



Behavior and social structure of the sperm whales of Dominica, West Indies

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ABSTRACT

There is substantial geographic variation in the behavior and social structure of sperm whales worldwide. The population in the Eastern Caribbean is thought to be isolated from other areas in the North Atlantic. We describe the behavior and social structure of the sperm whales identified off Dominica during an eight year study (2005–2012; 92% of photographic identifications) with supplementary data collected from seven other organizations dating as far back as 1981. A total of 419 individuals were identified. Resighting rates (42% of individuals between years) and encounter rates with sperm whale groups (mean = 80.4% of days at sea) among this population were both comparatively high. Group sizes were small (7–9 individuals) and were comprised of just one social unit (mean = 6.76 individuals, SD = 2.80). We described 17 units which have been reidentified off Dominica across 2–27 yr. Mature males are seen regularly off Dominica, but residency in the area lasts only a few days to a few weeks. Males were reidentified across years spanning up to a decade. Management of this population within the multinational Wider Caribbean Region will require governments to work towards international agreements governing sperm whales as a cross-border species of concern.

Key words: socio-ecology, social structure, group, unit, residency, photo-identification, *Physeter macrocephalus*, sperm whale, Caribbean.

There is substantial geographic variation in the behavior and social structure of sperm whales worldwide (*Physeter macrocephalus*, Linnaeus 1758; Whitehead *et al.* 2012). Much of what is known about sperm whale behavior has been garnered from a

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longitudinal study in the Eastern Tropical Pacific (see Whitehead 2003). However, more recent work in the Atlantic, particularly in the Gulf of Mexico, the Azorean archipelago, and the Mediterranean Sea, have demonstrated consistent social, vocal, and behavioral differences between regional populations and between ocean basins (Whitehead *et al.* 2012). Sperm whales exhibit both individual differences in behavior (Gero *et al.* 2008, 2013; Antunes *et al.* 2011; Schulz *et al.* 2011; Gero 2012), as well as group-specific behavioral traditions (Rendell and Whitehead 2003; Marcoux *et al.* 2007a, b; Gero *et al.* 2009; Gero 2012).

Although this degree of variation exists, management for this species is currently applied based on vaguely defined “stocks” covering vast areas of entire oceans (Dufault *et al.* 1999). However, recent genetic (Engelhaupt *et al.* 2009) and photographic evidence (Gero *et al.* 2007, Steiner *et al.* 2012) suggest that conservation and management initiatives should be undertaken on the female portion of the population as they exhibit regional philopatry. Small groups of female sperm whales form the base level of sperm whale social structure termed the “unit.” Female unit members are often related (Mesnick 2001, Mesnick *et al.* 2003, Gero *et al.* 2008), communally defend and care for their calves (Whitehead 1996, Gero *et al.* 2009), and roam across areas generally covering less than 2,000 km (Whitehead *et al.* 2008). As a result of the amount of behavior variation among groups and study sites and movement patterns of females, it can be argued that management decisions should be made over more biologically relevant scales.

As a species, the sperm whale’s distribution covers the entire Wider Caribbean Region (Ward *et al.* 2001, Reeves 2005), but the individuals found in the Caribbean appear to be isolated from other neighboring populations (Gero *et al.* 2007). In a condensed, multinational area, such as the Caribbean, no one country is able to manage highly mobile marine species, like the sperm whale, in isolation. Given that nations differ in their political, social, and economic attitudes towards conservation, when animals move between national jurisdictions management becomes increasingly more complex. Impacts in one national jurisdiction affect individuals in others.

In order to achieve efficient regional management, a thorough understanding of the behavior and social structure of the female social units in the region is required. Here, we address this need using the detailed data collected through longitudinal study across 8 yr while also linking with existing data from the region. It is rare in the study of pelagic cetaceans to have the opportunity to observe individuals over time in order to gain such a detailed insight into the social behavior and interactions among individuals and social groups. While not explicitly testing hypotheses, descriptive studies like this one, which establish residency times, resighting rates, group sizes, and other general features of a study population are needed in order to provide the framework for comparative studies with populations worldwide. Furthermore, these population parameters are critical from a conservation perspective within the complex multinational management area of the Wider Caribbean Region.

METHODS

Field Methods

Approximately 92% of the data set was collected by researchers from Dalhousie University during dedicated research between 2005 and 2012. During this research, groups of female and immature sperm whales were located and followed both

acoustically using hydrophones and visually by observers on one of four platforms (a dedicated 12 m auxiliary sailing vessel, a dedicated 5 m outboard skiff, a dedicated 11 m rigid-hulled inflatable boat with an outboard, or an 18 m whale watch vessel) in an area that covered approximately 2,000 km² along the entire west (leeward) coast of the island of Dominica (15.30°N, 61.40°W), in waters sheltered from the trade winds. Research was conducted in the winters and/or spring of 2005 through 2012 for a total of just over 3,056 h with whales across 388 d of effort. During outboard skiff seasons, the skiff was unable to operate on heavier weather days (wind above Beaufort 3) and so the research team boarded the larger whale-watch vessel to continue work. Since whale watch tours focused their effort on sperm whales, search patterns were consistent across all four platforms. Work from the whale watch was restricted only by the length of time spent at sea.

