Population estimate and inter-island movement of sperm whales, *Physeter macrocephalus*, in the Eastern Caribbean

SHANE GERO[1], JONATHAN GORDON[2], CAROLE CARLSON[3], PETER EVANS[4] AND HAL WHITEHEAD[1]

[1]*Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada*
[2]*Sea Mammal Research Unit, University of Saint Andrews, Fife, Scotland*
[3]*Provincetown, Massachusetts, USA*
[4]*Sea Watch Foundation, 11 Jersey Road, Oxford, UK*
Contact email: sgero@dal.ca

ABSTRACT

When a population extends across international boundaries management becomes more complex. This is especially true within a confined multinational area like the Caribbean Sea. Here we estimate the population size of sperm whales in the Eastern Caribbean and quantify the inter-island movements of individuals using a database of 1394 photographic identifications taken between 1984 and 2006 through the collaborative efforts of four research groups. A total of 194 individual sperm whales were identified off the leeward coasts of the Commonwealth of Dominica, Guadeloupe, Grenada, St. Lucia, and Martinique. The population size was estimated using two-component finite mixture models. About 94 (95% confidence interval. 75-126) sperm whales used Lesser Antillean waters in 1995 and this population appears to be growing slowly. There are differences amongst the individuals in their probability of identification. Of all individuals, 57 (29.4%) were identified in more than one year between 1995 and 2006. Long-term reidentification of associated females suggests that social units may be using the area for periods of at least 11 years. We made 27 confirmed matches between islands, the majority (92.6%) of which were between Guadeloupe and Dominica. Two longer movements by single individuals were confirmed between Dominica and the islands of St. Lucia and Grenada. High reidentification rates and no exchange between neighbouring seas suggest the population in the Eastern Caribbean Sea is small and quite isolated.

INTRODUCTION

An animal's movements are important to several facets of its biology, including behaviour, population structure, and conservation (Turchin, 1998; Whitehead, 2001). To effectively manage and conserve a nomadic species a good understanding of its modal and exceptional movements is needed over a range of temporal and spatial scales (Dufault *et al.*, 1999). As nations differ in their political, economic, and social attitudes to conservation, when animals move between national jurisdictions or if a population is spread across international boundaries management becomes more complex.

Cetacean species operate over relatively larger spatial (Stone *et al.*, 1990) and temporal (George *et al.*, 1999) scales than do most other mammalian species. As a result movements of cetaceans have often been a complicating issue when managing their populations (Donovan, 1991). This is especially true within a confined multinational area, such as the Caribbean Sea, where movements between countries is likely even for species whose movements are far from extreme. For such species it is important to gain and understanding of how many animals are present, how often they move between national jurisdictions, and how long animals are likely to stay within them. This information allows management decisions to be applied over biologically or culturally (Whitehead *et al.*, 2004) appropriate scales rather than be based on biologically arbitrary national boundaries.

The sperm whale (*Physeter macrocephalus*, Linnaeus, 1758) is a highly mobile species which inhabits the Caribbean Sea and is likely to move between islands and political jurisdictions. Over short time periods, of several hours to days, sperm whale movements are generally thought to be based on the need for food (Whitehead, 2003). When feeding success (determined by defecation rates) is good animals will remain in one area for longer periods than when feeding conditions are poor (Jaquet and Whitehead, 1999; Whitehead, 2003; Whitehead and Rendell, 2004).

Over longer time periods, it has been shown that movement patterns differ among the sexes as well as among clans of sperm whales. Mature male sperm whales travel large distances in moving from their high latitude feeding grounds to the breeding grounds in the tropical and subtropical waters and may even move between ocean basins (Dufault *et al.*, 1999; Whitehead, 2003). Females and immatures, which live in social units of often matrilineally related individuals (Richard *et al.* 1996; Lyrholm and Gyllensten 1998; Mesnick 2001; Mesnick *et al.* 2003), regularly travel over ranges spanning 1000 to 1500 km while remaining in tropical and subtropical waters year round (Dufault and Whitehead, 1995; Whitehead, 2003). In an extreme case, the same female sperm whales have been identified in two study areas 3500km apart, indicating movements from the Galapagos Islands to the Gulf of California (Jaquet *et al.*, 2003).

Different social units of sperm whales produce different repertoires of vocalizations which allow researchers to categorize units into acoustic clans (Rendell and Whitehead, 2003). Whitehead and Rendell (2004) showed that sperm whales in different clans exhibited different habitat-use and movement patterns suggesting that culture also impacts the movements of sperm whales.

