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

SHANE GERO+, JONATHAN GORDON*, CAROLE CARLSON#, PETER EVANS** AND HAL WHITEHEAD+

Contact e-mail: sgero@dal.ca

ABSTRACT

When a population extends across international boundaries, management becomes more complex. This is especially true within a confined multinational area such as the Caribbean Sea. The population size of sperm whales in the Eastern Caribbean is estimated and the inter-island movements of individuals are quantified using a database of 1,394 photographic identifications taken between 1984 and 2006 by several research groups. A total of 194 individual sperm whales were identified off the leeward coasts of the islands of Dominica, Guadeloupe, Grenada, St. Lucia and Martinique. Population size was estimated using two-component finite mixture models. About 145 (95% CI=94-219) 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 during 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. Twenty seven confirmed matches were made between islands, the majority (92.6%) of which were between Guadeloupe and Dominica, although there were two longer movements by single individuals between Dominica and the islands of St. Lucia and Grenada. High reidentification rates within the Lesser Antilles and no matches with identifications from nearby seas suggest the population in the Eastern Caribbean Sea is small and quite isolated. As such, we recommend that management actions be taken on a multi-island basis for the Eastern Caribbean, by encouraging the ratification of the SPAW protocols and that the current stock classification for the North Atlantic be reconsidered.

KEYWORDS: ABUNDANCE ESTIMATE; MOVEMENTS; SPERM WHALE; CARIBBEAN SEA; PHOTO-ID; MODELLING; MANAGEMENT; STOCK IDENTITY

INTRODUCTION

An animal's movements are important to several facets of its biology, including behaviour, population structure and conservation (Turchin 1998; Whitehead, 2001a). 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 towards conservation, when animals move between national jurisdictions or if a population is spread across international boundaries, management of the human activities that affect their conservation are made 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 and stock structure considerations have often been a complicating issue with respect to conservation and management (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 an understanding of how many animals are present, how often they move between national jurisdictions and how long animals are likely to remain within each. This information allows management decisions to be applied over biologically or culturally (discussed in Whitehead *et al*., 2004) appropriate scales rather than being 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 availability of 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 larger temporal and spatial scales, 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 (Lyrholm and Gyllensten, 1998; Mesnick, 2001; Mesnick *et al*., 2003; Richard *et al*., 1996), regularly travel over ranges spanning 1,000 to 1,500km while remaining in tropical and subtropical waters year round (Dufault and Whitehead, 1995b; Whitehead, 2003). In an extreme case, the same female sperm whales have been identified moving from the Galapagos Islands to the Gulf of California which are 3,500km apart (Jaquet *et al*., 2003).

Different social units of sperm whales produce different repertoires of vocalisations which allow researchers to categorise 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 for describing the movements of individuals in a number of areas (Gordon *et al*., 1998; Jaquet

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+ *Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada.*
* *Sea Mammal Research Unit, University of Saint Andrews, Fife, Scotland.*
\# *College of the Atlantic, Bar Habour, Maine, USA.*
** *Sea Watch Foundation, 11 Jersey Road, Oxford, UK.*

et al., 2003; Jaquet and Whitehead, 1999; Rendell *et al*., 2004; Whitehead, 1996;2001a; Whitehead and Rendell, 2004). However, only a few studies have examined sperm whale movement at large scales (Coakes, 2003; Jaquet *et al*., 2003; Whitehead, 2003). While small scale studies provide useful data on distribution and abundance within a particular area, 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).

Photo-identification also provides a powerful tool for estimating the abundance of whale populations when input into mark-recapture techniques (e.g. Hammond, 1986). In order to infer population parameters, most photographic mark-recapture analyses use likelihood techniques, or approximations of them, to find those parameter values most consistent with the temporal pattern of individual identifications, given an assumed population model. Some potential pitfalls exist when applying these methods to the study of live sperm whales. Issues such as mark loss (low in sperm whales; Childerhouse *et al*., 1996; Dufault and Whitehead, 1995a), mortality, geographic spreads of photo identification and whale movement (Cooke, 1986a;1986b) may inflate the population estimate; while heterogeneity reduces the estimate. Heterogeneity occurs when animals differ in their probability of identification due to variations in movement patterns or behaviour. Heterogeneity within female/immature social units appears to be only a small problem (Whitehead, 2001b), but units might differ considerably in their identifiability. Newer and more complex mark-recapture models attempt to account for some of these difficulties. Previous studies have successfully applied mark-recapture methods using photo-identifications to sperm whale populations in several areas (Childerhouse *et al*., 1995; Matthews *et al*., 2001; Whitehead *et al*., 1997; Whitehead *et al*., 1992).