During daylight hours, clusters of individuals visible at the surface were approached and photographed for individual identification. An individual was considered part of a cluster if it was within approximately three adult body lengths of any other cluster member, a ~40 m “chain rule,” and their behavior was coordinated, as in Whitehead (2003). If a calf was present in a given cluster, priority was given to taking dorsal fin pictures of the calf from alongside the larger animals, before moving the vessel behind the adults in the cluster to photograph distinct markings on the trailing edge of their flukes for individual identification purposes (Arnbom 1987).

Supplementary photo-identification data were collected off several islands in the Lesser Antilles by seven different organizations across 31 yr. Field methods were of two types based on platform (Table 1): research vessels dedicated to comprehensive sperm whale research, including photo-identification (D in Table 1), and opportunistic photo-identifications collected from whale watch vessels (W in Table 1). Results from work by Woods Hole Oceanographic Institution (WHOI; Watkins and Moore 1982; Watkins *et al.* 1985, 1993, 1999; Moore *et al.* 1993) and the International Fund For Animal Welfare (IFAW; Gordon *et al.* 1998) have been published. Data collected by researchers from Dalhousie University while in Guadeloupe in 2004 were collected in collaboration with Association Evasion Tropicale (AET). Finally, no data were available from 1985 to 1989, 1992 to 1994, and 1997 to 1998.

Age and Sex Class

Age/sex classification was completed in the field based primarily on size. Given that adult females and immatures of either sex are similar in size, we defined only three age/sex classes: *mature males*, distinguished primarily by their considerably larger size (Best 1979, Best *et al.* 1984) and additionally, in many cases, acoustically (Weilgart and Whitehead 1988); *adult female/immature*, adult females and older immature animals of either sex often cannot be distinguished by size alone; however, juvenile animals (visibly smaller in size than the adult females but no longer nursing and often already making fluke-up foraging dives) can often be distinguished but not easily sexed; and, *dependent calf*, small calves that are still nursing and do not make fluke-up foraging dives. Complementary data, such as the age/sex class of the animal identified, the exact date and time of the identification, start and end time of encounters, and information about associations, were only readily available for fieldwork completed by the Dalhousie University and IFAW groups; although mature males were noted in all opportunistic data. Some individuals were sexed genetically using sloughed skin following methods described in Gero *et al.* (2008).

Table 1. Details of the field projects, photographs, and individuals identified.

Dates	Nearest island	Project leader	Research group ^a	Type	# of photos	Individuals identified ^b
1981–1991	Dominica	William Watkins	WHOI	D	44	2
1984	Dominica	George Nichols	ORES	D	18	13
1995	Dominica	Jonathan Gordon	IFAW	D	218	59
1995	Grenada	Jonathan Gordon	IFAW	D	7	7
1996	Dominica	Jonathan Gordon	IFAW	D	81	36
2000	Guadeloupe	Carole Carlson	IFAW	D	7	6
1999	Dominica	Peter Evans	SWF	W	7	6
2000	Guadeloupe	Caroline Rinaldi	AET	D/W	9	8
2001	Guadeloupe	Caroline Rinaldi	AET	D/W	17	15
2002	Guadeloupe	Caroline Rinaldi	AET	D/W	11	9
2003	Guadeloupe	Caroline Rinaldi	AET	D/W	23	22
2005	Guadeloupe	Caroline Rinaldi	AET	D/W	275	75
2006	Guadeloupe	Caroline Rinaldi	AET	D/W	217	61
2007	Guadeloupe	Caroline Rinaldi	AET	D/W	170	46
2008	Guadeloupe	Caroline Rinaldi	AET	D/W	165	43
2009	Guadeloupe	Caroline Rinaldi	AET	D/W	6	4
2006	Dominica	Petra Charles	AWW	W	20	11
2007	Dominica	Pernell Francis	AWW	W	141	49
2008	Dominica	Pernell Francis	AWW	W	154	48
2009	Dominica	Pernell Francis	AWW	W	15	12
1999	Dominica	Andrea Steffen	GRD	W	7	3
2000	Dominica	Andrea Steffen	GRD	W	9	5
2001	Dominica	Andrea Steffen	GRD	W	48	14
2003	Dominica	Andrea Steffen	GRD	W	25	9
2004	Dominica	Andrea Steffen	GRD	W	11	6
2005	Dominica	Andrea Steffen	GRD	W	19	6
2006	Dominica	Andrea Steffen	GRD	W	18	6
February– March 2004	Guadeloupe	Shane Gero	Dalhousie	W	23	22
January– April 2005	Dominica	Hal Whitehead	Dalhousie	D	812	53
10 March 2005	Martinique	Hal Whitehead	Dalhousie	D	16	7
20 March 2005	St. Lucia	Hal Whitehead	Dalhousie	D	3	3
January– February 2006	Dominica	Shane Gero	Dalhousie	W	143	25
February 2007	Dominica	Shane Gero	Dalhousie	D/W	465	27
February– May 2008	Dominica	Shane Gero	Dalhousie	D	4,137	112
11 May 2008	St. Vincent	Hal Whitehead	Dalhousie	D	45	7
January– March 2009	Dominica	Shane Gero	Dalhousie	D	1,345	84