Photo-identification of individual sperm whales has proved to be effective in describing the movements of individuals within a number of field sites (Whitehead, 1996; Gordon *et al.*, 1998; Jaquet and Whitehead, 1999; Whitehead, 2001; Jaquet *et al.*, 2003; Rendell *et al.*, 2004; Whitehead and Rendell, 2004). However only a few studies have examined movements between sites for sperm whales (Coakes, 2003; Jaquet *et al.*, 2003). While small scale studies provide more accurate data on distribution and abundance within a particular field site, the pooling of identification data from a multitude of projects provides a relatively economical way of achieving a large data set over an extended area (e.g. Calambokidis *et al.*, 2001). Here we provide a population estimate for a region for which none was previously available and quantify the inter-island movements of individuals through a collaborative effort of four research groups based on photographic identifications taken between 1984 and 2006.

METHODS

Data Set

The data set consists of 1394 high quality (Q≥3; (Arnbom, 1987) photographic individual identifications of mature male, female, or immature sperm whales (calves were excluded) collected from waters adjacent to five Caribbean islands (Commonwealth of Dominica, Guadeloupe, Grenada, St. Lucia, and Martinique) in the Eastern Caribbean Sea between 1984 and 2006 (Table 1). The data set is made up of all photographs available from the Eastern Caribbean region in the North Atlantic and Mediterranean Sperm Whale Catalogue (NAMSC), curated by the International Fund for Animal Welfare (IFAW). An additional 439 identifications taken in the Sargasso Sea from May to June in both 2004 and 2005 were included in order to investigate movement between the two Seas.

Field Methods

As the data were collected from several organizations across 22 years, field methods varied among the projects. Field methods were of two types distinguished based on platform: research vessels dedicated to sperm whale research including photoidentification and photoidentifications collected from whale watch vessels. The 1984 data were collected while aboard the Ocean Research and Education Societies' vessel *R/V Rambler*. Photos were collected opportunistically and animals were not actively followed. The IFAW data from 1995 and 1996 (Gordon *et al.*, 1998) as with the data from Dalhousie University data from the Sargasso Sea in 2004 and 2005 as well as the Eastern Caribbean Sea in 2005 (Gero, 2005), were collected while groups of female and immature sperm whales were being actively located and followed twenty-four hours a day both acoustically, using a directional and towed hydrophone, and visually, by observers on dedicated auxiliary sailing vessels. The exceptions are the data collected in St. Lucia and Martinique, which were taken by the Dalhousie research vessel while in transit from Dominica to St. Lucia near the end of the field season. A small number of photographs were collected opportunistically aboard motorized catamaran whale watch vessels equipped with omnidirectional hydrophones while Peter Evans was in Dominica running a Multiple Land Use Project. Identifications collected by Association Evasion Tropical between 2000 and 2003 and by Dalhousie University while in Guadeloupe in 2004 were taken from the Association's whale watch auxiliary sailing vessel which actively searched for sperm whales using a directional hydrophone. Finally, the 2006 data from Dominica were collected while on daily trips aboard a motorized catamaran whale watch vessel also actively searching for whales using an omnidirectional hydrophone. Supplementary data, such as the age/sex class (as age/sex classification was completed in the field based on size, adult females and immatures are lumped as it is difficult to sex animals in the field, as

such only two age/sex classes are used: mature male, and adult female or immature) of the animal identified, the exact date and time of the identification, and information about associations, was only readily available for fieldwork completed by the Dalhousie University and IFAW groups.

Table 1
Details of the field projects and identifications (Q≥3) of sperm whales included in this synthesis for the Eastern Caribbean Sea.

Dates	Nearest Island	Project Leader	Research Group	Field Method	# of Photos	Individuals Identified
1984	Commonwealth of Dominica	Hal Whitehead	Dalhousie University	Dedicated vessel	18	13
1995	Commonwealth of Dominica	Jonathan Gordon	International Fund for Animal Welfare	Dedicated vessel	218	59
1995	Grenada	Jonathan Gordon	International Fund for Animal Welfare	Dedicated vessel	6	5
1996	Commonwealth of Dominica	Jonathan Gordon	International Fund for Animal Welfare	Dedicated vessel	81	35
1999	Commonwealth of Dominica	Peter Evans	Sea Watch Foundation	Whale watch	7	6
2000	Guadeloupe	Carole Carlson	International Fund for Animal Welfare	Dedicated vessel	7	6
2000	Guadeloupe	Renato and Caroline Rinaldi	Association Evasion Tropicale	Whale watch	9	8
2001	Guadeloupe	Renato and Caroline Rinaldi	Association Evasion Tropicale	Whale watch	17	15
2002	Guadeloupe	Renato and Caroline Rinaldi	Association Evasion Tropicale	Whale watch	11	9
2003	Guadeloupe	Renato and Caroline Rinaldi	Association Evasion Tropicale	Whale watch	23	22
Feb - Mar 2004	Guadeloupe	Shane Gero	Dalhousie University	Whale watch	23	22
Jan – Apr 2005	Commonwealth of Dominica	Hal Whitehead/ Shane Gero	Dalhousie University	Dedicated vessel	812	53
Mar 10 2005	Martinique	Hal Whitehead/ Shane Gero	Dalhousie University	Dedicated vessel	16	7
Mar 20 2005	St. Lucia	Hal Whitehead/ Shane Gero	Dalhousie University	Dedicated vessel	3	3
Jan – Feb 2006	Commonwealth of Dominica	Shane Gero	Dalhousie University	Whale watch	143	25
May– Jun 2004	Sargasso Sea	Hal Whitehead/ Shane Gero	Dalhousie University	Dedicated vessel	376	104
May– Jun 2005	Sargasso Sea	Hal Whitehead/ Shane Gero	Dalhousie University	Dedicated vessel	63	57