Given the multinational nature of the Eastern Caribbean region, some aspects of the conservation and protection of sperm whales might better 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 recognise that the Caribbean islands are interconnected ecosystems in which an environmental threat in one part represents a potential threat in other parts and stress the importance of establishing regional cooperation to protect marine species and their habitats in the Wider Caribbean Region (UNEP, 2005). Here a population estimate is provided using mark-recapture techniques for a region for which none was previously available and inter-island movements of individuals are identified through a collaborative photo-identification effort of several research groups in an attempt to investigate whether management should be considered on a multi-island basis. This study provides some quantitative support for the arguments to ratify the SPAW protocol.

METHODS

Field methods

As the data were collected from several organisations across 22 years, field methods varied among the projects. Photo-identifications were taken from two main types of study, which were distinguished based on the platform used: identifications collected from research vessels dedicated to sperm whale research and opportunistic identifications taken from whalewatching vessels. The 1984 data were collected while aboard the Ocean Research and Education Society's vessel *R/V Rambler*. Photographs were collected opportunistically and animals were not actively followed. The International Fund for Animal Welfare (IFAW) data from 1995 and 1996 (Gordon *et al*., 1998), the 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 24 hours a day both acoustically, using directional and towed hydrophones, and visually by observers, using dedicated auxiliary sailing vessels. The exceptions were the data collected off 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 motorised catamaran whalewatching 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 whalewatching 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 motorised catamaran whalewatching vessel also actively searching for whales using an omnidirectional hydrophone. Supplementary data, such as the age/sex class of the animal identified, the exact date and time of the identification and information about social associations, were only readily available for fieldwork completed by the Dalhousie University and IFAW groups.

Data set

The data set consisted of 1,394 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 (Dominica, Guadeloupe, Grenada, St. Lucia, and Martinique) in the Eastern Caribbean Sea between 1984 and 2006 (Table 1). The data set was made up of all photographs available from the Eastern Caribbean region in the North Atlantic and Mediterranean Sperm Whale Catalogue (NAMSC), curated by IFAW. An additional 439 identifications taken in the Sargasso Sea (roughly 1,800km north of the eastern Caribbean) from May to June in 2004 and 2005 (Gero, 2005) were included in order to investigate movement between the two Seas.

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.

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	No. of photos	Individuals identified
1984	Dominica	George Nichols	Ocean Research and Education Society	Dedicated vessel	18	13
1995	Dominica	Jonathan Gordon	IFAW	Dedicated vessel	218	59
1995	Grenada	Jonathan Gordon	IFAW	Dedicated vessel	6	5
1996	Dominica	Jonathan Gordon	IFAW	Dedicated vessel	81	35
1999	Dominica	Peter Evans	Sea Watch Foundation	Whale watch	7	6
2000	Guadeloupe	Carole Carlson	IFAW	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	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	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

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, a map was constructed showing the number of individuals identified off each island and the number of confirmed matches between islands (Fig. 1).

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*. (2003) and 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, p.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 $1\text{-}\alpha$ 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; and δ_B, mortality rate of class B animals per year.

