


Interaction between dietary and habitat niche breadth influences cetacean vulnerability to environmental disturbance

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Abstract. Ecosystems are experiencing elevated levels of disturbance, and species with narrower niches are often more vulnerable to disturbances. Niche breadth is often measured in terms of either diet or habitat use but diet and spatial use are infrequently considered in tandem. These different aspects of niche breadth potentially expose species to different types of disturbances; species with narrow dietary niches may be more affected by disturbances that alter trophic relationships, while species with narrow habitat niches may be more vulnerable to habitat loss and point-source pollutants. We examined dietary and habitat niche breadth of common bottlenose dolphins, *Tursiops truncatus truncatus*, from three different nearshore sites in the Gulf of Mexico (GoM). Using stable isotopes, we determined proportional contributions of different prey groups to dolphin diets at each site and through time at one site. We used satellite-linked telemetry at two sites to determine habitat use and site fidelity. Additionally, we examined the literature on cetacean diet, habitat use, movement, and IUCN status to determine relationships between niche breadth and population status for different species. Dolphin diets varied among sites as available prey varied, but Perciformes fish were the most frequently consumed prey. At the site for which we had temporal data, dolphins consumed more cephalopods in 2015 and 2018 but otherwise consumed primarily Perciformes fish. Dolphins had small utilization distributions and exhibited high site fidelity. Data from 31 cetacean species revealed that most species with vulnerable, threatened, or endangered IUCN statuses not only have specialized diets but also exhibit high site fidelity. Dolphins had diet characteristic of flexible generalists but were habitat specialists with high site fidelity. Dolphin populations in the GoM may have altered their diets in response to environmental changes that have altered community composition and trophic dynamics. On the other hand, their high site fidelity has exposed them to point-source pollutants, such as oil spills, persistent organic pollutants, and freshwater. Our broader analysis of cetaceans confirmed that species with specialized diets and high site fidelity were the most vulnerable to disturbances, providing a framework to predict which nearshore dolphin populations, and cetaceans in general, are most vulnerable to environmental changes.

Key words: bottlenose dolphins; cetaceans; environmental disturbance; mixing models; movement ecology; satellite-linked telemetry; site fidelity; stable isotopes; trophic ecology; *Tursiops truncatus*.

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INTRODUCTION

Ecosystems worldwide are undergoing substantial changes and impacts associated with anthropogenic and natural sources. Species niche breadth determines how organisms interact with their ecosystems and shapes how species respond to changes and disturbances (Voigt et al. 2007, Bellwood et al. 2019). Species with wider niches draw from a greater pool of resources and interact with a greater range of environments, making them more resilient and less prone to population declines and extinction compared to species with narrower niches (Swihart et al. 2003, Clavel et al. 2011). For example, species with wide dietary niches can potentially better withstand ecosystem changes that alter trophic dynamics and resource availability compared to species with narrower diets, and species with wide habitat niches can better withstand pollutants or other point-source disturbances that result in habitat degradation (Biesmeijer et al. 2006, Clavel et al. 2011). Accordingly, a wide range of taxa known to be dietary and habitat specialists have been theoretically predicted (Swihart et al. 2001) and empirically demonstrated to experience population declines (Swihart et al. 2003, Polus et al. 2007, Wilson et al. 2008, Stefanescu et al. 2011). Niche breadth is often measured in terms of diet or habitat use and movement (Wilson et al. 2008, Slatyer et al. 2013). Measuring these aspects of niche breadth in tandem can reveal a more complex relationship between organisms and their environments (Kiszka et al. 2011, Giménez et al. 2018), including how aspects of niche width may allow species to respond to different kinds of environmental disturbance.

The net influence of diet and habitat niches on vulnerability to disturbance depends on whether dietary or habitat quality and availability have been

altered (Swihart et al. 2003, Graham et al. 2011). Specialists use a narrow range of dietary resources and/or habitats, and changes in availability of both can have profound population consequences because these species are unable to exploit alternative dietary resources or habitats (Ford et al. 2009, Burstahler et al. 2016). For example, mortalities of resident killer whales (*Orcinus orca*) in the northeastern Pacific Ocean, which specialize on chinook salmon (*Oncorhynchus tshawytscha*), have been strongly correlated with environmentally driven declines in these salmon (Ford et al. 2009). Likewise, coral reef fish with narrower habitat requirements are more vulnerable to coral reef declines than those with broader habitat requirements (Wilson et al. 2008). Thus, species-specific responses to disturbance may vary depending on whether and how trophic dynamics or habitat quality are affected, but little work has connected different aspects of niche width to how disturbances affect ecosystems. Many disturbances have multi-faceted effects on ecosystems, and changes in trophic dynamics and habitat may interact and together drive population declines (Graham et al. 2011). For example, habitat degradation and loss can alter community composition in ways that ultimately affect dietary resources and trophic dynamics (Dobson et al. 2006, Waycott et al. 2009). Understanding how different elements of niche width make species vulnerable to ecosystem disturbances is vital to predicting species-specific responses to different disturbance types (Graham et al. 2011), and considering both dietary and habitat niche width is necessary to be able to make these predictions.

Another source of variation in vulnerability to disturbance is that generalist or specialist niche distinction can differ at population or individual levels (Bolnick et al. 2003, Rossman et al. 2015b, Cloyed and Eason 2016). Despite their relative

resilience, species and populations that are dietary or habitat generalists may actually be composed of individuals that use a subset of available resources and exhibit high site fidelity (Bolnick et al. 2003, Vander Zanden et al. 2010, Cloyed and Eason 2016), which is known as individual specialization and has important ecological consequences (Bolnick et al. 2011, Matich et al. 2011, Cloyed and Eason 2017). For example, common bottlenose dolphins, *Tursiops truncatus truncatus*, are habitat generalists with a global distribution, but populations inhabiting bays and estuaries can have high site fidelity and oftentimes spend their entire lives within, or very near, a specific bay or estuary (Gonzalvo et al. 2014, Wells 2014, Rossman et al. 2015b, Mullin et al. 2017, Wilson et al. 2017). Individual dolphins within these populations can also exhibit specialized foraging tactics that target certain prey or groups of prey (Connor et al. 2000, Wells 2003, Ronje et al. 2017). Thus, these particular populations and individuals can be more vulnerable to location-specific habitat loss or degradation from oil spills and other chemical pollutants (Wells 2010, 2014, Balmer et al. 2011, Schwacke et al. 2014), while the species as a whole is less vulnerable.

Bottlenose dolphins are an ideal species for testing interacting effects of dietary and habitat niche breadth on vulnerability to disturbance at individual and population levels. Common bottlenose dolphins that resided in areas of the northern Gulf of Mexico (GoM) affected by the *Deepwater Horizon (DWH)* oil spill did not leave these areas during the event and experienced adverse health impacts, reduced survival, and decreased population size (Schwacke et al. 2014, Lane et al. 2015, McDonald et al. 2017, Smith et al. 2017). Similarly, during severe harmful algae blooms common bottlenose dolphins remained within their home ranges in both coastal Texas and Sarasota Bay, Florida, and suffered increased injury and mortality during these blooms (Fire et al. 2007, 2011, Powell and Wells 2011). Dolphins in Texas had evidence of domoic acid and okadaic acids and brevetoxins in their stomachs, which are toxic compounds produced by the algae (Fire et al. 2011), and dolphins in Sarasota Bay changed their feeding behaviors in ways that likely resulted in a change in diet in response to harmful algae (McHugh et al. 2011b).

Thus, there is evidence that these habitat generalists that exhibit high site fidelity at the individual level may be functionally similar to habitat specialists (Rossman et al. 2015b) and more prone to the negative effects of site-specific environmental changes than individuals with low site fidelity and larger movement patterns.

Using stable isotopes and satellite-linked telemetry, we tested whether common bottlenose dolphins (hereafter referred to as dolphins) sampled in three estuaries had distinct niche breadths defined by the combination of diet and habitat use. First, we used stable isotopes to define spatial variation in the isotopic and dietary niches of live dolphins captured in Barataria Bay, Louisiana (BAR), Dauphin Island, Alabama (DAU), and Sarasota Bay, Florida (SAR) (Fig. 1), sites spanning a range of environmental attributes and associated disturbances. We also investigated temporal variation in isotopic and dietary niches by analyzing stable isotopes in archived tissues (liver, skin, muscle) from dolphins that stranded dead along the Alabama coast between 2011 and 2018. Second, we defined spatial variation in habitat use with satellite telemetry on dolphins at BAR and DAU. We predicted dolphins would consume a wide range of prey items, with the proportion of prey groups in diets varying among regions in the spatial analysis and among years in the temporal analysis, but that dolphins at each site would have distinct ranging patterns and relatively small utilization distributions. Third, we built a framework to determine how niche width affects potential vulnerability of other cetacean species to environmental disturbances by collecting information on the dietary and movement plasticity and IUCN or population status of 31 species of cetaceans, including estuarine, coastal, and offshore populations of common bottlenose dolphins. We predicted that species with the most vulnerable IUCN or population statuses will have narrow dietary and habitat niches.

MATERIALS AND METHODS

Study sites

Barataria Bay, Louisiana (BAR), is an estuary in southeast Louisiana bordered by the Mississippi River to the north and east and Bayou Lafourche to the west and is separated from the GoM along its southern end by barrier islands.