(Continued)

Table 1. (Continued)

Dates	Nearest island	Project leader	Research group ^a	Type	# of photos	Individuals identified ^b
January– March 2010	Dominica	Shane Gero	Dalhousie	D	7,322	83
March– April 2011	Dominica	Shane Gero	Dalhousie	D	2,996	69
May– June 2012	Dominica	Shane Gero	Dalhousie	D	2,868	52
Totals					21,872	419

^aWHOI, Woods Hole Oceanographic Institution; ORES, Oceanic Research and Education Society; IFAW, International Fund for Animal Welfare; SWF, Sea Watch Foundation; AET, Association Evasion Tropicale; AWW, Anchorage Whale Watch; GRD, German Society for Dolphin Conservation; Dalhousie, Dalhousie University. Type defines the research platform as either D, dedicated research vessel or W, whale watch.

^bIndividuals identified are unique within each field season (row). Total number of individuals identified is unique across all seasons.

Analyses

Identifications—A quality rating (Q) between 1 and 5 was assigned to each photograph, where 1 indicated a very poor photograph, and 5 indicated a very high quality photograph (Arnbom 1987, Dufault and Whitehead 1993). Only high quality photos of a $Q \geq 3$ were used for the analyses. Individuals with high quality identification photos but with no identifiable marks on their flukes were excluded from the analysis (132 high quality identification photos for a potential maximum of 33 individuals). The best photo for each identifiable individual within each encounter was assigned a temporary identification code and then matched between encounters and to a digital catalog using a computer-based matching program (Whitehead 1990). Calves, which do not regularly fluke, were individually identified using the shape of its dorsal fin and distinct markings on its dorsal fin and body (Gero *et al.* 2009). The best photo for each individual calf within each encounter was then matched between encounters by eye. An encounter was defined as the period of time from the first positive acoustic detection of sperm whales until 2 h since last detection or when it was decided to leave the animals. Encounter rates were determined as the proportion of days on which whales were encountered at sea during dedicated work between 2005–2012.

Assigning groups—During work off Dominica (Dalhousie only, 2005–2012), a “group” was defined as all individuals encountered on the same day that were coordinating their movement and behavior (adapted from Whitehead 2003). Groups are a temporary spatio-temporal assemblage of whales encountered at sea and do not imply social affiliation between all individuals present. Group size was estimated using only $Q \geq 3$ identification data from the dedicated research between 2005 and 2012. Observed group size was calculated by dividing the day’s identifications into two sets (either by splitting at midday or by using half of the day’s identifications) and then using a Petersen mark-recapture estimator to estimate the number of individuals present (Coakes and Whitehead 2004). Mean typical group size, an approximation of group size as experienced by a randomly chosen individual of the population as opposed to from an outside observer’s perspective (Jarman 1974), was then calculated

from those estimates as in Coakes and Whitehead (2004) using two levels of precision since the precision of these estimates decreases with increases in group size (Whitehead 2003).

Defining units—Units are the base level of sperm whale social structure. Unit members share a long-term, stable social relationship across years. Units were delineated using methods following Christal *et al.* (1998) but with more stringent minimum durations of association. We considered a unit to be the set of individuals for which each pair was observed associated during two different years (Christal *et al.* used a 30 d minimum rather than different years). The fact that unit members were associated across years suggests stable, long-term companionship as defined by Whitehead *et al.* (1991), but may also result in more conservative estimates of unit size than in previous work. Individuals were deemed to be associating if they were identified within 2 h of each other. This level of association allows for the inclusion of more individuals into defined units, but given the more stringent minimum durations between identifications (years apart) it still likely reflects stable, long-term companionship. Specifically, it includes individuals that might often be identified alone, as opposed to in clusters with other unit members, but still within close spatio-temporal association with its unit members across years. In addition, unit membership is transitive in that if A and B are unit members and so are B and C, then A and C are members of the same unit as well.