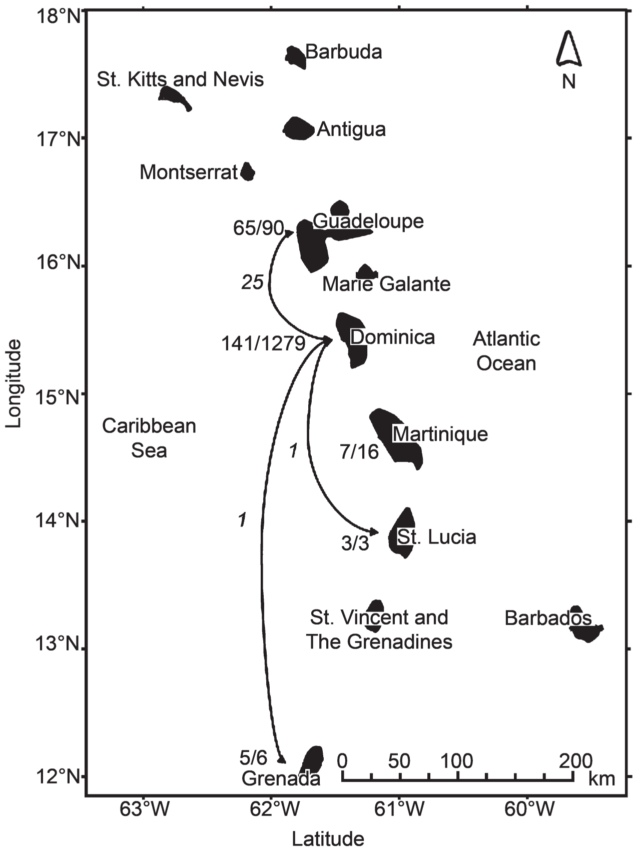

Fig. 1. Movements of identified sperm whales (Q≥3) in the Eastern Caribbean. Bold numbers indicate the number of individuals and the number of identifications separated by a slash and the italic numbers indicate the number of whales moving between islands.

Simpler models were investigated by using the following restrictions, or combinations of them: r=0, no population trend; α=1, no heterogeneity; β=1, no heterogeneity in identification; $\delta_A = \delta_B$, no heterogeneity in mortality; $\delta_A = \delta_B = 0$, α=1, r=0, closed, homogeneous population. The models examined are listed in Table 2.

Support for the different models was assessed using the Akaike Information Criterion (AIC), with the lowest AIC indicating the preferred model (Burnham and Anderson, 2002). The difference between the AIC of any model and the best fitting, ΔAIC, indicates the relative support for a model compared with the best. Parameter estimates were calculated using likelihood methods. A parametric bootstrap, in which 1,000 simulated data sets were produced using the estimated parameters and observed sampling scheme, was used to examine bias and precision in parameter estimates, following the methodology of Whitehead and Wimmer (2005).

RESULTS

A total of 194 individual sperm whales were identified off the five islands in the eastern Caribbean. The number of individuals identified off each island roughly corresponded

Table 2

Summary of population models fitted to photoidentification data. Models are presented in order of increasing AIC (Akaike Information Criterion). The lowest AIC, indicating the best fit to the data, is starred, and ΔAIC gives the difference between the AIC for a model and that of the best model. A ΔAIC less than 2 indicates there is substantial support for the less well fitting model. The final column indicates qualitatively the support for the model based upon ΔAIC using the criteria of Burnham and Anderson (2002, p.70).

	Closed?	Trend?	Heterogeneity in:				
Model	$\delta_A = \delta_B = 0$ $\alpha = 1, r = 0$	$r \neq 0$	Identifiability? $\beta \neq 1$	Mortality? $\delta_A \neq \delta_B$	AIC	ΔAIC	Support for model
Heterogeneity in identifiability + trend	No	Yes	Yes	No	544.00*	0	Yes
Full: Heterogeneity in mortality and identifiability + trend	No	Yes	Yes	Yes	548.98	4.98	Little
Mortality + trend	No	Yes	No	No	549.47	5.47	Little
Heterogeneity in mortality + trend	No	Yes	No	Yes	550.24	6.24	Little
Heterogeneity in identifiability	No	No	Yes	No	556.39	12.39	Very little
Heterogeneity in mortality and identifiability	No	No	Yes	Yes	557.26	13.26	Almost none
Mortality	No	No	No	No	558.35	14.35	Almost none
Heterogeneity in mortality	No	No	No	Yes	559.03	15.03	Almost none
Closed (Schnabel)	Yes	No	No	No	624.16	80.16	None

to the amount of effort within those waters, such that more individuals were identified where more pictures were taken (Table 1).

Identifications between years

A summary of confirmed re-identifications between years is found in Table 3. None of the animals identified in 1984 were identified in later years. Of the 194 individuals identified, 57 were re-identified in different years between 2 and 5 times between 1995 and 2006. Excluding the 1984 study, the longest possible identification span was 11 years (1995-2006), over which time five individuals were re-identified.