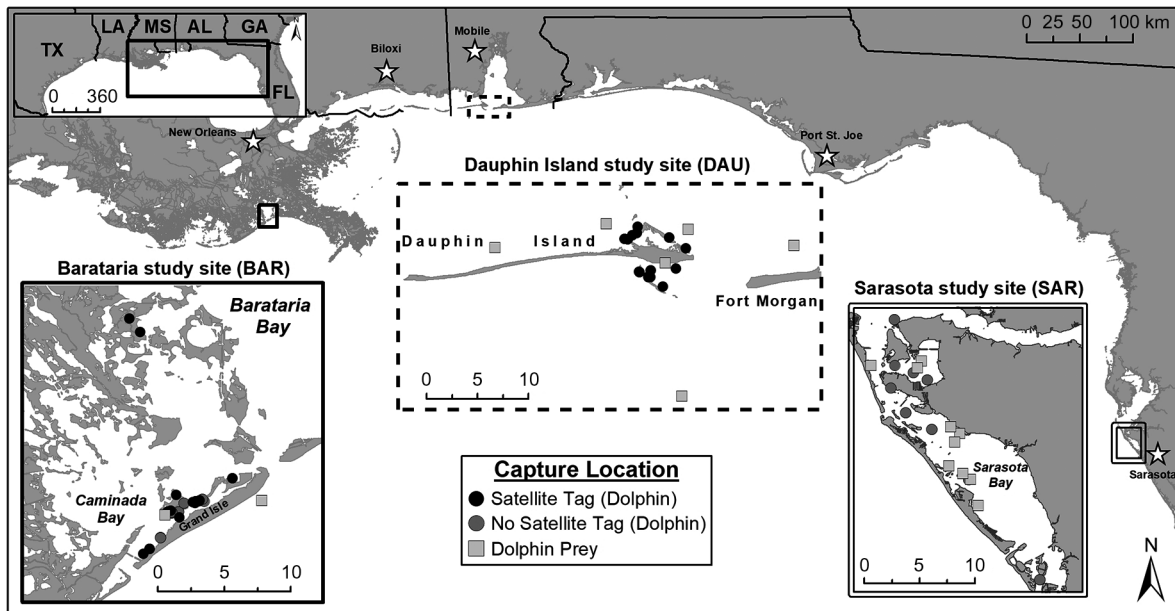


Fig. 1. Northern Gulf of Mexico study sites (Barataria Bay [BAR], Dauphin Island [DAU], and Sarasota Bay [SAR]), dolphin capture, sampling and tagging, and prey capture locations. Scale bars are in kilometers.

Spartina alterniflora marshes and non-vegetated bottoms are the dominate habitat types of BAR, but oyster shell (*Crassostrea virginica*) deposits are also common. BAR experiences freshwater influxes from the Mississippi River (Bianchi et al. 2011) and considerable fishing pressure from commercial fisheries (Chesney et al. 2000). However, BAR is a highly productive system (Conner and Day 1987), which might balance the pressures associated with fishing and changing environmental conditions. BAR is used extensively by the oil and gas industries and has experienced numerous oil spills, including extensive oiling due to the DWH oil spill in 2010 (Michel et al. 2013).

Dauphin Island, Alabama (DAU), is the easternmost barrier island that forms the Mississippi Sound (Eleuterius 1978). Primary habitats in the waters surrounding DAU include *S. alterniflora* marshes, oyster shell deposits, seagrass beds, and shallow, non-vegetated bottoms (Moncreiff 2007). Mobile Bay, east of DAU, receives considerable influxes of freshwater from the Mobile-Tensaw River system, making it the 3rd largest freshwater discharge among watersheds in the United States (Bureau, United States Census 2012). Discharge from Mobile Bay conveys

nutrients and contaminants from both rural (e.g., agriculture) and urban (e.g., wastewater, chemical industries, impervious surfaces) land uses (Biancani et al. 2012, Gancel 2020). The waters surrounding DAU experience pressure from fisheries as well as considerable ship traffic because the Intracoastal Waterway is located to the north and the Mobile Bay ship channel is east of the island. DAU experienced some oiling following the DWH oil spill, but to a lesser extent than BAR (Michel et al. 2013).

Sarasota Bay (SAR) is a series of shallow bays (<4 m deep) along the west-central Florida peninsula that are connected to the GoM by several narrow passes. SAR is characterized by extensive seagrass meadows, sandy bottom channels and open bays, and mangroves (Berens McCabe et al. 2010). SAR experiences high pressure from recreational fisheries (Powell and Wells 2011), comparable exposure to point-source contaminants as in BAR and DAU (Balmer et al. 2015), but minimal exposure to commercial fisheries as a result of a state-wide net ban in 1995 (Rossman et al. 2013). The long-term resident dolphins within this region form one of the most well-studied populations of free-ranging small cetaceans in the world, studied since 1970 (Wells 2014).

Dolphin sampling

Tissue samples for stable isotope analyses were collected at all three study sites, and telemetry tags were attached at two of the study sites (BAR and DAU; Fig. 1) during dolphin health assessments in 2018. Capture-release methodologies for small cetacean health assessments have been previously detailed (Schwacke et al. 2014, Barratclough et al. 2019). Briefly, dolphins were encircled with a 365 × 7 m deep seine net, depending on the site. For shallow-water sets (<1.5 m), well-trained handlers were deployed around the seine net, and when dolphins became entangled the handlers approached and restrained the dolphins. For deep-water sets (>1.5 m), handlers approached from a response vessel (6.7 m, center-console, rigid-hulled inflatable boats; Zodiac of North America, Stevensville, Maryland, USA), and once a dolphin became entangled, handlers used control lines to position the dolphin parallel to the response vessel and moved it to a 3 m long, tri-fold floating mat where it underwent evaluations (Schwacke et al. 2014). Tissue samples were collected from the dorsal fin using an 8 mm coring tool, and tags were attached while dolphins were in the water, on the floating mat, or onboard a specially designed processing vessel. Samples were stored at −20°C prior to sample processing. Tags attached on the dorsal fin dolphins included a KiwiSat 202 K2F (Lotek Wireless Inc., Newmarket, Ontario, Canada) satellite-linked transmitter at BAR or a SPOT299 (Wildlife Computers, Redmond, Washington, USA) satellite-linked transmitter at DAU (Balmer et al. 2014, Wells et al. 2017). The protocols for health assessments were designed with dolphin welfare and human safety being the utmost considerations, with samples collected efficiently to ensure all animals were handled safely and released as soon as possible by the capture team (Barratclough et al. 2019).

To define how diets may have changed through time, we determined stable isotope ratios in multiple tissues from dolphins that stranded dead along the Alabama coast, an area surrounding and including DAU. We analyzed liver, muscle, and skin samples from 30 randomly selected dolphins that stranded in 2011, 2013–2015, and 2017–2018 ($n = 5$ individual dolphins from each year): 2011 (all tissues $n = 5$), 2013 (liver: $n = 4$; skin: $n = 5$; muscle: $n = 3$),

2014 (liver: $n = 2$; skin: $n = 5$; muscle: $n = 5$), 2015, 2017, and 2018 (all tissues = 5). Tissue samples were obtained from the archival collection of the Alabama Marine Mammal Stranding Network, where they were stored frozen at −20°C prior to analyses. This analysis was performed with DAU animals only because archival dolphin tissues were not available for BAR or SAR.

Prey sample collection

We collected prey samples (fish, decapods, cephalopods) at all three study sites (Fig. 1) at times and locations to best align with sampled dolphins. In BAR, we collected prey samples in July 2018 from two locations using an otter trawl (4.6 m wide, 3.8 cm mesh) and categorized them into four groups for subsequent analysis: anchovy (*Anchoa mitchilli*), Ariidae (*Ariopsis felis*), decapoda (*Farfantepenaeus aztecus* and *Callinectes sapidus*), and Perciformes (*Micropogonias undulatus*, *Peprilus triacanthus*, and *Lagodon rhomboides*). Trawls were pulled at ~2 km/h for 20 min, after which time the contents of the trawl were checked, and if insufficient amounts of prey were captured (>6 individuals per group), then the trawl was repeated once. The trawl was not repeated after the second attempt if no additional prey items were obtained.

In DAU, during Oct 2018, we collected prey from four locations spanning the dolphin capture locations, using an otter trawl (4.9 m wide, 3.8-cm mesh). To define changes in available diet through time that may be related to environmental change or disturbance, at DAU we additionally analyzed prey previously collected during July 2011, 2013–2015, and 2017–2018, from two locations using an otter trawl (7.6 m wide, 3.8-cm mesh). We categorized prey from DAU into five taxonomic groups: anchovy (*A. mitchilli* and *Anchoa hepsetus*), cephalopods (*Loligo pealeii* and *Lolliguncula brevis*), non-anchovy clupeidae (*Brevoortia patronus*, *Dorosoma petenense*, and *Harengula jaguana*), decapoda (*F. aztecus* and *C. sapidus*), and Perciformes (*Chloroscombrus chrysurus*, *Cynoscion arenarius*, *Leiostomus xanthurus*, and *M. undulatus*). Trawling method was the same as at BAR.

In SAR, we collected prey samples in July 2018 from 10 locations (Fig. 1) by purse seine (183 × 6.6 m) and categorized them into six taxonomic groups: anchovy (*A. mitchilli*), Batrachoididae

(*Opsanus beta*), decapoda (*C. sapidus*), Elopidae (*Elops saurus*), Mugilidae (*Mugil cephalus*), and Perciformes (*Archosargus probatocephalus*, *Caranx hippos*, *Cynoscion nebulosus*, *L. rhomboides*, *L. xanthurus*, and *Orthopristis chrysoptera*). In general, the fish we sampled were between 10 and 30 cm total length, except anchovies, which were 3–11 cm, decapods were between 3–14 cm, and cephalopods were 4–15 cm.

Stable isotope analysis

For dolphin tissues, we removed blubber from skin, and all tissues (liver, muscle, and skin) were rinsed in UP water prior to lipid extraction (Cloyed et al. 2020). Because the process of lipid synthesis discriminates against ^{13}C , lipid-rich tissues often have depleted $\delta^{13}\text{C}$ values (DeNiro and Epstein 1977, Post et al. 2007) that can affect mixing model analyses. Extracting lipids before isotopic analysis is the primary way to account for these effects (Lesage et al. 2010, Tarroux et al. 2010, Ryan et al. 2012, Giménez et al. 2017, Cloyed et al. 2020). We used the modified Folch technique for lipid extraction (Sweeting et al. 2006, Cloyed et al. 2020), where samples were placed in 2 mL UP water and homogenized with a handheld rotor-stator (Waverly H100; Waverly Scientific, Waverly, Iowa, USA), after which 6 mL of 2:1 chloroform:methanol solution was added, and the samples were sonicated for 5 min and centrifuged for 10 min at 3353 g. The supernatant was removed, and the process was repeated 2–4 times until the supernatant was clear. Samples were dried at 60°C for 48 h and packed into tin capsules for isotope analysis. For prey samples, we dissected muscle from fish and decapods, and mantle tissue from cephalopods. All prey samples were rinsed with UP water, dried at 60°C for 48 h, homogenized with mortar and pestle, and packed into tin capsules for isotope analysis.