Distance to shore and depth of encounters—We calculated the distance to shore and depth of our position at the start of each encounter with whales. Associated distance and depth values were extracted using Spatial Analyst Tools in ArcGIS 10 and averaged across years. Depths were obtained from a 100 × 100 m resolution bathymetric model, with a 1 m accuracy, provided by the Institut de Physique du Globe de Paris (IPGP)/ Institut Francais de Recherche pour l'Exploitation de la Mer (IFREMER) and based on data collected by the IPGP/IFREMER in 1998 during the Aguadomar campaign. Distance from the shoreline was extracted from a 5 × 5 m resolution raster layer created in ArcGIS 10, with the Euclidean Distance Tool, from shoreline information obtained from the Government of the Commonwealth of Dominica, Land and Surveys Division. Calculated averages do not include data from 2006, since no GPS positions were available for that year.

RESULTS

Identifications Across Years

To date, 419 individual sperm whales (mature males, adult females/immatures, juveniles, and dependent calves) have been identified photographically in the Eastern Caribbean, primarily off the islands off Dominica and Guadeloupe. Of those, 274 (65.4%) were identified during dedicated research between 2005 and 2012 by researchers from Dalhousie University. While fewer new individuals are being identified each year, the discovery curves are still rising (Fig. 1). Of the 419 individuals, 175 (42%) were identified in multiple years between 2 and 14 times from 1984 to 2012 (Table 2). Only two individuals were resighted from the oldest data from 1984, one of which was resighted in 2011 with a total period spanning 27 yr between the first and most recent identifications.

Encounter rates were high from January through May during the longitudinal work off Dominica (2005–2012). Whales were followed across years on a mean of

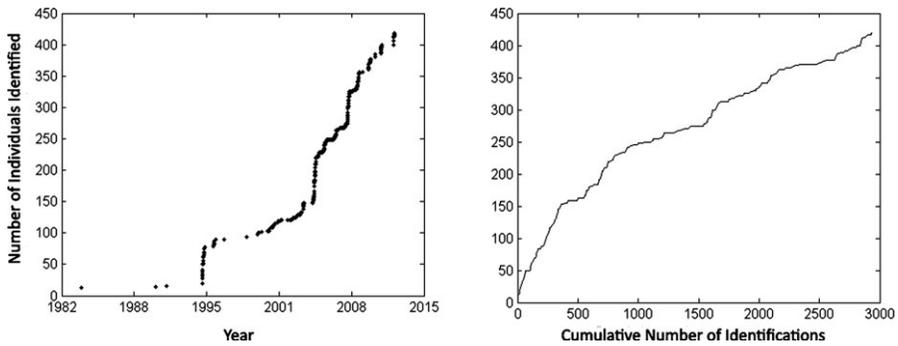


Figure 1. Discovery curves for individuals by date and by cumulative number of identifications.

80.4% of days at sea (or portion thereof; range = 54%–94%). The longest gap of time without any encounters with whales was 18 straight days during the 2009 season. When whales were encountered off Dominica, we were able to track the animals for just over 10 h on average but encounters ranged between 12 min and 5.5 d (133 h). Short encounters were often ended due to weather and sea state conditions, which are usually worse in the channels between islands. On average encounters began 9.3 km from shore (95% CI = 0.5–18.8 km) in waters that averaged 3,025 m deep (95% CI = 1,475–4,575 m).

Mean typical group sizes encountered off Dominica during longitudinal work were between 7 and 9 individuals, depending on the method used (Table 3). Mean unit size off Dominica was 6.76 (SD = 2.80; range = 3–12) indicating that most groups encountered at sea include only one social unit. Cluster sizes were usually small off Dominica with mean of only 1.75 individuals (SD = 1.24; range = 1–11) observed together at the surface. Within a day, the time lag between subsequent identifications of the same individual in different clusters has a mean of 94.1 min (maximum = 10.9 h). The multimodal distribution shown in Figure 2 would suggest that most individuals were identified every dive (~1 h), if not every other dive (~2 h); however, the longer lag times suggest that some individuals are not identified multiple times on any given day. While it is difficult to get an accurate measure of dive time (fluke-up to surfacing) based on our methods, the mean time lag between identifications (fluke-up to fluke-up, and therefore, including the surface interval, sometimes called “cycle time”) was 57.1 min, when limited to time lags between 40 and 70 min (the largest peak in Fig. 2).

Social Units

We identified 17 social units which use the waters off Dominica (Table 4). Residency off Dominica across years varied among units, but most have been consistently sighted off the island for the last decade (Fig. 3). The composition and membership described in Table 4 apply to the year of last sighting. We also identified “potential members,” which are individuals which were only identified associated with unit members within one season, but not at any other time. These individuals are likely members of the focal unit for which not enough data are available to assign them membership, or possibly members of an unidentified social unit that was associated

Table 3. Estimates of typical group size (TGS, mean and SD) observed off Dominica including only adults (excluding mature males and calves), calculated using Petersen mark-recapture methods with a day's identifications divided in half by two different methods and two levels of the coefficient of variation (CV; as in Coakes and Whitehead 2004).