Analyses

Individual identifications

A quality rating (Q) between 1 and 5 was given to each photograph, where 1 indicated a very poor photograph, and 5 indicated a very high quality photograph (Arnbom, 1987; Dufault and Whitehead, 1993). The Q-value was a function of the attributes of the photograph (focus, exposure, angle of fluke relative to the negative plane, angle between the axis of the fluke and the surface of the water, and the proportion of the frame filled by the fluke) but not the quality of the markings on the fluke (Arnbom, 1987; Dufault and Whitehead, 1993). This method assumes that all animals are adequately marked for the analysis (Dufault and Whitehead, 1993). Only pictures with a Q≥3 were used for the analyses. Pictures for each individual were matched within and between years, between islands and between Seas using a computer-based matching program (Whitehead, 1990).

Based on these identifications, two discovery curves were produced, as well as a map showing the number of individuals identified off each island and the number of confirmed matches between islands. The discovery curves were plotted of the number of identified individuals against the cumulative number of identifications (with only one identification per day per individual) and against date. These plots give an indication at what point individuals have entered the data set and what proportion of the population have been identified.

Population estimate

Assessments of the population of reliably marked individuals using Lesser Antillean waters were made with a variety of population models. To incorporate the possibility of heterogeneity in either mortality or identification rate (variability in the probability of recapture), two-component finite mixture models were constructed following the methods of Pledger *et al.* (Pledger *et al.*, 2003) and Whitehead & Wimmer (Whitehead and Wimmer, 2005). The models condition on the first identification of each individual, and assume overall identification rates in each year j of n_j/N_j (the number of animals identified during the year divided by the estimated population size that year, as in Seber 1982: 557). Heterogeneity is incorporated by having two classes of individual (A and B) which may have different identification and/or mortality rates. The population can also increase or decrease at a constant rate per year. Thus the full model has the following parameters: N_M, population of individuals using the study at mid-point of sampling (1995); r proportional rate of increase in population per year; α, proportion of population in class A (with 1-α in class B); β, ratio of identifiability of class B animals compared with class A animals; δ_A, mortality rate of class A animals per year; δ_B, mortality rate of class B animals per year.

Simpler models were investigated by using the following restrictions, or combinations of them: $r = 0$, no trend; $\alpha = 1$, no heterogeneity; $\beta = 1$, no heterogeneity in identification; $\delta_A = \delta_B$, no heterogeneity in mortality; $\delta_A = \delta_B = 0$, $\alpha = 1$, $r = 0$, closed, homogeneous population. The models examined are listed (Table 4).

Support for the different models was compared using the Akaike Information Criterion (AIC), with the lowest AIC indicating the preferred model (Burnham and Anderson, 2002), and the difference between the AIC of any model and the best fitting,)AIC, indicating the relative support for a model, compared with best. Parameter estimates were calculated using likelihood methods, and approximate confidence intervals using the bootstrap method with 1,000 replicates.

RESULTS

A total of 194 individual sperm whales were identified off the coast of the five islands in the Eastern Caribbean. The number of individuals identified off each island corresponds to the amount of effort within those waters, such that more individuals were identified where more pictures were taken. The discovery curves (Fig. 1) continue to show an upward trend as new individuals are identified with additional effort.