Carbon and nitrogen analyses were performed at the Stable Isotope Facility of University of California at Davis (<https://stableisotopefacility.ucdavis.edu>). Isotopic values were expressed using delta notation (δ) in parts per thousand (‰), where $\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, with R_{sample} and R_{standard} representing the molar ratios of $\text{C}^{13}/\text{C}^{12}$ and $\text{N}^{15}/\text{N}^{14}$ 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 (bovine liver, glutamic acid, and nylon 6 for C and N; repeated analyses of identical samples for S) showed that precision (SD) was $\pm 0.08\text{‰}$ and 0.07‰ for carbon and nitrogen, respectively.

To determine differences in the isotopic niches of dolphins among sites, we used stable isotope Bayesian ellipses in R corrected for small sample size (SIBER; Jackson et al. 2011). The area of these ellipses represents variation in two-dimensional graphical space, and in our analyses, we set ellipses to represent 95% credible intervals. We estimated the size of each ellipse and the pairwise proportional overlap of the ellipses among sites. We also estimated and compared ellipses of skin samples from dolphins that stranded each year in DAU. We used only dolphin skin samples in this analysis because it was the only tissue for which five samples were available from each year.

We used the package *stable isotope mixing model in r* (SIMMR; Parnell 2016) to estimate the proportional dietary contributions for each prey group. Different prey groups were used for each site because the prey captured during trawling varied among them. SIMMR uses a Bayesian framework, and we obtained prior information from previous studies of dolphins in the northern GoM for use in the models (Appendix S1: Table S1; Barros and Odell 1990, Berens McCabe et al. 2010, Dunshea et al. 2013). For skin samples, we obtained trophic discrimination factors (Appendix S1: Table S2) by averaging values from the literature (Browning et al. 2014, Giménez et al. 2016). Trophic discrimination values for both muscle and liver (Appendix S1: Table S2) were taken from fin whales (*Balaenoptera physalus*), which was the phylogenetically most similar species to common bottlenose dolphins for which this information was available (Borrell et al. 2016). We ran models using only consumer tissues that fell within the resource polygon after accounting for trophic discrimination factors (Smith et al. 2013b). We ran a mixing model for each site, using only prey and dolphin isotope values from that site and nearest the period of live capture (most recent sampling) for this analysis. For the temporal analysis on dolphins that stranded in Alabama, we additionally ran mixing models for each year and used only prey

captured during the July trawls of the associated year. We iterated the mixing models 20,000 times with a burn-in of 2000, which provided adequate convergence in all models.

Dolphin telemetry and spatial analyses

To spatially define habitat use, we used satellite telemetry on dolphins from BAR and DAU. We did not tag any dolphins from SAR because those dolphins have been well studied and their behaviors and movements are well documented (Irvine et al. 1981, Nowacek 2002, McHugh et al. 2011a). Satellite-linked transmitter specifications, programming, and attachment protocols have been detailed previously (Balmer et al. 2014, Wells et al. 2017). The KiwiSat 202 K2F and SPOT299 tags had a projected battery life of 168 and 280 d, respectively. To increase battery life and provide the highest quality location data, we programmed transmitters in the Advanced Research and Global Observation Satellite (ARGOS) data collection and location system (Collecte Localisation Satellites [CLS] 2011) to specifically target transmission windows with optimal satellite pass altitudes and durations. The BAR KiwiSat 202 K2F tags were programmed for 4, one-hour transmission windows (1300–1659 UTC), and the DAU SPOT299 tags were programmed for 6, one-hour transmission windows (0100–0259, 1300–1659 UTC). Tags were attached 38.4 mm from the trailing edge of the dorsal fin and affixed to the lower third of the dorsal fin. To reduce biogrowth, we coated tags, excluding the saltwater switches, with Prospeed (Oceanmax, Ltd., Auckland, New Zealand).

Telemetry data were received from the ARGOS CLS system. We then filtered the telemetry data through the Douglas ARGOS-filter algorithm (Douglas 2006), which evaluates the plausibility of locations based upon spatial redundancy, ARGOS Location Class (LC), movement rates across time, and angle of movement between locations (Udevitz et al. 2009). ARGOS LC 3, 2, and 1 data were used for subsequent spatial analyses, with estimated errors of <250 m, 250–500 m, and 500–1500 m, respectively.

Utilization distributions (UD) were used to define niche breadth in terms of space use and movement (Worton 1989). We used kernel density estimates (KDEs) to calculate UD (50% and

95%) for all tagged individuals in BAR and DAU study sites (Kie et al. 2010). Dolphins were grouped into cumulative ranging patterns post hoc based upon their individual locations from the telemetry data and general classification of the respective ranging pattern within each study site. Cumulative UD (50% and 95%) were calculated using all locations (i.e., all locations were given equal weight; Citta et al. 2018). Although this method biases the cumulative UD toward tags that transmit for longer durations, it is a more conservative approach given we do not know what proportion of the population is being evaluated (reviewed in Citta et al. 2018).

We used a KDE method that accounted for barriers to movement in Geostatistical Analyst and Spatial Analyst Tools (ArcGIS 10.6; ESRI, Redlands, California, USA) to calculate all UD in the Universal Transverse Mercator (UTM) Zone 15 and 16 North projection and the World Geodetic System (WGS) 1984 datum. The output grid cell size was 1 km² to account for ARGOS LC errors and to allow for fine-scale spatial resolution of the telemetry data (Jay et al. 2012, Sprogis et al. 2016). Because bandwidth selection, or the smoothing parameter (*h*), can strongly affect the KDE distribution (Gitzen et al. 2006, 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.

We used hot spot analyses to statistically quantify spatial clustering of dolphins with satellite-linked telemetry data (Block et al. 2011, Queiroz et al. 2016, Robinson et al. 2016). Getis-Ord G_i^* (Getis and Ord 1992) is a widely used spatial autocorrelation statistic that provides a *z*-score and significance (*P*-value) at each telemetry location or group of locations (reviewed in Feng et al. 2018). For example, at $P = 0.05$, $z > 2$ indicate hot spots, $z < -2$ indicate cold spots, and $-1 < z > 1$ indicate random spatial processes (reviewed in Feng et al. 2017). Satellite-linked tag locations for all cumulative ranging patterns in both BAR and DAU study sites were grouped into grid cells of 1 km² (Smith et al. 2013a, Mullen et al. 2017), and Getis-Ord G_i^* 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 G_i^* hot spot analysis (ESRI 2019). For each cumulative ranging pattern, hot spots were plotted at $P < 0.01$ and $P < 0.05$ levels to assess differences in spatial clustering.

Dietary and movement breadth in marine mammals

To determine whether patterns of dietary and habitat niche breadth influence the vulnerability of cetaceans to environmental disturbances and changes, we gathered information on diet, movement and site fidelity, habitat use, and IUCN status for a wide range of species. To measure breadth of diet, we counted the number of prey groups (fish, cephalopods, decapods, zooplankton) in each species' diets. If a prey group was only a small proportion of a species diet (i.e., < 0.15), we counted that prey group as 0.5 instead of 1 and thereby obtained a weighted estimate for diet. To measure variation in movement breadth and site fidelity, we considered three different movement patterns, low-area, high fidelity; high-area, high fidelity; and high-area, low fidelity. The low-area, high fidelity category included species that had movements contained to small areas (i.e., within bays and sounds or recorded to have small home ranges) and showed high fidelity to sites within that area. The high-area, high fidelity category included individuals that may move over large scales (i.e., along large sections of a continental shelf, among islands) but always returned to the same sites within that large area. The high-area, low fidelity category included species that moved large distances and did not exhibit fidelity to sites within that large area. We considered species to be habitat generalists if they used more than one habitat (inshore/estuary, nearshore/continental shelf, offshore/open ocean). Finally, we recorded the IUCN status of each species. If IUCN status was unavailable (i.e., killer whales), we sought primary literature sources that described population trends of each species and considered their population status according to those sources.

RESULTS

Dolphin health assessments and satellite tagging

The BAR health assessment was performed for 10 d (10–14, 16–20 July 2018) during which 34 dolphins were captured ($\varphi = 13$, $\sigma = 21$), 19 were tagged ($\varphi = 6$, $\sigma = 13$), 29 were used for the SIBER analysis ($\varphi = 11$, $\sigma = 18$), and 26 were used for isotopic mixing model analysis ($\varphi = 10$, $\sigma = 16$). The DAU health assessment was performed for 8 d (20–21, 23–28 September 2018), during which 18 dolphins were captured, 17 were tagged ($\varphi = 9$, $\sigma = 8$), 17 were used for the SIBER analysis ($\varphi = 8$, $\sigma = 9$), and seven were used in isotopic mixing model analysis ($\varphi = 3$, $\sigma = 4$). The SAR health assessment occurred for 5 d (11–15 June 2018), 20 dolphins were captured ($\varphi = 9$, $\sigma = 11$), 0 were tagged, 16 were used for the SIBER analysis ($\varphi = 7$, $\sigma = 9$), and 12 were used for the isotopic mixing model analysis ($\varphi = 5$, $\sigma = 7$).

Isotopic niches

The isotopic niches of live dolphins varied significantly among sites, but the ellipses of dolphins from BAR and DAU were more similar to each other than the ellipse of dolphins from SAR (Appendix S1: Table S3; Fig. 2A). Correspondingly, about 28% of the DAU ellipse overlapped with the BAR ellipse, 63% of the BAR ellipse overlapped with the DAU ellipse, and neither the DAU nor the BAR ellipses overlapped with the SAR ellipse (Fig. 2A). DAU and SAR had similar-sized ellipses ($P = 0.653$), although DAU trended slightly larger, and both were larger than BAR (DAU and BAR: $P = 0.005$; SAR and BAR: $P = 0.02$) (Appendix S1: Table S3; Fig. 2A).

