TITLE: Fine-scale social and genetic structure of common bottlenose dolphins (*Tursiops truncatus*) in the Barataria Basin, Louisiana, USA

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ABSTRACT

1. The Barataria Bay Estuarine System (BBES) Stock of common bottlenose dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico has been a focus of extensive research as a result of the Barataria Basin, Louisiana being one of the most heavily oiled estuaries following the *Deepwater Horizon* oil spill. The goal of this study was to build

upon previous research to better understand social and genetic structure of BBES dolphins.

2. Photo-identification data from 2010-2019 were analysed with SOCPROG to identify dolphin social clusters. Genetic analyses were conducted on samples obtained during remote biopsy surveys and health assessments (2010-2018) to assess if identified social clusters were congruent with genetic clustering results, and to evaluate relatedness and gene flow within and between social and genetic clusters. Spatial analyses of the cumulative photo-identification sighting histories from each cluster were also used to determine their geographic range and degree of overlap within the Barataria Basin.

3. Social analyses identified four distinct clusters with some degree of geographic overlap and similar utilization distributions as the three identified genetic clusters. Dolphins in the Barataria Basin were confirmed to be genetically differentiated from those in adjacent coastal waters.

4. In general, genetic analyses differentiate distinct dolphin communities established through long-term (generational) preferential breeding behaviour. In contrast, social associations can be more fluid over the short-term, may change in response to habitat or predator/prey changes, and strong associations can be formed between a mix of related and unrelated individuals. The combination of genetic and social methodologies is valuable for developing a better understanding of complex dolphin social interactions and provides unique insights into dolphin behaviour that can be important for developing effective management strategies.

KEYWORDS: association patterns, community structure, kernel density estimation, microsatellites, mtDNA, photo-identification, protected species

1. INTRODUCTION

Long-term studies have proven invaluable in understanding the social structure of both marine and terrestrial species (reviewed in Eisenberg, Muckenhirn & Rudran, 1972; Wells, 1991; Schradin & Hayes, 2017). Data collected from these studies can provide information on spatio-temporal shifts in abundance and distribution, reproductive success, and overall survival rates. In turn, this information can be used to assess impacts of anthropogenic stressors and develop conservation plans for a given population or species (reviewed in Hayes & Schradin, 2017). Bottlenose dolphins (*Tursiops* spp.) are long-lived, top-level predators characterized by fission-fusion societies wherein group composition can vary frequently with individuals changing associates over a period of hours to days (White, 1992; Connor et al., 2000). The social organization of dolphin societies can be influenced by density-dependent (e.g. predator and prey distribution) and density-independent (e.g. landscape complexity) factors (reviewed in Lusseau et al., 2006). For example, common bottlenose dolphins in Moray Firth, Scotland, were found to shift grouping patterns in relation to interannual variations in salmon (*Salmo salar*) abundance (Lusseau et al., 2004). In contrast, Lusseau et al. (2003) propose that common bottlenose dolphins in Doubtful Sound, New Zealand require a higher level of group stability as a result of the low productivity found within the local fjords.

In the United States, common bottlenose dolphins (*Tursiops truncatus*) have a similar fission-fusion social structure to that of other bottlenose dolphin populations around the world

(e.g. Quintana-Rizzo & Wells, 2001; Wells, 2003; Urian et al., 2009). In fission-fusion societies, most social interactions among dolphins occur within the same population or community (Connor et al., 2000). However, some individual dolphins occasionally move beyond their core areas into habitat utilized by different dolphin communities and high rates of interactions could promote genetic exchange among adjacent groups (Möller & Beheregaray, 2004), although it should be noted that physical dispersal to a new area does not necessarily equate with gene flow; dispersal and mating leading to successful production of offspring must both occur. Nevertheless, these associations between groups can complicate the development of effective management strategies for a given population or stock, even in the absence of gene flow between them (Vollmer & Rosel, 2013). For example, they may result in geographic overlap between adjacent stocks making it difficult to draw stock boundaries, assign individuals to a stock, or attribute dolphin mortalities to the proper stock (e.g. Balmer et al., 2019).

The United States Marine Mammal Protection Act defines a stock as a group of marine mammals of the same species or smaller taxa in a common spatial arrangement that interbreed when mature (MMPA, 16 USC }1361 et seq.). Currently, for common bottlenose dolphins in U.S. waters of the Gulf of Mexico, 32 bay, sound, and estuary (BSE) stocks are recognized, each generally associated with high, year-round site fidelity to a given BSE. Some BSE stocks form additional finer-scale groupings. For example, in Tampa Bay, Florida, Urian et al. (2009) used photo-identification (photo-ID) data to identify five social clusters of dolphins wherein there was minimal spatial overlap. Although genetic exchange may occur among these clusters, ecological factors such as habitat selection and foraging strategies may play a role in the delineation of these social groups over time. Other Southeast United States (SEUS) BSE stocks show evidence

of genetic subdivision, such as in Jacksonville, Florida (Rosel, Hansen & Hohn, 2009), Biscayne Bay, Florida (Litz et al., 2012), and the Indian River Lagoon, Florida (Richards et al., 2013).

The Barataria Basin, located in Louisiana in the northern Gulf of Mexico, was one of the most heavily oiled estuaries following the *Deepwater Horizon* (DWH) oil spill (Michel et al., 2013). As a result, the Barataria Bay Estuarine System (BBES) Stock of common bottlenose dolphins has been a focus of extensive research over the past decade. Since 2010, photo-ID surveys, remote biopsy sampling, health assessments, and telemetry studies have examined the impacts of oil exposure on dolphin abundance, health, reproduction, and survival. Long-term photo-ID data indicate BBES dolphins have year-round, multi-year site fidelity to the Barataria Basin (McDonald et al., 2017). Results from a study of BBES dolphins tagged with satellite-linked transmitters support long-term residence, and further showed that BBES dolphins have localized movements that, in general, can be classified into one of three ranging patterns: 1) western Barataria Basin, 2) barrier islands, and 3) eastern Barataria Basin (Wells et al., 2017). Photo-ID analysis has revealed limited movement of dolphins from the Barataria and Caminada Bays (Figure 1) into either the adjacent Terrebonne-Timbalier Bay estuarine system to the west (Mullin et al., 2018) or the south-eastern region of the basin (Garrison, Litz & Sinclair, 2020).

Genetic studies completed on BBES dolphin samples collected during 2010-2013 from remote biopsies and health assessments indicated the presence of at least two genetically distinct groups within the Barataria Basin (Rosel et al., 2017). The sample locations for one group were within estuarine waters of the western portion of the basin and the other group was found within estuarine waters of the central and eastern areas, with overlap of the two groups along the barrier islands. Using nuclear microsatellite data, significant differentiation was seen between the two groups, as well as between each BBES group and dolphins sampled > 2 km from shore,

belonging to the Western Coastal Stock (WCS). Rosel et al. (2017) also found evidence for three genetic groups within the basin, however, with weaker support than division into two groups, and therefore, differentiation of the three groups was not fully investigated. They suggested that further studies incorporating a larger sample size could increase our understanding of the genetic differentiation and distribution of groups within the Barataria Basin.

The goal of this study was to build upon previous research conducted within the Barataria Basin to better understand social and genetic structure of BBES dolphins. Specifically, the objective of this study was to determine the number of discrete social and genetic groups within this estuarine habitat and determine how those different units compare to one another. The results of this study offer a framework for using multiple sampling methods to provide insight into cetacean population structure and habitat use and can inform future stock management decisions and restoration planning.

2. METHODS

2.1 Study location

The Barataria Basin is located in southern Louisiana between Bayou Lafourche to the west and the Mississippi River to the east (Figure 1). This large, shallow estuary includes a variety of wetlands from fresh water to brackish to salt water. The basin is separated from the Gulf of Mexico by a chain of barrier islands and covers approximately 1,700 km^2 with an average depth of 2 m (USEPA, 1999). Tides are diurnal and the substrate comprises primarily a silty-clay sediment with varying amounts of detrital matter (Conner & Day, 1987). The basin's protected shores are characterized by tidal flats and brackish marshes. The marsh vegetation is

predominantly smooth cord grass (*Spartina alterniflora*) in the southern reaches transitioning to saltmeadow cordgrass (*S. patens*) further north (Baltz, Rakocinski & Fleeger, 1993). BBES dolphins generally inhabit the Barataria Basin in latitudes south of Little Lake (Figure 1).

2.2 Photo-ID data collection and analysis

Photo-ID data used to analyse dolphin social structure were collected during mark-recapture surveys conducted between 2010-2019. Surveys were completed in two phases: Phase 1 - 2010-2014 (10 primary periods; see McDonald et al., 2017 for field effort) as part of the DWH Natural Resource Damage Assessment (NRDA), and Phase 2 - March 2019 (1 primary period; see Garrison, Litz & Sinclair, 2020) as part of a study to inform an Environmental Impact Statement (EIS) required for the proposed Mid-Barataria Sediment Diversion (MBSD) project (U.S. Army Corps of Engineers, 2017). The DWH NRDA study area comprised the western and central portions of the BBES stock area, primarily the estuarine waters in and adjoining Barataria and Caminada Bays (Figure 1). Phase 1 survey transects ran east to west and generally covered the open portions of both bays. Phase 2 surveys covered Phase 1 transects in addition to smaller embayments and contours of marsh edge habitat (including south-eastern portions of the basin not previously surveyed) in order to include coverage of waters north of Bastian, Lanaux, and Pelican islands (Figure 1). Following the robust design for mark-recapture studies (Pollock, 1982), survey effort was divided into primary periods. Primary periods consisted of three to four secondary sessions, during each of which all survey transects were completed. During Phase 1, each transect was surveyed three times per primary period. During Phase 2, which only comprised one primary period, transects were surveyed four times in total. Each primary period was completed in 1-2 weeks.

Field methods were standardized across both survey phases and are detailed in Rosel et al. (2011) and McDonald et al. (2017). Briefly, when dolphins were encountered, data including GPS location and dolphin group size/composition were recorded for each group. A dolphin group was defined as all dolphins in relatively close proximity (~100 m), engaged in similar behaviour, and generally heading in the same direction (Wells, Scott & Irvine, 1987). During photo-ID surveys, effort was made to photograph each individual of the group with Canon EOS digital cameras (Canon Inc., Ota City, Tokyo, Japan) equipped with 100-400 mm telephoto lenses. During biopsy sampling, attempts were made to photograph sampled individuals for comparison to the Barataria dorsal fin catalogue.

Photo analysis techniques, described in Melancon et al. (2011), were followed to assure quality standards. All sorted photographs were scored independently for photo quality and distinctiveness (Urian et al., 2014). Standard photo-ID techniques were used to catalogue individuals based on dorsal fin characteristics (Würsig & Würsig, 1977; Würsig & Jefferson, 1990). The program finFindR was used to match all Phase 2 photos (Thompson et al., 2021). All matches made using finFindR were confirmed by two experienced researchers. All photos and associated sighting data were entered into the Barataria FinBase database created during Phase 1 (Adams et al., 2006). A discovery curve was plotted to display the number of marked dolphins and number of new individuals identified each year of sampling effort, as well as the total number of individuals catalogued across the study. Marked dorsal fins had two or more significant features or at least one major feature with a good probability of re-identification (Speakman et al., 2010; Urian et al., 2014). The average marked proportion was calculated by dividing the number of marked (distinctive) individuals identified by the number of marked and unmarked (not distinctive) individuals photographed during the study (Speakman et al., 2010).

To investigate associations among individual dolphins and identify social clusters, only high-quality photographs of individuals with distinctive dorsal fin characteristics, identifiable across surveys, were included in the association data set. The photo-ID data were analysed using the hierarchical cluster analysis feature in SOCPROG v2.9, a series of MATLAB programs designed specifically to analyse social structure from large datasets for species such as bottlenose dolphins (Whitehead, 2009). Analyses included only dolphins sighted 10 or more times across the study period (Quintana-Rizzo & Wells, 2001; Ingram & Rogan, 2002; Urian et al., 2009), excluding same day resights. Individuals with less than 10 sightings were excluded from the cluster analysis in order to minimize bias due to low sample size (Whitehead, 2008). Individuals were considered to be associated if observed in the same sighting on the same day (Whitehead & Dufault, 1999).

Association indices can be used to control for missed observations in social network analyses and are an important factor to consider when quantifying social relationships (Hoppitt & Farine, 2018). Only images collected during mark-recapture surveys, where the objective was to photograph every individual in the group, were used for the association analysis to minimize potential bias. A simple ratio association index (SRI) with the default average linkage algorithm was used to identify dolphin social clusters (Whitehead, 2009). The SRI, widely used in animal social network analyses, calculates the probability that two individuals are observed together given one has been seen. This index does not overestimate associations between individuals, which has been found with alternative methods such as using twice-weight and half-weight indices (Ginsberg & Young, 1992). Hoppitt & Farine (2018) found the SRI to be valid if the probability of failing to see two individuals together is the same as the probability of failing to see both when they are apart.

A dendrogram displays the results of the hierarchical cluster analysis and outlines the degree of association between individuals in the population. Newman's test of modularity (Q) was used to test whether the dolphins within the Barataria Basin can effectively be divided into social clusters (Newman, 2004; Whitehead, 2008). Newman (2004) suggests $Q > 0.3$ indicates accurately represented and well defined divisions. The effectiveness of hierarchical clustering was evaluated through the cophenetic correlation coefficient (CCC). This coefficient, calculated by SOCPROG, ranges from 0 to 1 and indicates how well the dendrogram correlates with the actual association indices, with a value of ≥ 0.8 representing reliable clustering (Whitehead, 2009). Median group size was calculated using the revised (post-photo analysis) best field estimate for all dolphin sighting groups containing each social cluster individual. Network analysis statistics (cluster means with bootstrap standard errors using 1,000 replicates) were calculated in SOCPROG to compare the social connectivity within and between social clusters (Newman, 2004). Five social network metrics were evaluated for each social cluster: 1) affinity - the weighted average strengths of all close associates; 2) clustering coefficient - how closely associates are themselves connected; 3) eigenvector centrality - a measure of how connected individuals are within their cluster; 4) reach - a measure of indirect connectedness; and 5) strength - the sum of all association indices with other individuals (Whitehead, 2009).

