Received: 10 August 2019 | Accepted: 16 January 2021

DOI: 10.1111/mms.12783

ARTICLE

Marine Mammal Science

Strandings provide insight into social group structure of Atlantic white-sided dolphins

Katie R. Pugliares-Bonner[1] | Kate LaSpina[2] | Kathryn S. Rose[3] | Steven E. Travis[1] | Kristina M. Cammen[2]

[1]Department of Biology, University of New England, Biddeford, Maine

[2]School of Marine Sciences, University of Maine, Orono, Maine

[3]International Fund for Animal Welfare, Yarmouthport, Massachusetts

Correspondence
Kristina Cammen, 5735 Hitchner Hall, School of Marine Sciences, University of Maine, Orono, ME 04469.
Email: kristina.cammen@maine.edu

Funding information
Norcross Foundation; Quebec-Labrador Foundation

Abstract

Atlantic white-sided dolphins (*Lagenorhynchus acutus*) are highly social odontocetes with a poorly understood tendency to mass strand. With limited capacity to study social ecology in the open ocean, mass strandings provide an opportunity to improve our understanding of group structure. Our study of 32 mass stranding events that occurred on Cape Cod, Massachusetts, between 1999 and 2009 identifies aspects of social ecology that vary across the year. A greater number of mass stranding events occurred outside of the breeding season and there was evidence of age-structuring during the breeding season. We find generally low average intragroup pairwise relatedness assessed across eight microsatellite loci in a subset of 16 mass stranding events. Mass stranded groups do not show higher than expected relatedness when compared to a baseline estimate derived from single-stranded individuals. Overall, our integration of genetic estimates of relatedness with data on sex and maturity-class from stranded specimens suggests that Atlantic white-sided dolphins fall near the more fluid end of the continuum from short-term, highly fluid social associations to long-term, stable groups represented among the odontocetes. Despite their tendency to mass strand, stable, kin-based associations are not a defining feature of social group structure in this species.

KEYWORDS
Atlantic white-sided dolphin, *Lagenorhynchus acutus*, mass strandings, odontocete, relatedness

1 | INTRODUCTION

Odontocetes, or toothed whales, employ a wide range of social strategies that may vary both within and among species, as well as across time and space within a single population (Möller, 2012). While some species are solitary or travel in pairs, others associate in fairly large, stable matrilineal groups (Read et al., 1996; Whitehead, 1998). Between these extremes, several dolphin species exhibit highly fluid social groups based on short-term associations, which may or may not be kin-based (Gowans et al., 2007). Social strategies may also vary between sexes (Connor et al., 1998). For example, in *Tursiops* sp. male alliances form in response to reproductive pressures, while female bands form in response to feeding pressures (Gowans et al., 2007) or shared reproductive condition (Connor et al., 2000; Wells, 1991). Among the more common driving forces that favor social group formation are predator avoidance, cooperative foraging, communal care of young, and enhanced reproductive opportunities, with the relative benefits of each varying according to prevailing environmental circumstances (Silk, 2007).

Attempts to better understand odontocete social group structure have been complicated by their oceanic marine habitat. Direct observations of individuals interacting at the ocean surface have been useful, but can be misleading, given that the majority of social interactions occur underwater (Connor et al., 1998; Whitehead, 1997). For practical reasons, much of what is known about odontocete social behavior stems from studies of species with coastal distributions or those whose individuals are easily identifiable by dorsal fin markings (e.g., Connor et al., 2000; Wells, 1991). Recently, mass strandings have been recognized as opportunities to better understand odontocete social behavior, especially if DNA analysis can be used to estimate genetic relationships (Mirimin et al., 2011; Viricel et al., 2008). Mass strandings are events in which two or more individuals, excluding mother-calf pairs, come ashore together. Assuming that animals mass strand within social units, these events provide a window of opportunity to analyze the age and sex composition, as well as genetic relatedness, of individuals within groups.

Mass strandings can be caused by a variety of environmental factors that affect multiple members of a group (Brabyn & McLean, 1992; Evans et al., 2005), including disease (Garrigue et al., 2016), algal toxins (Bengston et al., 2017), acoustic disturbance (Fernández et al., 2005), and anomalous weather (Mazzariol et al., 2011). Mass strandings can also reflect the strength of social bonds that lead to following a disoriented member of a pod into precarious and tidal areas (Mazzariol et al., 2018). In the latter case, where sociality plays a direct role in mass stranding, the assumption that mass strandings are reflective of natural social structure is likely to hold true. However, it is important to note that there are also cases when mass strandings may not reflect natural social structure, for example when a widespread disturbance affects multiple unaffiliated members of a species or multiple groups that cannot be differentiated on the beach. The largest recorded mass mortality event of baleen whales, which typically exhibit less sociality, was attributed to an unknown foraging aggregation during a harmful algal bloom (Häussermann et al., 2017). The number of individuals affected in mass strandings of Cuvier's beaked whales (*Ziphius cavirostris*) is also often several times the average size of groups of this species recorded at sea, suggesting either that the strandings involve multiple groups or the group size detected at sea does not accurately reflect true social structure for this species (MacLeod & D'Amico, 2006).

The Atlantic white-sided dolphin (*Lagenorhynchus acutus*) is one of the most commonly mass stranded odontocete species in the Northeast United States (Bogomolni et al., 2010). The cause of these mass strandings is typically unknown. Furthermore, while their tendency to mass strand may hint at group cohesion, the social dynamics of this species that is typically found offshore in open ocean environments remain poorly understood. Atlantic white-sided dolphins are largely restricted to continental shelves in temperate and subpolar waters of the North Atlantic, with a fairly widespread distribution stretching from North America to Europe (Hayes et al., 2018; Reeves et al., 1999). Prior analyses of genetic structure across this distribution found no evidence of significant differentiation between eastern and western North Atlantic populations, and limited differentiation between the North Sea and North Atlantic populations (Banguera-Hinestroza et al., 2014). Social groups of this species frequently number in the hundreds, although average group sizes were estimated at around 50 in two earlier studies of white-sided dolphins in the western Atlantic (Cetacean and Turtle Assessment Program, 1982; Weinrich et al., 2001).

In the Gulf of Maine, Atlantic white-sided dolphins exhibit seasonal shifts in distribution (Palka et al., 1997) and an annual reproductive cycle (Sergeant et al., 1980; Weinrich et al., 2001) that may drive seasonal differences in group size, and sex and age composition. Free-swimming groups tend to be smaller in the spring and early summer (April–June) than in the mid-summer and early fall (July–October). The latter period coincides with the presumed breeding season that follows peak calving (Sergeant et al., 1980; Weinrich et al., 2001). Seasonal differences in sex and age composition among mass stranded groups have been used to formulate hypotheses that juveniles leave their natal group after weaning at 18 months and that adult males and females associate in "bachelor herds" and "reproductive herds," respectively (Sergeant et al., 1980), yet these hypotheses have remained largely untested.

Genetic data from mass strandings of Atlantic white-sided dolphins have recently begun to shed light on the level of relatedness within groups. Mirimin et al. (2011) documented generally low levels of within-group relatedness and fairly high levels of genetic diversity in two mass strandings of Atlantic white-sided dolphins from the west coast of Ireland. Their findings suggest movement of individuals among groups for the purposes of mating and are generally consistent with prior observations in the Northwest Atlantic (Amaral, 2005). However, these prior studies have been limited in sample size (i.e., number of groups) and seasonal scope, leaving open questions of stability and composition of social structure across space and time. Is low intragroup relatedness typical of the species across the North Atlantic, and throughout the annual breeding cycle? To address this question, here we report on a larger study of *L. acutus* strandings along the northeastern coast of the United States throughout the year, inside and outside of the breeding season.

2 | METHODS

2.1 | Biological samples

All data and specimens for our study were collected in the vicinity of Cape Cod, Massachusetts, located on the northeastern coast of the United States (Figure 1). Cape Cod is a hook-shaped coastal land protrusion that extends into the southern Gulf of Maine. This region is characterized by gently sloping beaches and extreme tidal fluctuations. Within North America, this region reports the highest frequency and magnitude of mass strandings involving several species of odontocetes, including the Atlantic white-sided dolphin (Bogomolni et al., 2010). The coverage region for this study included an estimated 1,125 km of Massachusetts coastline, encompassing coastal portions of Cape Cod Bay, Nantucket Sound, and Buzzards Bay.