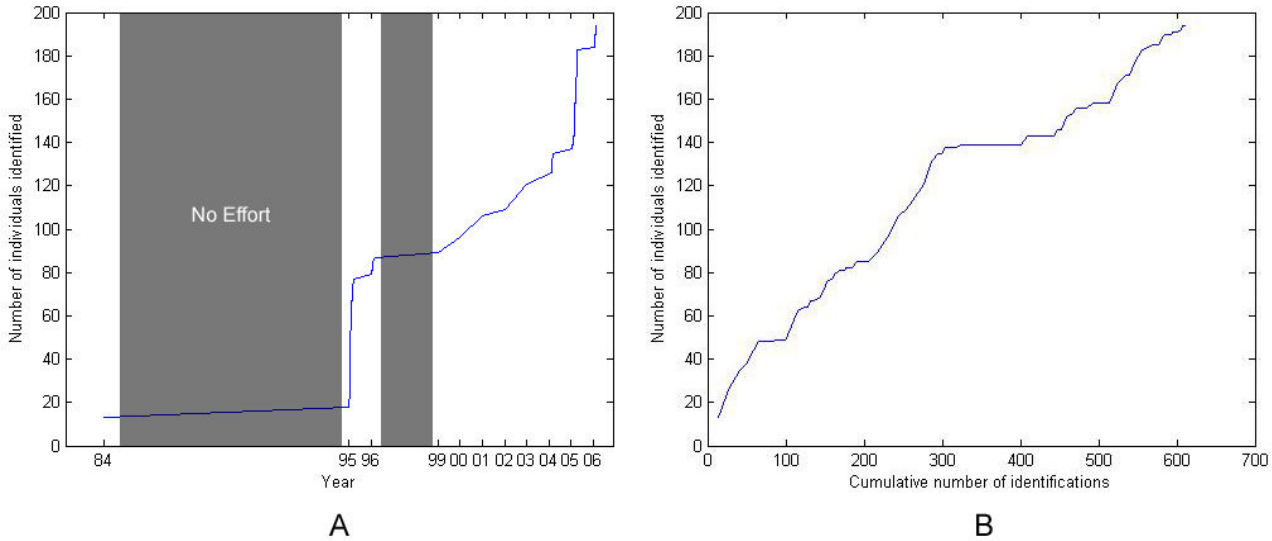

Fig. 1. Discovery curves plotting number of individuals identified by year (A) and by cumulative identifications (B).

Identifications between years

A summary of confirmed reidentifications between years is found in Table 2. None of the animals identified in 1984 were identified in later years. Of the 194 individuals identified, 57 were reidentified in different years between 2 and 5 times between 1995 and 2006. The longest period between an individual's identification and its subsequent reidentification was 9 years.

Following the pattern of identification of long-term companions in the Galapagos/Ecuador area (Whitehead *et al.*, 1991; Christal *et al.*, 1998), we looked for sets of animals identified between years. Eighteen sets of animals were identified across years (Table 3, following page). Of the 18 associates reidentified, only 4 were over longer time scales than one year. In one case, all five adult females (ID# 5130, 5560, 5561, 5563, 5722) of a well studied social unit, dubbed 'the Group of Seven' (Appendix 1; Gero, 2005), were observed together off the coast of Dominica on 14 different days in 1995 and 1996, three were reidentified in 2001 off the coast of Guadeloupe (association data were not available for the 2001 dataset), and were then reidentified in 2005 and 2006 off Dominica along with a juvenile male (ID# 5727) and a male calf (gender determined using sloughed skin in an ongoing genetic analysis; D. Engelhaupt, unpublished data). Two individuals (ID# 5151, 5562) were identified in 1995 and were subsequently associated in 1996 and again 2004. Another set of animals (ID# 5143, 5150) identified first in 1996 was later identified in 2004. Finally, a pair of animals (ID# 5756, 5757) was identified together every year between 2004 and 2006.

Table 2

Observed reidentifications of individual sperm whales in the Eastern Caribbean including waters off of the Commonwealth of Dominica, Guadeloupe, Grenada, Martinique, and St. Lucia between 1984 and 2006. *Note*: the numbers of identified individuals in each year are given along the diagonal

	1984	**1995**	**1996**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
1984	13	0	0	0	0	0	0	0	0	0	0
1995	0	64	25	2	6	5	4	6	3	7	5
1996	0	25	35	3	0	2	3	4	4	7	5
1999	0	2	3	6	0	0	0	0	1	1	1
2000	0	6	0	0	13	0	0	2	2	0	0
2001	0	5	2	0	0	15	3	4	2	5	0
2002	0	4	3	0	0	3	9	1	2	2	0
2003	0	6	4	0	2	4	1	22	4	1	0
2004	0	3	4	1	2	2	2	4	22	4	4
2005	0	7	7	1	0	5	2	1	4	63	13
2006	0	5	5	1	0	0	0	0	4	13	25

Table 3
Sets of individuals identified together across years. Individuals were considered associated if they were identified on the same day. Only data from the IFAW and Dalhousie research groups, for which association data were available, were considered for this analysis.