2.3 Genetic data collection and analysis

Skin samples for genetic analyses were collected during four remote biopsy surveys (2010-2012; Balmer et al., 2015) and during health assessment studies (2011-2018, except 2012 and 2015; Schwacke et al., 2014) conducted within Barataria and Caminada Bays (Figure 1). All skin samples were preserved in a 20% DMSO/saturated NaCl solution. Remote biopsy field

sampling methods are detailed in Sinclair et al. (2015). The genetic samples included 126 samples collected between 2010 and 2013 that were processed and analyzed by Rosel et al. (2017). An additional 106 skin samples collected in 2014-2018 were added to this study for a total of 232 genetic samples. DNA was extracted from the new samples using a Qiagen DNeasy Blood & Tissue kit following manufacturer's protocols. DNA quality was examined via gel electrophoresis and quantity measured by fluorometry (GE Healthcare Hoefer DyNA Quant 200 or Invitrogen/Thermo Fisher Scientific Qubit 4 Fluorometer). The sex from each sample collected by remote biopsy was genetically determined via PCR using ZFXY and SRY specific primers (Rosel 2003). The sexes of individuals captured during health assessment studies were determined in the field by examining the genital slit and the presence/absence of mammary slits (Smolker et al., 1992).

Samples were genotyped at 43 nuclear polymorphic microsatellite loci previously optimized for *T. truncatus* (Rosel, Hansen & Hohn, 2009; Rosel et al., 2017; Vollmer et al., 2021; see Supporting Information Table S1). Modifications to original primer sequences were made for D08, DlrFCB12, EV94, and MK8 (Rosel et al., 2017; Vollmer & Rosel, 2017; Vollmer et al., 2021). Excluding MK6, the reverse primer of each microsatellite locus or the forward primer of D22 was PIGtailed as described in Brownstein, Carpten & Smith (1996) to reduce one base pair (bp) stutter. All primer sequences are provided in Supporting Information Table S1. Three of the loci used in this study, Ttr20, Ttr51, and Ttr98, were amplified by Rosel et al. (2017) but were excluded from their final analyses due to evidence of null alleles in one of their studied populations. Primer sequences and PCR conditions for those loci were, therefore, not reported in the previous study but have been included in Supporting Information Table S1. The 43 loci were genotyped using a Qiagen Type-it Microsatellite PCR kit in eight multiplexes, each

containing four to seven loci, plus one locus (KWM12a) amplified alone and co-loaded with one of the multiplexes (see Supporting Information Table S1 for PCR multiplexing and conditions). A positive and negative control were included with each PCR reaction. All PCR products, including controls, were run on an ABI 3130 or ABI 3500 Genetic Analyzer using GeneScan 500 LIZ or GeneScan 600 LIZ v2.0 size standards (Applied Biosystems), respectively. Microsatellite fragments were analysed and allele sizes determined using GeneMapper v6 (Life Technologies/Applied Biosystems). The two instruments were calibrated using a broad set of *Tursiops* samples to ensure allele calling was consistent. In addition, the genotypic data from the Rosel et al. (2017) study were collected in the same lab with the same protocols.

A genotyping error rate was calculated by re-genotyping 10% of the samples at all 43 loci. Microsatellite Toolkit (Park, 2002) was used to identify any dolphins that had been sampled more than once and probability of identity estimators, $P_{(ID)}$ and $P_{(ID)sib}$ (Waits, Luikart & Taberlet, 2001), were calculated in GenAlEx v6.5 (Peakall & Smouse, 2012). One member of each duplicate pair was removed from further microsatellite analyses.

The inclusion of closely related individuals in a data set can bias methods used to estimate genetic diversity that rely on allele frequencies such as Bayesian clustering analysis, as well as diversity estimators such as heterozygosities, Hardy-Weinberg equilibrium (HWE), and linkage disequilibrium (Anderson & Dunham, 2008; Rodríguez-Ramilo & Wang, 2012; Wang, 2018). Therefore, closely related individuals are often removed from genetic analyses. During Barataria Basin field sampling, it was possible that individuals from the same family group were sampled during health assessments when a capture set involved multiple dolphins or during remote biopsy surveys when more than one animal was sampled from a single sighting. Furthermore, photo-ID evidence indicated that several mother-calf pairs were sampled during

health assessments. Following standard practice, one individual from each of the mother-calf pairs was removed and one individual was removed from pairs with high pairwise relatedness values (r) from the same capture set or biopsy sighting, to prevent introducing bias from these related pairs. The R package *related* (Pew et al., 2015) was used to calculate r for six relatedness estimators [four moment estimators (Queller & Goodnight, 1989; Li, Weeks & Chakravarti, 1993; Lynch & Ritland, 1999; Wang, 2002) and two likelihood-based estimators (Milligan, 2003; Wang, 2007)] in RStudio v1.3.1093 (RStudio Team, 2020) with R v3.6.2 (R Core Team, 2019). To determine the best relatedness estimator given the data, simulations were conducted using allele frequencies from the Barataria Basin samples to generate 100 pairs of each of the four relationship types (parent-offspring, full-sibling, half-sibling, and unrelated). Pearson correlation coefficients were calculated between observed and expected relatedness values of the simulations. The relatedness estimator with the highest coefficient, the triadic likelihood estimator (trioml; Wang, 2007), was then used to estimate r and identify closely related pairs ($r \geq 0.45$).

The optimal number of genetic clusters (K) within the Barataria Basin was evaluated using the Bayesian clustering program STRUCTURE v2.3.4 (Pritchard, Stephens & Donnelly, 2000). An initial STRUCTURE run was completed in which microsatellite data from 29 dolphins of the WCS from Rosel et al. (2017) were included to determine if any dolphins sampled within the Barataria Basin would cluster more closely with this coastal stock and therefore merit exclusion from further analyses. This run was completed using the admixture model, correlated allele frequencies, 20 independent runs for K = 1-10, with a burn-in length of 1 X 10^6 iterations followed by 5 X 10^6 Markov Chain Monte Carlo (MCMC) repetitions, and location priors were set for the two sampling locations (Barataria Basin or WCS). Program defaults were used for all

other parameters. All STRUCTURE runs were performed on multi-core processors using the program ParallelStructure (Besnier & Glover, 2013) on the CIPRES Science Gateway v3.3 server (Miller, Pfeiffer & Schwartz, 2010). The most likely number of clusters was evaluated using three methods for estimating the best value of *K*: the mean log-likelihood of the data (ln Pr(*X*/*K*)) (Pritchard, Stephens & Donnelly, 2000), Δ*K* (Evanno, Regnaut & Goudet, 2005), and the parsimony index in KFinder (Wang, 2019). Structure Harvester v0.6.94 (Earl & vonHoldt, 2012) was used to visualize Δ*K* and ln Pr(*X*/*K*) plots and to generate input files for the program CLUMPP v1.1.2 (Jakobsson & Rosenberg, 2007). The *Greedy* algorithm in CLUMPP was then applied to average the membership coefficient (*q*) from all replicate runs of the best *K*. Using the output files from CLUMPP, individuals were assigned to each cluster using a threshold of $q \geq 0.50$. Further STRUCTURE runs were completed on each of the identified clusters to determine if hierarchical levels of population structure were present. STRUCTURE parameters were set as previously described but without the use of location priors information and with a burn-in length of 1×10^5 iterations followed by 5×10^5 MCMC repetitions. The optimal number of clusters was determined by evaluating the three methods for estimating *K* as before and individuals were assigned to clusters with $q \geq 0.50$. Subsequent STRUCTURE runs were conducted until no sub-clustering was indicated.

For each of the Barataria Basin genetic clusters identified by STRUCTURE and for the WCS, Microchecker v2.2.0.3 (van Oosterhout et al., 2004) was used to test each locus for the presence of null alleles, large allelic dropout, and genotype scoring errors due to stuttering. Deviation from HWE proportions and linkage disequilibrium were measured using Genepop v4.2 (Rousset, 2008) with 10,000 dememorizations, 1,000 batches, and 10,000 iterations per batch. Levels of significance were adjusted for multiple comparisons using the sequential

Bonferroni technique (Holm, 1979). The number of alleles, private alleles, and observed and expected heterozygosities per locus were calculated using ARLEQUIN v3.5.2.2 (Excoffier & Lischer, 2010). Allelic richness was calculated in FSTAT v2.9.4 (Goudet, 1995; Goudet, 2003). Differences in mean observed heterozygosity and allelic richness were tested using an analysis of variance (ANOVA). To investigate genetic differentiation among STRUCTURE clusters, global and pairwise F_{ST} values were estimated with the microsatellite data in ARLEQUIN and significance levels were adjusted using sequential Bonferroni.

The 5' end of the mitochondrial DNA (mtDNA) control region and flanking transfer-RNA gene was amplified using PCR and the primers L15824 (Rosel et al., 1999) and H16498 (Rosel, Dizon & Heyning, 1994) with conditions from Vollmer & Rosel (2017), including a negative no-DNA control with each PCR reaction. Amplified products were purified from low melting point agarose gels by agarose digestion and then sequenced in the forward and reverse directions using a BigDye Terminator v1.1 cycle sequencing kit (Applied Biosystems) on an ABI 3130 or ABI 3500 Genetic Analyzer. The forward and reverse reads were edited independently using Sequencher v5.4.6 (GeneCodes) or Geneious Prime 2000.0.5 (https://www.geneious.com), then assembled for final consensus sequences. Haplotypes were identified using Geneious Prime and heteroplasmic sequences (Vollmer et al., 2011) were excluded from further mtDNA analyses. ARLEQUIN was used to calculate nucleotide and haplotype diversities (Nei, 1987) for each Barataria Basin cluster identified with STRUCTURE and the WCS, and to estimate global and pairwise levels of differentiation using F_{ST} and Φ_{ST}. The Tamura & Nei (1993) model was identified as the best model of evolution to use in ARLEQUIN for estimating Φ_{ST} from the program JModeltest v2.1.10 (Darriba et al., 2012) run on the CIPRES Science Gateway v3.3

server and using the Bayesian Information Criterion (BIC). Levels of significance for pairwise estimates of F_{ST} and Φ_{ST} were corrected for multiple comparisons using sequential Bonferroni.

2.4 Combined analyses using data from social and genetic clusters

Spatial data were analysed to determine the geographic range and overlap of dolphin clusters identified via the social analyses and the genetic data. Utilization distributions (UDs) [i.e. per cent volume contours (PVCs)] represent the probability that an animal or group of animals is found in a given space (Worton, 1989). Kernel density estimates (KDEs) (Worton, 1989) were estimated using the cumulative photo-ID sighting locations of each social and genetic cluster using the Geostatistical Analyst and Spatial Analyst Toolboxes in ArcGIS 10.7.1 (ESRI, Redlands, CA, USA; reviewed by MacLeod, 2013). Using KDEs, 95th (i.e. the entire range or where an individual can likely be found 95% of the time) and 50th (i.e. the core area or where an individual is likely to be found 50% of the time) percentile UDs were determined. KDE distributions can be over or under-estimated depending on the bandwidth value (or smoothing parameter) that is used (Horne & Garton, 2006). The appropriate bandwidth was determined by using a rule-based ad hoc method (Kie, 2013). Genetic samples that qualified for the SOCPROG analysis by having 10 or more photo-ID sightings were compared to their satellite telemetry assignment group reported by Wells et al. (2017).

To compare kinship within the identified genetic and social clusters, average pairwise relatedness and variance for pairs of individuals within each cluster and for the entire Barataria Basin data set were calculated using the 43 microsatellite loci and the trioml estimator in the program COANCESTRY v1.0.1.0 (Wang, 2011). The difference in average relatedness between each cluster (social and genetic) and the entire data set was calculated and tested for significance

using the bootstrap method (10,000 repetitions) and a 95% confidence level in COANCESTRY to determine if relatedness within any group was higher than that of the overall dataset.

To test for evidence of sex-biased dispersal in the genetic and social clusters, two methods were used. First, the assignment-based procedure developed by Favre et al. (1997) and extended by Mossman & Waser (1999) was implemented in GenAlEx. This method detects sex-biased dispersal by calculating the mean Assignment Index correction (AIc) for males and females. Next, non-parametric tests for significance between the mean AIc values of the sexes were performed using a Mann Whitney U-test. The more dispersing sex generally has a negative mean AIc (Goudet, Perrin & Waser, 2002). For the second method, average relatedness was compared between the female-female and male-male pairs of each cluster. The significance of differences in mean relatedness between the two sexes within a cluster was then tested in COANCESTRY using the bootstrap method as previously described. The average relatedness of the more dispersing sex would be expected to be lower than the average relatedness of the more philopatric sex. This relatedness-based method has been shown to detect lower levels of sex-biased dispersal not identified by the assignment-based method (Phillips et al., 2014). To further investigate any differences in gene flow between the sexes, ARLEQUIN was used to calculate overall estimates of F_{ST} and Φ_{ST} among the genetic clusters for males and females separately, using mtDNA data.

3. RESULTS

3.1 Photo-ID data and social analysis

From 2010 to 2014 (Phase 1), 132 small vessel-based mark-recapture surveys were completed (McDonald et al., 2017), while 36 vessel surveys were completed in 2019 as part of Phase 2. In total, survey vessels during both phases covered over 15,000 km of trackline across 1,087 hours and took 99,916 photographs. Crews spent 408 hours in dolphin sightings over the 10 years with an average sighting time of 17 min 46 sec. In total, 1,379 dolphin groups were encountered with an average group size of 8 individuals (SD = 10.1; range: 1-71; median = 4). Through photo analysis, a total of 2,091 unique individual dolphins were identified with an average marked proportion of 75%. The highest proportion of dolphins (48%; n = 995) was seen during a single primary period while only one individual was observed in all 11 primary periods. The discovery curve showed an increase in catalogued individuals at every mark-recapture primary period including a steep increase between primary period 10 and 11, coinciding with a 5-year gap between surveys and the inclusion of previously unsurveyed regions in 2019 (Figure 2). From 2010 to 2014, the number of new dolphins added to the catalogue following each primary period ranged from 34 to 312 (mean = 158). The 2019 effort added 507 new individuals to the catalogue, 44% of which were sighted in the previously unsurveyed south-eastern region.