Data were available from 32 Atlantic white-sided dolphin mass stranding events on Cape Cod occurring between 1999 and 2009, involving a total of 242 live and dead animals (Table 1). Note that most mass strandings were observed or reported after individuals were already on shore, so it was generally uncertain whether the stranded animals made up an entire pod. During this same time period in this geographic region, there were 134 Atlantic white-sided dolphins observed to have stranded singly, with no indication of an associated pod. For all strandings, date and location of event, group size, and the body lengths of individuals were recorded. The season during which each group stranded was characterized as either "breeding/calving" or "nonbreeding," where May to September was considered the breeding/calving season, and October to April was considered the nonbreeding season. Seasons were defined based on the previously described calving season of May to September and gestation period of 11 months (Sergeant et al., 1980; Weinrich et al., 2001). Maturity-class and sex were determined by physical examination for most individuals.

Maturity-class was not recorded for 20 males, 81 females, and 41 individuals of unknown sex at the time of stranding, but could be estimated for individuals of known sex using body length data. For the females, maturity-class was estimated using sex-specific body size limits determined from postmortem gonad inspections and the Sum-of-Fraction-of-Immatures model of Murphy et al. (2009). Gonad and standard straight length data from 62 sexually mature and 19 immature bycaught or stranded females were used to calculate a threshold of 199.5 cm for maturity

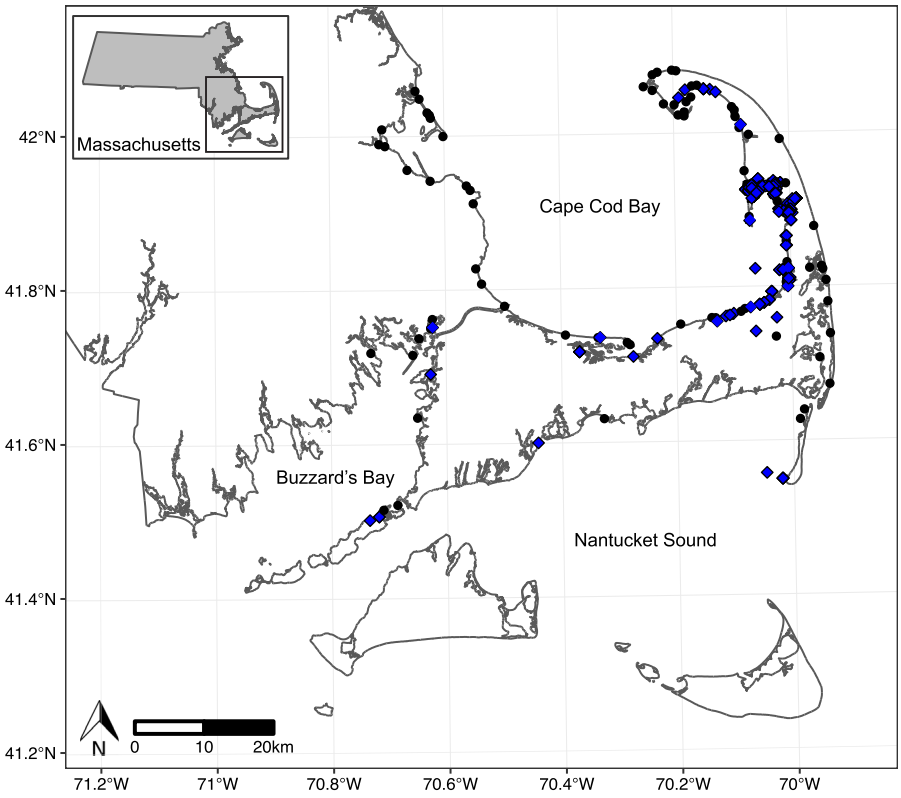

FIGURE 1 Map of Atlantic white-sided dolphin strandings on Cape Cod, Massachusetts, from 1999 to 2009. Black circles represent individuals that stranded alone (single stranded); blue diamonds represent individuals that stranded as part of a group of animals (mass stranded).

in females. Females that were ≥ 199.5 cm in length were deemed to be mature, and all other animals (excluding dependent calves) were considered juveniles. Sufficient data were not available to confidently categorize males using the same method. However, gonad inspection of 61 bycaught or stranded males revealed that all males >240.0 cm were mature. This finding was consistent with Rogan et al. (1997) who report a length at sexual maturity for male Atlantic white-sided dolphins of the northeastern Atlantic as 240.0 cm. All males in our data set (excluding dependent calves) <240.0 cm were therefore considered juveniles.

Sex remained undetermined for 64 individuals at the time of stranding. For nine of these individuals with available tissue (see below), we used genetic markers to determine sex. Total genomic DNA was multiplexed in a PCR with three odontocete sex-determining primers (ZFYX0582F, ZFY0767R, ZFX0923R) described by Bérubé and Palsbøll (1996) following the reaction conditions outlined in Palsbøll et al. (1992). Reactions were run alongside one male and one female of known sex (through gonad examination) that served as positive controls, as well as one reaction without added dolphin DNA that served as a negative control to check for reaction contamination. The PCR products were separated by electrophoresis on a 2% agarose gel, and sex was confirmed through the visualization of sex-specific bands.

Tissue of 89 (36.8%) dolphins from 16 of the 32 mass stranding events were sampled for further genetic analysis (Table 1). The proportion of animals sampled within groups ranged from 0% to 100% (mean = 32.6% ± 35.3% *SD*). Tissue samples were also collected from 74 dolphins (55.2%) that stranded alone. Samples were obtained either as a skin plug from live animals as they were being tagged prior to release, or as a dorsal fin clip (approximately 3 × 3 cm) from dead animals. Prerelease tagging of all live cetaceans is required per stranding agreements between the

TABLE 1 Demographic data for Atlantic white-sided dolphin mass stranding (MS) and single stranding (SS) events on Cape Cod, Massachusetts from 1999 to 2009.

		Females			Males			Unknown sex				
Group	Date	Adult	Juvenile	Calf	Adult	Juvenile	Calf	Adult	Juvenile	Calf	CBD	Total
MS1	March 1999	3 (3)	1	1	0	0	1	0	0	0	0	6 (3)
MS2	March 1999	2	9	1	13	20	5	0	0	0	1	51
MS3	April 2000	1	0	0	1	0	0	0	0	0	0	2
MS4	August 2000	0	0	1	0	1	0	0	0	0	0	2
MS5	August 2000	2 (1)	0	0	5 (2)	0	4 (2)	0	0	0	0	11 (5)
MS6	March 2001	1	0	0	1	0	0	0	0	0	0	2
MS7	April 2001	1 (1)	1 (1)	0	2 (2)	2	0	0	0	0	0	6 (4)
MS8	March 2002	1 (1)	0	1 (1)	1 (1)	4 (3)	0	0	1	0	6	14 (6)
MS9	March 2002	4	0	1	2	0	0	0	0	0	0	7
MS10	August 2002	0	1 (1)	0	0	2 (1)	0	0	0	0	0	3 (2)
MS11	January 2003	0	1 (1)	0	2 (2)	0	0	0	1	0	0	4 (3)
MS12	April 2003	4 (3)	2 (1)	0	8 (6)	6 (4)	1 (1)	0	0	0	4	25 (15)
MS13	April 2003	0	0	0	1	2	0	0	0	0	0	3
MS14	December 2003	2 (2)	0	0	2 (2)	0	0	0	0	0	0	4 (4)
MS15	December 2004	2	0	0	0	0	0	0	0	0	0	2
MS16	February 2005	3 (3)	1 (1)	0	1 (1)	3	0	0	0	0	0	8 (5)
MS17	April 2005	1	0	0	4	1	0	0	0	0	0	6
MS18	May 2005	0	0	0	1	1	0	0	0	0	0	2
MS19	May 2005	0	0	0	0	3 (2)	1	0	0	0	0	4 (2)
MS20	December 2005	1	0	0	0	0	0	1	0	0	0	2
MS21	January 2006	3 (3)	1	0	4 (2)	5 (4)	2 (2)	0	0	0	0	15 (11)
MS22	January 2006	0	0	0	1 (1)	1 (1)	1 (1)	0	0	0	0	3 (3)
MS23	January 2006	0	0	0	0	5	0	0	0	0	0	5
MS24	February 2006	0	0	0	1	2	1	0	1	0	0	5
MS25	July 2006	4 (2)	0	2 (1)	2	0	1	0	0	0	0	9 (3)

(Continues)

TABLE 1 (Continued)

		Females			Males			Unknown sex				
Group	Date	Adult	Juvenile	Calf	Adult	Juvenile	Calf	Adult	Juvenile	Calf	CBD	Total
MS26	January 2007	2 (2)	1 (1)	0	2 (1)	2 (1)	0	0	0	0	2	9 (5)
MS27	January 2008	7 (6)	0	1 (1)	8 (8)	1 (1)	0	0	0	0	0	17 (16)
MS28	February 2008	0	1	1	0	1	0	0	0	0	0	3
MS29	April 2009	1 (1)	0	1	1 (1)	0	0	0	0	0	0	3 (2)
MS30	September 2009	0	0	1	0	0	0	0	0	0	2	3
MS31	September 2009	1	0	0	0	1	0	0	0	0	0	2
MS32	September 2009	0	0	0	0	0	0	0	0	0	4	4
MS total		46 (28)	19	11 (3)	63 (29)	63 (17)	17 (6)	1	2	1	19	242 (89)
SS total		15	9	10	25	35	8	2	0	8	22	134 (74)

Note. CBD = could not be determined. The numbers in the parentheses indicate the number of individuals genotyped at microsatellite loci. Values that are not followed by parenthetical numbers are cases where none of these individuals were genotyped.

responding agency and the National Oceanic and Atmospheric Administration. All tissue samples were archived at −20°C prior to DNA extraction. We extracted total genomic DNA from approximately 25 mg of tissue using the Qiagen DNeasy Blood and Tissue kit (Valencia, CA) and measured DNA concentration using a fluorometer.