The isotopic niches of stranded dolphins in DAU overlapped among years but became larger through time (Appendix S1: Table S4; Fig. 2B). Ellipses from all years overlapped, and differences in the amount of overlap was driven by ellipsis sizes (Fig. 2B). 2011 and 2013 ellipses were similar in size ($P = 0.295$), but ellipses from both years were smaller than all other years (2011–2014: $P = 0.006$; 2011 and 2015: $P = 0.024$; 2011 and 2017: $P = 0.006$; 2011 and 2018: $P = 0.002$; 2013 and 2014: $P = 0.022$; 2013 and 2015: $P = 0.079$; 2013 and 2017: $P = 0.020$; 2013 and 2018: $P = 0.013$) (Appendix S1: Table S4; Fig. 2B). Ellipses from all other years were

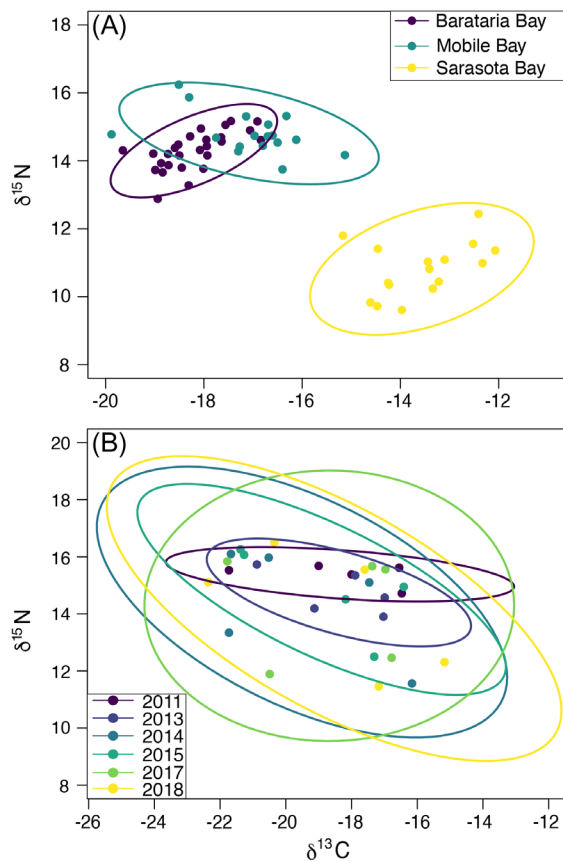


Fig. 2. Isotopic niches of live-captured dolphins from Barataria, Dauphin Island (DAU), and Sarasota Bay (A) and stranded dolphins from DAU (B) measured using stable isotope Bayesian ellipses in R. Ellipses represent 95% credible intervals in two-dimensional graphical space.

statistically similar in size, with estimates for 2014, 2017, and 2018 trending larger than the 2015 ellipse (Appendix S1: Table S4; Fig. 2B).

Prey sampling

In BAR, a total of 68 individual prey were used for isotopic analyses (18 anchovies, seven *Aridia*, 10 decapods, and 33 Perciformes). For the October 2018 trawl around DAU, a total of 67 individual prey species were used for isotopic analysis (seven anchovies, two clupeids, 19 decapods, 37 Perciformes, and two cephalopods). For archived prey around DAU, a total of 217 individual species were analyzed, including 37 in 2011 (six anchovies, five clupeids, seven

decapods, 12 Perciformes, and seven cephalopods were sampled for isotope analysis), 24 in 2013 (eight anchovies, two clupeids, one decapod, eight Perciformes, and five cephalopods), 41 in 2014 (six anchovies, five clupeids, seven decapods, 11 Perciformes, and 12 cephalopods), 46 in 2015 (12 anchovies, one clupeid, 12 decapods, nine Perciformes, and 12 cephalopods), 20 in 2017 (three anchovies, one clupeid, six decapods, 10 Perciformes, and 0 cephalopods), and 49 in 2018 (12 anchovies, five clupeids, 10 decapods, 10 Perciformes, and 12 cephalopods). In SAR, a total of 58 individual prey were analyzed (two anchovies, three Batrachoidiformes, nine decapods, six Elopidae, nine Mugiliformes, and 29 Perciformes).

Dietary patterns

Mixing model estimates suggested that diets varied among study sites for live-captured dolphins. At BAR, dolphins likely fed almost exclusively on Perciformes fish, much less on other fish types (*Anchoa* spp. and *A. felis*), and the least on decapods (Fig. 3; Appendix S1: Table S5). At DAU, dolphins also likely fed predominately on Perciformes fish but included a large proportion of cephalopods (which were absent from our prey sampling at BAR) and a greater proportion of other fish compared to BAR dolphins (Fig. 3; Appendix S1: Table S6). Dietary estimates of dolphins from SAR followed previous reports on diets, finding that they fed entirely on fish, which consisted mostly of Perciformes followed by Batrachoidae (toadfish), Elopidae (ladyfish), and Mugilidae (mullet) (Fig. 3; Appendix S1: Table S7). Unlike other sites, mixing models indicated that few to no anchovies and no decapods were consumed by SAR dolphins (Fig. 3; Appendix S1: Table S7).

Mixing model estimates of diets from stranded dolphins from DAU differed among years. In most years (2011, 2013–2014, 2017), Perciformes fish likely dominated the diets of stranded dolphins, a finding common among tissues (Fig. 4; Appendix S1: Table S6). Cephalopods were estimated as the second most common prey item, and dolphin diets in 2015 and 2018 likely had a slightly higher proportion of cephalopods compared with other years, a finding consistent among tissue types (Fig. 3; Appendix S1: Table S6). Diets between DAU 2018 stranded

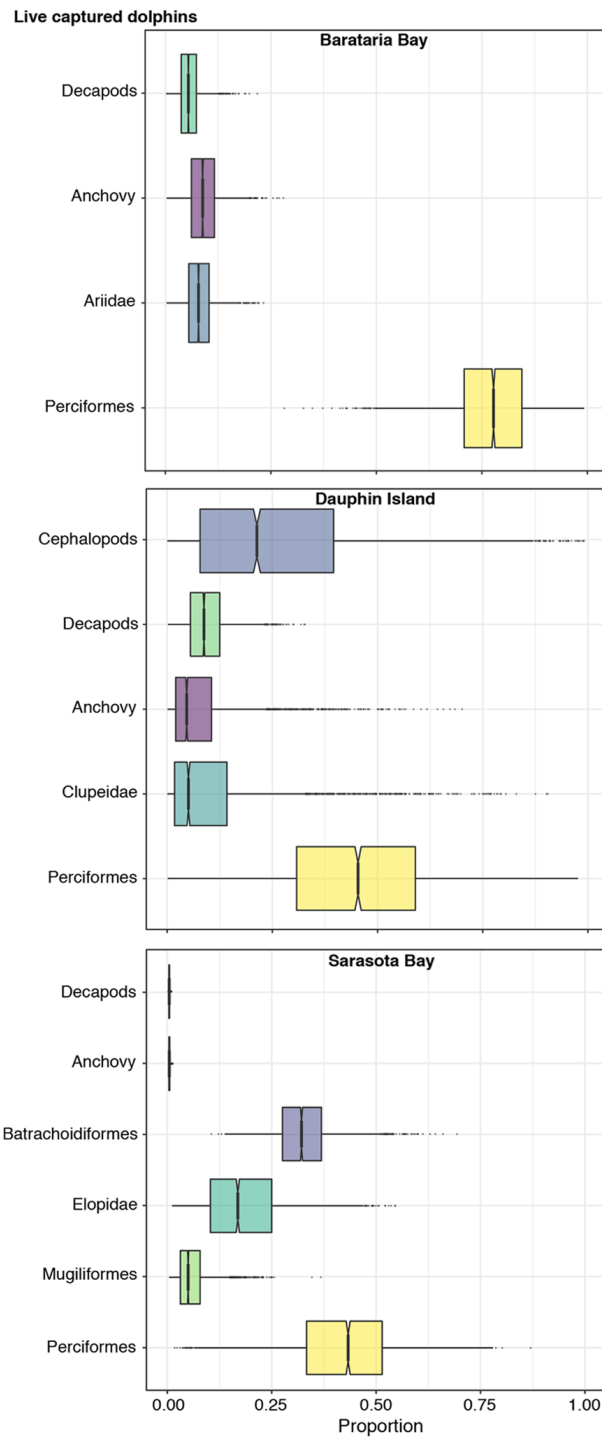


Fig. 3. Proportional contributions of prey groups to live-captured common bottlenose dolphin diets from 2018 health assessments in Barataria Bay (top), Dauphin Island (middle), and Sarasota Bay (bottom). The boxes represent the first and third quartiles of the posterior distributions, the black bars represent the medians, and the dots outside the boxes represent posterior estimates outside the first and third quartiles.

and live-captured dolphins were similar (Figs. 3, 4; Appendix S1: Table S6). Decapods were likely more common than either Anchovy or other Clupeidae fish in the diets of dolphins from DAU compared with the dolphins from BAR, although their 95% CIs overlapped in all years (Fig. 4; Appendix S1: Table S6).