A total of 112 individuals were sighted more than 10 times (mean = 12 sightings; range 10-24) and were included in the association analysis. Based on associations among these individuals, SOCPROG identified four distinct social clusters (Figure 3). The resulting cophenetic correlation coefficient of 0.80 and modularity value of 0.34 indicated a good fit of the data with valid clustering and well-defined community divisions. The island (red) cluster was the largest with 65 individuals followed by the western (yellow) cluster with 40 individuals. Both the east-central (green) and west-central (blue) clusters were small, containing just three and four individuals, respectively. The east-central social cluster was characterized by the largest median

group size (n=17) but lower social metrics, while the western cluster was the opposite with the smallest group size (n=8) and higher social metrics (Table 1).

3.2 Genetic analyses

DNA was successfully extracted from all Barataria Basin skin samples and all were genotyped at 43 microsatellite loci. Nine samples were identified as having matching genotypes to individuals analysed by Rosel et al. (2017). The probability of identity estimates was low ($P_{(ID)} = 3.6 \times 10^{-35}$ and $P_{(ID)sib} = 1.3 \times 10^{-14}$), therefore it is unlikely that two dolphins would share the same genotype at all 43 loci. Furthermore, each duplicate pair had matching sexes and mtDNA control region haplotypes. One sample from each of the nine duplicates was removed, resulting in a total of 223 individuals from the Barataria Basin used in further analysis. Re-genotyping of 10% of the samples resulted in a genotyping error rate of 0.00%.

The *r* values of 19 known mother-calf pairs ranged from 0.50-0.68 and each pair had identical mtDNA control region haplotypes. Four additional pairs of individuals each sampled within the same capture set had *r* values ≥ 0.45. One individual from each of these pairs as well as from the mother-calf pairs was excluded from further analyses, resulting in a final sample size of 203 for the Barataria Basin.

The optimal number of clusters identified from the initial STRUCTURE run, which included dolphins from the Barataria Basin and the WCS, was $K = 2$ using the ΔK method. The parsimony index and the ln Pr(X/K) method identified a best K of 4 and 5, respectively (Supporting Information Table S2). Because hierarchical population structure was expected when including individuals from the WCS, ΔK estimation was used to determine the initial best number of clusters. All dolphins of the WCS grouped into a single cluster with the addition of

seven individuals sampled within the Barataria Basin using $q \geq 0.50$ (Supporting Information Figure S1). The second STRUCTURE cluster contained 195 dolphins sampled within the Barataria Basin. One individual had a q value of 0.50 to each cluster and therefore was not assigned to either cluster. This individual plus the seven dolphins with higher assignment coefficients to the WCS were removed from further analysis of the Barataria Basin data set. The average q values of the WCS and Barataria Basin groups were 0.94 and 0.90, respectively. Running the WCS through STRUCTURE alone revealed no hierarchical structure (Supporting Information Table S2).

STRUCTURE analysis of the Barataria Basin data set alone (n=195) estimated a best K = 3 using all three methods for estimating K (Supporting Information Table S2). These three genetic clusters are geographically distributed, with one group located primarily near the barrier islands of Grand Isle and Grand Terre Islands and the other two groups utilizing either the western or the central and eastern estuarine habitats of the basin with overlap near the barrier islands (Figure 4A). Using a q-value cutoff of 0.50, individuals were grouped into 'western', 'east-central' or 'island' genetic clusters with average q values per cluster ranging from 0.71 to 0.76. Approximately 18% of the samples were not assigned to any cluster due to q-values lower than the 0.50 threshold (Figure 4B). Re-running each of the Barataria Basin clusters alone through STRUCTURE revealed no further partitioning of samples (Supporting Information Table S2).

No microsatellite loci showed significant departure from HWE after Bonferroni correction for any of the Barataria Basin genetic clusters or the WCS (Supporting Information Table S3). Ttr61 and Ttr71 showed evidence of linkage disequilibrium in the Barataria Basin island cluster only. No evidence of null alleles was found in the Barataria Basin western or island

clusters, however Ttr19, Ttr20, and TexVet5 in the east-central cluster and Ttr51 in the WCS did show evidence of null alleles due to homozygote excess. Since evidence of linkage disequilibrium and null alleles were not present for the same loci across groups, all loci were retained for genetic analyses. The number of alleles and private alleles, allelic richness, heterozygosity values, and HWE *P*-values per locus for each group is provided in Supporting Information Table S3. Observed heterozygosity was not significantly different among groups (ANOVA, $F = 0.58$, $df = 3$, $P = 0.63$) and values ranged from 0.6170 (±0.1833) to 0.6632 (±0.1793) with the lowest and highest values estimated for the east-central cluster and the WCS, respectively. Mean allelic richness was also not significantly different among groups (ANOVA, $F = 1.25$, $df = 3$, $P = 0.29$). Among the Barataria Basin clusters, the mean number of alleles per locus ranged from 5.4 to 6.2 and the number of private alleles were 5, 13, and 23 for the western, east-central, and island clusters, respectively.

All pairwise comparisons of microsatellite F_{ST} were significant (Table 2A). Pairwise F_{ST} values between the WCS and each of the Barataria Basin clusters ranged from 0.021 to 0.044 (all $P < 0.0001$; Table 2) with the highest F_{ST} estimated between the WCS and the Barataria Basin western cluster. Among the Barataria Basin clusters, the lowest level of differentiation ($F_{ST} = 0.023$, $P < 0.0001$) was seen between the east-central and island clusters and similar values were seen between the western cluster and the east-central and island clusters ($F_{ST} = 0.031$ and 0.030, respectively, $P < 0.0001$).

The final mtDNA control region alignment length was 353 bp. A total of 24 haplotypes were found, 16 in the Barataria Basin samples and 12 in the WCS. Of the 24 haplotypes, eight were heteroplasmic (Supporting Information Table S4). After removal of the heteroplasmic haplotypes, seven of the haplotypes were unique to the WCS and five were unique to the

Barataria Basin data set. Novel sequences were submitted to GenBank (MZ615655-MZ615665; Supporting Information Table S4). Haplotype and nucleotide diversity for the Barataria Basin clusters ranged from 0.6456 (±0.0539) to 0.5933 (±0.0626), and 0.0030 (±0.0023) to 0.0044 (±0.0029), respectively. Diversity indices were higher for the WCS, with a haplotype diversity of 0.8439 (±0.0533) and nucleotide diversity of 0.0079 (±0.0048). Pairwise comparisons of F_{ST} and Φ_{ST} were significant between the WCS and each of the three Barataria Basin clusters (Table 2B). Pairwise F_{ST} was also significant between the Barataria Basin east-central cluster and the other two Barataria Basin clusters, but not for Φ_{ST} after correcting for multiple comparisons (Table 2B). Significant differences were not seen between the Barataria Basin western and island clusters for either estimator.

Average overall relatedness within each of the Barataria Basin genetic clusters and within the western SOCPROG social cluster was significantly higher using a 95% confidence level than the relatedness of the entire Barataria Basin sample set ($r = 0.0262$) (Figure 5; Supporting Information Table S5A). Average relatedness within the island social cluster ($r = 0.0235$) was not significantly different from the overall Barataria Basin sample set (Supporting Information Table S5A). Relatedness within the east-central and west-central social clusters could not be calculated because there were not enough samples with genetic data assigned to those two clusters.

Tests of sex-biased dispersal for the genetic and social clusters were not significant using the assignment-based method implemented in GenAlEx (comparisons of mean AIc values; Table 3). Using the bootstrapping method of COANCESTRY (relatedness-based estimates) with a 95% confidence level, the mean difference in r between male and female pairs was significant only for the east-central genetic cluster with males having a higher average relatedness but relatedness

values were generally low for both sexes and the difference between female and male pairs was small (*r* observed average difference = -0.0132; Supporting Information Table S5B). Among the genetic clusters, overall estimates of F_{ST} based on mtDNA data were significant ($P < 0.05$) for females ($F_{ST} = 0.100$, $P = 0.0027$) but not significant for males ($F_{ST} = 0.025$, $P = 0.1190$). Estimates of Φ_{ST} were identical and not significant for either sex (females: $\Phi_{ST} = 0.032$, $P = 0.0865$; males: $\Phi_{ST} = 0.032$, $P = 0.0937$).

3.3 Spatial analysis

Cumulative UDs derived from the KDE analysis indicated a spatial distinction between the SOCPROG social clusters with some degree of overlap in geographic ranges (Figure 6). The smallest amount of spatial overlap occurred between the east-central (green) and western (yellow) social clusters while the greatest amount of overlap occurred between the island (red) and west-central (blue) clusters. The western cluster had the largest 50% and 95% UDs, with 4.8 km^2 and 37.1 km^2, respectively (Table 4). The east-central social cluster had the smallest UDs, with 0.99 km^2 area for the 50% UD and 7.6 km^2 area for the 95% UD (Table 4).

Kernel density estimate analysis of the cumulative photo-ID sightings for each genetic cluster exhibited a large degree of overlap in their geographic ranges (50% UDs for all three genetic clusters overlapped along the north side of Grand Isle and in Barataria Pass between Grand Isle and Grand Terre Islands; Figure 6). The UDs for the western and island genetic clusters were congruent with the western and island social clusters. The east-central genetic cluster had similar UDs as the east-central and west-central social clusters' combined UDs. The western genetic group had all of its 95% UD west of Barataria Bay and the Grand Terre Islands. The east-central genetic group had the largest 50% and 95% UDs, with 7.2 km^2 and 48.8 km^2,

respectively (Table 4). Conversely, the western genetic cluster had the smallest UDs, with 3.9 km^2 area for the 50% UD and 31.4 km^2 area for the 95% UD (Table 4).

A total of 28 individuals met the criteria to be included in both the genetic and social clustering analyses (Table 5). The lone west-central social cluster individual (Y22) was assigned to the western genetic group. This aligned with satellite tag data placing Y22 in the western group as well (Table 5; Wells et al., 2017). For the island social cluster, 55% of those individuals matched with their genetic assignment to the island group. A similar proportion (60%) of the western social cluster showed agreement with their genetic assignments. The largest agreement (83%) between social cluster and satellite tag assignments was with western cluster individuals.

4. DISCUSSION

The Barataria Basin is habitat for common bottlenose dolphin residents with long-term site fidelity (some dolphins documented over a 10-year period and across seasons) and fine-scale habitat partitioning. The abundance of dolphins in this estuarine system is one of the largest of any surveyed SEUS BSE [2,071 (95% CI: 1,832–2,309)] (Garrison, Litz & Sinclair, 2020). Evidence that the dolphins inhabiting this basin are separated into distinct groups has been previously presented, based on satellite-telemetry (Wells et al., 2017; Cloyed et al., 2021) and genetic data (Rosel et al., 2017). This study provides additional evidence supporting partitions within the basin. Multiple unique social and genetic groups were identified within the studied areas of the Barataria Basin and it is possible that more partitions could be discovered with higher coverage in other parts of the basin, such as the south-eastern and north-central portions. Genetic analysis, with an increased sample size, reinforced the presence of three distinct genetic

groups previously identified by Rosel et al. (2017). The degree of nuclear genetic differentiation among the three Barataria Basin genetic clusters was similar to that estimated by Rosel et al. (2017) between the two Barataria groups evaluated in their study. The level of genetic differentiation among these groups was similar to estimates among other dolphin communities of the SEUS, such as BSE groups within the Indian River Lagoon, Florida (Richards et al., 2013), as well as between BSE and coastal stocks of the Gulf of Mexico and Atlantic Ocean (Sellas, Wells & Rosel, 2005; Rosel, Hansen & Hohn, 2009, Rosel et al., 2017). This study also confirmed significant genetic differentiation between dolphins in the Barataria Basin and those from the adjacent coastal waters, as previously revealed by Rosel et al. (2017). Out of the 203 dolphins sampled within the Barataria Basin, only seven grouped with the coastal stock in clustering analysis and had much lower membership values (q = 0.54-0.72) than the overall average for the WCS (q = 0.94). The STRUCTURE results also indicated low levels of admixture between the Barataria Basin and nearshore coastal populations.

Using nuclear genetic data, the western genetic cluster showed the highest level of divergence when compared to all other clusters within the Basin. In fact, estimates of F_{ST} were higher between the western cluster and the other two Barataria Basin clusters than between the WCS and the Barataria island or east-central clusters, demonstrating how genetically distinct the western group is from other dolphin groups of the same BSE. The western social cluster had the smallest median group size (Table 1) with high strength and affinity social metrics, further supporting distinction of the western group from the other three social clusters.

Kernel density estimate analysis of the cumulative photo-ID sightings indicated spatial distinction between the four social clusters with varying degrees of geographic overlap. There was little to no geographic overlap between the western and east-central social clusters (Figure

6). The Barataria Waterway and land formations on the edges of West Champagne Bay separate these two clusters, appearing to serve as a social barrier. The highest degree of geographic overlap was between the island and western social clusters near Grand Isle. The kernel density estimate analysis of the genetic clusters also showed a great amount of geographic overlap near the barrier islands with the majority of the 50% UDs for all three clusters near Grand Isle (Figure 6). The east-central genetic cluster was more widespread than the other clusters, with the 95% UD extending to both the western and eastern portions of the Barataria Basin; however, it is the only group with UDs located near the south-eastern region of the basin. Interestingly, when comparing distributions between the social and genetic groups, the western clusters had very similar geographic ranges between the two analysis methods, unlike any of the other clusters. This could indicate that the dolphins in the western portion of the basin are both socially and genetically more unique than the other groups.

The east-central, western, and island social and genetic clusters identified by this study generally corresponded to the ranging patterns identified from tracking satellite-tagged dolphins in the Barataria Basin (Wells et al., 2017). However, when comparing the social cluster assignments to the satellite telemetry classifications, less than half of the island social cluster individuals aligned with the island satellite telemetry group (Table 5). There was better agreement when comparing the western social cluster, as over 80% of individuals matched with their corresponding satellite telemetry assignments, further supporting the uniqueness of the dolphins in the western portion of the Basin. The low correspondence between the two studies could be the result of a small sample size of satellite-tagged individuals that qualified for the SOCPROG analysis. Additionally, satellite telemetry represents short-term (< 6 months) movements [mean tag duration was 140 days; Wells et al., (2017)] while the SOCPROG clusters

were derived from long-term (10 years) photo-ID sighting records. This temporal difference between the two methodologies could help explain some of the discrepancies in the satellite telemetry and SOCPROG cluster assignments and has been observed in other studies when comparing different sampling methods to assess dolphin movements (e.g. Balmer et al., 2014; Nekolny et al., 2017; Balmer et al., 2021).