We assessed relatedness in single and mass stranded individuals via microsatellite genotyping. Mitochondrial control region sequences provided additional data to exclude inferred mother-calf relationships if the adult female and calf did not share a haplotype. As has been done elsewhere (Viricel et al., 2008), we used data from single stranded individuals to approximate relatedness levels among presumed unrelated individuals. While there is no way to fully test the assumption that single stranded individuals are unrelated, they represent the best approximation for this study. All Atlantic white-sided dolphins in the western North Atlantic are considered one population (Banguera-Hinestroza et al., 2014), and as such it is fair to assume that the single stranders derive from the same population as the mass stranders.

2.2 | Genetic analysis of microsatellites and relatedness estimation

We genotyped samples using eight polymorphic di- or tetra-nucleotide microsatellite loci developed from other cetacean species, previously confirmed to successfully cross-amplify microsatellite DNA from the Atlantic white-sided dolphin (Dde65, Dde66, Dde69, Dde70, and Dde72 from Coughlan et al., 2006; Sco11, Sco28, and Sco31 from Mirimin et al., 2006). Microsatellite loci were amplified individually (i.e., without multiplexing) in reaction volumes of 10 μl including approximately 80 ng of DNA, 1× PCR buffer (200 mM Tris HCl [pH 8.4], 500 mM KCl; Invitrogen, Inc.), 2.0 mM $MgCl_2$, 0.25 mM dNTPs, 1.0 μM of each primer, and 0.5 U of Taq DNA polymerase (Invitrogen, Inc.). Slight deviations from these reaction conditions included 0.1 μM of each primer for Dde66 and 2.0 μM of each primer for Dde70, Sco11, and Sco31. Thermal profiles matched published protocols (Table S1) except for Dde70: 95°C for 3 min, followed by 25 cycles at 95°C for 30 s, 56°C for 30 s, and 72°C for 15 s. Alleles were separated on an ABI Prism 310 Genetic Analyzer, and scored for size using GENEMAPPER, version 3.7 software (Applied Biosystems, Inc.). Allele sizes were determined by comparison with an internal size standard (GeneScan 500 LIZ Size Standard, Applied Biosystems, Inc.).

These data were collected prior to the establishment of best practices for microsatellite genotyping (Morin et al., 2010), so no genotyping error rate was calculated at the time of data collection. However, several samples were genotyped multiple times when peaks were questionable and there were no indications of genotyping issues. Furthermore, we have assessed the genotypes using multiple metrics to test for evidence of scoring error and for their utility to estimate relatedness, and no measures deviated from expectations (see details in the Results section). The following analyses were performed on the genotypes from the single stranded data set of presumed unrelated individuals. We used MICROCHECKER (Van Oosterhout et al., 2004) and INEst ver. 1.0 (Chybicki & Burczyk, 2009) to test our microsatellite genotypes for evidence of null alleles. MICROCHECKER was run using 1,000 runs and 95% confidence intervals. INEst was run using 10,000 iterations of the Individual Inbreeding Model, which simultaneously estimates inbreeding in order to avoid upwardly biased estimates. We used GENEPOP ver. 4.2 (Roussett, 2008) to test for deviations from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium. HWE was evaluated using an exact probability test based on the Markov chain method with 10,000 iterations. Linkage disequilibrium was evaluated using Fisher's exact test based on the Markov chain method and 10,000 iterations. We used FSTAT 2.93 (Goudet, 2001) to calculate inbreeding coefficients, F_{IS}, on a locus-by-locus basis and to evaluate whether any of these values deviated significantly from zero (based on 8,000 randomizations). Because of the multiple loci involved, sequential Bonferroni corrections were used to gauge statistical significance among the results of each of the above tests.

Prior to evaluating kinship within each mass stranded group, we further assessed the discriminatory power of our microsatellite markers in two ways. First, we calculated the probability of two individuals sharing a genotype by chance using the program FaMoz (Gerber et al., 2003). Second, we performed a rarefaction analysis based on 10,000 simulations using the program RERAT (Schwacke et al., 2005) and the Queller and Goodnight (1989) method to estimate symmetric pairwise relatedness with no bias correction. The rarefaction analysis allowed us to evaluate the

stability of relatedness estimates using our eight microsatellite markers. Relatedness estimates are expected to increase in accuracy with increasing numbers of markers, with stability achieved at the point where the relationship between the average change in estimated relatedness and the number of markers used begins to approach a horizontal asymptote (Schwacke et al., 2005).

We used the R package *related* (Pew et al., 2015) to calculate pairwise relatedness and determine whether average intragroup relatedness was significantly greater than expected by chance within mass stranded groups. We first evaluated relatedness estimators by comparing pairwise relatedness estimates among 400 pairs of simulated individuals representing 100 unrelated pairs, 100 half-sibs, 100 full-sibs, and 100 parent-offspring pairs. Individuals were simulated using the allele frequencies from the single-stranded data set with expected values of r = 0, 0.25, and 0.5 for unrelated pairs, half-sibs, and both full-sibs and parent-offspring pairs, respectively. With this approach, we evaluated relatedness estimators from Queller and Goodnight (1989), Li et al. (1993), Lynch and Ritland (1999), Ritland (1996), and Wang (2002), as well as dyadic and triadic maximum likelihood estimators from Milligan (2003) and Wang (2007). Pearson's correlation coefficient was used to select the best estimator for our data set.

Relatedness for each pair of dolphins within each mass stranded group was then calculated using the best estimator and a 95% confidence interval based on 100 bootstraps over loci. If the 95% confidence interval fell at or above a relatedness value of 0.25 but below 0.5, individuals were considered to be putative half-sib pairs. If the 95% confidence interval fell at or above a relatedness value of 0.5, individuals were considered to be putative full-sib or parent-offspring pairs. This conservative approach to identifying putative parent-offspring pairs was complemented by a direct comparison of microsatellite genotypes that identified any pair within a stranding event that contained an adult and nonadult sharing one allele at each locus to be a candidate parent-offspring pair.

To compare observed and expected relatedness values, the average pairwise relatedness within each mass stranded group was compared to a neutral expectation for relatedness in a group of the same size. Neutral expectations of relatedness were generated by simulating 1,000 groups through random draws from the single stranded individuals for each group size from 2 to 16, representing the range in genotyped group sizes for our mass stranded individuals. Group simulations and relatedness estimates were performed using the *grouprel* function in the package *related* (Pew et al., 2015). Estimated relatedness values for mass stranded groups were thus compared to an associated null distribution of relatedness values for the simulated groups of the same size; p values associated with this comparison were calculated as the proportion of simulated groups that had a relatedness estimate greater than or equal to the average estimated relatedness value. The threshold for significance was adjusted using a sequential Bonferroni approach.

2.3 | Genetic analysis of mitochondrial control region

The relationship between adults and immature individuals (including both juveniles and dependent calves) was further evaluated through a direct comparison of microsatellite genotypes and mitochondrial haplotypes. All pairs of mature females and immature individuals (of either sex) that shared at least one allele for all genotyped microsatellite loci were sequenced at the mitochondrial control region to further assess pairwise relationships. Matching haplotypes support designation of a putative mother-offspring relationship, while identification of distinct haplotypes between the two individuals refutes this relationship.

We sequenced a portion of the mitochondrial control region using primers MTCRF and MTCR-R first described by Hoelzel and Green (1998) using a protocol modified from Mirimin et al. (2011). Unfortunately, due to funding and personnel limitations, there was a 10-year gap between microsatellite genotyping and mitochondrial control region sequencing, and during their storage in a − 80°C freezer many samples had evaporated as a result of poorly sealed tubes. We attempted to re-elute these samples with sterile water but 3 of the 18 samples selected for this analysis failed to amplify despite several attempts at the following PCR protocol.