Ranging patterns

In BAR, KiwiSat tags transmitted for a mean of 75 ± 46 (SD) days with a mean of 184 ± 151 cumulative usable quality locations. Individual UD_s ranged from 0.2 to 17.7 km² (50%) and 0.3 to 76.5 km² (95%) and extended northward to the southern edge of Little Lake and southward to the coastal waters of the GoM (Table 1). In BAR, two cumulative ranging patterns emerged, Interior (West Champagne Bay, Bassa Bassa Bay northward) and Island-associated (Caminada Bay, southern Barataria Bay, waters surrounding Grand Isle; Fig. 5; Appendix S1: Figs. S3, S4). For cumulative ranging patterns, individuals were grouped ad hoc into the Interior ranging pattern ($N = 4$; $\eta = 2$, $\sigma = 2$) and the Island-associated ranging pattern ($N = 15$; $\eta = 4$, $\sigma = 11$). Cumulative 50% and 95% UD_s for the Interior ranging patterns were 10.1 and 47.9 km², respectively, and for the Island-associated ranging patterns were 36.8 and 225.7 km², respectively (Table 2, Fig. 5; Appendix S1: Figs. S3, S4). Hot spot analyses identified significant differences in spatial clustering ($P < 0.05$ and $P < 0.01$) between Interior and Island-associated ranging patterns, with the four Interior animals clustered to the west of Bassa Bassa Bay and the 15 Island-associated animals clustered in Caminada Bay and the waters surrounding Grand Isle (Fig. 5; Appendix S1: Figs. S5, S6).

In DAU, SPOT satellite-linked tags ($\eta = 9$, $\sigma = 8$) transmitted for a mean of 153 ± 37 (SD) days, with a mean of 607 ± 214 cumulative usable quality locations. Individual UD_s ranged from 4.7 to 37.4 km² (50%) and 7.3 to 166.0 km² (95%) and extended from the eastern tip of Dauphin Island to the western tip of Ship Island (Table 1). In DAU, two cumulative ranging patterns also emerged, Island-east (coastal/estuarine Dauphin Island) and Island-west (coastal/estuarine waters from western Dauphin Island-east to Petit Bois and Horn Islands; Fig. 6; Appendix S1: Figs. S5, S6). For cumulative ranging patterns,

individuals were grouped ad hoc into the Island-east ranging pattern ($N = 11$; $\eta = 4$, $\sigma = 7$) and the Island-west ranging pattern ($N = 6$; $\eta = 5$, $\sigma = 1$). Cumulative 50% and 95% UD_s for the Island-east were 49.0 and 337.1 km² and for the Island-west ranging patterns were 43.3 and 311.7 km², respectively (Table 2, Fig. 6; Appendix S1: Figs. S5, S6). Hot spot analyses identified significant differences in spatial clustering ($P < 0.05$ and $P < 0.01$) between the Island-east and Island-west ranging patterns, with Island-east animals clustered along the eastern and western tips of Dauphin Island and the Island-west animals clustered along the eastern tip of Horn Island and western tip of Petit Bois Island (Fig. 6; Appendix S1: Figs. S5, S6).

Dietary and movement flexibility in cetaceans

We found data on diet, movement, habitat use, and population status on 31 cetacean species and three ecotypes of bottlenose dolphins (estuarine, nearshore, and offshore; Appendix S1: Table S8). In general, species with IUCN status of vulnerable or endangered (orange or red, respectively) had very specialized diets and movements patterns that had high-area, high-fidelity (Fig. 7). Species with flexible diets and low site fidelity were all species of least concern (Fig. 7).

DISCUSSION

Our findings show that nearshore common bottlenose dolphins are generalist foragers with some site-specific selective feeding, suggesting that they have a broad dietary niche in the GoM. *SIBER* analyses indicated that isotopic niches varied across sites, likely driven by differences in baseline values among sites. For example, both BAR and DAU are heavily influenced by freshwater inputs from terrestrial runoff, which likely contributed to the overlap among ellipses, whereas SAR has greater marine influence, with considerable seagrass coverage and seagrass-associated fish (Berens McCabe et al. 2010, Rossman et al. 2015a). Mixing model results further support the idea that differences in isotopic niches among sites are driven by varying isotopic baselines rather than major differences in diet. Mixing model estimates indicated that dolphins foraged mostly on fish in BAR and DAU and exclusively on fish in SAR, likely preferring fish

**Mobile Bay, Alabama
Stranded dolphins**

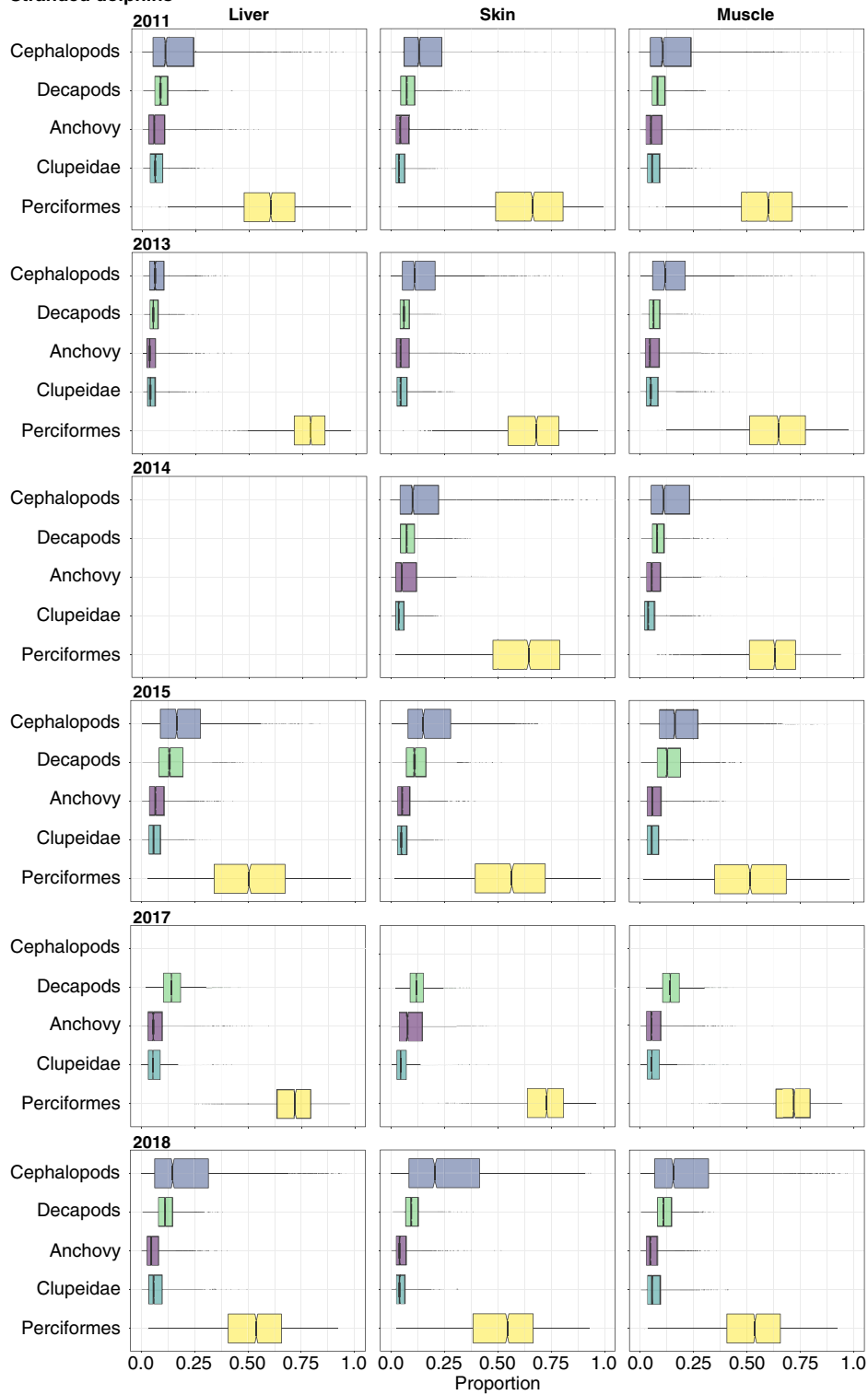


Fig. 4. Proportional contributions of prey groups to the diets of common bottlenose dolphin that stranded along the Alabama coast in 2011, 2013-2015, and 2017-2018. See Fig. 2 legend for information on the boxes and estimates outside the boxes.

Table 1. Satellite tagging summary for common bottlenose dolphins in the Barataria and Dauphin Island, including tag type, sex, deployment (Dep) and final satellite transmission (FST) dates, number of cumulative quality locations (CQL [3, 2, and 1]), number of days transmitting (DT), ranging pattern classification (RP), and individual utilization distributions (UDs) (50% and 95%).