The two largest social clusters, the island and the western, totalled 65 and 40 individuals, respectively. Both of these larger clusters displayed high strength of associations, connectedness, and gregariousness, especially when compared with the two smaller clusters (east-central and west-central; Table 1). However, group sizes for individuals of the island and western clusters were smaller than the east-central cluster. Individuals in the east-central cluster were seen in much larger group sizes with looser associations when compared to the other three clusters (Table 1). This suggests that east-central individuals form many loose associations with other Barataria dolphins but have strong associations with only a few individuals to form a social cluster. Bottlenose dolphins in southern Australia have shown a similar pattern, potentially in response to higher prey abundance, where one community is characterized by larger aggregations and loose social bonds, and the other by smaller groups but stronger associations, perhaps as a consequence of having to search for limited prey (Diaz-Aguirre et al., 2019). Association patterns can also be influenced by predatory threats (Heithaus & Dill, 2002; Gowans, Würsig & Karczmarski, 2007). Nearly one-third of captured Barataria dolphins showed some degree of shark bite scars (Zolman E., 2020, unpublished data), supporting the possibility that predation risk could be influencing social structure and habitat use, as seen with dolphins in Sarasota Bay, Florida (Wells, Scott & Irvine, 1987; Wilkinson et al., 2017).

The dendrogram and network analysis statistics compare the social connectivity within and between social clusters. The position of the west-central social cluster in the dendrogram, between the east-central (with which it shares a node) and island clusters (Figure 3), suggests its four members also have some association with the east-central or island community. This is supported by the equal amount of spatial overlap between the west-central UDs with the east-central and island UDs (Figure 6). When comparing the network analysis measures, the west-central cluster had a greater between-class strength value with the island (0.45) cluster compared to the east-central (0.03) or western (0.09) clusters (Table 1), suggesting the west-central and island clusters are more strongly associated. The western cluster appears to be the most isolated social cluster based on its position in the dendrogram and low between-class strength values with the other social clusters. Additional surveys are needed to increase the number of individuals with 10 or more sightings to elucidate the social structure of the smaller clusters.

Fine-scale habitat partitioning by common bottlenose dolphins within BSEs has been found elsewhere in the SEUS. Using photo-ID data, Urian et al. (2009) found five discrete dolphin communities within Tampa Bay, Florida. However, unlike the Barataria Basin social and genetic clusters, Tampa Bay communities exhibited very little spatial overlap. Dolphins within the Barataria Basin have spatial cluster patterns more similar to those inhabiting the Moray Firth, Scotland. There, using photo-ID data, Lusseau et al. (2006) found two communities of dolphins with differences in associations but overlapping ranges.

Photo-ID data in the present study suggest that all four Barataria Basin social clusters exhibit spatial overlap around Grand Isle. Some dolphins within the Barataria Basin have been observed using a specialized foraging strategy ("drilling") during which they presumably burrow into the substrate (Quigley et al., 2022). Only six individuals observed "drilling" qualified for the

SOCPROG analysis with three from the western cluster, two from the island cluster, and one from the west-central cluster. This behaviour was observed primarily along the north side of Grand Isle and in southern Caminada Bay and could be a driver for the high degree of overlap between the western and island social clusters. Grand Isle began forming around 750 years ago and is one of the most stable Louisiana barrier islands (Torres et al., 2020). Perhaps dolphins from different clusters have shifted their core usage area towards Grand Isle, a preferred area for the "drilling" foraging strategy.

A higher number of social clusters (4) than genetic clusters (3) was identified within the Barataria Basin. Two of the social clusters contained only 3-4 individuals, possibly due to the data restrictions of the cluster analysis requiring 10 or more sightings, only including mark-recapture surveys, and a lack of sufficient time series in the eastern part of the basin. However, social clusters containing very few individuals have been observed in other dolphin studies (Genov et al., 2019; Hawkins et al., 2020). It may be that individuals from the two small Barataria social clusters (east-central and west-central) are part of a larger social group with individuals not included in the analysis. One other explanation for the small number of members of the east-central social cluster is the lack of survey effort in that region. With additional central and eastern surveys, the east-central and west-central clusters will likely increase in sample size.

Other studies of common bottlenose dolphins in the SEUS have revealed discrepancies in the number of social versus genetic clusters within a single habitat, and similar to findings from this study, a higher number of social versus genetic clusters were reported. For example, using photo-ID data, Mazzoil et al. (2008) identified three communities of dolphins within the Indian River Lagoon of Florida, but only two genetic clusters were differentiated by Richards et al. (2013) using microsatellite data. Furthermore, analysis of telemetry and photo-ID data of

dolphins inhabiting Mississippi Sound, Mississippi/Alabama in the northern Gulf of Mexico (Mullin et al., 2017) identified at least two social groups but microsatellite data supported only a single population (Vollmer et al., 2021). The fission-fusion nature of dolphin societies might also explain why more social than genetic groups were found in the Barataria Basin. Connor et al. (2000) suggested that dolphins need to spread out more to reduce feeding competition, resulting in multiple social interactions.

If kinship is an important factor in the formation of social bonds within a population, one would expect higher levels of relatedness within social communities than between them. Higher levels of genetic relatedness have been reported for social groups of bottlenose dolphins (*Tursiops* spp.) in other studies (Diaz Aguirre et al., 2019; Chabanne et al., 2021). In this study, two of the four social clusters had large enough sample size to investigate genetic relatedness. Compared to all Barataria samples analysed together as a single group, the western social cluster had significantly higher overall relatedness while the island cluster did not (Supporting Table S5A). This result further supports the uniqueness of the western dolphins. When examining average relatedness within the sexes of both social clusters, the observed average pairwise relatedness was higher for female pairs than male pairs in both clusters, although differences lay within the 2.5% and 97.5% quantiles of the bootstrapped sample (Supporting Table 5B). Tests for sex-biased dispersal based on mean AIc values also did not indicate a significant difference between males and females in the social clusters (Table 3). However, sample sizes for both social clusters were small for the tests (≤ 8 individuals per sex) so the power to detect a difference may have been low. While not significant, the lower levels of relatedness and negative mean AIc values of male dolphins within the BBES social groups may suggest that males within the Barataria Basin are the more dispersive sex, but larger sample sizes are necessary to

comprehensively examine this question. There was also no overall support for sex-biased dispersal in the genetic clusters except when testing differences in relatedness within the east-central cluster. It should be noted that a lack of evidence for sex-biased dispersal inferred from genetic data has been reported for other common bottlenose dolphin populations in the SEUS (Sellas, Wells & Rosel, 2005; Rosel, Hansen & Hohn, 2009; Richards et al., 2013; Vollmer & Rosel, 2017; Vollmer et al., 2021).

Further evidence suggesting movement of male dolphins across social clusters comes from the lower percentage of matching social and genetic assignments for males compared to females. Males had 40% and 50% matching cluster assignments compared to 80% and 60% for females in the western and island clusters, respectively. Females also had higher assignment matches between social and telemetry groups than males. Although the sample size is small, this result supports the hypothesis that dolphin social clusters could include males that have dispersed from their natal genetic populations. Fewer matches between the genetic and social assignments could also indicate that dolphins are socializing between different genetic populations but not breeding at rates that would produce panmixia throughout the basin since there is significant genetic differentiation among groups. Longer-term studies of social interactions and additional genetic data from an increased number of individuals will continue to improve our understanding of dolphin interactions within the BBES.

There was also evidence of female philopatry in the matrilineally inherited mtDNA data. Overall estimates of F_{ST} were higher for females than for males (F_{ST} = 0.100 and 0.025, respectively). Also, pairwise values of F_{ST} between the western and east-central genetic groups and the east-central and island groups were significantly different from zero, allowing rejection of the null hypothesis of panmixia (Table 2B). Levels of differentiation were, however, not

significant between the western and island clusters. The similarities in mtDNA data for those two clusters could indicate a founder event in which the western population first colonized inshore waters of the Barataria Basin and then a subset of individuals separated from the group and inhabited areas surrounding the barrier islands that formed within the last 750 years. Also, all comparisons among the Barataria Basin genetic clusters using Φ_{ST} were not significant. Measurements of Φ_{ST} use haplotype frequencies and genetic distance information combined, whereas F_{ST} estimates use haplotype frequency information only. As populations diverge, frequency differences are expected to emerge prior to divergence of the haplotypes through mutation and drift. The low amount of sequence variability between mtDNA haplotypes of dolphins within the basin could be due to historical colonization of the BSE by a single population that then diverged into multiple genetic groups. Low mtDNA diversity has been reported among other BSE populations of *T. truncatus* and, as a result, mtDNA data can have lower statistical power needed to detect genetic structure within these communities (Sellas, Wells & Rosel, 2005; Litz et al., 2012; Richards et al., 2013).

Combining social and genetic analyses in this study has further demonstrated that dolphin population structure is complex, and both analytical approaches can provide unique and valuable insights. Overall, genetic analyses can differentiate communities of dolphins established through long-term (generational) preferential breeding behavior. In contrast, associations can be more fluid and may change in response to habitat or predator/prey changes, and strong associations can be formed between a mix of related and unrelated individuals. Combining the two data types can provide insights on different timescales into dolphin population structure versus using one technique alone. Our results suggest underlying social and relatedness groupings of common bottlenose dolphins within the Barataria Basin, coupled with evidence for multiple

demographically independent groups that are unique with respect to dolphin populations in coastal waters (i.e. the WCS). Furthermore, it is likely that additional social groups, and possibly genetically distinct groups, occupy the neighbouring estuarine habitats of the Barataria Basin that have yet to be fully investigated. Additional genetic sampling and photo-ID efforts in the south-eastern portion of the basin would improve our understanding of the social and genetic structure throughout the entire basin, and future research should aim to understand habitat and/or behavioral differences that could be drivers of differentiation.

Understanding the unique characteristics of these groups, such as social bonds, feeding behavior, prey preference, and habitat specialization, and also the most pressing threats for the distinct communities may help managers to design more effective mitigation or restoration plans, and to monitor their effectiveness to adapt as needed. For example, the MBSD project is intended to divert sediment and nutrients from the Mississippi River to the mid-Barataria Basin to reduce land loss and create and maintain wetlands. The sediment diversion will result in large volumes of fresh water moving into the basin (U.S. Army Corps of Engineers, 2017). Models predict a 34% decrease in dolphin survival for a given year of diversion operations, with dolphins occupying the western and central portions of the Barataria Basin likely to experience the greatest impacts (Garrison, Litz & Sinclair, 2020). This will potentially compound the significant health effects suffered by BBES dolphins as a result of the DWH oil spill (Schwacke et al., 2014; Lane et al., 2015; Smith et al., 2017). The current study shows discrete social and genetic groups in the western and central regions, which could be severely impacted if these regions are subjected to prolonged durations (multiple months) of fresh water. The information on social structure and evidence for demographically independent groups can aid decisions on management, mitigation, and/or conservation projects, and allow them to be designed to best

address the unique threats to given groups of animals, rather than attempting to apply a broad-stroke approach that may not maintain the complex structure and ecosystem roles of the dolphins in the Barataria Basin.

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TABLE 1. Median group size and mean social network metrics of individual social clusters. Standard error is in parentheses. n: number of individuals in each cluster.

Metric	E-central (n=3)	W-central (n=4)	Island (n=65)	Western (n=40)
Number of sightings	31	40	270	267
Group size	17.0 (2.07)	8.5 (2.06)	12.0 (0.96)	8.0 (0.68)
Affinity	1.64 (1.08)	2.06 (0.38)	2.72 (0.19)	2.45 (0.22)
Clustering coefficient	0.04 (0.04)	0.07 (0.01)	0.07 (0.02)	0.07 (0.02)
Eigenvector centrality	0.02 (0.02)	0.02 (0.01)	0.11 (0.04)	0.06 (0.02)
Reach	1.06 (1.18)	1.05 (0.93)	7.18 (2.41)	5.35 (2.03)
Strength	0.48 (0.42)	0.46 (0.40)	2.61 (0.76)	2.16 (0.74)

TABLE 2. Genetic differentiation among the Barataria Basin genetic clusters (western, east-central, and island) identified by STRUCTURE analysis and the Western Coastal Stock (WCS). A: Pairwise estimates of F_{ST} using nuclear microsatellite data. B: mtDNA pairwise estimates of Φ_{ST} above and F_{ST} below the diagonal. *P*-values are in parentheses and significant pairwise comparisons after sequential Bonferroni correction are in bold. n: number of samples.

A:	n	Western	East-central	Island	WCS
Western	53				
East-central	49	**0.031 (< 0.0001)**			
Island	57	**0.030 (< 0.0001)**	**0.023 (< 0.0001)**		
WCS	29	**0.044 (< 0.0001)**	**0.027 (< 0.0001)**	**0.021 (<0.0001)**	

Overall $F_{ST} = 0.029$, $P < 0.0001$

B:	n	Western	East-central	Island	WCS
Western	52		0.032 (0.0451)	0.023 (0.0661)	**0.243 (< 0.0001)**
East-central	46	**0.076 (0.0030)**		0.039 (0.0304)	**0.156 (< 0.0001)**
Island	55	0.010 (0.1787)	**0.113 (0.0002)**		**0.163 (0.0001)**
WCS	28	**0.196 (< 0.0001)**	**0.102 (0.0001)**	**0.227 (< 0.0001)**	

Overall $\Phi_{ST} = 0.099$, $P < 0.0001$
Overall $F_{ST} = 0.112$, $P < 0.0001$

TABLE 3. Tests of sex-biased dispersal in the Barataria Basin genetic clusters (GEN) and social clusters (SOC) using the mean Assignment Index correction (mAIc) values calculated in GenAlEx. Significance test results are shown for a two-tailed Mann Whitney U-test (Z and Probability). No values were significant between male and female pairs for any group. n: number of samples.

	n		mAIc			
Group	**Male**	**Female**	**Male**	**Female**	**Z**	**Probability**
GEN-western	29	24	0.360	-0.435	-0.643	0.520
GEN-east-central	20	29	0.322	-0.222	0.590	0.555
GEN-island	29	28	0.546	-0.565	-1.660	0.097
SOC-western	8	5	-0.514	0.823	1.171	0.242
SOC-island	7	7	-0.292	0.292	-0.447	0.655
Barataria Basin	100	95	0.195	-0.205	-0.873	0.383

TABLE 4. Number of individuals (n), cumulative number of sighting locations, bandwidth, and 50% and 95% utilization distributions (UDs) areas (km^2) for each social (SOC) and genetic (GEN) cluster.