Mitochondrial control region amplifications were conducted in a total volume of 20 μl using the following reaction concentrations: 20–50 ng of DNA, 1× Standard *Taq B*uffer (10 mM Tris–HCl [pH 8.3], 50 mM KCl, 1.5 mM $MgCl_2$; New England Biolabs), 0.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.6 mg/ml BSA, 0.3 μM of each primer, and 0.5 U of Taq DNA polymerase (New England Biolabs). The amplification thermal profile was: 94°C for 5 min, followed by 35 cycles at 94°C for 30 s, 56°C for 30 s, and 72°C for 30 s, and a final elongation step at 72°C for 10 min. PCR products were visualized on an agarose gel. The remaining 10 μl of each successful PCR product was enzymatically purified through the addition of 1 unit Exonuclease I (New England Biolabs), 0.25 units Antarctic Phosphatase (New England Biolabs), and 1× Exonuclease I buffer (67 mM Glycine-KOH, 6.7 mM $MgCl_2$, 10 mM β-ME, pH 9.5); purification reactions were incubated at 37°C for 1 hr, followed by 15 min at 85°C to denature the enzymes.

BigDye sequencing reactions were conducted in a final volume of 10 μl including 2 μl purified PCR product, 5 pM primer, 1× BigDye Sequencing Buffer (Applied Biosystems), and 0.2× BigDye Terminator Ready Reaction Mix v 3.1 (Applied Biosystems). The sequencing profile consisted of 25 cycles of 96°C for 30 s, 50°C for 15 s, and 60°C for 4 min. Sequencing products were purified using Princeton Separations Centrisep columns and sequenced in both directions on an Applied Biosystems ABI 3730 Genetic Analyzer. Sequencing reactions, purification, and sequencing was carried out by the University of Maine DNA Sequencing Facility. Resulting sequences were manually edited and aligned using CodonCode Aligner v8.0.2 and trimmed to 599 bp for comparison with existing haplotypes in GenBank (Accession No. FR668237-FR668246, FR682916-FR682924).

An additional 113 individuals from this study, beyond the putative mother-offspring pairs described above, were also sequenced to address other research objectives. All haplotypes identified were named following the convention of Mirimim et al. (2011) and uploaded to GenBank under accession numbers MT450724-MT450751.

3 | RESULTS

3.1 | Stranding demographics and seasonal stranding trends on Cape Cod

From 1999 to 2009, almost twice the number of Atlantic white-sided dolphins came to shore during mass strandings on Cape Cod compared to single strandings (Table 1). Males were significantly more common than females in both single (M:F = 2, Exact binomial test $p < .001$) and mass strandings (M:F = 1.88, Exact binomial test $p < 1 \times 10^{-5}$). There was a significant difference in maturity-class composition between mass strandings and single strandings ($\chi^2 = 7.578$, $df = 2$, $p < .05$). Adults made up a larger proportion (mass: 49.3%, single: 37.5%, Exact binomial test $p < .001$) and calves made up a smaller proportion (mass: 12.5%, single: 23.2%, Exact binomial test $p < .0001$) of the mass strandings than the single strandings; there was no difference in the proportion of juvenile individuals (mass: 38.1%, single: 39.3%, Exact binomial test $p = .732$).

There was an average of 7.56 (± 9.51 *SD*) individuals per mass stranding event. Of the 23 stranding events for which complete sex and maturity-class information were available, 15 (65%) were of mixed sex (mean size: 6.53 ± 4.75 *SD*), 6 (26%) consisted exclusively of males (mean size: 3.17 ± 1.20 *SD*), and 2 (9%) consisted exclusively of females (mean size: 4 ± 2.83 *SD*; Table 1). Of the mixed-sex strandings, nearly half (47%) consisted exclusively of adults. Of the all-male strandings, the largest proportion (50%) consisted exclusively of juvenile individuals. All-female strandings were too rare to discern a meaningful pattern relative to maturity.

Mass strandings on Cape Cod were observed more frequently during the nonbreeding season ($n = 23$) than during the breeding/calving season ($n = 9$), though the difference between seasons in number of mass stranding events per month was not significant ($t = -1.314$, $p = .220$). We detected no significant differences between seasons in size ($t = 0.961$, $p = .362$; Figure 2a) or sex-composition ($\chi^2 = 0$, $df = 1$, $p = 1$; Figure 2b) of mass stranding events. However, there was a significant difference in maturity-class composition between seasons ($\chi^2 = 10.726$, $df = 2$, $p < .01$), with a greater proportion of juveniles and fewer calves in the nonbreeding season. Excluding calves, we also

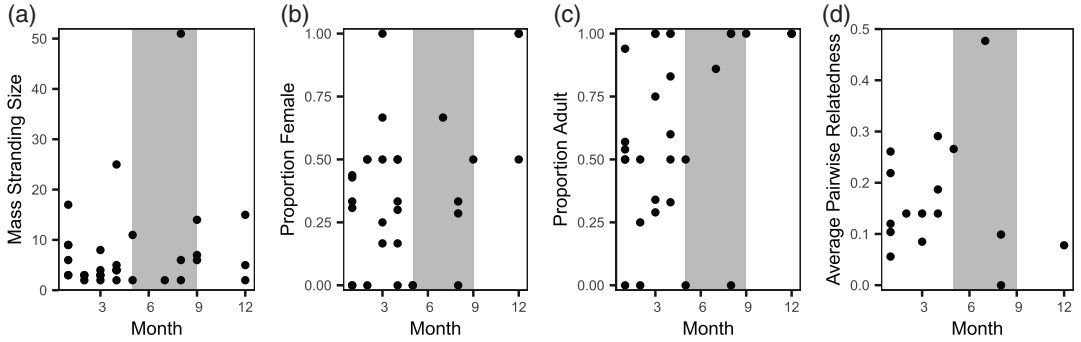

FIGURE 2 Seasonal trends in (a) size of mass stranding events, (b) sex ratio, (c) maturity-class structure, and (d) average pairwise relatedness of mass stranded Atlantic white-sided dolphin groups from Cape Cod between 1999 and 2009. The proportion of females and adults were calculated excluding dependent calves and individuals of unknown age. The average pairwise dyadic maximum likelihood estimate of relatedness within groups is based on eight microsatellite loci. Shaded area indicates breeding/calving season.

TABLE 2 Summary statistics for eight microsatellite loci used to genotype Atlantic white-sided dolphins.

Locus	Allele size range (bp)	No. of alleles	H_o	H_e	F_{IS}	F_{IS} *p*-value	Null allele frequency
Dde65	187–211	7	0.743	0.805	0.077	.131	0.006
Dde66	348–374	11	0.824	0.755	−0.093	.988	0.003
Dde69	193–213	6	0.595	0.629	0.055	.288	0.004
Dde70	131–161	13	0.797	0.777	0.080	.181	0.004
Dde72	213–241	8	0.730	0.684	−0.067	.906	0.002
Sco11	200–224	7	0.432	0.467	0.085	.188	0.005
Sco28	151–171	6	0.541	0.480	−0.126	.975	0.002
Sco31	252–284	9	0.784	0.739	−0.062	.888	0.002
Mean		8.375	0.681	0.667	−0.004	.569	
SD		2.5	0.141	0.131			

Note. H_o = observed heterozygote frequency; H_e = expected heterozygote frequency. F_{IS} = inbreeding coefficient; F_{IS} *p*-value is outcome of test for significant deviation from 0. Allele size range and number of alleles are counted from the full data set of 163 genotyped individuals. All other statistics were generated from 74 dolphins stranded singly on Cape Cod between 1999 and 2009.

observed a trend of mostly single maturity-class stranding groups during the breeding/calving season, and mostly mixed maturity-class stranding groups during the nonbreeding season (Figure 2c).

3.2 | Intragroup relatedness of mass stranded dolphins

The eight microsatellite loci used in our study appeared robust to all deviations tested for using the baseline single-stranded data set (N = 74). Within this subset of the data, we found no evidence of scoring error due to stuttering, no evidence for large allele dropout, and no evidence for null alleles. Our estimates of null allele frequencies never exceeded 0.01 (Table 2), which should have rendered their effects on relatedness estimates negligible. No locus was found to significantly deviate from HWE, and we found no evidence of linkage between any pair of loci. We did not observe any evidence of inbreeding, as reflected in locus-by-locus F_{IS} estimates that did not deviate significantly from 0 (Table 2).