Table 3

Observed reidentifications of individual sperm whales in the East Caribbean including waters off 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	13										
1995	0	64									
1996	0	25	35								
1999	0	2	3	6							
2000	0	6	0	0	13						
2001	0	5	2	0	0	15					
2002	0	4	3	0	0	3	9				
2003	0	6	4	0	2	4	1	22			
2004	0	3	4	1	2	2	2	4	22		
2005	0	7	7	1	0	5	2	1	4	63	
2006	0	5	5	1	0	0	0	0	4	13	25
	1984	**1995**	**1996**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**

Following the pattern of identification of long-term companions in the Galapagos/Ecuador area (Christal *et al*., 1998; Whitehead *et al*., 1991), we looked for sets of animals identified with one another between years. Eighteen sets of animals were identified across years (Table 4). Of the 18 associates re-identified, only four were over time scales longer than one year. In one case, all five adult females (ID No. 5130, 5560, 5561, 5563, 5722) of a well studied social unit, dubbed 'the Group of Seven' (Gero, 2005), were observed together off Dominica on 14 different days in 1995 and 1996, three were re-identified in 2001 off the coast of Guadeloupe (association data were not available for the 2001 dataset), and all were then re-identified in 2005 and 2006 off Dominica along with a juvenile male (ID No. 5727) and a male calf (gender determined using sloughed skin in an ongoing genetic analysis; D. Engelhaupt, unpublished data).

Identifications between islands and seas

The total number of individuals identified, along with the total number of identifications, in the waters off each island is shown in Fig. 1. Movements between islands are shown as arrows on the map of the Eastern Caribbean (Fig. 1), along with the number of confirmed inter-island matches. Twenty seven confirmed matches were made 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. 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. 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. 1). An adult female or immature animal was observed off the coast of Dominica in 1995 then re-identified off St. Lucia in 2005. No class data were 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. It is also important to note that no matches were made between years within the Sargasso Sea.

Population size

The results of the two-component finite mixture models are listed in order of best fit in Table 2. The lowest AIC indicated that the heterogeneity in identifiability (variability in the probability of recapture) plus trend model was best supported by the data (Table 2). Although a ΔAIC of <2 has been used as the convention for an indicator of substantial support for a less well fitting model, the full model still had some support, as did the model without heterogeneity in identifiability but including mortality and a trend, and the model with heterogeneity in mortality plus a trend. This same pattern of relative fits of the different models to the

Table 4

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	
ID Nos	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		

data was found when the data for 1984 (collected a decade earlier than any other) were excluded from the analysis. The parameter estimates from the best supported model and the parametric bootstrap estimates of bias and precision are shown in Table 5. Using the best supported model, the estimated population size using the Lesser Antillean waters in 1995 was N_M=93.8. However, the parametric bootstrap analysis suggests that this is biased downwards, after correcting for bias the estimate is 144.7 (95% CI=93.8-218.5). The estimated rate of mortality plus emigration plus mark change was δ=0.094 yr^{-1} (95% CI=0.035-0.169). The estimated trend in the population size was r=+0.157 yr^{-1} (95% CI= −0.119-0.357), so not significantly different from zero. The estimated proportion of low-identifiability individuals in the population, and the ratio of identifiability between the two classes were too imprecise to bear interpretation (Table 5).

As Pledger *et al*. (2003) and Whitehead and Wimmer (2005) noted, 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.

DISCUSSION

The photo-identification analysis conducted here indicates 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 within social units, although younger animals tend to be identified less often (Whitehead, 2001b). 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) found that some large males have been re-identified between years off Dominica, it is still unknown how predictably males return to the same area year after year (Whitehead, 2003). Consistent photo-identification effort from several islands is needed to investigate male breeding ranges. The models also suggest that the Eastern Caribbean population numbers in the low hundreds and may be growing. While this is encouraging, the estimated trend is not significantly different from zero.

Table 5

Parameter estimates for heterogeneity in identifiability plus trend model, together with the mean of the estimates from 1,000 parametric bootstrap replicates, and their 95% confidence intervals. The bias is the mean of the parametric bootstrap estimates of a parameter divided by its original estimate. Corrected estimates and corrected 95% confidence intervals were derived by dividing by the bias.

Parameter	Estimate	Mean of parametric bootstraps	95% CI (lower limit)	95% CI (upper limit)	Bias	Corrected estimate	Corrected 95% CI (lower limit)	Corrected 95% CI (upper limit)
Population in 1995	93.8	60.8	39.4	91.8	0.6	144.7	93.8	218.5
Mortality yr^{-1}	0.119	0.150	0.055	0.269	1.261	0.094	0.035	0.169
Trend yr^{-1}	0.104	0.069	-0.008	0.157	0.663	0.157	-0.019	0.357
Proportion of high identifiability animals	0.28	0.461	0.000	1.000				
Ratio of identifiabilities	0.048	0.265	0.000	1.000				

It is apparent from Fig. 1 that individuals, and probably associated sets of animals, 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 it likely that the actual number of inter-island movements was higher than reported here. 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 generally consistent with patterns of social organisation and movement reported elsewhere, summarised in Whitehead (2003).