	First Identification		Second Identification		Third Identification		Fourth Identification	
IDS	**Year**	**Island**	**Year**	**Island**	**Year**	**Island**	**Year**	**Island**
5583, 5964	1995	Dominica	1996	Dominica				
5579, 5585	1995	Dominica	1996	Dominica				
5555, 5559	1995	Dominica	1996	Dominica				
5142, 5559	1995	Dominica	1996	Dominica				
5550, 5554	1995	Dominica	1996	Dominica				
5144, 5554	1995	Dominica	1996	Dominica				
5146, 5550	1995	Dominica	1996	Dominica				
5550, 5722	1995	Dominica	1996	Dominica				
5151, 5564, 5571, 5579, 5722	1995	Dominica	1996	Dominica				
5151, 5562, 5564 5130, 5560, 5561, 5722	1995	Dominica	1996	Dominica				
5130, 5560, 5561, 5563, 5722	1995	Dominica	1996	Dominica	2005	Dominica		
5560, 5561, 5563, 5722	1995	Dominica	1996	Dominica	2005	Dominica	2006	Dominica
5560, 5561,5563, 5722, 5727	2005	Dominica	2006	Dominica				
5563, 5726	2005	Dominica	2006	Dominica				
5151, 5562	1995	Dominica	1996	Dominica	2004	Guadeloupe		
5143, 5150	1996	Dominica	2004	Guadeloupe				
5752, 5753	2005	Dominica	2006	Dominica				
5753, 5757	2005	Dominica	2006	Dominica				
5755, 5756, 5757	2004	Guadeloupe	2005	Dominica				
5756, 5757	2004	Guadeloupe	2005	Dominica	2006	Dominica		

Identifications between islands and seas

The total number of individuals identified, along with the total number of identifications, in the waters off of each island is shown in figure 2. Movements between islands are shown as arrows on the map of the Eastern Caribbean (Fig. 2), along with the number of confirmed inter-island matches. We made 27 confirmed matches between islands. The majority (92.6%) of these were between the neighbouring islands of Guadeloupe and Dominica (the islands for which effort was highest). Of the individuals which moved between Dominica and Guadeloupe for which age/sex data were available (13 of the 25 individuals), all were adult females or immatures. No matches were made between Dominica and its neighbouring island to the south, Martinique. Four sets of animals were identified together in one year off the coast of one island and then in another year off another. In all cases, the islands were Dominica and Guadeloupe as only single animals were identified between non-neighbouring islands.

Two longer movements by single individuals between non-neighbouring islands were confirmed between Dominica and the islands of St. Lucia and Grenada (Fig. 2). An adult female or immature animal was observed off the coast of Dominica in 1995 then reidentified off of St. Lucia in 2005. No class data was available for the animal which was identified in 1995 off Dominica and then again off Grenada 15 days later.

No matches were made between the identifications in the Caribbean Sea and the Sargasso Sea to the north separating Bermuda from the Lesser Antilles. It is also important to note that no matches were made between years within the Sargasso Sea.

