2018). In the short term, individual dolphins that use nearshore habitats and those that use more open systems may be more susceptible to DMV, but in the longer term the naïve populations may be at higher risk if they do not have antibodies and encounter a DMV carrier. Some evidence exists that declines in DMV seroprevalences within populations over time can also increase risk (Raga *et al.* 2008; Rowles *et al.* 2011), which would alter how the pathogen can spread among populations and individuals. As a paramyxovirus, however, it is likely that DMV antibody concentrations remain elevated for at least several decades if not a lifetime (Rowles *et al.* 2011; Van Bressem *et al.* 2014). Furthermore, many estuarine populations are exposed to other stressors associated with human activities nearshore, such as fisheries interactions (Samuels & Bejder 2004), biotoxins (Fire *et al.* 2011), and contaminants (Schwacke *et al.* 2014) that may suppress immune function and place potentially disease-naïve populations at higher risk (Schwacke *et al.* 2011). Thus, the interaction between spatial distribution of habitat use and geography is critical to exposure and transmission of DMV and likely other diseases that spread via contact among individuals. Although our study focuses on a single species and has relatively low samples sizes, we demonstrated an exciting link between movement, individual habitat use, and disease exposure in wild populations. More work is needed to better understand the global relationships among ranging patterns, habitat use, and infectious diseases. Future work needs to place these results in the context of social networks that drive contacts among groups and populations and determine how different types of movement distribute individuals across the landscape (Craft *et al.* 2011; Boulinier *et al.* 2016). Satellite telemetry and stable isotopes provide a potent combination of tools that can reveal if patterns of infectious disease are associated with habitat use, including species that harbor zoonotics with pandemic potential (Bridge *et al.* 2014).

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Author Contributions: CSC led the stable isotope analysis and BCB led the movement analysis. JTS analyzed dolphin morbillivirus. CRS, FIT, and DAF were lead veterinarians for the health assessments. ESZ led health assessment captures in BAR and MSS. CSC and BCB together led the writing of the manuscript. All authors participated in at least one health assessment, participated in discussing the results, and editing the manuscript.

Data accessibility: A stable isotope data and telemetry data from the 2018 captures are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at https://data.gulfresearchinitiative.org (telemetry data: doi: https://data.gulfresearchinitiative.org/data/R6.x809.000:0011; stable isotope data: https://data.gulfresearchinitiative.org/data/R6.x809.000:0020). The 2011 and 2013 telemetry data are publicly available through the NRDA data warehouse, https://www.diver.orr.noaa.gov, where the data can be found through the *Search Data in DIVER* link under *Deepwater Horizon Natural Resource Damage Assessment Data* and then expanding *Field Collected Data Records* and clicking on *Telemetry Tracks,* filtering by Species Name, and adding Bottlenose Dolphins. Telemetry data from dolphins in Barataria Bay and Mississippi Sound were used in this study.

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Table 1: DMV antibody prevalence among age classes and sexes in BAR and MSS.

Site	Sex	Age Class	N Total	DMV Positive N	% DMV Positive (± 95% CI)
BAR	—	Subadult	18	6	33 (15 – 56)
BAR	—	Adult	22	8	36 (19 – 57)
BAR	Male	—	25	10	40 (23 – 60)
BAR	Female	—	16	5	31 (13 – 56)
MSS	—	Subadult	20	8	40 (21 – 62)
MSS	—	Adult	12	6	50 (24 – 76)
MSS	Male	—	20	10	50 (29 – 71)
MSS	Female	—	13	4	31 (11 – 58)

Table 2: Cumulative ranging pattern summary for Barataria (BAR) and Mississippi Sound (MSS) study sites including number of quality locations (3, 2, and 1), dolphin morbillivirus (DMV) antibody prevalence, and 50 and 95% utilization distributions (UD).