FB	Tag type	Sex	Dep date	FST date	CQL	DT	RP	UD (km ²)	
								50%	95%
Barataria									
Y36	KiwiSat 202 K2F	M	12 July 2018	22 August 2018	45	41	Interior	1.1	3.3
YX9	KiwiSat 202 K2F	F	12 July 2018	24 July 2018	47	12	Interior	0.6	1.6
YN4	KiwiSat 202 K2F	M	20 July 2018	25 September 2018	252	67	Interior	2.0	4.3
YZ1	KiwiSat 202 K2F	F	20 July 2018	10 August 2018	108	21	Interior	0.9	2.5
Y70	KiwiSat 202 K2F	M	10 July 2018	19 August 2018	107	40	Island	1.0	1.8
YF8	KiwiSat 202 K2F	M	10 July 2018	28 July 2018	53	18	Island	0.2	0.3
YX7	KiwiSat 202 K2F	F	10 July 2018	9 December 2018	529	152	Island	6.8	28.7
YJ2	KiwiSat 202 K2F	M	12 July 2018	30 July 2018	81	18	Island	2.0	2.6
Y21	KiwiSat 202 K2F	F	13 July 2018	20 October 2018	179	99	Island	3.6	12.4
YJ4	KiwiSat 202 K2F	M	13 July 2018	16 September 2018	32	65	Island	0.5	1.1
YJ6	KiwiSat 202 K2F	M	13 July 2018	15 August 2018	102	33	Island	3.0	8.2
YV7	KiwiSat 202 K2F	F	13 July 2018	7 October 2018	188	86	Island	3.1	12.8
YJ8	KiwiSat 202 K2F	M	14 July 2018	8 November 2018	72	117	Island	1.9	7.9
YK0	KiwiSat 202 K2F	M	14 July 2018	2 November 2018	88	111	Island	4.3	5.3
YA6	KiwiSat 202 K2F	M	16 July 2018	29 November 2018	370	136	Island	17.7	68.4
YK4	KiwiSat 202 K2F	M	16 July 2018	21 September 2018	185	67	Island	4.4	9.5
YY3	KiwiSat 202 K2F	F	16 July 2018	17 November 2018	408	124	Island	1.6	4.2
YK8	KiwiSat 202 K2F	M	19 July 2018	25 September 2018	199	68	Island	1.6	4.2
YN2	KiwiSat 202 K2F	M	19 July 2018	12 December 2018	454	146	Island	14.7	76.5
Dauphin Island									
679	SPOT299-A	F	20 September 2018	25 November 2018	298	66	East	6.3	19.7
684	SPOT299-A	M	20 September 2018	18 February 2019	558	151	East	37.4	166.0
686	SPOT299-A	M	20 September 2018	3 March 2019	392	164	East	7.1	17.8
688	SPOT299-A	M	21 September 2018	27 February 2019	526	159	East	30.8	124.3
690	SPOT299-A	M	21 September 2018	19 February 2019	419	151	East	28.9	104.6
681	SPOT299-A	F	21 September 2018	27 November 2018	335	67	East	4.7	7.3
692	SPOT299-A	M	21 September 2018	31 March 2019	993	191	East	18.4	79.8
694	SPOT299-A	M	23 September 2018	3 April 2019	774	192	East	21.5	93.5
683	SPOT299-A	F	23 September 2018	19 February 2019	381	149	East	6.6	16.3
689	SPOT299-A	F	26 September 2018	23 February 2019	571	150	East	8.8	26.0
6A2	SPOT299-A	M	28 September 2018	21 February 2019	627	146	East	20.3	119.3
685	SPOT299-A	F	25 September 2018	16 March 2019	855	172	West	14.8	38.4
687	SPOT299-A	F	26 September 2018	17 March 2019	797	172	West	22.1	102.2
698	SPOT299-A	F	26 September 2018	29 March 2019	450	184	West	29.8	109.5
691	SPOT299-A	F	26 September 2018	28 February 2019	748	155	West	6.0	20.0
693	SPOT299-A	F	26 September 2018	14 April 2019	907	200	West	7.5	20.6
6A0	SPOT299-A	M	28 September 2018	13 February 2019	696	138	West	35.1	130.9

over non-fish prey because the former are more energetically profitable (Benoit-Bird 2004). At all sites, dolphins fed mostly on Perciformes fish compared with other fish groups, similar to findings from prior GoM studies (Barros and Wells

1998, Berens McCabe et al. 2010, Wilson et al. 2017), and Perciformes fish were the most abundant fish within the observed prey size range in these areas (Baltz et al. 1993, Barros and Wells 1998, Berens McCabe et al. 2010, Hernandez Jr.

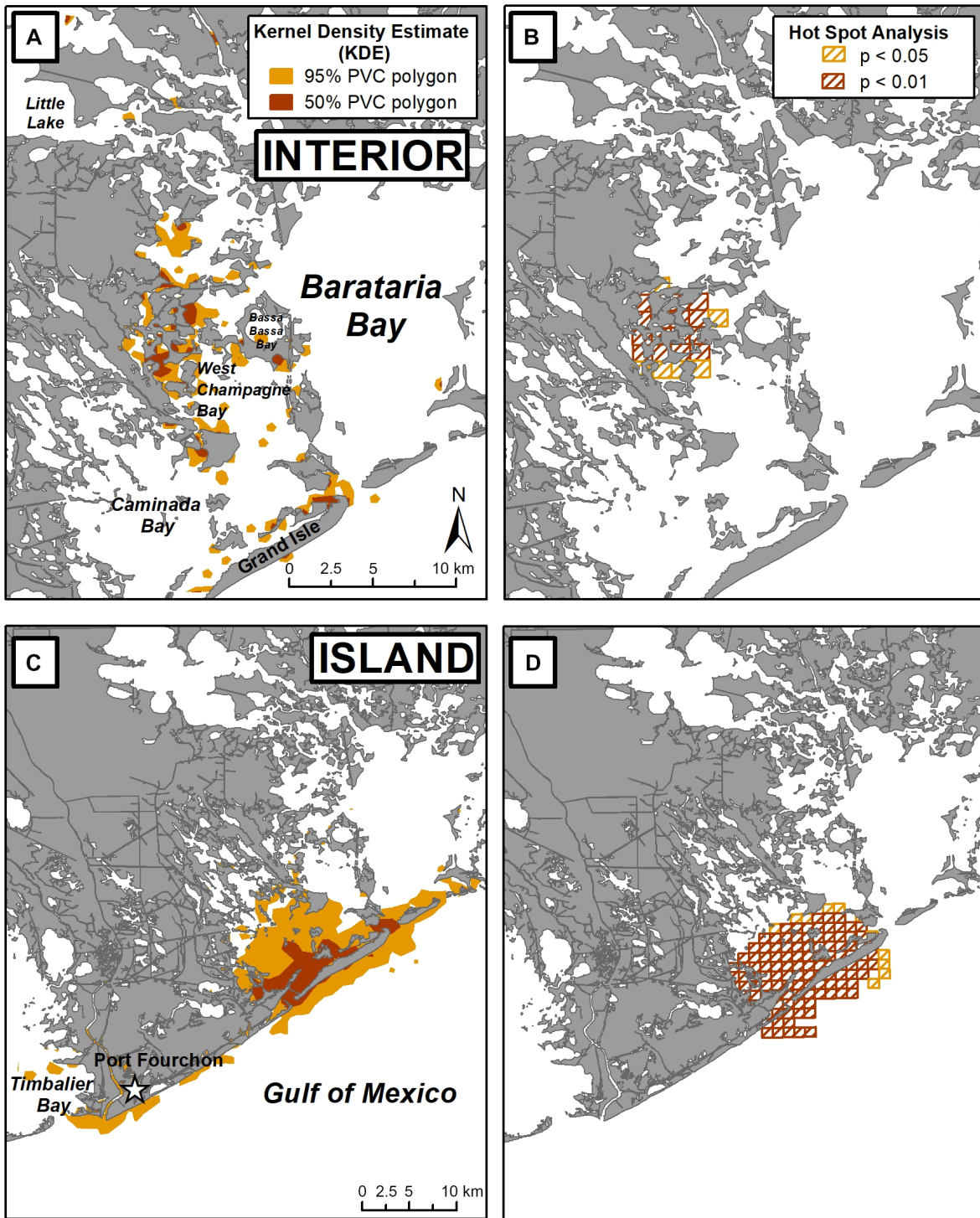


Fig. 5. Movement patterns of common bottlenose dolphins in Barataria Bay, including 50% and 95% utilization distributions and hot spot analysis ($P < 0.05$ and $P < 0.01$) for individuals in the Interior (A, B) and Island-associated (C, D) ranging patterns.

Table 2. Cumulative ranging pattern (RP) satellite tagging summary for common bottlenose dolphins in the Barataria (BAR) and Dauphin Island (DAU) study sites, including number of individuals, number of cumulative quality locations (CQL [3, 2, and 1]), and utilization distributions (UD; 50% and 95%).

Study site	RP	N	CQL	50% UD (km ²)	95% UD (km ²)
BAR	Interior	4	546	10.1	47.9
BAR	Island	15	3046	36.8	225.7
DAU	East	11	5874	49.0	337.1
DAU	West	6	4453	43.3	311.7

et al. 2010). As the presence of prey groups other than Perciformes varied among sites, so did the overall diet of dolphins from each site. Dolphins from BAR and DAU included decapods and cephalopods, as is documented from other studies in the northern GoM and globally (Barros and Odell 1990), and these species were more abundant at BAR and DAU compared with SAR (Berens McCabe et al. 2010, Judkins et al. 2017). Similarly, fish such as Elopidae and Batrachoidae were common in the diets of dolphins in SAR but not BAR and DAU and are more abundant in peninsular Florida compared with BAR and DAU (McBride and Horodysky 2004, Hernandez Jr. et al. 2010). While our study demonstrated differences in dolphins' diets among sites separated by hundreds of kilometers, these same types of differences can occur even at proximal sites. For example, dolphins in SAR previously were shown to prefer fish associated with seagrasses (Barros and Wells 1998, Berens McCabe et al. 2010), but in Clearwater Beach (<70 km away), dolphins do not show this preference (Allen et al. 2001). Across the GoM, therefore, we found a consistent pattern of using the most abundant and likely energetically profitable prey (Benoit-Bird 2004), with proportion of prey varying based on availability, which is a hallmark characteristic of generalist foragers.

Although the isotopic niches of dolphins that stranded in DAU overlapped among all years, dolphin diets likely varied among years along the Alabama coast, potentially related to a combination of natural and anthropogenic disturbances. At DAU, cephalopod consumption was likely higher in 2015 and 2018, a pattern

consistent among tissues and live-captured and stranded dolphins. While dolphins are known to consume cephalopods in the northern GoM and elsewhere, they typically do so much less frequently (Barros and Odell 1990, Blanco et al. 2001, Gannon and Waples 2004). The higher consumption of cephalopods during 2015 and 2018 could have been caused by an increase in cephalopod abundance around DAU during these years. Cephalopods prefer warm, high salinity waters (Waluda and Pierce 1998, Bartol et al. 2002), and 2015 and 2018 were both dry years with some drought conditions along the Alabama coast; most of 2015 was abnormally dry with periods of moderate drought conditions and 2018 began with exceptional drought and abnormally dry and moderate drought conditions lasted throughout most of the year (National Drought Mitigation Center 2020). The observed interannual diet variation, particularly the shift to consuming larger amounts of cephalopods in 2015 and 2018, demonstrates the dietary plasticity of dolphins in the region.