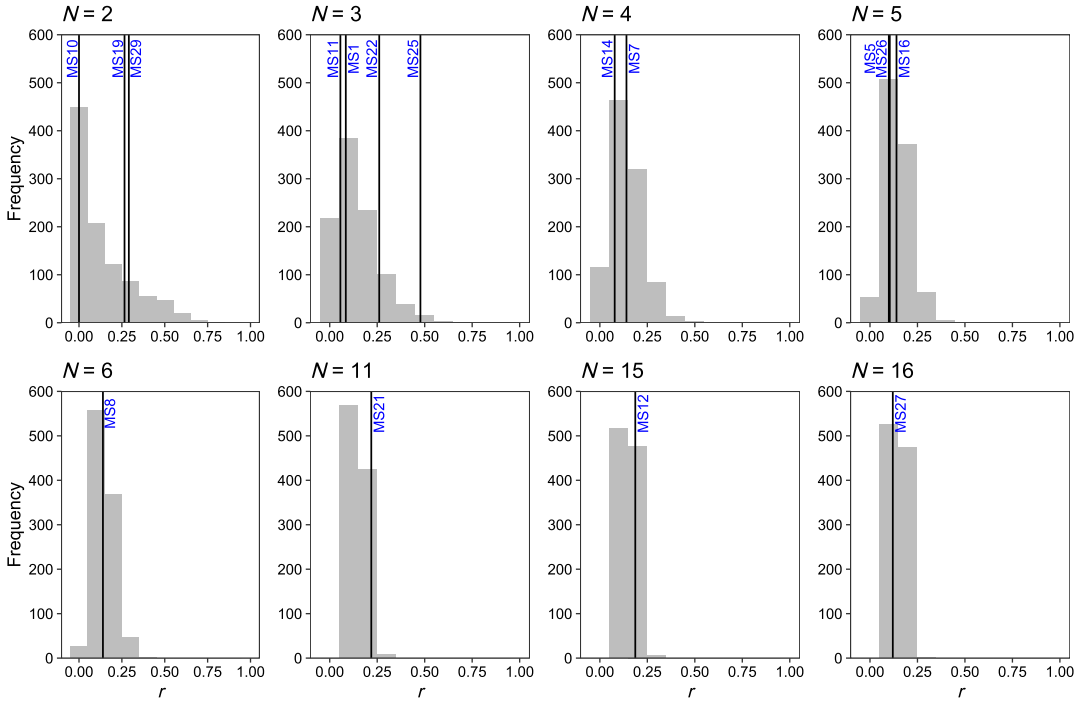

FIGURE 3 Comparison of observed and expected estimates of average pairwise relatedness among groups of stranded Atlantic white-sided dolphins of different sizes. Histograms show distribution and frequency of relatedness estimates derived from 1,000 simulations of groups of individuals randomly drawn from the set of 74 genotyped dolphins that stranded singly on Cape Cod between 1999 and 2009. The vertical bars show observed average intragroup pairwise relatedness estimates for 16 mass stranding events that occurred during this same time period. Relatedness estimates represent the average pairwise dyadic maximum likelihood estimate of relatedness within groups based on eight microsatellite loci.

All loci were polymorphic with a mean of 8.37 (± 2.5 *SD*) alleles per locus (range = 6–13), which produced observed heterozygosities averaging 0.681 (± 0.141 *SD*) per locus (range = 0.432–0.824; Table 2). This level of diversity generated a low-to-moderate probability of a chance match between the multilocus genotypes of distinct individuals, at 1 in 8,772. Our rarefaction analysis indicated that estimates of relatedness were reasonably stable, as indicated by a 6.40% and 7.43% change in average relatedness estimates between the use of 7 and 8 loci and 6 and 7 loci, respectively. 98.16% of individuals (*N* = 160 of 163) were successfully genotyped for at least 7 of 8 loci (*N* = 113, 69.33% at all 8 loci). Most of the missing data derived from a single locus, Dde70, for which genotypes could not be confidently called due primarily to large and closely overlapping stutter peaks obscuring allelic distinctions observed in 30.06% of individuals. Subsequent analyses were run both with and without this locus; no difference in conclusions was noted so only results from analyses with all eight loci are included below.

Simulations of pairs of individuals with varying levels of relatedness using allele frequencies from the single-stranded dataset identified the dyadic likelihood estimator (Milligan, 2003) as the best fit for our data (Table S2). Estimates of relatedness presented here are thus calculated with this maximum likelihood estimator. Average intragroup pairwise relatedness was generally low within mass stranding events. We found no significant difference in pairwise relatedness (*t*-test $p = .470$) between individuals that stranded as part of mass stranding events which occurred during the breeding/calving vs. nonbreeding seasons (Figure 2d). Two events (MS21 and MS25) exhibited average pairwise relatedness that neared significance (MS1 $p = .054$; MS25 $p = .019$), but following correction for multiple tests, no event exhibited significantly higher average pairwise relatedness than expected based on simulations of groups of the same size populated with a random set of genotypes from single stranded individuals (Figure 3, Table S3). Similarly, no group contained a significantly

greater number of individual pairwise comparisons suggestive of full-sib or parent-offspring relationships (relatedness lower 95% CI ≥0.5), or of half-sib relationships (relatedness lower 95% CI ≥0.25 and < 0.5), following correction for multiple tests. With this conservative approach based on the 95% confidence interval around the relatedness estimate, only one group contained pairs identified as putative full-sibs or parent-offspring (MS12: 2.86% of pairs), and two groups contained pairs identified as half-sibs (MS12: 2.86% and MS21: 3.63% of pairs).

Further analyses of potential parent-offspring relationships identified additional adult-immature pairs (N = 17) within mass stranding events that shared one allele at each microsatellite locus. The fact that all of these pairs were not identified by the above approach using the lower bound of the 95% confidence interval around the relatedness estimate suggests that the conservative approach may have a relatively high rate of false negatives. When possible, we further evaluated these potential parent-offspring relationships through the consideration of mitochondrial haplotypes. This was not possible for two pairs that involved adult females for which no haplotype could be successfully obtained, one pair that involved an immature individual for which no haplotype could be successfully obtained, and seven pairs that involved an adult male. Of the seven remaining pairs that involved both an immature individual and an adult female with a sequenced mitochondrial haplotype, four putative mother-offspring pairs with matching haplotypes were identified: one mother-calf pair in MS25, one mother-calf and one mother-juvenile pair involving different adult females in MS27, and one mother-juvenile pair in MS12. Both calves were female and the two juveniles were male. It is important to remind readers here that our genetic data for mass stranded groups do not always represent the full group of associated live individuals, both because tissue samples were not available for all stranded individuals and because it is possible that some members of the group survived or were not recovered. The latter could explain the groups that contain dependent calves but no adult females (MS4, MS19, MS22, MS24, MS28, MS30).

4 | DISCUSSION

Our integration of genetic estimates of relatedness with data on sex and maturity-class from stranded specimens supports a relatively fluid, nonkin-based social structure in the Atlantic white-sided dolphins of the western North Atlantic, both within and outside the presumed breeding/calving season. We draw conclusions on the fluidity of social structure based on comparisons of group composition between mass strandings that occurred throughout the year, in particular comparing stranding events that occurred within and outside the breeding/calving season. We further provide evidence for a nonkin-based social structure based on a comparison of genetic estimates of relatedness within mass strandings and among those dolphins that strand singly. Overall, our study of a recent decade of Atlantic white-sided dolphin strandings on Cape Cod, including 32 mass stranding events, expands significantly upon and is generally consistent with prior studies in the eastern and western North Atlantic.

From our analysis, we can infer seasonal differences in some but not all aspects of Atlantic white-sided dolphin social ecology. Despite the fact that Atlantic white-sided dolphins are commonly observed from spring to autumn near Cape Cod (Katona et al., 1993), prior studies have reported that strandings occur more frequently in Massachusetts during the non-breeding season (Amaral, 2005; Palka et al., 1997). These prior studies include a review of the Smithsonian Strandings Database from 1970 to 1995 (Palka et al., 1997) and an unpublished Master's thesis which analyzed single and mass-stranding data from the western Atlantic white-sided dolphin population collected between 1973 and 1999 (Amaral, 2005). The average number of mass stranding events per month has also been consistently higher during the nonbreeding season since the 1970s, as observed by Amaral (2005) from 1973 to 1999 and during our study period from 1999 to 2009, though this difference between seasons was not statistically significant during either time period. These trends may be driven by seasonal variation in environmental conditions, prey and predator abundance and distribution, and reproductive ecology. However, it has yet to be convincingly explained, as it is not a clear reflection of the limited data we have on shifts in seasonal distribution of free-swimming groups (Palka et al., 1997).

The sizes of mass strandings recorded from 1999 to 2009 also do not reflect seasonal trends in group size observed among free-swimming groups. We observed no significant difference in the sizes of mass strandings that occurred within and outside the breeding season (Figure 2a), though Weinrich et al. (2001) have previously reported free-swimming groups tend to be larger during the breeding season. Importantly, however, the sizes of mass stranded groups were typically much smaller than the average group size observed at sea (Cetacean and Turtle Assessment Program, 1982; Weinrich et al., 2001), suggesting that mass strandings may represent only a subset of the individuals that compose a free-swimming group.