Slightly less than 30% of individuals were re-identified in more than one year. 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 five adult females were identified associated with five 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 drawn from studies in the eastern tropical Pacific (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 (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, in the eastern tropical Pacific, units of females and immatures possess ranges spanning 1,000-1,500km (Dufault and Whitehead, 1995b; Whitehead, 2003). Sperm whales have been estimated to be able to travel at average speeds of about 4km h^{-1} (Gordon, 1987; Watkins *et al*., 1999; Whitehead, 1989; Whitehead *et al*., 1992) whether at the surface or at depth foraging. Although sperm whales may potentially cover as much as 96km day^{-1} (4km $h^{-1} \times 24h$), Whitehead (2001a) estimated root-mean-squared displacement to be approximately 50km day^{-1}, 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.

Of the five islands included in this study, only three have ratified the SPAW protocols (Guadeloupe and Martinique under France in 2002, and St. Lucia in 2000). Dominica and Grenada have neither signed nor ratified this agreement. With whalewatching growing as a business on all of these islands, these findings indicate that neighbouring islands, in particular Dominica and Guadeloupe, have a vested interest in jointly protecting this shared resource and encouraging their neighbours to ratify and meet international treaty commitments, such as the SPAW protocols. Dominica, Grenada and St. Lucia are members of the International Whaling Commission (IWC), which may provide them a forum to collaborate on these issues.

From a management perspective, it is interesting that no matches were made between any of the identifications in the Caribbean Sea and photo-identifications from the Sargasso Sea, about 1,800km to the north. Similarly, there have been no matches with the Gulf of Mexico 2,700km to the northwest (J. Gordon and N. Jaquet, pers. comm.). The status and stock structure sperm whales of the North Atlantic have not been considered by the International Whaling Commission since the early 1980s. A single stock is listed in the IWC Regulations (Donovan, 1991), supposed partially due to the capture of a male off Spain that had been tagged off Nova Scotia (Mitchell, 1975) and two findings linking males in the Azores to Spain and Iceland (Aguilar, 1985; Martin, 1982). 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, 1995b; Whitehead, 2003). It is, therefore, the ranging patterns and habitat-use of the female and immature component of the population which is most relevant for management and conservation. Our findings suggest that the female and immature component of the small Caribbean population, estimated here to be approximately 145 individuals (95% CI=94-219) in 1995, is somewhat segregated from the once heavily hunted Sargasso population (Maury, 1852; Townsend, 1935). If interchange between the seas is minimal and reidentification within the Caribbean is high, it suggests that animals in the Caribbean are able to successfully exploit resources available in a smaller range restricted to the Lesser Antilles, making movement between seas unnecessary. Previous studies support this hypothesis, indicating that animals that are feeding successfully (using defecation rate as a proxy) cover less ground when foraging (Whitehead, 1996; Whitehead and Rendell, 2004). Gero (2005) showed, using defecation as a proxy for feeding success, that the animals in the Eastern Caribbean are foraging more successfully than those in the Sargasso, which is consistent with the hypothesis of a reduced foraging range in the Caribbean. In addition, foraging strategies seem to be culturally inherited (Whitehead and Rendell, 2004) and preliminary results find no evidence of the Caribbean vocal clan occurring anywhere else in the North Atlantic (L. Rendell, unpublished data) such that a restricted foraging range may be passed on between generations within social units of the Caribbean clan. These findings suggest that the Caribbean population is quite isolated, such that impacts on the population in the Eastern Caribbean are unlikely to have repercussions on neighbouring populations. Given that all sperm whales in the North Atlantic are presently considered one management region by the IWC, our findings suggest that reclassification of the stock boundaries should be considered.

CONCLUSIONS

Defining sperm whale stocks is a difficult task as this species is highly mobile (Jaquet *et al*., 2003), sexually segregated (Whitehead and Mesnick, 2003), shows little genetic differentiation within an ocean basin (Dufault *et al*., 1999; Lyrholm and Gyllensten, 1998; Lyrholm *et al*., 1996; Mesnick, 2001) and has socially and culturally complex behaviour and movement patterns, summarised 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. In this paper, an estimate is provided for a region for which none was previously available and it is shown that movement between national boundaries within the Caribbean Sea is common, but that movement between adjacent seas may not be. Management of this species should be considered on a cooperative, multi-national basis across the Eastern Caribbean area and stock reclassification for the entire North Atlantic should be considered.

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