Splitting Method	CV < 0.25		CV < 0.40	
	<i>n</i>	TGS	<i>n</i>	TGS
Split at Midday	125	8.65 (4.40)	145	9.20 (4.10)
Split by half of Identifications	216	7.93 (4.55)	258	8.52 (4.25)

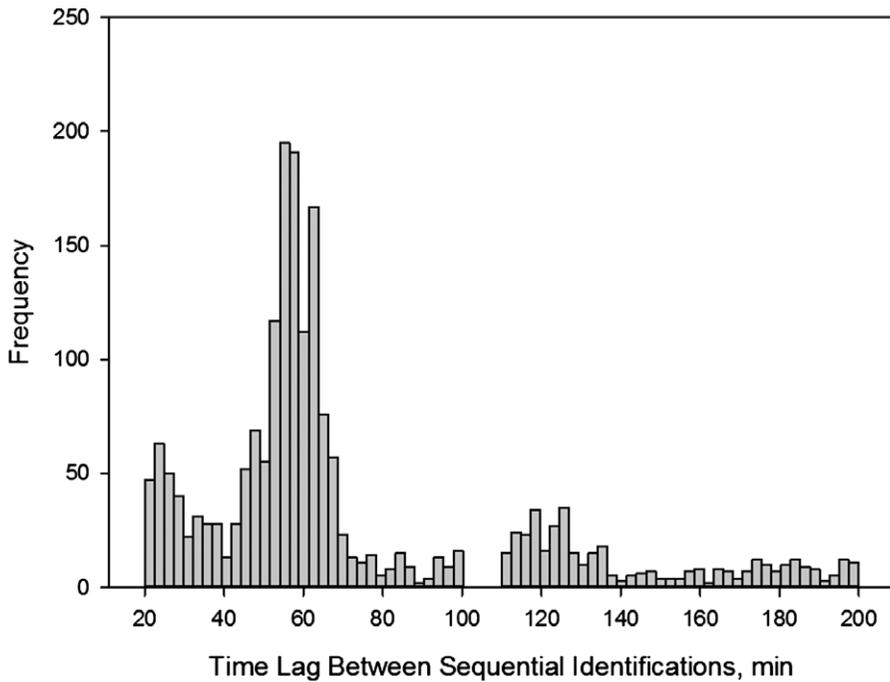


Figure 2. Time lags between sequential identifications of individuals on the same day for all lags less than 200 min.

with the focal unit. As a result, many of the units for which fewer data were available have several individuals which are designated only as potential members.

Dependent Calves, Nursing, and Allonursing

The majority of units observed off Dominica contained one or more dependent calves (Table 4). Calves appear to nurse for at least 3 yr but may continue to do so as late as 8 yr in one case in Unit A. In some units, the adult females babysit each other's calves but appear not to nurse them (Units: A, D, F, and U); in two other units, however, there is evidence of allonursing or attempted allonursing. Interestingly, both units appear to have different systems. In Unit J, the calf attempted to suckle from every adult in the unit. In Unit T, each of the two calves was nursed predominantly

Table 4. The 17 social units identified off Dominica. First and last year sighted, number of years and days in which at least one member was identified, total number of identifications (1984–2012), number of individuals, and composition as of the most recent year are given (A = adult, C = calf). Potential members are individuals which were identified as associated with unit members within only one year but never identified otherwise.

Unit	First	Last	Years	Days	Identifications	Composition	Potential
A	1996	2010	8	39	1,943	7A 4C	1A
C	2004	2006	3	14	56	6A	3A
D	1984	2011	6	36	1,223	5A 2C	None
F	1995	2012	15	173	3,583	5A 2C	None
G	2007	2010	3	3	76	3A 1C	3A 1C
I	2008	2009	2	2	60	3A 1C	None
J	1995	2011	8	57	1,496	4A 1C	None
K	2008	2012	3	6	128	4A 2C	3A
L	2005	2008	2	2	89	2A 1C	5A
N	1995	2012	12	119	1,304	7A 2C	1A
P	1995	2012	10	21	426	9A	4A 3C
Q	2006	2011	5	9	105	5A	2A 2C
R	2001	2011	8	55	873	6A 2C	None
S	2004	2012	7	37	557	3A	None
T	1995	2011	11	68	1,872	7A 2C	None
U	1990	2012	17	105	913	3A 1C	None
V	1995	2011	11	64	619	9A 3C	None

by their mothers, but also made attempts on their specific primary babysitters. In addition, they also attempted to suckle from a third female, often at the same time when she accompanied them both while neither of their primary babysitters was around.