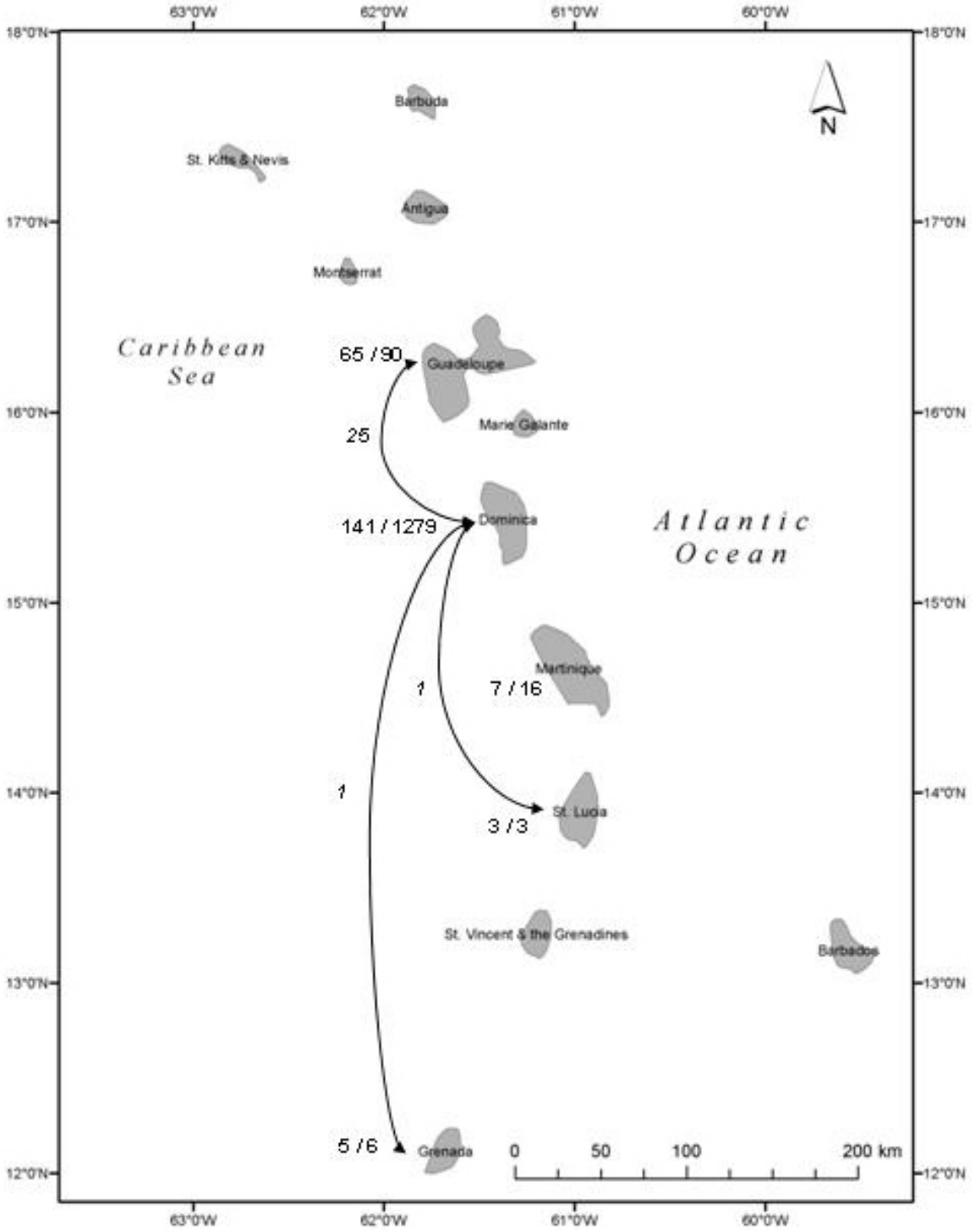

Fig. 2. Movements of identified sperm whales (Q≥3) in the Eastern Caribbean. Bold numbers indicate the number of individuals and the number of identifications separated by a slash and the italic numbers indicate the number of whales moving between islands.

Population size

Using methods as in Whitehead and Wimmer (2005), we estimated the population of sperm whales in the Eastern Caribbean Sea to have been approximately 94 individuals in 1995, the mid-point of the time period for which identifications were available.

AIC indicated that the heterogeneity in identifiability (variability in the probability of recapture) plus trend model is best supported by the data (Table 4). The model without heterogeneity in identifiability but including mortality and a trend is also quite well supported. There is little evidence that heterogeneity in mortality is a large factor in the identification history, but mortality itself and a trend in population size are well supported by the data, and heterogeneity in identifiability seems to be present. The most general model seems to fit the data well (observed and expected distributions of the number of years in which individuals were identified are not significantly different; =2.19; 4 d.f.; p=0.70), suggesting a variance inflation factor less than 1.0, and so no need to use the quasi-likelihood version of AIC for overdispersed count data (Burnham & Anderson 2002, p. 69).

Using the best supported model, the estimated population size using the Lesser Antillean waters in 1995 was N_M=93.8(95% c.i. 75.2-125.7), the estimated rate of mortality plus emigration plus mark change was δ=0.119/yr (95% c.i. 0.075-0.175), the estimated trend in the population size was r=+0.104/yr (95% c.i. 0.047-0.173), and the estimated proportion of low-identifiability individuals in the population at any time was α=0.28 (95% c.i. 0.06-0.47), with the high-identifiability individuals being identified at a rate β=20.8 times (95% c.i. 18.7-21.5) greater than the low identifiability individuals. As female sperm whale move around in fairly permanent social units (Whitehead, 2003), the bootstrap method is theoretically invalid because of non-independence, so the indicated confidence intervals are probably somewhat too narrow. A rough-and-ready alternative in such situations is the temporal jackknife in which annual sets of data are omitted in turn when calculating pseudovalues (Whitehead, 2001) but this did not work on this data set because of the very uneven annual identification effort.