We can interpret our other findings related to group composition within the context of the dolphin's annual reproductive cycle, with peak calving in June and July, followed by breeding (Sergeant et al., 1980; Weinrich et al., 2001). Amaral (2005) previously reported a non-significant trend toward female-skewed sex ratios of mass stranding events during the spring and summer and male skewed-sex ratios during the fall and winter. However, we found no difference in sex-composition between the nonbreeding and breeding/calving season (Figure 2b). We do report a significant difference in age structure within mass stranded Atlantic white-sided dolphin groups between seasons, as well as between mass strandings and single strandings, which may be explained by selection pressures related to mating that vary seasonally. For example, we commonly found pure groups of either adults or juveniles during the breeding/calving season and a greater frequency of mixed groups during the nonbreeding season (Figure 2c). We also found a larger than expected ratio of adults to juveniles overall among the mass stranding events, as compared to a ratio close to one among single stranded individuals. This finding is consistent with Sergeant's (1980) hypothesis that juveniles leave their family group upon weaning and may be found as solitary animals or in loose groupings thereafter. Amaral (2005) similarly reports finding fewer mass-stranding juveniles than expected in adult-dominated groups. Our evidence for age segregation in Atlantic white-sided dolphins is further corroborated by several previously reported cases of single age-class mass strandings, including two cases that occurred in the month of September at the end of the breeding/calving season, one in the northeast United States consisting of 12 male juveniles (Amaral, 2005) and one in Ireland consisting of 19 individuals and no juveniles (Rogan et al., 1997).

These trends may be rooted in the disparate reproductive strategies employed by females and males (Gibson & Mann, 2008; Hartmann et al., 2008; Möller, 2012). Pregnant and nursing (i.e., mature) females may preferentially group together during the breeding/calving season, because of similar dietary requirements and a shared need for increased vigilance in predator detection (Connor et al., 2000; Gero et al., 2006; Möller, 2012; Möller & Beheregaray, 2004). Outside of the breeding/calving season, juvenile females may seek out groups including mature females as a means of learning to take care of young through participation in allomaternal care (Mann & Smuts, 1998; Rogers et al., 2004). The advantage of forming age-structured groups for males during the breeding season could relate to the formation of mating coalitions (Krützen et al., 2003), a common tactic for securing access to mates (Olsen & Blumstein, 2009; Parsons et al., 2003; Rogers et al., 2004). Such behavior has been observed in male bottlenose dolphins (*Tursiops* sp.), which form long-term pair bonds (Connor et al., 2001; Krützen et al., 2003; Parsons et al., 2003), a strategy that serves both to increase the copulatory success of males and as a defense against other roving male alliances (Connor et al., 2001; Möller et al., 2001; Wells, 1991). During such times, juvenile males may be forced to form their own, temporary social groups.

Our evidence supporting the relatively fluid nature of Atlantic white-sided dolphin group composition across the year is consistent with our genetic data that support a nonkin-based social structure (though some highly fluid social groups of dolphins can exhibit kin-based relationships: Gowans et al., 2007). We found generally low average intra-group pairwise genetic relatedness within 16 mass stranding events that occurred on Cape Cod between 1999 and 2009. Compared to simulated estimations of relatedness in groups of varying sizes populated randomly by individuals that stranded singly over the same time period, mass stranded groups did not show significantly higher than expected levels of relatedness (Figure 3). We were able to identify a small number of putative mother-offspring pairs, who matched in at least one allele at each microsatellite locus and mitochondrial haplotype. Two of these pairs included animals identified as juveniles (the other two included dependent calves), both of which were male and from

stranding events that occurred outside the breeding season. It is currently hypothesized that juveniles leave their natal group after weaning at 18 months (Sergeant et al., 1980); without more precise age information from these juveniles, it is not possible to know if they had not yet weaned, had weaned but did not leave the natal group, or returned to their natal group after disassociation.

Our genetic data are generally consistent with those of Mirimin et al. (2011), who conducted a similar analysis of Atlantic white-sided dolphins based on two mass stranding events on the western shores of Ireland. We found similar allelic diversity, observed heterozygosities, and inbreeding levels across the seven microsatellite loci shared between the two studies. Both our study and that of Mirimin et al. (2011) leverage the opportunity to investigate social structure of an oceanic dolphin through a study of mass strandings. While we have readily acknowledged several of the limitations of this approach above (i.e., not all individuals in a group are sampled, stranded individuals may not reflect the typical social behaviors of healthy individuals in the population), we also contend that strandings present a valuable resource for understanding cetacean ecology. Particularly for oceanic dolphins, research on stranded animals is less costly than boat-based studies, results in little to no disruption to natural populations, and is in many instances the only window of opportunity to learn about these elusive species.

To draw broader conclusions on the social structure of Atlantic white-sided dolphins, we place our results within the context of prior studies of genetic relatedness in mass-stranded odontocetes across species representing the full spectrum of kin associations—from the extraordinarily cohesive, matrilineal social structure observed among long-finned pilot whales (*Globicephala melas*; Amos et al., 1993) to the complete lack of kin-based bonds in short-beaked common dolphins (*Delphinus delphis*; Viricel et al., 2008). Studies of species exhibiting matrilineal social structure tend to show high levels of relatedness in small mass stranded groups (Mazzariol et al., 2018, 2011; Téllez et al., 2014) and decreasing relatedness with increasing group size (Téllez et al., 2014). Moderate to large-sized groups may include multiple maternal lineages, and both related and unrelated individuals (Mesnick, 2001; Oremus et al., 2013; Téllez et al., 2014). In contrast, a prior study of delphinids typified by large oceanic aggregations report little evidence for kin associations within mass stranded groups (Viricel et al., 2008). Overall, our results, together with those of Amaral (2005) and Mirimin et al. (2011), suggest that Atlantic white-sided dolphins fall near the fluid end of the continuum of associations represented among the odontocetes. Despite their tendency to mass strand, stable or kin-based associations are not a defining feature of social group structure in this species.

ACKNOWLEDGMENTS

This work was supported by the University of New England Marine Science Graduate Student Program; a Quebec-Labrador Foundation Sounds Conservancy Grant; and the Norcross Foundation A. V. Stout Fund. We are grateful to the current and previous staff of the International Fund for Animal Welfare (IFAW) who contributed to the present study during their tenure: S. Sharp, C. T. Harry, J. Hoppe, M. Niemeyer, A. Bogomolni, K. Patchett, B. Lentell, and W. B. Sharp. A. Kennedy at the New England Aquarium (NEAQ) provided additional data and samples. We thank M. Moore, K. Ono, two anonymous reviewers, and Patricia Rosel for their feedback on earlier versions of this manuscript. All stranding response was conducted by IFAW or NEAQ and authorized through Stranding Agreements with the National Oceanic and Atmospheric Administration Greater Atlantic Region Stranding Network Coordinator.

AUTHOR CONTRIBUTIONS

Katie Pugliares-Bonner: Conceptualization; formal analysis; investigation; writing-original draft. **Kate LaSpina:** Investigation; writing-review and editing. **Kathryn Rose:** Resources; writing-review and editing. **Steven Travis:** Conceptualization; methodology; resources; supervision; writing-review and editing. **Kristina Cammen:** Methodology; resources; supervision; writing-original draft.

ORCID

Kristina M. Cammen https://orcid.org/0000-0002-3923-6438

REFERENCES

Amaral, K. (2005). *Atlantic white-sided dolphins* (Lagenorhynchus acutus) *social structure based on stranding trends and genetics* (Master's thesis). University of Massachusetts Dartmouth.