Dietary plasticity may enhance resistance to ecological disturbances and longer-term changes in the northern GoM. Dolphins are known to alter their diets in response to environmental changes and disturbances that affect community composition and trophic relationships (Clavel et al. 2011). For example, during a severe harmful algae bloom in SAR in 2004–2007, fish abundances decreased, and dolphins were forced to survive on fewer primary prey and more alternative food sources (Gannon et al. 2009). In addition, carbon stable isotope analysis of a long-term data set (1944–2010) of dolphins from SAR indicated a potential shift away from seagrass-associated fish as seagrass meadows shrank in size throughout the 20th century (Rossman et al. 2013). In other cases, the introduction of invasive prey have led to dietary shifts (López et al. 2005, Marcoux et al. 2012). In all these cases, dolphins effectively foraged through the food web, switching among prey at a similar trophic level (Essington et al. 2006). In this study, dolphins along the Alabama coast varied their diets through time, likely due to natural environmental variation that affected cephalopod abundances. There were no clear disturbance-related differences through time or among sites that could be clearly related back to the *DWH* oil spill or residual

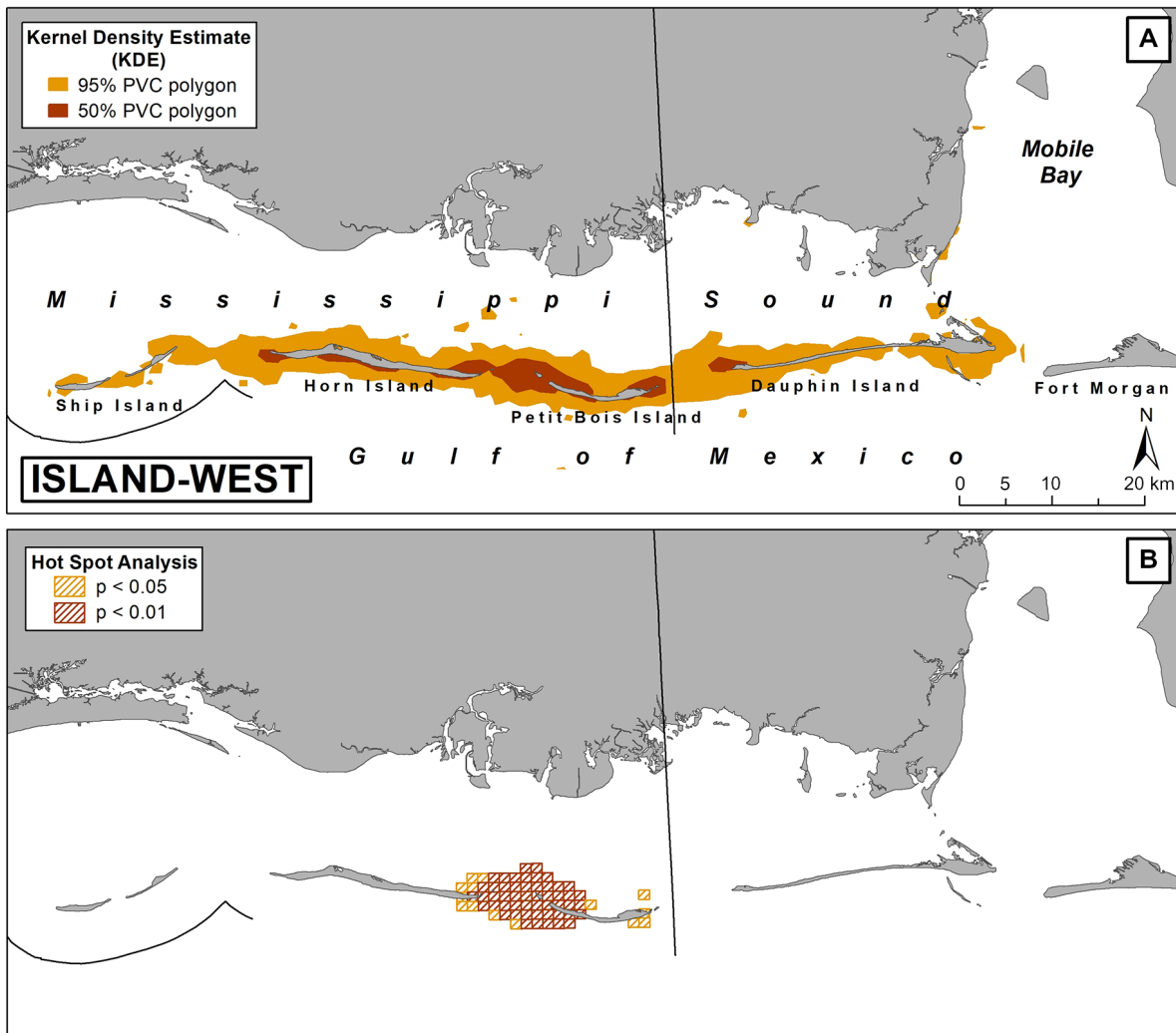


Fig. 6. Movement patterns of common bottlenose dolphins around Dauphin Island, including 50% and 95% utilization distributions and hot spot analysis ($P < 0.05$ and $P < 0.01$) for individuals in the Island-west (A, B) and Island-east (C, D) ranging patterns.

effects on fisheries. A wide dietary niche and trophic plasticity, therefore, likely help GoM dolphins manage ongoing seasonal and interannual environmental change as well as facilitates their resilience to point-source disturbance events such as *DWH* oil spill. These traits help explain how dolphins as a species maintain a cosmopolitan global distribution (Louis et al. 2014).

Dolphin ranging patterns were more limited in BAR compared with DAU but overall were small at both sites and consistent with known habitat and resource use. Dolphins in this study showed

variation in range among habitats consistent with previous findings that dolphins inhabiting bays, sounds, and estuaries (BSE) typically have smaller ranges (Wells et al. 2017) than those in nearshore and offshore areas (Klatsky et al. 2007, Balmer et al. 2018). Range sizes are often driven by resource abundance and distribution (Ford et al. 1998, Andrews et al. 2008), which seems to be the case for BAR and DAU dolphins in this study. Accordingly, BAR dolphins had the smallest known UD in the southeastern United States (Owen et al. 2002, Urian et al. 2009, McHugh

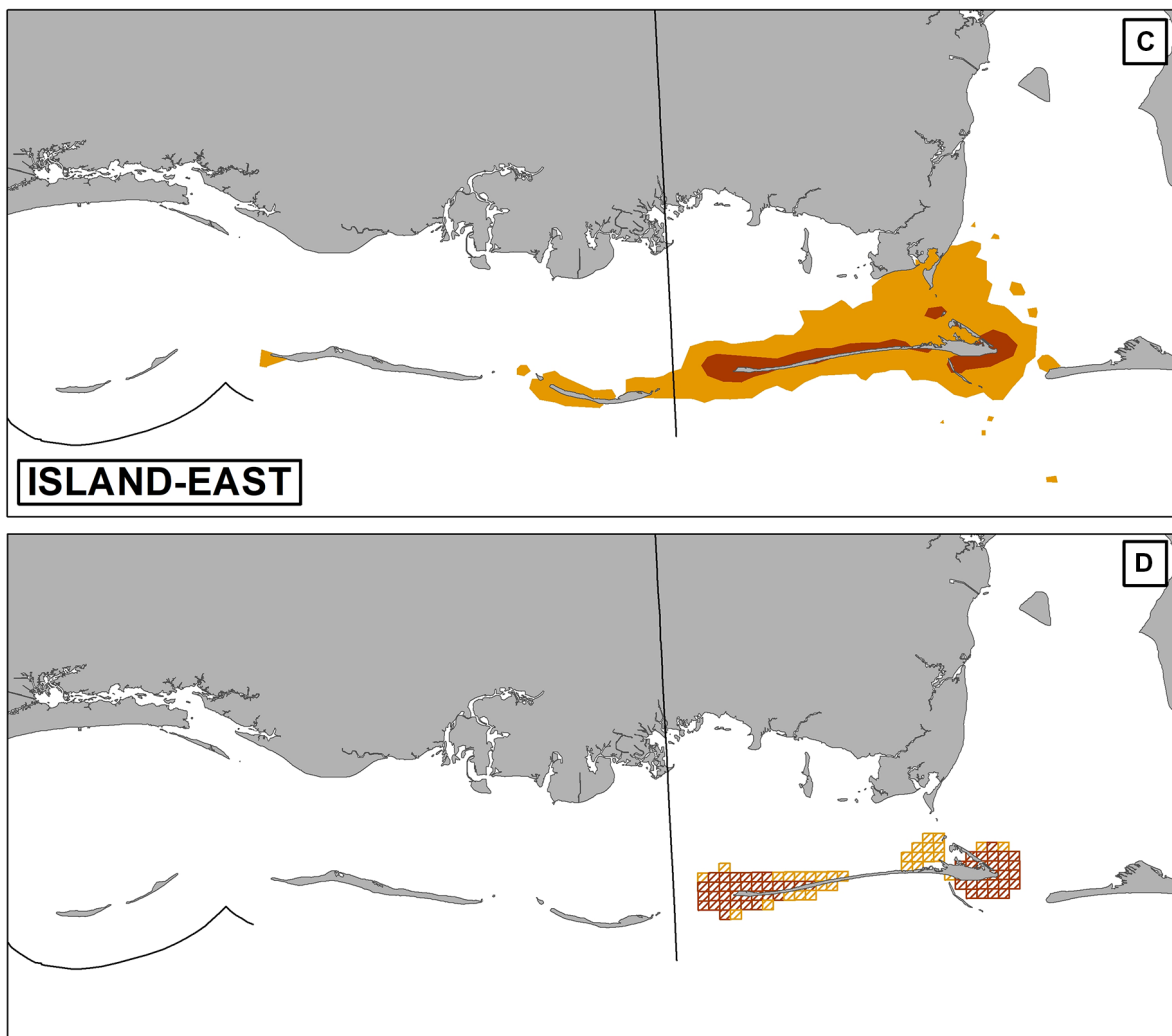


Fig. 6. Continued.

et al. 2011a), with hot spots primarily in edge habitat surrounding salt marshes (Interior) and barrier islands (Island-associated), where fish diversity and abundance in BAR are highest (Baltz et al. 1993). BAR is known to be a highly productive system (e.g., nekton biomass is 7–12 times greater in a Louisiana salt marsh than adjacent GoM waters; Day Jr. et al. 1982, Conner and Day 1987). The extremely small ranges for BAR dolphins may be driven by this productivity, where prey are readily available and predictably distributed, and dolphins need to move little to obtain their nutritional requirements compared with more offshore dolphins (Wells 1980).