Singletons

Two individuals have been identified in multiple years, but with different well-known units. Individual #5988 was first identified with Unit F twice in 2006 and then spent all of 2007 with Unit F, in particular in clusters with the juvenile male from Unit F. In 2008, however, #5988 was consistently identified in clusters with Unit J. Individual #5989 showed a similar pattern spending the whole 2007 season with Unit J, but was only identified with members of Unit P in 2008. Neither singleton has been seen since, even though all of the units have been encountered in subsequent years.

Mature Males

A total of 25 mature males have been identified between 2005 and 2012 off Dominica. Mature males were observed in 6 of the 8 yr with between two and six different males in a given year (none seen in 2009 and 2012). Clusters are twice as large when mature males are present (with males: mean = 3.75, SD = 3.16, $n = 78$; without males: mean = 1.70, SD = 1.10, $n = 2,967$, Mann-Whitney: $P < 0.001$). Most males were only sighted on a single day, but a total of six males were identified on different days within the same year. The longest span between sightings of males within a year was 34 d, suggesting that residency of mature males in the waters off Dominica

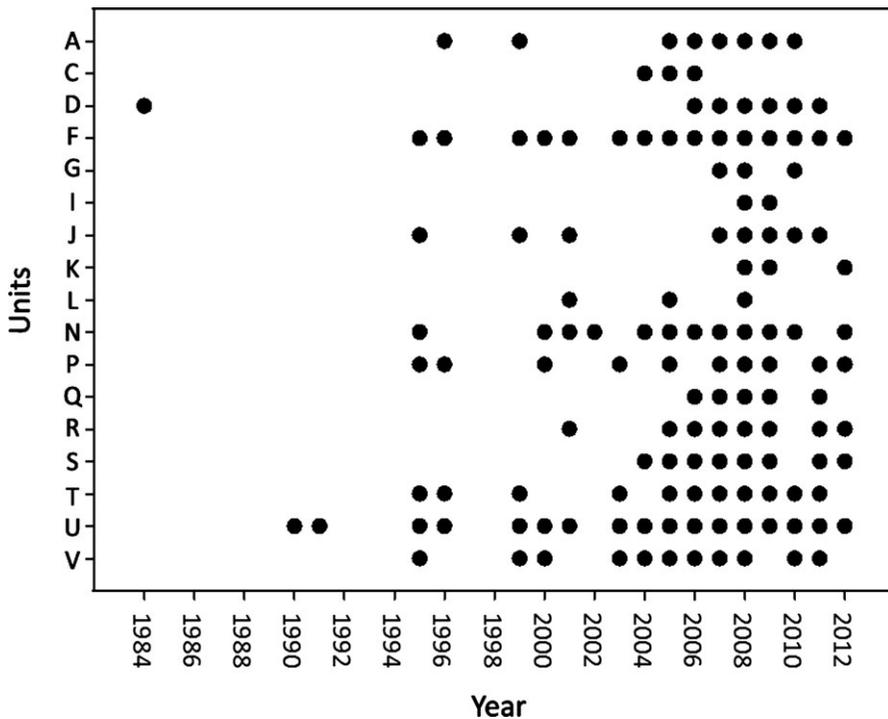


Figure 3. Years in which at least one member of a given unit was identified. No data available for 1985–1989, 1992–1994, and 1997–1998.

is on the order of a few days to a few weeks at a time (observed mean = 3.76 d, range = 1–34 d). While males were observed in clusters with females with dependent calves, mature males were never seen escorting a calf alone. When associating with units of females, males were not always initiating social or breeding behavior. Males often behave in qualitatively similar ways to the females, making foraging dives with them or resting when the units rest. In one extreme case, a mature male charged in from offshore swimming purposefully and quickly at the surface, while making the sex-specific “clang” vocalization (Weilgart and Whitehead 1988), towards members of Unit J. However, Unit J had just gone into a resting/sleep state (vertical suspension underwater; Miller *et al.* 2008). Rather than the females waking in response to its arrival, the male began to rest/sleep within a few minutes of joining them. Several hours later, upon waking up, there was an exchange of codas with little interaction and the male departed in the opposite direction of the unit which resumed normal foraging behavior.

On only one occasion (2 d with a 4 d span between) were two mature males sighted together. In this case, both produced clangs when with the females. The two were seen with the same unit on different days (Unit R), and only one of the two males was identified with the unit 2 d later. Their interactions were not antagonistic and were seen in clusters together at the surface without females in close proximity.

Only two males were identified in multiple years, one of which was identified in three different years. The first was sighted in 2001 and then again in 2004. While association data were not available for 2001, in 2004, this male was seen on the same

day as Unit C. The other was first identified in 2000 and then again in 2008 and 2010. In 2008, this second male was identified on three different days each with members of a different unit: Unit A, Unit R, and Unit U. Then he was identified again in 2010 with members of Unit J and Unit D on one day. Association data were not available for this male in 2000.