Amos, W., Schlotterer, C., & Tautz, D. (1993). Social structure of pilot whales revealed by analytical DNA profiling. *Science*, *260*, 670–672. http://dx.doi.org/10.1126/science.8480176

Banguera-Hinestroza, E., Evans, P. G. H., Mirimin, L., Reid, R. J., Mikkelsen, B., Couperus, A. S., Deaville, R., Rogan, E., & Hoelzel, A. R. (2014). Phylogeography and population dynamics of the white-sided dolphin (*Lagenorhynchus acutus*) in the North Atlantic. *Conservation Genetics*, *15*, 789–802. http://dx.doi.org/10.1007/s10592-014-0578-z

Bengston Nash, S. M., Baddock, M. C., Takahashi, E., Dawson, A., & Cropp, R. (2017). Domoic acid poisoning as a possible cause of seasonal cetacean mass stranding events in Tasmania, Australia. *Bulletin of Environmental Contamination and Toxicology*, *98*, 8–13. http://dx.doi.org/10.1007/s00128-016-1906-4

Bérubé, M., & Palsbøll, P. (1996). Identification of sex in Cetaceans by multiplexing with three ZFX and ZFY specific primers. *Molecular Ecology*, *5*, 283–287. http://dx.doi.org/10.1111/j.1365-294X.1996.tb00315.x

Bogomolni, A., Pugliares, K. R., Sharp, S. M., Patchett, K., Harry, C. T., LaRocque, J., Touhey, K. M., & Moore, M. (2010). Mortality trends of stranded marine mammals on Cape Cod and southeastern Massachusetts, USA: 2000 to 2006. *Diseases of Aquatic Organisms*, *88*, 143–155. https://doi.org/10.3354/dao02146

Brabyn, M. W., & McLean, I. G. (1992). Oceanography and coastal topography of herd-stranding sites for whales in New Zealand. *Journal of Mammalogy*, *73*, 469–476. http://dx.doi.org/10.2307/1382012

Cetacean and Turtle Assessment Program. (1982). *A characterization of marine mammals and turtles in the mid- and North Atlantic areas of the U.S. outer continental shelf*. (Executive Summary for 1979 Cetacean and Turtle Assessment Program). University of Rhode Island.

Chybicki, I. J., & Burczyk, J. (2009). Simultaneous estimation of null alleles and inbreeding coefficients. *Journal of Heredity*, *100*, 106–113. http://dx.doi.org/10.1093/jhered/esn088

Connor, R. C., Heithaus, M. R., & Barré, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *268*, 263–267. http://dx.doi.org/10.1098/rspb.2000.1357

Connor, R. C., Mann, J., Tyack, P. L., & Whitehead, H. (1998). Social evolution in toothed whales. *Trends in Ecology & Evolution*, *13*, 228–232. http://dx.doi.org/10.1016/S0169-5347(98)01326-3

Connor, R. C., Wells, R., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of whales and dolphins* (pp. 91–126). University of Chicago Press.

Coughlan, J., Mirimin, L., Dillane, E., Rogan, E., & Cross, T. F. (2006). Isolation and characterization of novel microsatellite loci for the short-beaked common dolphin (*Delphinus delphis*) and cross-amplification in other cetacean species. *Molecular Ecology Notes*, *6*, 490–492. http://dx.doi.org/10.1111/j.1471-8286.2006.01284.x

Evans, K., Thresher, R., Warneke, R. M., Bradshaw, C. J. A., M, P., Thiele, D., & Hindell, M. A. (2005). Periodic variability in cetacean strandings: Links to large-scale climate events. *Biology Letters*, *1*, 147–150. http://dx.doi.org/10.1098/rsbl.2005.0313

Fernández, A., Edwards, J. F., Rodríguez, F., Espinosa de los Monteros, A., Herráez, P., Castro, P., Jaber, J. R., Martín, V., & Arbelo, M. (2005). "Gas and fat embolic syndrome" involving a mass stranding of beaked whales (family Ziphiidae) exposed to anthropogenic sonar signals. *Veterinary Pathology*, *42*, 446–457. http://dx.doi.org/10.1354/vp.42-4-446

Garrigue, C., Oremus, M., Dodémont, R., Bustamante, P., Kwiatek, O., Libeau, G., Lockyer, C., Vivier, J. C., & Dalebout, M. (2016). A mass stranding of seven Longman's beaked whales (*Indopacetus pacificus*) in New Caledonia, South Pacific. *Marine Mammal Science*, *32*, 884–910. http://dx.doi.org/10.1111/mms.12304

Gerber, S., Chabrier, P., & Kremer, A. (2003). FAMOZ: a software for parentage analysis using dominant, codominant and uniparentally inherited markers. *Molecular Ecology Notes*, *3*, 479–481. http://dx.doi.org/10.1046/j.1471-8286.2003.00439.x

Gero, S., Bejder, L., Whitehead, H., & Connor, R. C. (2006). Behaviorally specific preferred associations in bottlenose dolphins, *Tursiops* spp. *Canadian Journal of Zoology*, *83*, 1566–1573. http://dx.doi.org/10.1139/Z05-155

Gibson, Q. A., & Mann, J. (2008). Early social development in wild bottlenose dolphins: Sex differences, individual variation and maternal influence. *Animal Behaviour*, *76*, 375–387. http://dx.doi.org/10.1016/j.anbehav.2008.01.021

Goudet, J. (2001). FSTAT, a program to estimate and test gene diversities and fixation indices (Version 2.9.3) [Computer software]. University of Lausanne. https://www2.unil.ch/popgen/softwares/fstat.htm

Gowans, S., Würsig, B., & Karczmarski, L. (2007). The social structure and strategies of delphinids: Predictions based on an ecological framework. *Advances in Marine Biology*, *53*, 195–293. http://dx.doi.org/10.1016/S0065-2881(07)53003-8

Hartmann, K. L., Visser, F., & Hendriks, A. J. E. (2008). Social structure of Risso's dolphins (*Grampus griseus*) at the Azores: A stratified community based on highly associated social units. *Canadian Journal of Zoology*, *86*, 294–306. http://dx.doi.org/10.1139/Z07-138

Häussermann, V., Gutstein, C. S., Bedington, M., Cassis, D., Olavarria, C., Dale, A. C., Valenzuela-Toro, A. M., Perez-Alvarez, M. J., Sepúlveda, H. H., McConnell, K. M., Horwitz, F. E., & Försterra, G. (2017). Largest baleen whale mass mortality during strong El Niño event is likely related to harmful toxic algal bloom. *PeerJ*, *5*, e3123. http://dx.doi.org/10.7717/peerj.3123

Hayes, S. A., Josephson, E., Maze-Foley, K., & Rosel, P. E. (2018). *US Atlantic and Gulf of Mexico Marine mammal stock assessments – 2017*. (NOAA Technical Memorandum NMFS NE-245). NOAA NMFS Northeast Fisheries Science Center.

Hoelzel, A. R., & Green, A. (1998). PCR protocols and population analysis by direct DNA sequencing and PCR-based fingerprinting. In A. R. Hoelzel (Ed.), *Molecular genetic analysis of population, a practical approach*). Oxford University Press.

Katona, S. K., Rough, V., & Richardson, D. T. (1993). *A field guide to whales, porpoises, and seals from Cape Cod to Newfoundland*. Smithsonian Institution Press.

Krützen, M., Sherwin, W. B., Connor, R. C., Barré, L. M., Van De Casteele, T., Mann, J., & Brooks, R. (2003). Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *270*, 497–502. http://dx.doi.org/10.1098/rspb.2002.2229

Li, C. C., Weeks, D. E., & Chakravarti, A. (1993). Similarity of DNA fingerprints due to chance and relatedness. *Human Heredity*, *43*, 45–52. http://dx.doi.org/10.1159/000154113

Lynch, M., & Ritland, K. (1999). Estimation of pairwise relatedness with molecular markers. *Genetics*, *152*, 1753–1766.

MacLeod, C. D., & D'Amico, A. (2006). A review of beaked whale behaviour and ecology in relation to assessing and mitigating impacts of anthropogenic noise. *Journal of Cetacean Research and Management*, *7*, 211–221.

Mann, J., & Smuts, B. B. (1998). Natal attraction: Allomaternal care and mother-infant separations in wild bottlenose dolphins. *Animal Behaviour*, *55*, 1097–1113. http://dx.doi.org/10.1006/anbe.1997.0637

Mazzariol, S., Centelleghe, C., Cozzi, B., Povinelli, M., Marcer, F., Ferri, N., Di Francesco, G., Badagliacca, P., Profeta, F., Olivieri, V., Guccione, S., Cocumelli, C., Terracciano, G., Troiano, P., Beverelli, M., Garibaldi, F., Podestà, M., Marsili, L., Fossi, M. C., … Di Guardo, G. (2018). Multidisciplinary studies on a sick-leader syndrome-associated mass stranding of sperm whales (*Physeter macrocephalus*) along the Adriatic coast of Italy. *Scientific Reports*, *8*, 11577. http://dx.doi.org/10.1038/s41598-018-29966-7

Mazzariol, S., Di Guardo, G., Petrella, A., Marsili, L., Fossi, C. M., Leonzio, C., Zizzo, N., Vizzini, S., Gaspari, S., Pavan, G., Podestà, M., Garibaldi, F., Ferrante, M., Copat, C., Traversa, D., Marcer, F., Airoldi, S., Frantzis, A., De Bernaldo Quirós, Y., … Fernández, A. (2011). Sometimes sperm whales (*Physeter macrocephalus*) cannot find their way back to the high seas: A multidisciplinary study on a mass stranding. *PLoS ONE*, *6*, e19417. http://dx.doi.org/10.1371/journal.pone.0019417

Mesnick, S. L. (2001). Genetic relatedness in sperm whales: Evidence and cultural implications. *Behavioral and Brain Sciences*, *24*, 346–347. http://dx.doi.org/10.1017/S0140525X01463965

Milligan, B. G. (2003). Maximum-likelihood estimation of relatedness. *Genetics*, *163*, 1153–1167.