Cluster	n	Cumulative # of locations	Bandwidth	50% area (km^2)	95% area (km^2)
SOC-East-central	3	33	467	0.99	7.6
SOC-West-central	4	42	700	2.6	13.2
SOC-Island	65	765	667	1.5	22.4
SOC-Western	40	504	567	4.8	37.1
GEN-East-central	49	493	1267	7.2	48.8
GEN-Island	57	883	1100	4.0	37.6
GEN-Western	53	861	933	3.9	31.4

TABLE 5. Comparison of genetic samples (n=28) that qualified for the SOCPROG analysis along with satellite telemetry assignment group. Genetic assignments are based on STRUCTURE membership coefficients (q) ≥ 0.50. SOC-GEN represents the proportion of social clusters that matched the genetic assignment. SOC-GEN-TEL represents the proportion of social clusters that matched both genetic and satellite telemetry assignments. SOC-TEL represents the proportion of social clusters that matched the satellite telemetry assignment. Clusters in bold represent matches. nd: data not available.

Field #	SOCPROG cluster	Genetic cluster (*q*)	Sat telemetry	Sex	Age	SOC-GEN match	SOC-GEN-TEL match	SOC-TEL match
Y22	west-central	western (0.75)	western	M	nd	0/1 (0%)	0/1 (0%)	0/1 (0%)
BW120223-06	island	western (0.89)	na	M	nd	6/11 (55%) M: 3/6 (50%) F: 3/5 (60%)	2/6 (33%) M: 1/3 (33%) F: 1/3 (33%)	3/7 (43%) M: 1/3 (33%) F: 2/4 (50%)
Y75	island	western (0.93)	western	F	>10			
TYP100814-03	**island**	**island** (0.82)	na	M	nd			
Y20	island	east-central (0.90)	western	M	30			
YF8	**island**	**island** (0.63)	**island**	M	12			
R3100511-03	island	unassigned	na	M	nd			
Y60	**island**	**island** (0.58)	na	M	11			
Y63	**island**	**island** (0.83)	na	F	>10			
YV5	**island**	**island** (0.54)	na	F	24			
BW120220-03	island	unassigned	na	F	nd			
Y03	island	unassigned	western	F	15			
Y17	**island**	**island** (0.89)	**island**	F	14			
Y19	**island**	western (0.68)	**island**	F	15			
Y18	island	east-central (0.85)	western	M	nd			
YJ2	**western**	unassigned	**western**	M	23	6/10 (60%) M: 2/5 (40%) F: 4/5 (80%)	2/4 (50%) M: 0/2 (0%) F: 2/2 (100%)	5/6 (83%) M: 3/4 (75%) F: 2/2 (100%)
Y00	**western**	island (0.76)	**western**	M	17			
R3100511-01	western	unassigned	na	M	nd			
BW120223-01	western	island (0.75)	na	M	nd			
Y53	**western**	**western** (0.88)	na	F	10			
Y45	**western**	**western** (0.78)	na	F	19			
YK4	**western**	unassigned	**western**	M	nd			
Y08	**western**	**western** (0.59)	island	M	22			
YX7	**western**	**western** (0.51)	**western**	F	>10			
Y73	western	island (0.76)	na	F	17			
BW120223-03	**western**	**western** (0.88)	na	M	nd			
Y06	western	island (0.56)	na	M	13			
Y15	**western**	**western** (0.74)	**western**	F	13			

FIGURE 1. Barataria Basin study area with photo-ID tracklines from the two phases of field effort. Phase 1 (black dashed line): 2010-2014 (10 primary periods; see McDonald et al., 2017 for details) as part of the *Deepwater Horizon* (DWH) Natural Resource Damage Assessment (NRDA), and Phase 2 (solid colored lines): March 2019 as part of an Environmental Impact Statement required for the Mid-Barataria Sediment Diversion (MBSD). The inset in the upper right depicts the same area outlined in the main image, and shows the biopsy sample locations (black dots) within the basin used for the genetic analysis.

FIGURE 2. Number of identified individuals, including previously and newly identified, observed within each primary period, and total number of individuals in the Barataria Basin photo-ID catalog observed during mark-recapture surveys.

FIGURE 3. SOCPROG dendrogram showing the result from the association analysis using average linkage and simple ratio index for the 112 Barataria Basin dolphins with 10 or more sightings from mark-recapture photo-ID surveys (2010 - 2019). Dolphin catalog ID's are listed on the y-axis. Dolphin clusters are joined by vertical black lines and differentiated by color: east-central (green), west-central (blue), island (red), and western (yellow). The analysis resulted in a cophenetic correlation coefficient of 0.80 and modularity value of 0.34.

FIGURE 4. Genetic clustering assignments of individual dolphins within Barataria Basin from STRUCTURE analysis ($K = 3$). A) Sampling locations of the three genetic clusters: east-central

(green circles), island (red circles), and western (yellow circles); and the unassigned individuals (black circles). Number of samples (n) assigned to each cluster and average membership coefficient (q) values are shown for each. B) STRUCTURE bar plot. Each vertical column represents one individual and proportional membership assignments to each of the three clusters is represented by the different colors based on q-value (y-axis). Individuals are grouped into clusters using a q-value threshold of 0.50 and separated by a black line.

FIGURE 5. Average pairwise relatedness and variance (error bars) estimated using COANCESTRY within the genetic clusters (GEN), social clusters (SOC), and the entire genetic data set (Barataria Basin). Values are shown for the overall pairs (gray bars), female-female pairs (red), and male-male pairs (blue). Significant differences between the overall relatedness of each cluster and Barataria Basin data set are denoted with * above the bar. Tests of differences between female and male pairs were only significant for the east-central genetic cluster.

FIGURE 6. 95% and 50% percent volume contours (PVC) (i.e. utilization distributions (UDs)) calculated using kernel density estimates (KDEs) from cumulative photo-ID sightings for each of the four Barataria Basin SOCPROG clusters (top row): western (yellow); island (red); east-central (green); west-central (blue) and the three Barataria Basin genetic groups from the STRUCTURE analyses (bottom row): western (yellow); island (red); east-central (green).

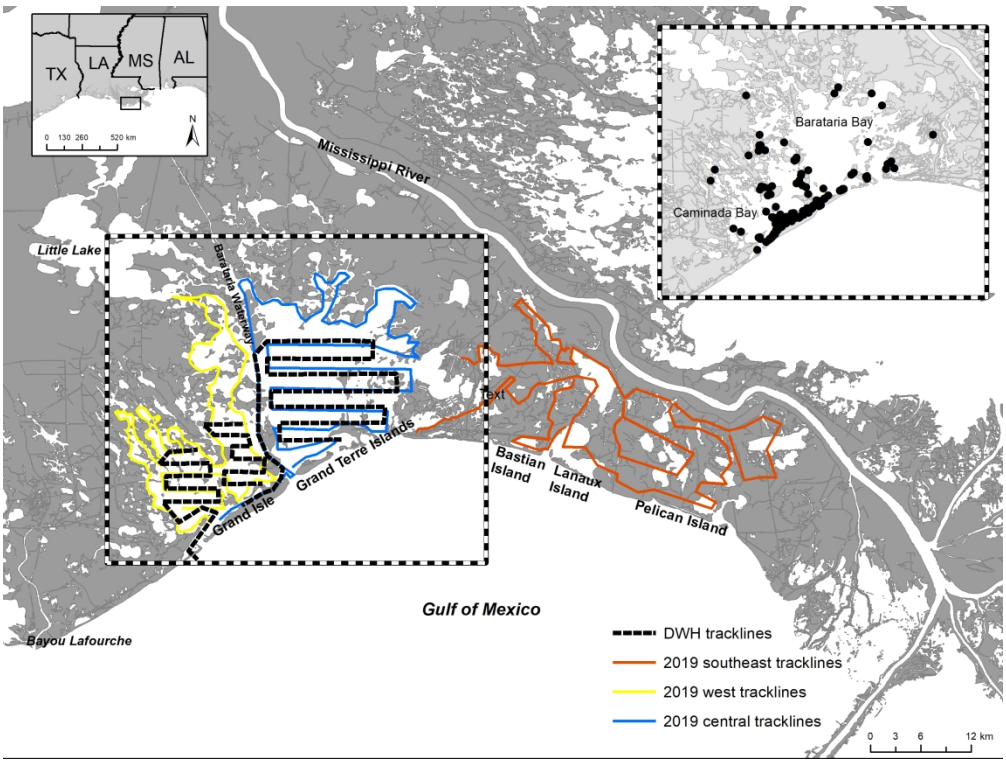

FIGURE 1. Barataria Basin study area with photo-ID tracklines from the two phases of field effort. Phase 1 (black dashed line): 2010-2014 (10 primary periods; see McDonald et al., 2017 for details) as part of the Deepwater Horizon (DWH) Natural Resource Damage Assessment (NRDA), and Phase 2 (solid colored lines): March 2019 as part of an Environmental Impact Statement required for the Mid-Barataria Sediment Diversion (MBSD). The inset in the upper right depicts the same area outlined in the main image, and shows the biopsy sample locations (black dots) within the basin used for the genetic analysis.

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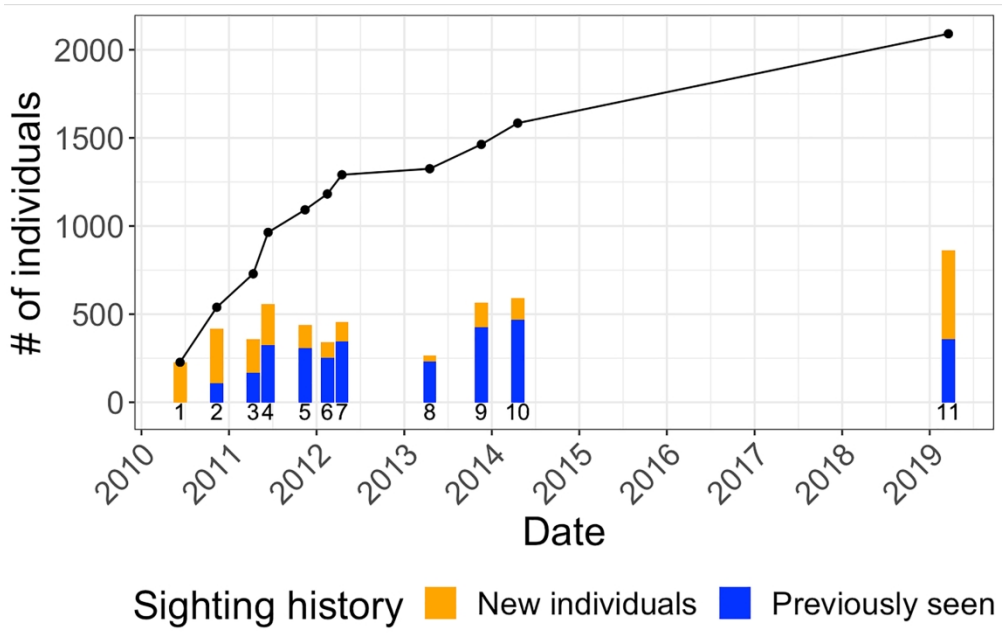

FIGURE 2. Number of identified individuals, including previously and newly identified, observed within each primary period, and total number of individuals in the Barataria Basin photo-ID catalog observed during mark-recapture surveys.

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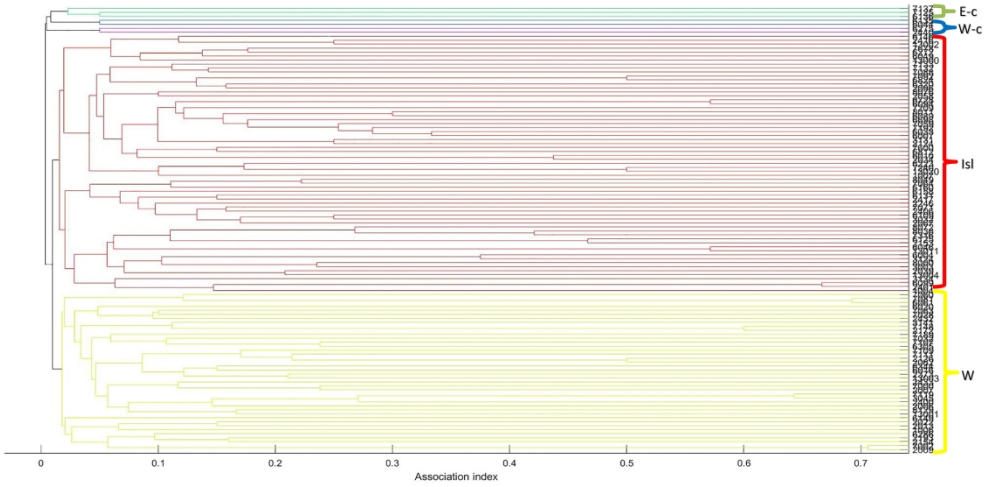

FIGURE 3. SOCPROG dendrogram showing the result from the association analysis using average linkage and simple ratio index for the 112 Barataria Basin dolphins with 10 or more sightings from mark-recapture photo-ID surveys (2010 - 2019). Dolphin catalog ID's are listed on the y-axis. Dolphin clusters are joined by vertical black lines and differentiated by color: east-central (green), west-central (blue), island (red), and western (yellow). The analysis resulted in a cophenetic correlation coefficient of 0.80 and modularity value of 0.34.