As Pledger *et al.* (2003) and Whitehead & Wimmer (2005) note, two-component mixture models fit well to data with heterogeneity of more than two classes. Thus the parameter estimates relating to the two supposed classes of sperm whale should not be taken literally. Rather the analysis indicates that there are differences among the sperm whales using the Eastern Caribbean in their probability of identification in studies based primarily around Dominica and Guadeloupe.

Table 4

Summary of population models fitted to photoidentification data. AIC (Akaike Information Criterion) is given for each model. The lowest AIC, indicating the best fit to the data, is starred, and the)AIC gives the difference between the AIC for a model and that of the best model. The final column indicates qualitatively the support for the model based upon)AIC using the criteria of Burnham and Anderson (p. 70)

Model	**Closed?**	**Trend?**	**Heterogeneity in:**				
	$\delta_A = \delta_B = 0$ $\alpha = 1, r = 0$	$r \neq 0$	Identifiability? $\beta \neq 1$	Mortality? $\delta_A \neq \delta_B$	AIC	)AIC	Support for model
Closed (Schnabel)	Yes	No	No	No	624.16	80.16	None
Mortality	No	No	No	No	558.35	14.35	Very little
Mortality + trend	No	Yes	No	No	549.47	5.47	Little
Heterogeneity in mortality	No	No	No	Yes	559.03	15.03	Almost none
Heterogeneity in mortality + trend	No	Yes	No	Yes	550.24	6.24	Little
Heterogeneity in identifiability	No	No	Yes	No	556.39	12.39	Almost none

Heterogeneity in identifiability + trend	No	Yes	Yes	No	544.00*	0	Yes
Heterogeneity in mortality & identifiability	No	No	Yes	Yes	557.26	13.26	Almost none
Full: Heterogeneity in mortality & identifiability + trend	No	Yes	Yes	Yes	548.98	4.98	Little

DISCUSSION

It is apparent from figure 2 that individuals and potentially associated sets of animals do move across the entire area of the Eastern Caribbean for which data were available, a linear distance of 460km. Furthermore, given that the photographs were collected opportunistically and not systematically throughout the region, it is likely that not all individuals in a given area were identified making the actual number of inter-island movements higher than those reported here. As such, continued sampling in this area, and from different islands, should be encouraged. Although these data are sparse, and effort differed between sites and among years, the information provided by this multinational collaboration is consistent with patterns of social organization and movement reported elsewhere.

Slightly less than 30% of the individuals were reidentified in more than one year. This is a relatively high reidentification rate. Although Gordon *et al.* (1998) had a reidentification rate between years of more than 50% off Dominica, a reidentification rate of only 12.1% of 'medium-sized whales' (likely indicative of females and immatures) was reported for the Galapagos Islands (Whitehead, 1993) and of about 18% for 'females' and 6% for 'others' off the Azores (Matthews *et al.*, 2001). Repeated identification of sets of associated individuals suggests that social units of female and immature sperm whales may use this area over periods of at least 11 years. In a particularly detailed case, a core set of 5 adult females (Appendix 1) were identified associated with several other animals with lags of up to one year (1995 to 1996), but later identified together without those associates (2005 and 2006). These findings are consistent with the current model of sperm whale social structure (Whitehead *et al.*, 1991), although it is difficult to determine whether these associates were unit members who have since died or members of another social unit with which the first is preferentially grouped, as units tend to group with units of their own clan (Whitehead, 2003).

The confirmed inter-island movements are also consistent with current knowledge. Sperm whales are thought to cover distances much greater than the roughly 460km between the islands of Guadeloupe and Grenada as units of females and immatures forage within ranges spanning 1000 to 1500 km (Dufault and Whitehead, 1995; Whitehead, 2003). Sperm whales have been estimated to be able to travel at average speeds of about 4km/h (Gordon, 1987; Whitehead, 1989; Whitehead *et al.*, 1992; Watkins *et al.*, 1999) whether at the surface or at depth foraging, but are thought to be able to sustain speeds up to 18-22km/h over several minutes (Caldwell *et al.*, 1966). Although sperm whales may potentially cover as much as 96km/d (4km/h * 24h/d), Whitehead (2001) estimated root-mean-squared displacement to be approximately 50km/d based on a likelihood movement analysis on opportunistic sperm whale identification data from the Pacific. Either value would allow for animals to cover the distance between any of the five islands included in this analysis within a matter of days.