Mirimin, L., Banguera-Hinestroza, E., Dillane, E., Hoelzel, A. R., Cross, T. F., & Rogan, E. (2011). Insights into genetic diversity, parentage, and group composition of Atlantic white-sided dolphins (*Lagenorhynchus acutus*) off the west of Ireland based on nuclear and mitochondrial genetic markers. *Journal of Heredity*, *102*, 79–87. http://dx.doi.org/10.1093/jhered/esq106

Mirimin, L., Coughlan, J., Rogan, E., & Cross, T. F. (2006). Tetranucelotide microsatellite loci from the striped dolphin (*Stenella coeruleoalba* Meyen, 1833). *Molecular Ecology Notes*, *6*, 493–495. https://doi.org/10.1111/j.1471-8286.2006.01285.x

Möller, L. M. (2012). Sociogenetic structure, kin associations and bonding in delphinids. *Molecular Ecology*, *21*, 745–764. http://dx.doi.org/10.1111/j.1365-294X.2011.05405.x

Möller, L. M., & Beheregaray, L. B. (2004). Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). *Molecular Ecology*, *13*, 1607–1612. http://dx.doi.org/10.1111/j.1365-294X.2004.02137.x

Möller, L. M., Beheregaray, L. B., Harcourt, R. G., & Krützen, M. (2001). Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *268*, 1941–1947. http://dx.doi.org/10.1098/rspb.2001.1756

Morin, P. A., Martien, K. K., Archer, F. I., Cipriano, F., Steel, D., Jackson, J., & Taylor, B. L. (2010). Applied conservation genetics and the need for quality control and reporting of genetic data used in fisheries and wildlife management. *Journal of Heredity*, *101*, 1–10. http://dx.doi.org/10.1093/jhered/esp107

Murphy, S., Winship, A., Dabin, W., Jepson, P. D., Deaville, R., Reid, R. J., Spurrier, C., Rogan, E., López, A., González, A. F., Read, F. L., Addink, M., Silva, M., Ridoux, V., Learmonth, J. A., Pierce11, G. J., & Northridge, S. P. (2009). Importance of biological parameters in assessing the status of *Delphinus delphis*. *Marine Ecology Progress Series*, *338*, 273–291. http://dx.doi.org/10.3354/meps08129

Olsen, L. E., & Blumstein, D. T. (2009). A trait-based approach to understand the evolution of complex coalitions in male mammals. *Behavioral Ecology*, *20*, 624–632. http://dx.doi.org/10.1093/beheco/arp040

Oremus, M., Gales, R., Kettles, H., & Baker, C. S. (2013). Genetic evidence of multiple matrilines and spatial disruption of kinship bonds in mass strandings of long-finned pilot whales, *Globicephala melas*. *Journal of Heredity*, *104*, 301–311. http://dx.doi.org/10.1093/jhered/est007

Palka, D., Read, A. J., & Potter, C. (1997). Summary of knowledge of white-sided dolphins (*Lagenorhynchus acutus*) from US and Canadian Atlantic waters. *Report of the International Whaling Commission*, *47*, 729–734.

Palsbøll, P., Vader, A., Bakke, I., & El-Gewely, M. R. (1992). Gender determination in cetaceans by the polymerase chain reaction. *Canadian Journal of Zoology*, *70*, 2166–2170. http://dx.doi.org/10.1139/z92-292

Parsons, K. M., Durban, J. W., Claridge, D. E., Balcomb, K. C., Noble, L. R., & Thompson, P. M. (2003). Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Animal Behaviour*, *66*, 185–194. http://dx.doi.org/10.1006/anbe.2003.2186

Pew, J., Muir, P. H., Wang, J., & Frasier, T. R. (2015). related: An R package for analysing pairwise relatedness from codominant molecular markers. *Molecular Ecology Resources*, *15*, 557–561. http://dx.doi.org/10.1111/1755-0998.12323

Queller, D. C., & Goodnight, K. F. (1989). Estimating relatedness using genetic markers. *Evolution*, *43*, 258–275. http://dx.doi.org/10.2307/2409206

Read, A. J., Nicolas, J. R., & Caddock, J. E. (1996). Winter capture of a harbor porpoise in a pelagic drift net off North Carolina. *Fishery Bulletin*, *94*, 381–383.

Reeves, R. R., Smeenk, C., Brownell, R. L., Jr., & Kinze, C. C. (1999). Atlantic white-sided dolphin *Lagenorhynchus acutus* (Gray 1828). In S. H. Ridgway & R. Harrison (Eds.), *Handbook of marine mammals* (pp. 31–56). Academic Press.

Ritland, K. (1996). Estimators for pairwise relatedness and inbreeding coefficients. *Genetical Research*, *67*, 175–186. http://dx.doi.org/10.1017/S0016672300033620

Rogan, E., Baker, J. R., Jepson, P. D., Berrow, S., & Keily, O. (1997). A mass stranding of white-sided dolphins (*Lagenorhynchus acutus*) in Ireland: Biological and pathological studies. *Journal of Zoology*, *242*, 217–227. http://dx.doi.org/10.1111/j.1469-7998.1997.tb05798.x

Rogers, C. A., Brunnick, B. J., Herzing, D. L., & Baldwin, J. D. (2004). The social structure of bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Marine Mammal Science*, *20*, 668–708. http://dx.doi.org/10.1111/j.1748-7692.2004.tb01188.x

Roussett, F. (2008). GENEPOP'007: A complete re-implementation of the GENEPOP software for Windows and Linux. *Molecular Ecology Resources*, *8*, 103–106. http://dx.doi.org/10.1111/j.1471-8286.2007.01931.x

Schwacke, L., Schwacke, J., & Rosel, P. E. (2005). RERAT: relatedness estimation and rarefaction analysis tool [Computer software]. http://people.musc.edu/~schwaclh/

Sergeant, D. E., St. Aubin, D. J., & Geraci, J. R. (1980). Life history and northwest Atlantic status of the Atlantic white-sided dolphin (*Lagenorhynchus acutus*). *Cetology*, *37*, 1–12.

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *362*, 539–559. http://dx.doi.org/10.1098/rstb.2006.1994

Téllez, R., Mignucci-Giannoni, A. A., & Caballero, S. (2014). Initial description of short-finned pilot whale (*Globicephala macrorhynchus*) genetic diversity from the Caribbean. *Bioechemical Systematics and Ecology*, *56*, 196–201. http://dx.doi.org/10.1016/j.bse.2014.06.001

Van Oosterhout, C., Hutchinson, W. F., Willis, D. P. M., & Shipley, P. (2004). MICRO-CHECKER: Software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, *4*, 535–538. http://dx.doi.org/10.1111/j.1471-8286.2004.00684.x

Viricel, A., Strand, A. E., Rosel, P. E., Ridoux, V., & Garcia, P. (2008). Insights on common dolphin (*Delphinus delphis*) social organization from genetic analysis of a mass-stranded pod. *Behavioral Ecology and Sociobiology*, *63*, 173–185. http://dx.doi.org/10.1007/s00265-008-0648-7

Wang, J. (2002). An estimator for pairwise relatedness using molecular markers. *Genetics*, *160*, 1203–1215.

Wang, J. (2007). Triadic IBD coefficients and applications to estimating pairwise relatedness. *Genetical Research*, *89*, 135–153. http://dx.doi.org/10.1017/S0016672307008798

Weinrich, M. T., Belt, C. R., & Morin, D. (2001). Behavior and ecology of the Atlantic white-sided dolphin (*Lagenorhynchus acutus*) in coastal New England waters. *Marine Mammal Science*, *17*, 231–248. http://dx.doi.org/10.1111/j.1748-7692.2001.tb01268.x

Wells, R. (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 199–225). University of California Press.

Whitehead, H. (1997). Analyzing animal social structure. *Animal Behaviour*, *53*, 1053–1067. https://doi.org/10.1006/anbe.1996.0358

Whitehead, H. (1998). Cultural selection and genetic diversity in matrilineal whales. *Science*, *282*, 1708–1711. http://dx.doi.org/10.1126/science.282.5394.1708

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Pugliares-Bonner KR, LaSpina K, Rose KS, Travis SE, Cammen KM. Strandings provide insight into social group structure of Atlantic white-sided dolphins. *Mar Mam Sci*. 2021;1–18. https://doi.org/10.1111/mms.12783