Site	Ranging Pattern	N	DMV Positive N	% DMV Positive (95% CI)	Cumulative # of Quality Locations	50% UD (km^2)	95% UD (km^2)
BAR	INTERIOR	8	0	0 (0 – 21)	1307	41	200
BAR	ISLAND-ASSOCIATED	33	15	45 (29 – 60)	6786	71	429
MSS	INTERIOR	15	9	60 (35 – 82)	12443	81	495
MSS	ISLAND-EAST	10	2	20 (13 – 77)	5482	43	324
MSS	ISLAND-WEST	7	3	43 (4 – 50)	4655	46	343

Table 3: Statistics for the parameters of the best-fitting models for δ^{13}C and δ^{15}N in Barataria Bay and Mississippi Sound study sites.

	Parameter	Estimate (± SE)	*t*	*p*
Barataria Bay: δ^{13}C				
	Intercept	181.65 (50.85)	3.57	0.001
	Mean Latitude	-6.81 (1.74)	-3.92	0.004
	Morbillivirus titer (0/1)	182.08 (0.22)	1.96	0.06
	Year-2013	180.56 (0.28)	-3.94	0.004
	Year-2018	180.81 (0.24)	-3.55	0.001
Barataria Bay: δ^{15}N				
	Intercept	169.90 (52.82)	3.22	0.003
	Mean Latitude	-6.42 (1.80)	-3.56	0.001
Mississippi Sound: δ^{13}C				
	Intercept	643.56 (99.72)	6.45	< 0.001
	Mean Latitude	-21.85 (3.29)	-6.63	< 0.001
Mississippi Sound: δ^{15}N				
	Intercept	-14.71 (59.68)	-0.25	0.81
	Mean	0.97 (1.97)	0.49	0.62

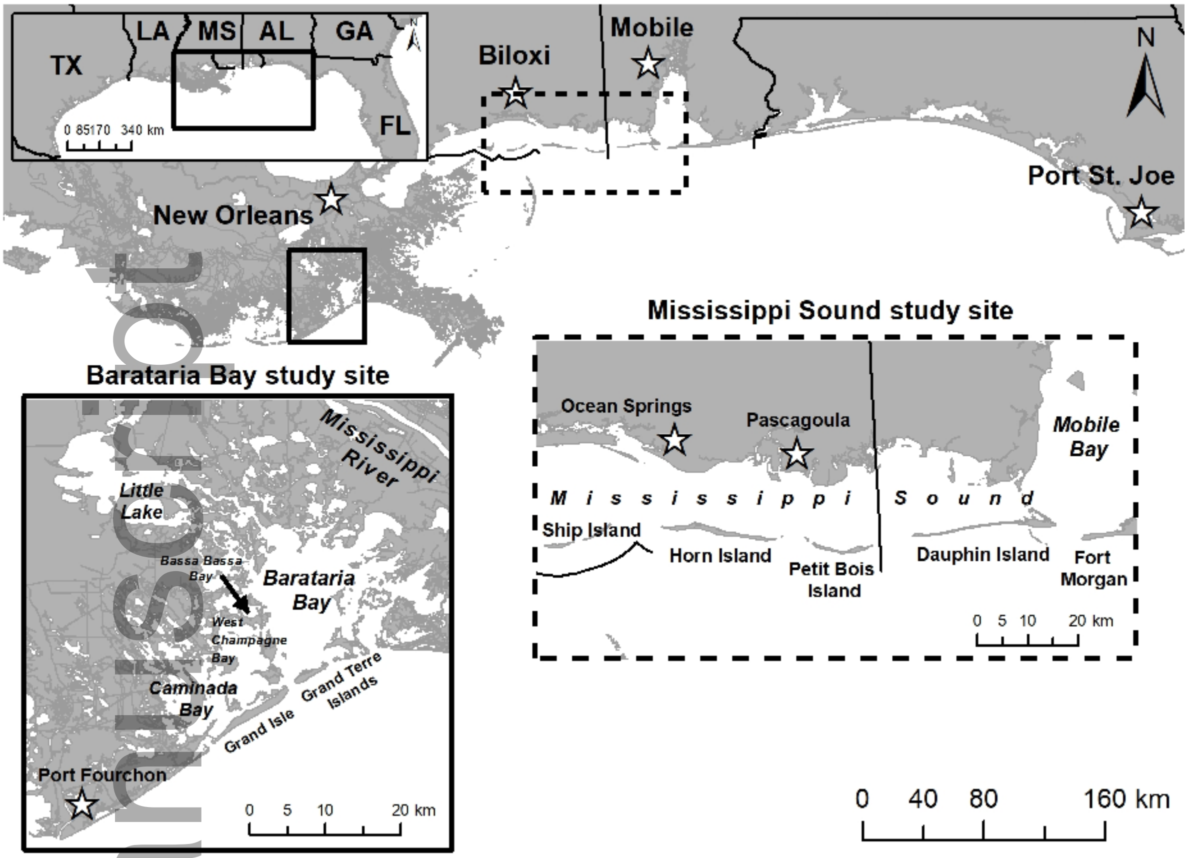
Figure 1. Map of study sites (Barataria Bay and Mississippi Sound) along the northern Gulf of Mexico. Inset in the upper left is the southeastern U.S.A.