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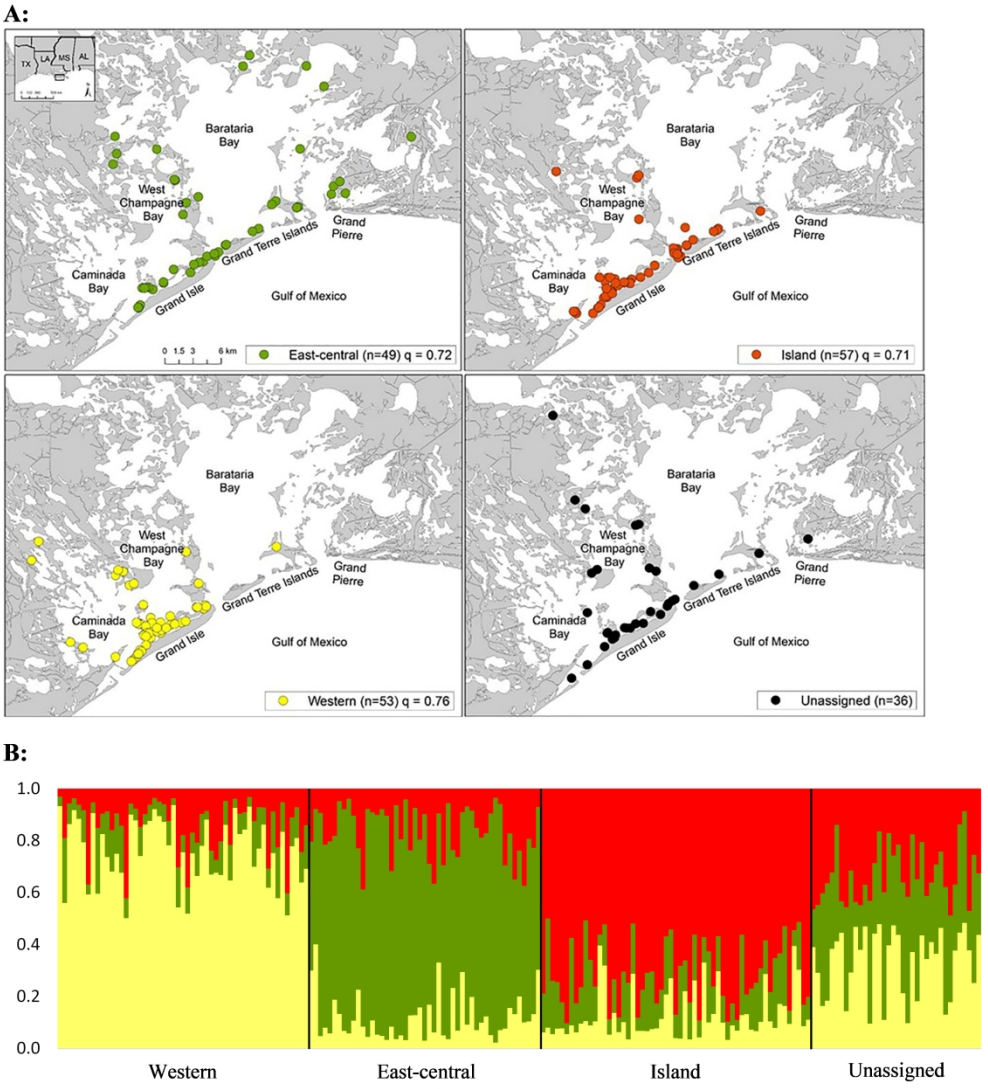

FIGURE 4. Genetic clustering assignments of individual dolphins within Barataria Basin from STRUCTURE analysis (K = 3). A) Sampling locations of the three genetic clusters: east-central (green circles), island (red circles), and western (yellow circles); and the unassigned individuals (black circles). Number of samples (n) assigned to each cluster and average membership coefficient (q) values are shown for each. B) STRUCTURE bar plot. Each vertical column represents one individual and proportional membership assignments to each of the three clusters is represented by the different colors based on q-value (y-axis). Individuals are grouped into clusters using a q-value threshold of 0.50 and separated by a black line.

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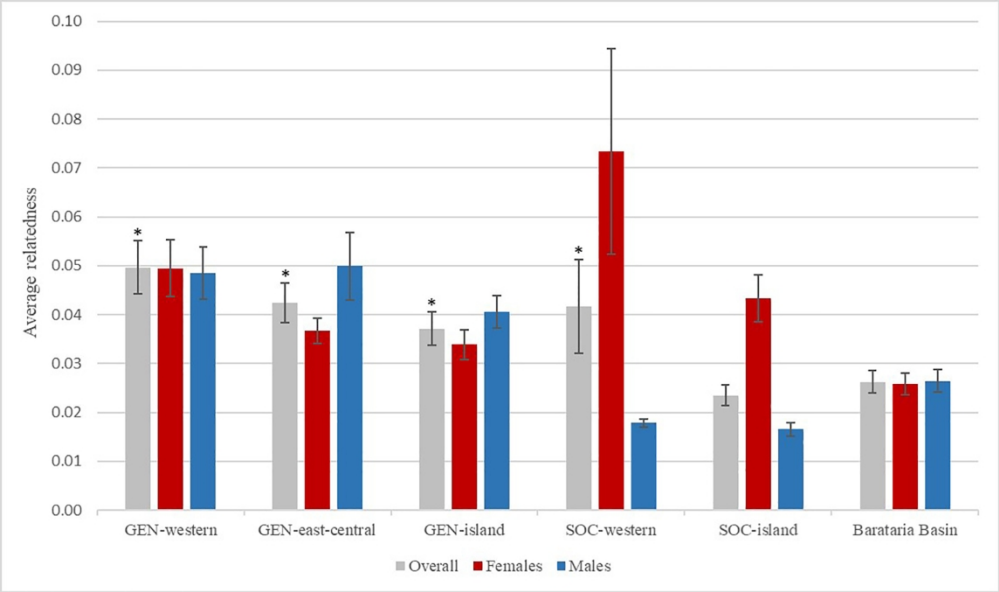

FIGURE 5. Average pairwise relatedness and variance (error bars) estimated using COANCESTRY within the genetic clusters (GEN), social clusters (SOC), and the entire genetic data set (Barataria Basin). Values are shown for the overall pairs (gray bars), female-female pairs (red), and male-male pairs (blue). Significant differences between the overall relatedness of each cluster and Barataria Basin data set are denoted with * above the bar. Tests of differences between female and male pairs were only significant for the east-central genetic cluster.

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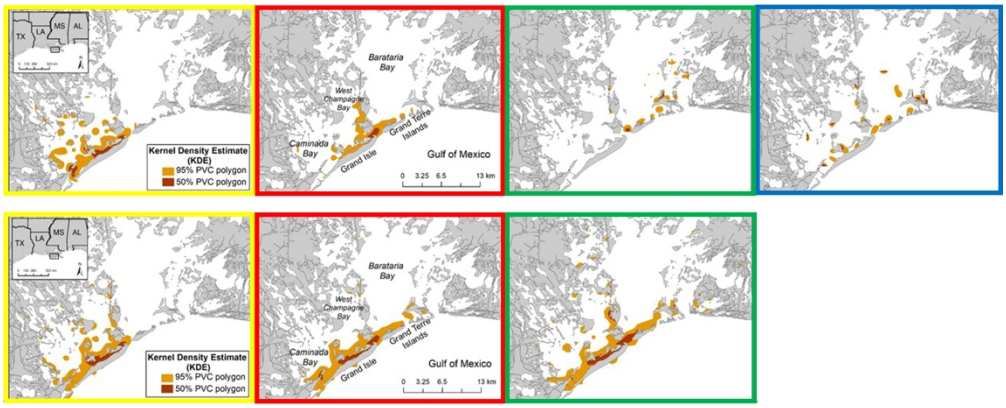

FIGURE 6. 95% and 50% percent volume contours (PVC) (i.e. utilization distributions (UDs)) calculated using kernel density estimates (KDEs) from cumulative photo-ID sightings for each of the four Barataria Basin SOCPROG clusters (top row): western (yellow); island (red); east-central (green); west-central (blue) and the three Barataria Basin genetic groups from the STRUCTURE analyses (bottom row): western (yellow); island (red); east-central (green).

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Supporting Information

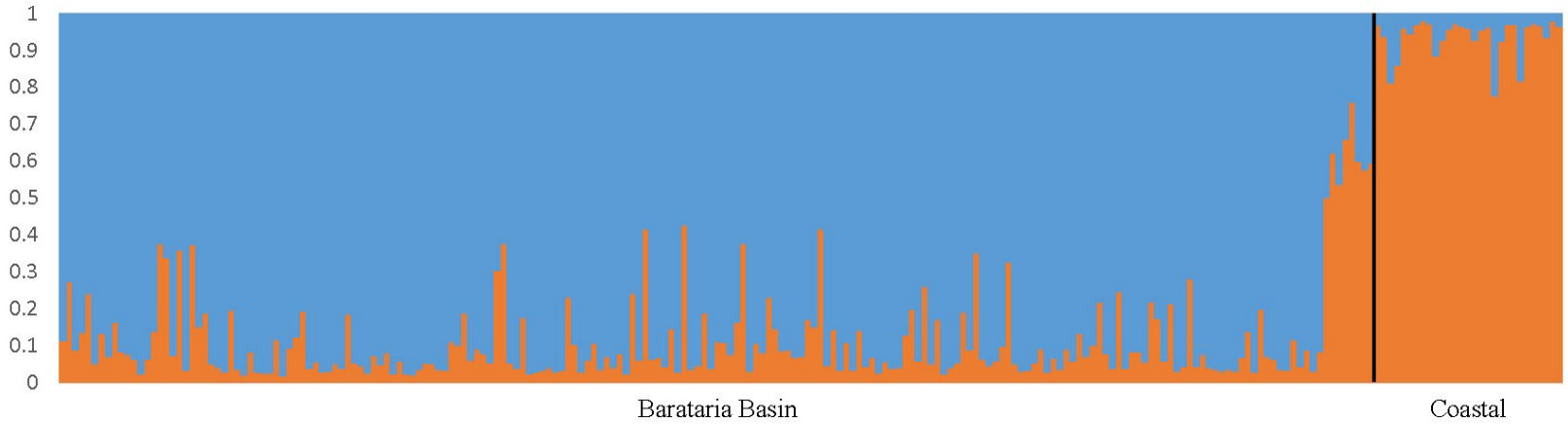


FIGURE S1. Bayesian clustering assignments of dolphins from STRUCTURE analysis of the Barataria Basin and Western Coastal Stock samples. Each individual is represented by a vertical column along the *x*-axis and proportional membership coefficients (*q*) to the two clusters are shaded in blue or orange. Sampling locations (inside Barataria Basin versus in coastal waters > 2 km from shore) are separated by a black line.

TABLE S1. PCR conditions for the eight multiplexes used to amplify 43 microsatellite loci using the Qiagen Type-it Microsatellite PCR kit. PCR reactions were completed in 10 µL volumes and contained 1x Type-it Multiplex PCR Master Mix and 10 ng of DNA. Thermocycler profiles started with a denaturation step of 95°C for 5 min followed by 26-29 cycles of 95°C for 30 sec, 50-60°C (Ta) for 90 sec, and 72°C for 30 sec with a final extension step at 60°C for 30 min.