DISCUSSION

During this work in Dominica, we were able to track social units of sperm whales across days, months, and between years. In many ways, their behavior differs from the model of animals in the Pacific. Caribbean units appear to range over smaller areas than in other regions (Whitehead *et al.* 2012), which has allowed us to collect an unparalleled data set at the level of the individual and to observe differences between social units. More time has been spent with Unit F, “The Group of Seven,” than with any other unit by a large margin. As a result, they have served as the exemplar for sperm whale behavior in the Eastern Caribbean. However, other units do differ from the way Unit F behaves. Based primarily on observations of Unit F, it had been concluded that allonursing was not occurring in the Caribbean (Gero *et al.* 2009). The females of Unit F babysit each other’s calves but appear not to nurse them; however, more recent observations of two other units provide evidence of allonursing or attempted allonursing in the Caribbean. Furthermore, we found evidence that calves make suckling attempts for up to 8 yr, suggesting that mothers may also lactate for that period, which bears some similarity to elephants (Lee and Moss 1986, Lee 1996). Calves are present in the vast majority of units, which is in strong contrast to those studied in the Pacific in which calves were rare (Whitehead *et al.* 2012). Calves appear to create much of the social dynamics within units (Gero *et al.* 2013) and babysitting appears to be one factor leading to the formation of social groups with long-term stable membership (Best 1979, Best *et al.* 1984, Whitehead 1996).

Units in the Caribbean differ in several characteristics. While Unit F is about average in size, the largest of the units have nearly twice as many members and the smallest units are composed of only two mature females and their offspring. Overall, units in the Caribbean are smaller when compared to the Pacific and other parts of the Atlantic (Jaquet and Gendron 2009, Whitehead *et al.* 2012). However, our estimates, which include only animals that were associated across years would result in conservative estimates of units size. Units also appear to differ vocally, in that different units have distinguishable coda repertoires, while all share the predominant coda types of the Eastern Caribbean Clan (Gero 2012).

There appears to be a large component of the population which has only been identified in a single year. Of the 419 individuals, 58% or 244 individuals were identified in only one year. This can be interpreted in several ways: (1) a proportion of these individuals can be explained by undersampled “potential” members of units outlined above (26 individuals), which were identified only once but with units that have been sighted across years; dependent calves, which are not always identified during every encounter of less sighted units; or animals that have died prior to the onset of dedicated research in 2005; (2) there is a component of the population that is under-sampled because they only transit through the Caribbean, however, the identification of distinct vocal patterns in the Caribbean (Gero 2012) and a lack of photoidentification matches between neighboring areas (Gero *et al.* 2007) suggest that units are localized to the Caribbean Sea; (3) there may be some inshore-offshore stratification of

units in terms of habitat preferences. Our research, which is generally restricted to within 20 km of shore, may be undersampling units that are less island associated; and/or (4) units have a complex pattern of overlapping home ranges, as is seen among African elephants (Charif *et al.* 2005) and the units regularly reidentified here have a larger portion of this, which overlaps with our study area. Some units certainly are more often identified off one island even though concurrent effort exists from a neighboring island. Unit V provides a good example of multiple sightings off Guadeloupe in years when constant effort was undertaken off Dominica during which Unit V was not identified. Satellite telemetry studies are needed to examine small scale habitat use by the units around the islands and movements between them in order to outline unit level home ranges. While most units have only been identified off the coasts of both Dominica and Guadeloupe, it should be noted that these islands have received by far the most effort in the region. Identifications off islands further south are primarily based on opportunistic photographs. The longest distance between reidentifications is between the islands of Dominica and Grenada (~450 km; Gero *et al.* 2007). However, all of the Lesser Antilles are separated by less than 1,000 km in a straight line, which would suggest that units may range across the entire eastern Caribbean given that sperm whales are known to travel distances over 1,000 km regularly (Whitehead *et al.* 2008).

The two roving singleton animals provide interesting new insight into the immature years of male sperm whales. A plausible interpretation of their association patterns is that these are subadult males who have recently separated from their natal family units. Separating from the natal unit occurs slowly, and can take several years, as immature males spend less and less time with their mothers and their unit members (Gero 2012). Young males who have recently left their natal unit may fill this lack of social interactions by seeking companionship with other young males, as may have been the case with individuals #5988 and #5989 in 2007. We can speculate that these encounters with roving subadult males may encourage immature males to leave their units to join them in a bachelor group.