From a management perspective, it is interesting that no matches were made between any of the identifications in the Caribbean Sea and those made in the Sargasso Sea, immediately to the north (similarly there have been no matches with the Gulf of Mexico to the West; J.Gordon and N.Jaquet, pers. comm.). The sperm whales of the North Atlantic are considered a single stock (Donovan, 1991) primarily due to a single confirmed recapture of a male tagged off Nova Scotia and later killed off Spain (Mitchell, 1975) and two findings linking males in the Azores to Spain and Iceland (Martin, 1982; Aguilar, 1985). While males may be wide ranging (Dufault *et al.*, 1999; Whitehead, 2003), social units of females and immatures appear to have much more confined home ranges (Dufault and Whitehead, 1995; Whitehead, 2003), and thus it is the ranging patterns and habitat-use of the female and immature component of the population which is relevant for management and conservation. Our findings contradict the current stock

classification for the female and immature component of the population and suggest that the small Caribbean population, estimated here to be approximately 94 individuals (95% confidence interval. 75-126) in 1995, is somewhat segregated from the once heavily hunted Sargasso population (Maury, 1852; Townsend, 1935). No reidentifications between years suggest that the Sargasso population is larger and perhaps more wide ranging. If interchange between the seas is minimal, reidentification within the Caribbean is high, and preliminary results find no evidence of that Caribbean clan occurring anywhere else in the North Atlantic (L. Rendell, unpublished data), it suggests that animals in the Caribbean are able to successfully exploit the resources available in a smaller range restricted to the Lesser Antilles making movement between seas unnecessary. Previous studies support this hypothesis suggesting that foraging strategy is culturally inherited (Whitehead and Rendell, 2004), that animals which are feeding successfully (using defecation rate as a proxy) cover less ground when foraging (Whitehead, 1996; Whitehead and Rendell, 2004) and that the animals in the Eastern Caribbean are foraging more successfully than those in the Sargasso (Gero, 2005).

As such, the conservation and management of sperm whales in the Eastern Caribbean should be considered on a multi-island basis. Protocols concerning specially protected areas and wildlife in the Wider Caribbean Area (SPAW Protocol) have already been established by the United Nations Environment Programme (UNEP). Under this agreement, parties recognize that the Caribbean islands are interconnected ecosystems in which an environmental threat in one part represents a potential threat in other parts, and stresses the importance of establishing regional co-operation to protect marine species and their habitats in the Wider Caribbean Region (UNEP, 2006). Of the five islands included in this study, only three have ratified this agreement (Guadeloupe and Martinique under France in 2002, and St Lucia in 2000). Dominica and Grenada have neither signed nor ratified these protocols. With whale watching growing as a business on all of these islands, neighbouring islands, in particular Dominica and Guadeloupe, have a vested interest in jointly protecting this shared population of sperm whales and lobbying their neighbours to ratify and meet international treaty commitments, such as the SPAW protocols.

These models indicate that the animals differ in their identifiability (variability in the probability of recapture). Heterogeneity of capture by differences in movement patterns based on sex, clan membership, and behaviour affect population estimates. Typically, heterogeneity of photographic capture appears only to be a small problem between female and immature sperm whales, although younger animals tend to be identified less often (Whitehead, 2001). It is likely that the lack of sex class information for much of the data, and the inclusion of males in the analysis, has resulted in an increase in heterogeneity of identification. Differences of range use by females of the eastern Caribbean are also likely to have contributed towards the heterogeneity in identification. Although Gordon *et al.* (1998) suggest that some large males have been reidentified between years off Dominica, it is still unknown if males return to the same area year after year (Whitehead, 2003). We need consistent photoidentification effort from several islands to investigate range use.

The models also suggest that the Eastern Caribbean population is growing. While this is encouraging, it should be considered a tentative result, as there has been no study of the robustness of estimates of rates of population change in mixture model mark-recapture estimates (in contrast to population size and mortality rate; Whitehead & Wimmer 2005), and aspects of data structure might affect estimates of rates of population change.

CONCLUSIONS

Defining sperm whale stocks is a complex task as this species is highly mobile (Jaquet *et al.*, 2003), sexually segregated (Whitehead, 2003), shows little genetic differentiation within an ocean basin (Lyrholm *et al.*, 1996; Lyrholm and Gyllensten, 1998; Dufault *et al.*, 1999; Mesnick, 2001), and has socially and culturally complex behaviour and movement patterns (summarized in Whitehead, 2003). With an increase in the proportion of sperm whale habitat for which there are population estimates and a better understanding of sperm whale movements, stock definitions can be refined. Here we provide an estimate for a region for which none was previously available and show that movement between national boundaries within the Caribbean Sea is common, but that movement between adjacent seas may not be; such that management of this species should be considered on a co-operative, multi-national basis across the Caribbean area.

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APPENDIX 1: Identification photographs of the 'Group of Seven', the most commonly sighted social unit. These animals were resighted over an 11 year period both off of Guadeloupe (2001) and Dominica (1995, 1996, 2005, 2006)