Locus	Forward primer (5'-3')	Reverse primer (5'-3')	Repeat type	Multiplex set	Primer final concentration (µM)	Ta (°C), # of cycles	Species of origin	Reference
MK5	CTCAGAGGGAAATGAGGCTG	GTTTGTCTAGAGGTCAAAGCCTTCC	Di	1	0.10 µM	56, 27	*T. aduncus*	Krützen et al., 2001
MK6	GTCCTCTTTCCAGGTGTAGCC	GCCCACTAAGTATGTTGCAGC	Di	1	0.10 µM	56, 27	*T. aduncus*	Krützen et al., 2001
MK8	TCCTGGAGCATCTTATAGTGGC	GTTTCTGTGTCTCTTTGACATGCCCTCACC	Di	1	0.075 µM	56, 27	*T. aduncus*	Vollmer et al., 2021 modification of Krützen et al., 2001
MK9	CATAACAAAGTGGGATGACTCC	GTTTATCCTGTTGGCTGCAGTG	Di	1	0.10 µM	56, 27	*T. aduncus*	Krützen et al., 2001
TexVet7	TGCACTGTAGGGTGTTCAGCAG	GTTTCTTAATTGGGGGCGATTTCAC	Di	1	0.10 µM	56, 27	*T. truncatus*	Rooney, Merritt & Derr, 1999
KWM12a[†]	CCATACAATCCAGCAGTC	GTTTCACTGCAGAATGATGACC	Di	1	0.10 µM	50, 27	*O. orca*	Hoelzel, Dahlheim & Stern, 1998
Ttr58	TGGGTCTTGAGGGGTCTG	GTTTGCTGAGGCTCCTTGTTGG	Di	2	0.0375 µM	52, 27	*T. truncatus*	Rosel, Forgetta & Dewar, 2005
Ttr63	CAGCTTACAGCCAAATGAGAG	GTTTCTCCATGGCTGAGTCATCA	Di	2	0.20 µM	52, 27	*T. truncatus*	Rosel, Forgetta & Dewar, 2005
TexVet5	GATTGTGCAAATGGAGACA	GTTTGAGATGACTCCTGTGGG	Di	2	0.05 µM	52, 27	*T. truncatus*	Rooney, Merritt & Derr, 1999
EV37	AGCTTGATTTGGAAGTCATGA	GTTTAGTAGAGCCGTGATAAAGTGC	Di	2	0.30 µM	52, 27	*M. novaeangliae*	Valsecchi & Amos, 1996
PPHO130	CAAGCCCTTACACATATG	GTTTATTGAGTAAAAGCAATTTTG	Di	3	0.30 µM	50, 29	*P. phocoena*	Rosel et al., 1999
TtrFF6	AAGTAAGTGCTCCTTTGACTGG	GTTTGGCAGAGAGATATTAGGACAGC	Di	3	0.15 µM	50, 29	*T. truncatus*	Rosel, Forgetta & Dewar, 2005
Ttr04	CTGACCAGGCACTTTCCAC	GTTTGTTTCCCAGGATTTTAGTGC	Di	3	0.075 µM	50, 29	*T. truncatus*	Rosel, Forgetta & Dewar, 2005
Ttr11	CTTTCAACCTGGCCTTTCTG	GTTTGGCCACTACAAGGGAGTGAA	Di	3	0.05 µM	50, 29	*T. truncatus*	Rosel, Forgetta & Dewar, 2005
Ttr19	TGGGTGGACCTCATCAAATC	GTTTAAGGGCTGTAAGAGG	Di	3	0.10 µM	50, 29	*T. truncatus*	Rosel, Forgetta & Dewar, 2005
Ttr34	GCACATGAGTATGTGGACAGG	GTTTCCTCCTTGGGAGTGTCCTCT	Di	4	0.05 µM	58, 28	*T. truncatus*	Rosel, Forgetta & Dewar, 2005
Ttr48	AAGAGGATGCAAATGGCAAG	GTTTGGTAAGAAAATACCAAAGTCC	Di	4	0.0375 µM	58, 28	*T. truncatus*	Rosel, Forgetta & Dewar, 2005
EV14	TAAACATCAAAGCAGACCCC	GTTTCCAGAGCCAAGGTCAAGAG	Di	4	0.30 µM	58, 28	*P. macrocephalus*	Valsecchi & Amos, 1996
EV94	ACATGGCCATCGCTCTTAAC	GTTTATAAGGGTGAATTTTATGG	Di	4	0.30 µM	58, 28	*M. novaeangliae*	Vollmer & Rosel, 2017 modification of Valsecchi & Amos, 1996
Ttr36(tetra)	GGACATAACTAGCTTTCTTGCTTGC	GTTTGTCTGCATAGTGCGAGGCG	Tetra	5	0.05 µM	54, 27	*T. truncatus*	Rosel et al., 2017
Ttr54	GAAGGGCAAACAAGATATCGG	GTTTCTCCGTCTCCTGTTCAATGC	Di	5	0.125 µM	54, 27	*T. truncatus*	Rosel et al., 2017
Ttr55	CAAGACTCTGAAGGATTTCTCAGG	GTTTCCAAAGAGCATTGCAGAGG	Di	5	0.125 µM	54, 27	*T. truncatus*	Rosel et al., 2017
Ttr61	GCCATCGTGAATAAAGACGC	GTTTGGAAGTTCTTACTTGTATTGAGGGC	Di	5	0.10 µM	54, 27	*T. truncatus*	Rosel et al., 2017
Ttr90	AGGGTTCTCCAGAAACATAGGG	GTTTCACAATCATGAGAGCCAGTTCC	Di	5	0.10 µM	54, 27	*T. truncatus*	Rosel et al., 2017
Ttr98	CCATTGCATTTCAATACCACC	GTTTCAGAGAATTCAGAAACGGAGC	Di	5	0.10 µM	54, 27	*T. truncatus*	this study, Rosel et al., 2017
Ttr100	GTCTTGGATTACACGGGCG	GTTTGGCAGGCAGAAGATAAAGC	Di	5	0.05 µM	54, 27	*T. truncatus*	Rosel et al., 2017
Ttr12	AAATTCTTCTTAGTCATGTTTCCACC	GTTTCACATCACATTCAGAATAGTCTTTGC	Tetra	6	0.10 µM	60, 26	*T. truncatus*	Rosel et al., 2017
Ttr20	CCAATCTCTAAGGTGGTTCTGGG	GTTTCCCATTGGTCACTTGGTTACG	Tetra	6	0.025 µM	60, 26	*T. truncatus*	this study, Rosel et al., 2017
Ttr41	TGCTTCCTAATGCCACATCC	GTTTCAGAGCCATTGCTCATAAACC	Tetra	6	0.05 µM	60, 26	*T. truncatus*	Rosel et al., 2017
Ttr51	GCTAAGATATTGACATATTTCCCTGG	GTTTGGTGGTTGATTCAGAACC	Di	6	0.05 µM	60, 26	*T. truncatus*	this study, Rosel et al., 2017
Ttr52	TGGACTCAGAGAGATAGGTGG	GTTTGGCTGCCTTGTGTCTGTAAGC	Di	6	0.125 µM	60, 26	*T. truncatus*	Rosel et al., 2017
DlrFCB1	TGCATCTCCATGGTATGTCTTATCC	GTTTAGCCTCTGCTATGCCTGGAACGC	Di	6	0.10 µM	60, 26	*D. leucas*	Buchanan et al., 1996
Ttr56	CTGCATTCACCTCCTCACC	GTTTATGATGCAATCACAGGCTGC	Di	7	0.15 µM	60, 26	*T. truncatus*	Rosel et al., 2017
Ttr83	TGCATATTTGAGATTTCTAGCTCC	GTTTGCAGAAGTATCGGTCAAGC	Di	7	0.10 µM	60, 26	*T. truncatus*	Rosel et al., 2017
D08	ATCCATCATATTGTCAAGTT	GTTTTCCTGGGTGATGAGTCTTC	Di	7	0.20 µM	60, 26	*T. truncatus*	Rosel et al., 2017 modification of Shinohara, Domingo-Roura & Takenaka, 1997
D22	GTTTGGAAATGCTCTGAGAAGGTC	CCAGAGCACCTATGTGGAC	Di	7	0.035 µM	60, 26	*T. truncatus*	Shinohara, Domingo-Roura & Takenaka, 1997
Dde70	ACACCAGCACCTACATTCACA	GTTTTCAGCAGCATTCTAACCAAAC	Di	7	0.05 µM	60, 26	*D. delphis*	Coughlan et al., 2006
Ttr71	CCCTTATTAATCAGAGAGAGAGGG	GTTTCTCTTACCTCTTCTTTCCTGTGG	Tetra	8	0.025 µM	54, 27	*T. truncatus*	Rosel et al., 2017
Ttr78	AAAGCTGAGGAGACTTGAGATGG	GTTTGGCTAAGGATGCCATTGAGG	Tetra	8	0.035 µM	54, 27	*T. truncatus*	Rosel et al., 2017
Ttr84	TTATCTATTCACTTCAACCACACG	GTTTAAATGTGTCTTAGGAAGACTGAACC	Di	8	0.10 µM	54, 27	*T. truncatus*	Rosel et al., 2017
DlrFCB3	CAAGTGCCTATCAGTAGATGAATG	GTTTCTTGTATCTATAACTCTGGTTATGG	Di	8	0.25 µM	54, 27	*D. leucas*	Buchanan et al., 1996
DlrFCB12[‡]	CTCAGTTAATATACATGTAATGCATGC	GTTTCAAAGAATAGCTAAATAAACAGTAAC	Di	8	0.20 µM	54, 27	*D. leucas*	this study, modification of Buchanan et al., 1996
SW19	GTAGTTTTCTTTAACAGTAATG	GTTTAGTTCTGGGCTTTTCACCTA	Di	8	0.075 µM	54, 27	*P. macrocephalus*	Richard, Whitehead & Wright, 1996

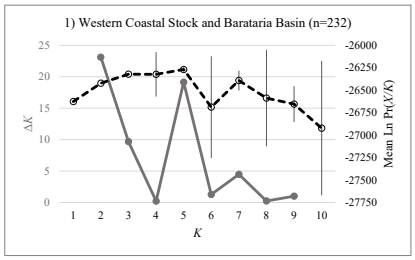
[†]KWM12a was amplified alone and then 2 µL of the PCR reaction was coloaded with 2 µL of the MK5/MK6/MK8/MK9/TexVet7 PCR reaction.

[‡]Buchanan DlrFCB12 reverse primer sequence is CAAAGA**G**ATAGCTAAATAAACAGTAAC; a G (in bold & underlined) has been removed from our primer sequence.

TABLE S2. Estimations for the optimal number of clusters (K) using Evanno's ΔK, Pritchard's mean log-likelihood of the data (ln Pr(X/K)) with standard deviation (Stdev), and Wang's parsimony index (PI) for each STRUCTURE run. The most likely K from each method is bolded in each table. When the most likely ΔK was below a value of 10, samples could not be assigned to more than one cluster for that K, therefore the best K was determined to be 1 as estimated by the other two methods. Plots of ΔK (solid gray line) and mean ln Pr(X/K) (dashed black lines with Stdev plotted) are provided for each STRUCTURE run. n: number of samples.

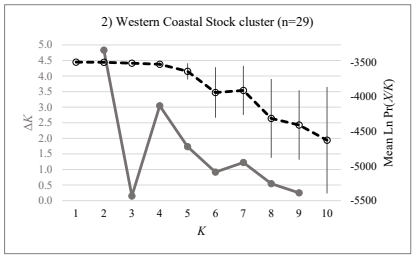
1) Western Coastal Stock and Barataria Basin (n=232)

K	Evanno's ΔK	Pritchard's Mean ln Pr(X/K)	Stdev ln Pr(X/K)	Wang's PI
1	-	-26625.62	0.70	0.500
2	**23.10**	-26421.70	4.52	0.753
3	9.69	-26322.12	10.39	0.824
4	0.23	-26323.21	247.16	**0.842**
5	19.13	**-26268.68**	24.79	0.623
6	1.26	-26688.55	566.83	0.015
7	4.47	-26392.27	109.73	0.276
8	0.24	-26586.83	537.05	-0.053
9	1.01	-26653.77	199.14	0.129
10	-	-26922.44	747.59	0.147



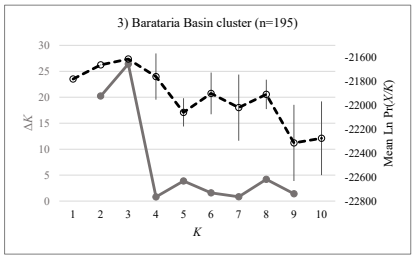
2) Western Coastal Stock alone (n=29)

K	Evanno's ΔK	Pritchard's Mean ln Pr(X/K)	Stdev ln Pr(X/K)	Wang's PI
1	-	**-3498.92**	1.04	**0.500**
2	**4.83**	-3500.38	2.44	-0.280
3	0.15	-3513.64	17.10	-0.609
4	3.05	-3529.40	28.57	-0.551
5	1.73	-3632.23	116.80	-0.599
6	0.92	-3937.17	365.06	-0.853
7	1.23	-3907.04	354.96	-0.563
8	0.54	-4312.00	569.59	-0.614
9	0.25	-4407.30	501.30	-0.798
10	-	-4626.95	769.21	-0.813



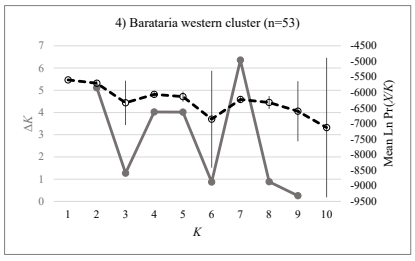
3) Barataria Basin cluster alone (n=195)

K	Evanno's ΔK	Pritchard's Mean ln Pr(X/K)	Stdev ln Pr(X/K)	Wang's PI
1	-	-21781.33	0.56	0.500
2	20.23	-21663.16	3.44	0.724
3	**26.42**	**-21614.48**	7.37	**0.824**
4	0.79	-21760.49	192.95	0.620
5	3.87	-22059.25	117.98	0.497
6	1.59	-21901.12	174.13	0.491
7	0.83	-22020.10	276.12	0.723
8	4.21	-21909.31	122.68	0.819
9	1.40	-22314.44	317.94	0.691
10	-	-22275.61	307.70	0.722



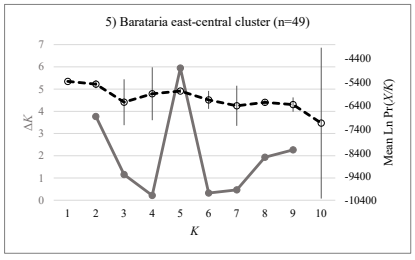
4) Barataria western cluster alone (n=53)

K	Evanno's ΔK	Pritchard's Mean ln Pr(X/K)	Stdev ln Pr(X/K)	Wang's PI
1	-	**-5596.07**	1.18	**0.500**
2	5.11	-5702.94	102.45	-0.169
3	1.27	-6333.57	712.24	-0.037
4	4.03	-6058.74	87.05	0.367
5	4.02	-6134.39	161.49	0.102
6	0.87	-6858.95	1557.67	-0.050
7	**6.35**	-6226.53	114.69	0.077
8	0.88	-6322.90	206.75	-0.028
9	0.25	-6602.23	965.67	-0.371
10	-	-7127.34	2241.66	-0.371



5) Barataria east-central cluster alone (n=49)

K	Evanno's ΔK	Pritchard's Mean ln Pr(X/K)	Stdev ln Pr(X/K)	Wang's PI
1	-	**-5359.08**	0.81	**0.500**
2	3.77	-5478.58	171.24	-0.227
3	1.15	-6243.02	973.29	0.078
4	0.22	-5883.74	1121.84	-0.153
5	**5.95**	-5770.11	81.92	-0.083
6	0.33	-6143.68	380.33	-0.289
7	0.47	-6393.57	850.41	-0.449
8	1.93	-6245.38	127.15	-0.074
9	2.26	-6342.93	304.23	-0.376
10	-	-7129.08	3199.31	-0.777



6) Barataria island cluster alone (n=57)

K	Evanno's ΔK	Pritchard's Mean ln Pr(X/K)	Stdev ln Pr(X/K)	Wang's PI
1	-	**-6358.53**	0.80	**0.500**
2	**9.76**	-6412.61	63.94	-0.079
3	0.08	-7090.64	595.45	-0.044
4	1.30	-7719.12	856.30	-0.329
5	0.31	-7236.98	1071.97	-0.400
6	2.08	-7089.52	174.86	-0.240
7	1.16	-7306.14	217.95	0.124
8	1.30	-7269.66	289.18	-0.056
9	0.38	-7607.82	2299.61	-0.658
10	-	-7077.94	161.66	-0.042

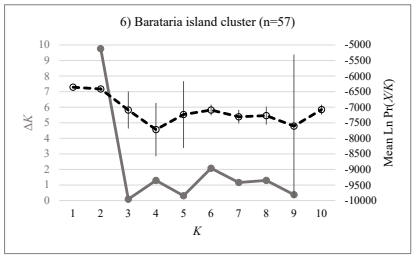


TABLE S3. Genetic diversity based on the 43 microsatellite loci genotyped for the Western Coastal Stock (WCS) and the Barataria Basin western, east-central, and island clusters identified by STRUCTURE analysis. N_A: number of alleles, PA: number of private alleles with values in parentheses showing PA among the Barataria Basin clusters only, AR: allelic richness, H_o: observed heterozygosity, H_e: expected heterozygosity, and HWE *P*-value: tests for departure from Hardy-Weinberg equilibrium (no *P*-values were significant after Bonferroni correction). s.d. = standard deviation. n: number of samples.