While mature males have sometimes been sighted alone without any females in close proximity, generally mature males appear to aggregate otherwise dispersed units of females. Cluster sizes are significantly larger when males are present. Residency of mature males in the waters off Dominica appears to be on the scale of a few days to a few weeks which is comparable to previous results off Dominica (Watkins *et al.* 1999) and the Galapagos Islands (Whitehead 1993). In one case, members from six different units were identified off the coast of Dominica on the same day within proximity of a single male. If we assume all unit members were present, it would have resulted in an aggregation of 44 females and immatures, a substantial part of the whole eastern Caribbean population. This would provide some support for the suggestion that female choice plays an important role in their mating system (Whitehead 2003). Another mature male was reidentified off Dominica in three different years spanning a total of ten years. Unfortunately, we can only speculate as to the ranging behavior between resightings of males such as this one. Males may (1) leave the Caribbean on a regular or irregular basis for colder, more productive, waters but return annually or repeatedly over several years; (2) leave the Caribbean but roam widely through the tropics in search of mates over long periods of time, making multiple visits to the Caribbean, followed by long periods in colder waters feeding; or (3) remain in the Caribbean to breed for several years, or some combination of these. Currently, we have little evidence favoring any one of these possibilities. Mature males are difficult to study as they cover large spatial and temporal scales. It is now known

that immature males use a similar coda repertoire to that of their natal unit (Schulz *et al.* 2011). What still remains to be seen is if males ever return to their natal waters to breed or if the coda repertoire is used to prevent inbreeding (Whitehead 2003). The nuclear genetic homogeneity across oceans and clear female philopatry (Lyrholm *et al.* 1999, Engelhaupt *et al.* 2009) would suggest that males may show a preference for females from vocal clans other than their own (Rendell *et al.* 2005). Alternatively, this pattern may be the result of females showing a preference for males from different vocal clans than their own such that males avoid areas which are predominantly populated by units from their natal clan. In either case, the males seen in the Eastern Caribbean likely originate from elsewhere in the Atlantic as vocal clans are geographically structured in the Atlantic (Antunes 2009).

Almost half (42%) of the individuals have been reidentified across years in the study area. Several units have been identified off the islands every year for the last decade and there is some evidence that members of one unit have been using the waters off Dominica for at least the last 27 yr. High residency times and resighting rates off Dominica would suggest that this is preferred habitat for these social units, thereby, leaving these animals vulnerable to local disturbance or habitat degradation. Furthermore, this residency, and close proximity to populated coasts, exposes these small units to repeated exposure to anthropogenic activity, including whale watching for which Dominica is well known. This population would be vulnerable should the current whale watching activities in the Caribbean grow substantially. Groups encountered off Dominica are small, often containing only one unit, and typically there is only one group off the island. While our data was predominantly restricted to the first half of the year, we have little reason to suspect that grouping behavior differs during the summer and fall, and what data are available from months with lower effort fits the patterns outlined here. These results would indicate that at any one time there are only about seven animals off the western coast of Dominica. With so few animals offshore on any given day, tour boat effort is not easily diffused, although current whale watching in Dominica appears not to be preventing these units from using preferred habitat over many years. Nonetheless, based on research into the impacts of whale watching and boat traffic in other regions (Williams *et al.* 2002a, b, 2006; Lusseau and Higham 2004; Scheidat *et al.* 2004; Lusseau 2005; Bejder *et al.* 2006a, b; Williams and Ashe 2007), this could easily change with the addition of only one or two more commercial vessels, with an increase in noncommercial approaches from private yachts, or increased commercial shipping or cruise ship activity into Dominica. Specifically, sperm whales appear to alter their surface intervals, breathing rates, and echolocation patterns in response to boat presence (Richter *et al.* 2006). Alternatively, we might already be dealing with a shifted baseline so that the animals we observe, or most of them, are already habituated to anthropogenic disturbance, and tolerate high levels of boat traffic, whereas the more sensitive animals have already emigrated from the area (Bejder *et al.* 2006b).

Perhaps of even greater concern are the escalating commercial swim-with-the-whale operations in Dominica. Operators have begun offering tourists the opportunity to swim with cetaceans. The focus of these operations is primarily the sperm whales, but in-water observations have been attempted with several other species including short-finned pilot whales (*Globicephala macrorhynchus*), rough-toothed dolphins (*Steno bredanensis*), as well as, pygmy (*Feresa attenuata*), and false killer whales (*Pseudorca crassidens*). Current knowledge indicates that in many cases swim-with activities are disturbing to targeted animals (Constantine 2001, Samuels *et al.* 2003, Lundquist *et al.* 2012). Nevertheless, intense popular demand for swim-with

programs is pushing the growth of the industry, in Dominica and elsewhere, beyond what might be considered prudent based on current data. Effective management of tourism operations will be vital in securing a long-term future for this small sperm whale population.

The animals present in Dominican waters are members of an isolated population that spans the waters of most of the nations in the Eastern Caribbean. As a result, individual states will not be able to effectively manage the population in isolation, as they will only be managing a part of the individuals' range, and any threat to these species in one jurisdiction will therefore represent a threat in others. As such, local governments should consider working towards drafting international agreements governing management of sperm whales as a cross-border species of concern.

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