Figure 2: Barataria Bay study site (A and C) utilization distributions (50%, 95%) with capture locations and presence of dolphin morbillivirus antibodies (positive, negative) and (B and D) hot spots separated by Interior and Island-associated ranging patterns.

Figure 3: Mississippi Sound study site (A, C, and E) utilization distributions (50%, 95%) with capture locations and presence of dolphin morbillivirus antibodies (positive, negative) and (B, D, and F) hot spots, separated by Island-west, Island-east, and Interior ranging patterns.

Figure 4: Boxplots with mean latitude by dolphin morbillivirus antibody presence for (A) BAR and (B) MSS study sites. Minimum and maximum values are indicated by the horizontal lines at the bottom and top, the box represents the interquartile range (1st-3rd quartiles), and the line in the middle of the box is the median.

Figure 5: δ^{13}C and δ^{15}N values by mean latitude, year, and dolphin morbillivirus antibody presence (+ black symbols, - grey symbols). (A) δ^{13}C and (B) δ^{15}N values in BAR study site. (C) δ^{13}C and (D) δ^{15}N values in MSS study site. Lack of regression line indicates no significant relationship.



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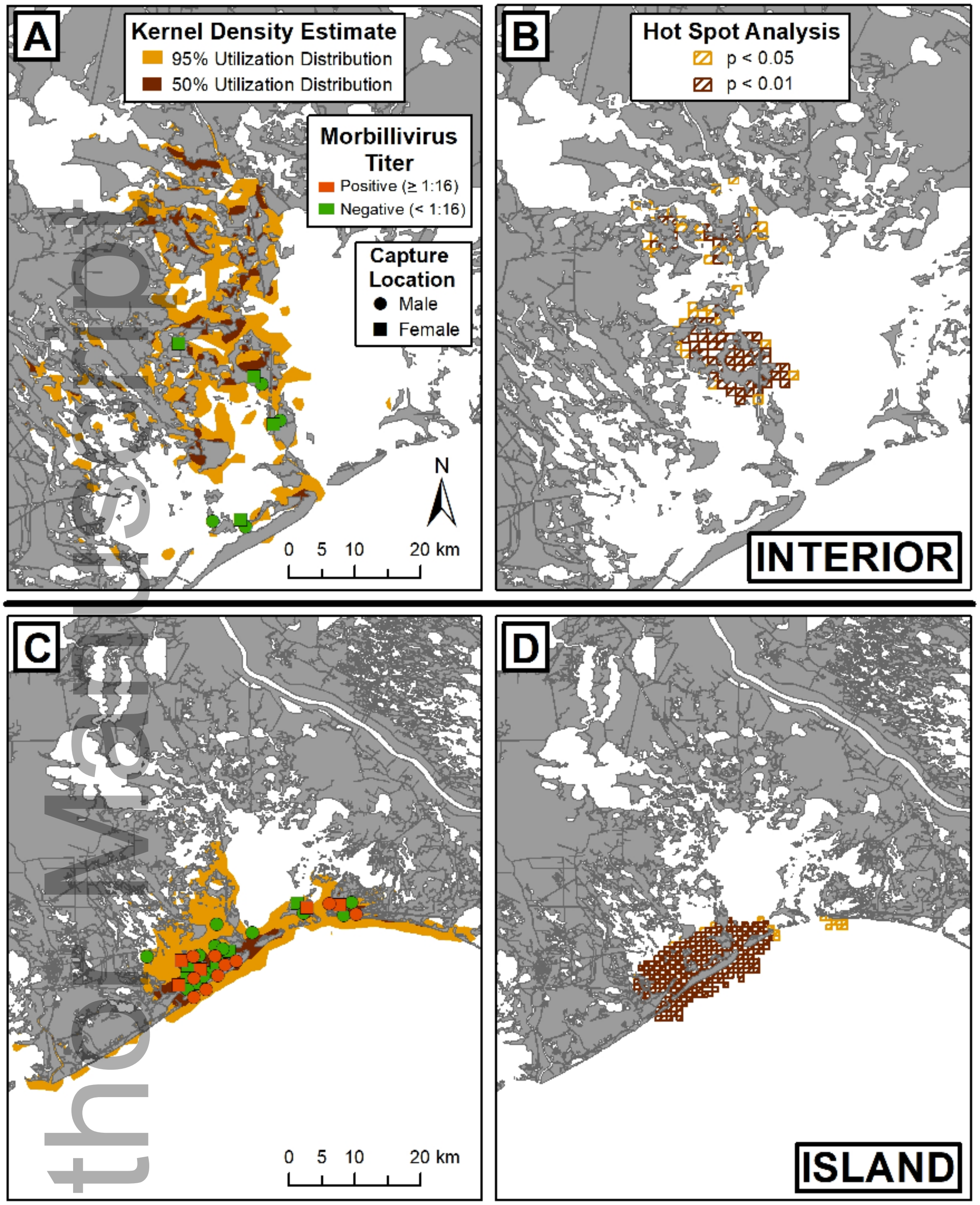

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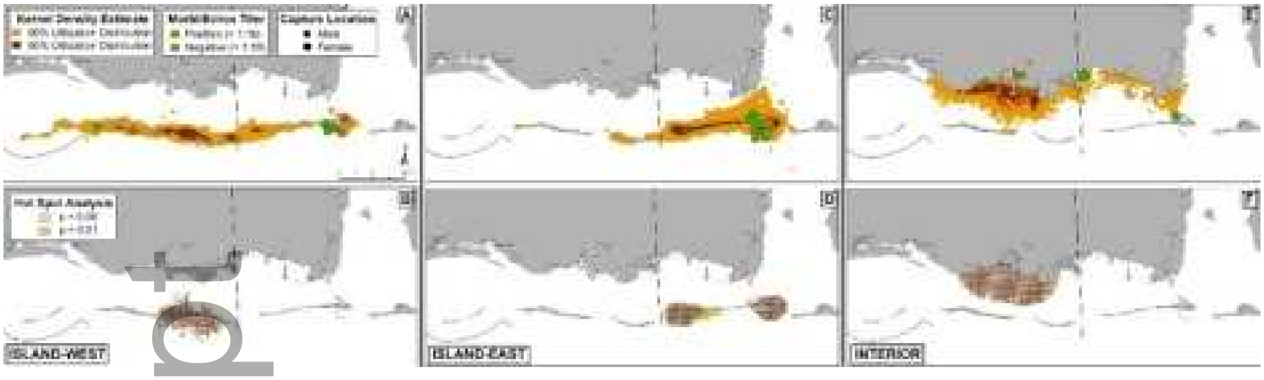