	Western (n=53)						**East-central (n=49)**						**Island (n=57)**						**WCS (n=29)**					
Locus	N_A	PA	AR	H_o	H_e	HWE *P*-value	N_A	PA	AR	H_o	H_e	HWE *P*-value	N_A	PA	AR	H_o	H_e	HWE *P*-value	N_A	PA	AR	H_o	H_e	HWE *P*-value
Ttr04	8	0	7.83	0.792	0.786	0.864	9	0	8.02	0.816	0.838	0.467	11	1 (1)	8.93	0.825	0.796	0.200	9	0	9.00	0.793	0.806	0.749
Ttr19	3	0	3.00	0.491	0.457	0.554	3	0	3.00	0.347	0.552	0.002	3	0	3.00	0.456	0.499	0.486	5	2	5.00	0.621	0.564	0.434
Ttr11	7	0	6.51	0.736	0.772	0.615	8	1 (1)	7.16	0.694	0.729	0.137	7	0	6.47	0.754	0.756	0.105	6	0	6.00	0.655	0.716	0.585
Ttr48	2	0	2.00	0.264	0.231	0.576	2	0	2.00	0.224	0.232	1.000	2	0	1.97	0.088	0.085	1.000	2	0	2.00	0.241	0.216	1.000
Ttr34	4	0	3.79	0.358	0.316	1.000	5	0	4.42	0.306	0.338	0.028	5	0	4.02	0.333	0.349	0.429	5	1	5.00	0.276	0.256	1.000
Ttr63	13	0	12.73	0.887	0.905	0.938	15	1 (1)	13.29	0.857	0.871	0.112	16	1 (1)	14.07	0.807	0.882	0.254	12	0	12.00	0.897	0.845	0.631
Ttr58	3	0	3.00	0.660	0.635	0.963	3	0	3.00	0.592	0.612	0.198	3	0	3.00	0.667	0.560	0.047	3	0	3.00	0.621	0.615	0.600
EV37	11	0	10.14	0.906	0.884	0.081	17	1 (4)	14.79	1.000	0.911	0.784	15	0 (3)	12.86	0.912	0.888	0.879	20	3	20.00	0.897	0.924	0.269
TexVet5	4	1 (1)	3.55	0.755	0.634	0.084	3	0	3.00	0.367	0.498	0.009	4	1 (1)	3.51	0.614	0.589	1.000	3	0	3.00	0.310	0.406	0.174
EV14	8	0	7.82	0.849	0.827	0.654	10	1 (1)	9.01	0.857	0.835	0.237	11	2 (2)	9.74	0.895	0.855	0.027	8	0	8.00	0.828	0.841	0.772
EV94	3	0	3.00	0.528	0.563	0.832	3	0	2.94	0.571	0.507	0.727	3	0	3.00	0.632	0.531	0.094	4	1	4.00	0.621	0.579	0.352
MK6	7	0	6.98	0.755	0.802	0.615	7	0	6.72	0.755	0.738	0.173	7	0	6.93	0.825	0.773	0.338	9	2	9.00	0.897	0.831	0.008
MK8	5	0	4.98	0.528	0.587	0.068	5	0	4.81	0.429	0.526	0.326	5	0	4.88	0.579	0.591	0.931	6	1	6.00	0.724	0.718	0.145
MK9	4	0	4.00	0.736	0.673	0.319	5	1 (1)	4.18	0.837	0.656	0.026	4	0	3.95	0.667	0.630	0.670	4	0	4.00	0.586	0.642	0.262
KWM12a	5	1 (1)	4.88	0.491	0.436	0.818	6	0	5.57	0.653	0.702	0.657	6	0	5.50	0.649	0.669	0.218	4	0	4.00	0.690	0.626	0.974
MK5	5	0	4.89	0.434	0.474	0.179	6	0	5.43	0.735	0.708	0.690	6	0	4.99	0.772	0.681	0.299	6	1	6.00	0.793	0.688	0.256
TexVet7	4	0	3.80	0.434	0.396	0.561	4	0	3.93	0.551	0.501	0.887	4	0	3.51	0.596	0.581	0.984	4	0	4.00	0.586	0.649	0.458
TtrFF6	7	2 (2)	5.85	0.566	0.580	0.632	5	0	4.83	0.612	0.644	0.579	8	3 (3)	6.48	0.456	0.443	0.288	5	0	5.00	0.724	0.714	0.486
PPHO130	5	0	4.09	0.623	0.594	0.404	4	0	3.94	0.592	0.537	0.114	6	1 (1)	5.39	0.596	0.537	0.841	6	1	6.00	0.655	0.699	0.390
Ttr36(tetra)	5	0	4.91	0.811	0.736	0.482	7	1 (1)	6.15	0.714	0.677	0.566	6	0	5.65	0.737	0.704	0.718	7	2	7.00	0.724	0.765	0.329
Ttr54	9	0	8.51	0.962	0.832	0.713	8	0	7.57	0.816	0.848	0.195	10	0 (1)	9.42	0.842	0.844	0.373	11	1	11.00	0.931	0.855	0.018
Ttr55	5	0	4.96	0.774	0.713	0.717	5	0	4.77	0.796	0.669	0.585	5	0	4.74	0.614	0.621	0.161	4	1	4.00	0.621	0.591	1.000
Ttr61	8	0	7.09	0.774	0.805	0.661	8	0	7.16	0.837	0.803	0.697	9	0	8.10	0.912	0.833	0.973	11	3	11.00	0.897	0.866	0.861
Ttr90	5	0	4.34	0.642	0.606	0.204	6	0	5.86	0.571	0.596	0.124	6	0	5.63	0.579	0.603	0.250	5	1	5.00	0.621	0.583	0.971
Ttr98	4	0	3.80	0.755	0.660	0.637	4	0	3.84	0.633	0.570	0.875	5	1 (1)	4.45	0.614	0.608	0.590	5	1	5.00	0.552	0.554	0.283
Ttr100	7	0	6.46	0.698	0.776	0.263	7	0	6.83	0.816	0.803	0.955	8	1 (1)	6.41	0.649	0.745	0.084	6	0	6.00	0.828	0.754	0.574
Ttr12	5	0	4.99	0.642	0.640	0.336	4	0	3.99	0.714	0.616	0.708	7	2 (2)	6.34	0.439	0.501	0.485	5	0	5.00	0.552	0.578	0.199
Ttr20	6	0	5.00	0.491	0.471	0.409	6	0	5.36	0.429	0.555	0.020	6	0	5.02	0.561	0.581	0.400	6	1	6.00	0.586	0.633	0.097
Ttr41	3	0	3.00	0.604	0.590	0.778	3	0	3.00	0.531	0.519	0.829	3	0	3.00	0.772	0.671	0.128	5	2	5.00	0.690	0.719	0.817
Ttr51	4	0 (1)	3.34	0.208	0.223	0.568	3	0	2.84	0.388	0.457	0.320	3	0	2.99	0.509	0.491	0.860	5	1	5.00	0.310	0.525	0.017
Ttr52	6	0	4.64	0.717	0.671	0.659	6	0 (1)	5.42	0.571	0.621	0.192	6	0	5.27	0.632	0.578	0.711	7	1	7.00	0.655	0.710	0.346
DlrFCB1	6	0	5.78	0.736	0.756	0.102	8	0	7.56	0.796	0.810	0.543	9	0	8.46	0.719	0.755	0.607	10	1	10.00	0.862	0.825	0.336
Ttr56	4	0	3.96	0.491	0.433	0.800	5	1 (1)	4.53	0.388	0.449	0.194	4	0 (1)	3.99	0.439	0.491	0.422	8	3	8.00	0.724	0.719	0.296
Ttr83	6	0	5.79	0.755	0.701	0.761	5	0	5.00	0.714	0.704	0.940	6	0	5.50	0.614	0.580	0.496	5	0	5.00	0.690	0.700	0.767
D08	5	0	4.67	0.358	0.370	0.323	5	0	4.67	0.469	0.487	0.903	4	0	3.97	0.421	0.460	0.294	5	1	5.00	0.621	0.628	0.163
D22	7	0	6.48	0.698	0.705	0.385	7	0	6.81	0.735	0.724	0.274	7	1 (1)	6.88	0.807	0.809	0.186	6	0	6.00	0.828	0.796	0.975
Dde70	3	0	2.80	0.453	0.523	0.216	3	0	3.00	0.449	0.464	0.352	5	2 (2)	4.71	0.544	0.518	0.433	3	0	3.00	0.552	0.529	0.834
Ttr71	3	0	3.00	0.623	0.599	0.258	4	0	4.00	0.735	0.700	0.667	4	0	4.00	0.772	0.695	0.616	5	1	5.00	0.828	0.752	0.292
Ttr78	2	0	2.00	0.226	0.203	1.000	3	0	2.94	0.286	0.284	0.033	3	0	3.00	0.386	0.392	0.100	3	0	3.00	0.207	0.194	1.000
Ttr84	7	0	6.85	0.698	0.736	0.871	8	1 (1)	7.38	0.633	0.686	0.484	8	1 (1)	7.27	0.719	0.740	0.734	7	1	7.00	0.724	0.747	0.836
DlrFCB3	5	0	4.46	0.755	0.643	0.671	5	0	5.00	0.673	0.639	0.959	5	0	5.00	0.772	0.753	0.611	6	1	6.00	0.724	0.765	0.390
DlrFCB12	6	0	5.98	0.604	0.587	0.788	7	0 (1)	6.16	0.592	0.557	0.577	7	1 (1)	6.87	0.684	0.675	0.189	7	0	7.00	0.724	0.757	0.493
SW19	5	0	4.51	0.491	0.492	0.806	4	0	3.59	0.449	0.468	0.857	4	0	3.27	0.596	0.519	0.383	3	0	3.00	0.655	0.550	0.229
Total	234	4 (5)					251	8 (13)					266	18 (23)					266	34				
Mean	5.4		5.120	0.6222	0.6052		5.8		5.428	0.6170	0.6195		6.2		5.630	0.6385	0.6247		6.2		6.186	0.6632	0.6612	
s.d.	2.3		2.134	0.1817	0.1766		3.0		2.560	0.1833	0.1559		3.0		2.572	0.1687	0.1594		3.2		3.157	0.1793	0.1642	

TABLE S4. Mitochondrial DNA haplotypes from Barataria Basin and the Western Coastal Stock (WCS). Counts for the Barataria Basin samples are given for the clusters identified with STRUCTURE analyses (western, east-central, and island) and the unassigned individuals (no $q \geq 0.50$ for any cluster), as well as individuals removed from the Barataria Basin data set due to $q \geq 0.50$ to the WCS in the initial STRUCTURE run. Haplotype name and sample size for haplotypes used in pairwise tests of genetic differentiation are in bold. Heteroplasmic haplotypes are labeled with 'hpl'.

	Barataria Basin							
Haplotype name	Western	East-central	Island	Unassigned	Removed	WCS	GenBank Accession	Reference
Ttr2	**28**	**10**	**33**	12	4	**2**	AY997308	Sellas et al., 2005
Ttr16	**2**	**2**	0	2	0	**10**	AY997309	Sellas et al., 2005
GTtr18	**1**	**6**	**2**	1	0	0	GQ504051	Rosel et al., 2009
GTtr19	0	**3**	**4**	4	0	**4**	AY997307	Sellas et al., 2005
GTtr23	**1**	0	**3**	0	0	0	GQ504062	Kingston et al., 2009
GTtr30	**11**	**17**	**12**	9	4	**4**	AY997311	Sellas et al., 2005
GTtr45	0	0	0	0	0	**1**	JN944196	Vollmer and Rosel, 2017
GTtr46	0	0	0	0	0	**1**	JN944197	Vollmer and Rosel, 2017
GTtr48	0	0	0	0	0	**2**	JN944199	Vollmer and Rosel, 2017
GTtr54	0	0	0	0	0	**1**	JN944205	Vollmer et al., 2021
GTtr57	0	0	0	1	0	0	JN944208	this study
GTtr62	0	0	0	0	0	**1**	JN944213	Vollmer and Rosel, 2017
GTtr72	**9**	**7**	**1**	6	0	0	MZ615655	this study
GTtr73	0	**1**	0	0	0	0	MZ615656	this study
GTtr75	0	0	0	0	0	**1**	MZ615657	this study
GTtr76	0	0	0	0	0	**1**	MZ615658	this study
11Tt079hpl	0	1	0	0	0	0	MZ615659	this study
16Tt269hpl	0	1	0	0	0	0	MT380121	Vollmer et al., 2021
21Tt086hpl	0	0	1	0	0	0	MZ615660	this study
24Tt052hpl	1	0	0	0	0	0	MZ615661	this study
24Tt074hpl	0	0	1	0	0	0	MZ615662	this study
24Tt139hpl	0	0	0	1	0	0	MZ615663	this study
26Tt083hpl	0	1	0	0	0	0	MZ615664	this study
40Tt011hpl	0	0	0	0	0	1	MZ615665	this study
Total used in analysis:	**52**	**46**	**55**	0	0	**28**		

TABLE S5. Average pairwise relatedness (*r*) and variance estimated using COANCESTRY and tests for signficant differences between A) the genetic clusters (GEN), social clusters (SOC) and the entire genetic data set (Barataria Basin) and B) for each sex within the groups. The 2.5% and 97.5% quantiles obtained from the bootstrapping method to test differences in average relatedness between groups are given. Significant differences in *r* using a 95% confidence level are in bold when comparing A) each cluster to the entire data set and B) male and females pairs within each group. n: number of samples.

A:

Group	n	average *r*	variance	*r* observed average difference	2.5% quantile	97.5% quantile
GEN-western	53	0.0497	0.0054	**0.0234**	-0.0023	0.0025
GEN-east-central	49	0.0425	0.0041	**0.0162**	-0.0026	0.0027
GEN-island	57	0.0371	0.0034	**0.0109**	-0.0022	0.0023
SOC-western	13	0.0417	0.0096	**0.0154**	-0.0096	0.0116
SOC-island	14	0.0235	0.0021	-0.0027	-0.0087	0.0108
Barataria Basin	195	0.0262	0.0023			

B:

	n		average *r*		variance		*r* observed average		
Group	Male	Female	Male	Female	Male	Female	difference	2.5% quantile	97.5% quantile
GEN-western	29	24	0.0485	0.0495	0.0054	0.0058	0.0010	-0.0111	0.0114
GEN-east-central	20	29	0.0499	0.0367	0.0068	0.0026	**-0.0132**	-0.0112	0.0106
GEN-island	29	28	0.0405	0.0339	0.0033	0.0030	-0.0067	-0.0081	0.0077
SOC-western	8	5	0.0178	0.0734	0.0008	0.0210	0.0556	-0.0353	0.0639
SOC-island	7	7	0.0165	0.0433	0.0013	0.0048	0.0268	-0.0307	0.0347
Barataria Basin	100	95	0.0264	0.0258	0.0023	0.0022	-0.0006	-0.0019	0.0019

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