Interior dolphins had much smaller ranges than Island-associated dolphins, which may also be driven by resource distribution and patchiness. The ranges of DAU dolphins were larger than in BAR and other estuarine systems, but they were smaller than those of nearshore coastal dolphins (Balmer et al. 2018). The larger UD for DAU dolphins may be a result of the more open water environment of Mississippi Sound that is less productive than the salt marshes of BAR (Conner and Day 1987), prompting these animals to move more to meet their nutritional requirements. The relatively discrete ranging patterns of dolphins from both BAR and DAU suggest that they are

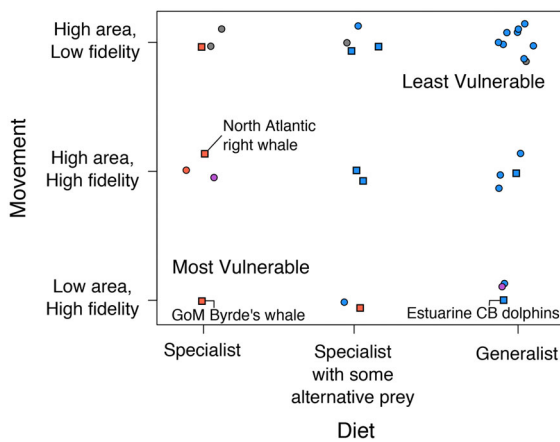


Fig. 7. Biplot with dietary and movement flexibility. Colors refer to IUCN status (blue = least concern, purple = vulnerable and threatened, red = endangered, gray = data deficient). Squares indicate habitat specialists, and circles indicate habitat generalists.

individual habitat specialists, similar to other populations in the northern GoM and that their niche size may be largely driven by resource availability (Rossman et al. 2015b, Wilson et al. 2017).

The ranging patterns we observed in BAR and DAU support and build upon previous studies (Smith et al. 2013a, McDonald et al. 2017, Mullin et al. 2017, Wells et al. 2017). In our study, most Interior dolphins at BAR likely correspond to dolphins previously defined as having a West distribution, and most Island-associated dolphins in our study correspond to Island dolphins in those studies (McDonald et al. 2017, Wells et al. 2017). Based on the additional data provided in this study, we opted to use Interior and Island-associated ranging patterns to better reflect the combination of behavior of the animals (ranging size), ecology of the system (estuarine–marine gradient), and potential threats that may affect each sub-group (freshwater and disease exposure, human interactions; Wissel et al. 2005, McDonald et al. 2017, Wells et al. 2017, Balmer et al. 2018). The finding that DAU dolphin movements primarily surrounded the barrier island along the southern edge of MS Sound is consistent with previous studies (Smith et al. 2013, Mullin et al. 2017), but our study also identified a more distinct eastern distribution

than previously described. It is likely, given the relatively small ranges of dolphins in our study and others (Smith et al. 2013, Mullin et al. 2017), that groups of dolphins are associated with certain islands along the southern edge of the Mississippi Sound. While these previous studies also identified a mainland-associated group, our limited sampling to waters surrounding Dauphin Island likely resulted in us only capturing island-associated dolphins. Thus, our described ranging patterns not only expand our knowledge of the distribution of dolphin groups but also capture important ecological gradients and differences in range sizes within and among sites.

In the northern GoM, the National Marine Fisheries Service currently manages for 31 BSE and three coastal stocks (Hayes et al. 2017). Bays, sounds, and estuaries stocks are associated with long-term site fidelity (multiple seasons and years; Tyson et al. 2011, Balmer et al. 2019), while coastal stocks are associated with potential seasonal movements that extend along the coastline (Balmer et al. 2016). The different ranging patterns of these stocks can influence the effects of a given anthropogenic stressor on the stock. For example, nine BSE stocks are estimated to reside within the cumulative oiling footprint of the *DWH* oil spill (NOAA 2015). BAR dolphins had strong, negative, and long-lasting health effects following *DWH* oiling (Schwacke et al. 2014, Lane et al. 2015, Smith et al. 2017), and the majority of individuals in the Barataria Bay Estuarine System (BBES) stock may have been impacted by the *DWH* oil spill (Schwacke et al. 2017, Wells et al. 2017). An estimated 35% (15–49%, CI) of the BBES stock was killed following *DWH* oiling of local waters, while an estimated 22% (13–29%, CI) of the Mississippi Sound, Lake Borgne, Bay Boudreau, and Mobile Bay stocks were killed (NOAA 2015), in which the DAU dolphins currently are hypothesized to be members (Hayes et al. 2017). The lower instances of injury and mortality in Mississippi Sound compared with Barataria Bay may result, at least in part, from the larger range sizes of DAU dolphins combined with more patchy and less sustained oiling in Mississippi Sound (Michel et al. 2013, Schwacke et al. 2017). Thus, the size of ranging patterns and site fidelity are important parameters in determining how populations will be impacted by disturbances that degrade habitats (Schwacke et al. 2014, Balmer et al. 2015, Lane et al. 2015).

In addition to the *DWH* oil spill, dolphins in the GoM and elsewhere are exposed to other pollutants and disturbances that result in habitat degradation. In the southeastern United States, many BSE populations are exposed to persistent organic pollutants (POPs; Balmer et al. 2011, Kucklick et al. 2011), and individuals with ranging patterns closer to pollutant sources have higher concentrations of POPs (Balmer et al. 2011). Although maximum POP levels reported for BAR and DAU dolphins are several times lower than in other southeastern U.S. dolphin populations (Kucklick et al. 2011, Balmer et al. 2015), contaminant concentrations may be an additive stressor on GoM dolphin populations. Many of these BSE populations are also exposed to prolonged periods of low salinity that may contribute to ongoing mortality events for dolphins (Carmichael et al. 2012, Meager and Limpus 2014). Populations of bottlenose dolphins with high site fidelity in the GoM and elsewhere have also been negatively affected by tourism and increased boat traffic (Constantine et al. 2004, Bejder et al. 2006). Thus, dolphin populations with small ranges and high site fidelity may be particularly vulnerable to cumulative stressors associated with pollution and other point sources of disturbance such as fishery and other human interactions.

Our literature search showed that, in general, cetaceans with very specialized diets and high site fidelity were the most likely to be classified as vulnerable or endangered by the IUCN. Vulnerable and endangered cetaceans generally had more restricted diets than movement patterns, and the majority of these cetaceans were categorized into the high-area, high-fidelity group. While the causes for population declines in these species include a combination of factors such as habitat loss, ship collisions, and legacy of whale hunting (Baylis et al. 2015, Pirotta et al. 2019), dietary specialization may further constrain and stress these populations, increasing their vulnerability to environmental disturbances and changes. For example, killer whale populations that specialize on different prey (e.g., chinook salmon, other marine mammals) are thought to be particularly vulnerable (Ford et al. 2009), and the decline in abundance of short-beaked common dolphins, *Delphinus delphis*, in the Mediterranean Sea has been associated with over-fishing

and fishery collapse (Bearzi et al. 2006, 2008). While many of these species have extended movement patterns, they exhibit high site fidelity within those areas. For example, the critically endangered GoM subspecies of Byrde's whale, *Balaenoptera edeni*, specializes on sardines and has highly localized movements in small areas of the northeast GoM (Siciliano et al. 2004). The use of different habitats within extended ranges also may expose cetaceans to adverse conditions at a few sites that may have important population consequences. For example, North Atlantic right whales, *Eubalaena glacialis*, periodically use areas of high ship traffic and suffer numerous ship collisions (Laist et al. 2014). Likewise, the more highly restricted movements of BSE dolphins have exposed them to potentially dangerous pollutants such as oil-derived contaminants and POPs, and some of these populations are threatened (Schwacke et al. 2012, 2014, Smith et al. 2017). Hence, while common bottlenose dolphins as a species fit into the broader pattern of species of least concern that generally have higher dietary flexibility and less-restricted movement patterns, local BSE populations are more likely to be threatened due to their restricted movements and despite dietary flexibility. These results provide strong support that species with narrower dietary or habitat niche breadths may be at greater risk from environmental disturbances.

CONCLUSIONS

We found that populations of estuarine common bottlenose dolphins in the GoM had general and flexible diets but exhibited high site fidelity within small areas, an example of an "ecological cul-de-sac," in which animals must be flexible in some niche dimension if they are unwilling to leave a relatively small home range (Wells 2014). These differences in niche breadth potentially make them less vulnerable to changes in community composition (Gannon et al. 2009, Rossman et al. 2013) and more vulnerable to point-source or location-specific pollutants (Balmer et al. 2011, Schwacke et al. 2014). For cetaceans in general, species with highly specialized diets and high site fidelity were more likely to be listed as vulnerable and endangered by the IUCN. Together, our results support the growing body of research demonstrating species and populations with

narrow niche breadths are more likely to be affected by environmental change and highlight that different axes of niche breadth—dietary and habitat or movement—expose them to different types of disturbance and change. Our results provide a roadmap for predicting which cetacean species may be most vulnerable in the future, as ecosystems around the world continue to experience pulse disturbances and longer-term change.

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EJBM led the collection of dolphin prey in DAU, BAR, and SAR, respectively. All authors participated in planning of the studies and subsequent analyses, participated in discussing the analyses and results, and reviewed and provided edits to the manuscript.

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DATA AVAILABILITY

Data are available from the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at <https://data.gulfresearchinitiative.org> (telemetry, <https://doi.org/10.7266/n7-15s1-9j90>; stable isotope values, <https://doi.org/10.7266/n7-e5ry-ck72>; mixing model results, <https://doi.org/10.7266/n7-4knr-kj95>).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3759/full>