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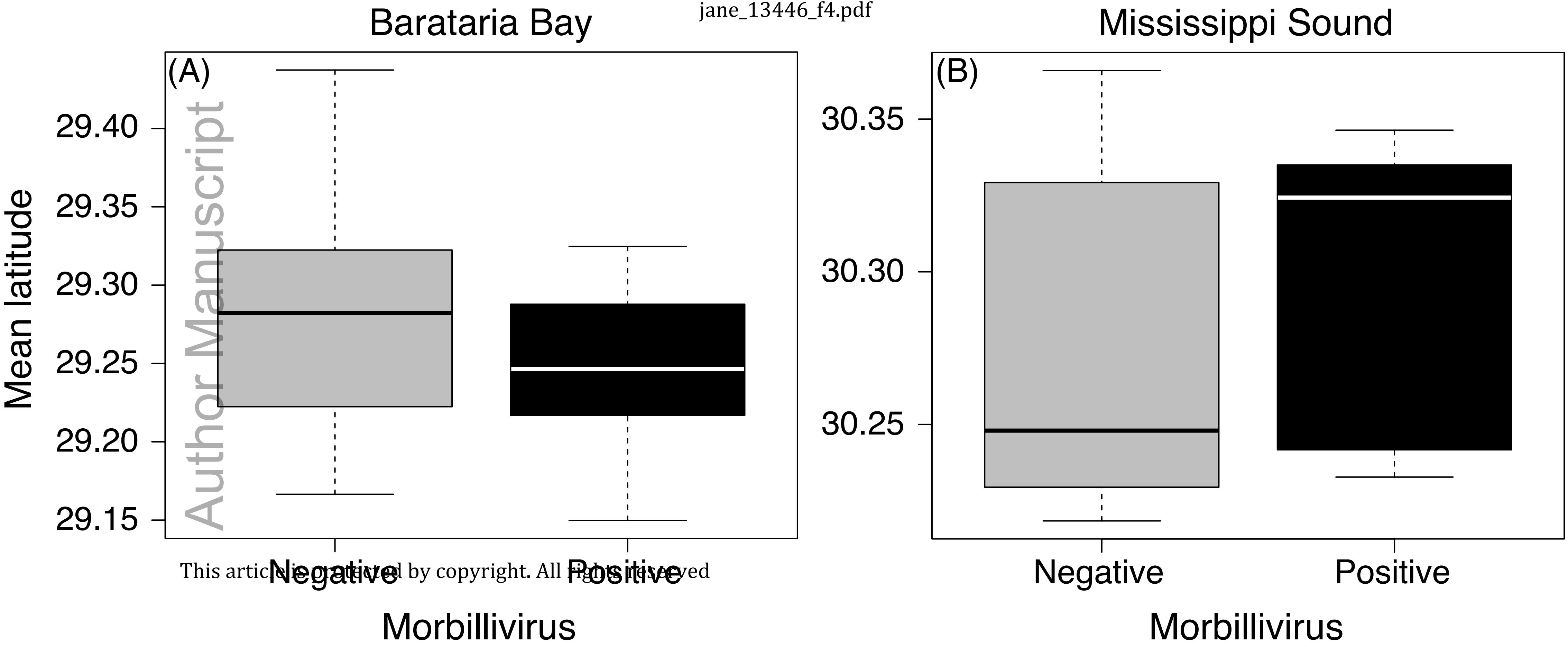
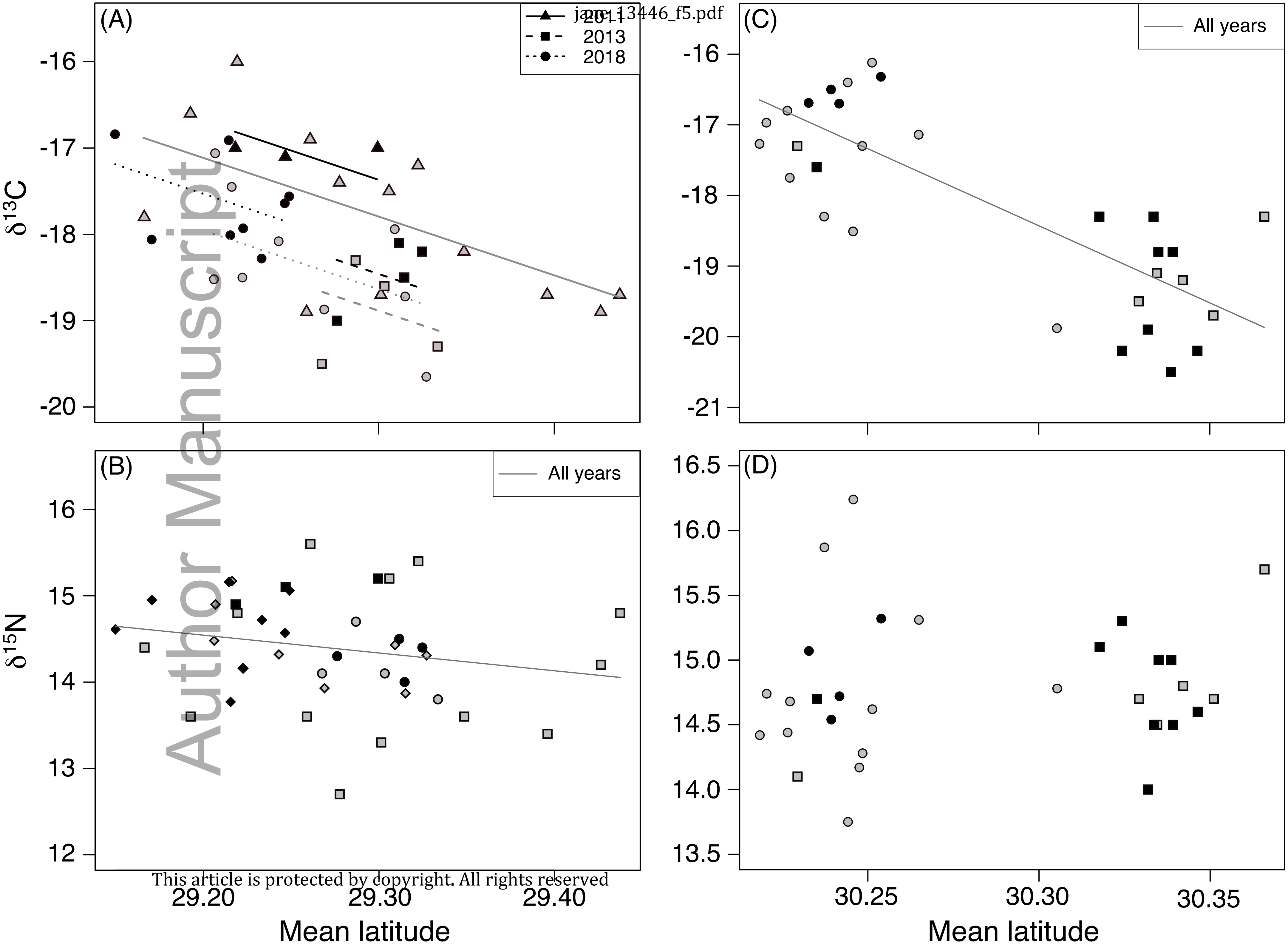

Barataria Bay
Mississippi Sound
(A)
(B)
Mean latitude
29.40
29.35
29.30
29.25
29.20
29.15
30.35
30.30
30.25
Negative
Positive
Negative
Positive
Morbillivirus
Morbillivirus


(A)
2011
2013
2018
-16
-17
-18
-19
-20
δ13C
(B)
All years
16
15
14
13
12
δ15N
29.20
29.30
29.40
Mean latitude
(C)
All years
-16
-17
-18
-19
-20
-21
(D)
16.5
16.0
15.5
15.0
14.5
14.0
13.5
30.25
30.30
30.35
Mean latitude