NRC Research Press

ARTICLE

North Atlantic humpback whale (*Megaptera novaeangliae*) hotspots defined by bathymetric features off western Puerto Rico

M.M. MacKay, B. Würsig, C.E. Bacon, and J.D. Selwyn

Abstract: North Atlantic humpback whales (*Megaptera novaeangliae* (Borowski, 1781)) are increasing in number, necessitating current data from winter areas for assessing potential interactions with humans. Occurrence patterns of humpback whales wintering off Puerto Rico were investigated to predict where whales aggregate in nearshore areas. Here we describe the relationship between group associations of humpback whales and bathymetric features off western Puerto Rico. Data were collected from 2011 to 2014. Effort consisted of 240.9 vessel h, 13.0 aerial h, and 303.6 h of land observations conducted over 165 days. A total of 197 humpback whale groups were observed with n = 331 individuals: 91 (46.2%) singletons, 67 (34%) dyads, 17 (8.6%) mother–calf pairs, 8 (4.1%) competitive groups, 8 (4.1%) mother–calf–escort groups, and 6 (3.1%) mixed-species associations. A linear regression model supported that group composition correlated with hotspots associated with four bathymetric features. Dyads and competitive groups were dispersed among features in deeper water. Singletons were observed farther from a shelf edge, whereas singing males were closely associated with a shelf edge. Mother–calf pairs occurred nearshore in shallow water; however, when mother–calf pairs were sighted with an escort, they were offshore. This study is especially important ahead of possible removal from the Endangered Species list.

Key words: humpback whale, *Megaptera novaeangliae*, North Atlantic, Caribbean, Puerto Rico, Mona Passage, seasonal occurrence, bathymetry, resources management, migration.

Résumé : Le nombre de rorquals à bosse (*Megaptera novaeangliae* (Borowski, 1781)) de l'Atlantique Nord augmente, d'où la nécessité de données à jour provenant des aires d'hivernage pour évaluer les interactions potentielles avec les humains. Les motifs de présence de rorquals à bosse hivernant dans la région de Puerto Rico ont été étudiés afin de prédire où ces rorquals se regroupent dans les zones littorales. Nous décrivons le lien entre les associations en groupe de rorquals à bosse et des éléments bathymétriques le long de la côte ouest de Puerto Rico. Des données ont été recueillies de 2011 à 2014 dans un effort qui a consisté en 240,9 h, 13,0 h et 303,6 h, respectivement, d'observation en mer, aérienne et de la terre, réparties sur 165 jours. Au total, 197 groupes de rorquals à bosse ont été observés comptant n = 331 individus, soit 91 singletons (46,2 %), 67 dyades (34 %), 17 paires mère–veau (8,6 %), 8 groupes de concurrents (4,1 %), 8 groupes mère–veau–escorte (4,1 %) et 6 associations de différentes espèces (3,1 %). Un modèle de régression linéaire appuie le fait que la composition des groupes est corrélée à des points chauds associés à quatre éléments bathymétriques. Les dyades et les groupes de concurrents étaient dispersés entre les éléments en eau profonde. Les singletons ont été observés plus loin d'une bordure de plateforme, alors que les mâles chanteurs étaient étroitement associés une bordure de plateforme. Si les paires mère–veau se trouvaient près des côtes en eau peu profonde, les paires mère–veau observées avec une escorte étaient au large. L'étude est particulièrement importante dans l'optique d'un éventuel retrait de l'espèce de la liste des espèces en voie de disparition. [Traduit par la Rédaction]

Mots-clés : rorqual à bosse, *Megaptera novaeangliae*, Atlantique Nord, Caraïbes, Puerto Rico, passage de Mona, présence saisonnière, bathymétrie, gestion des ressources, migration.

Introduction

Humpback whales (*Megaptera novaeangliae* (Borowski, 1781)) migrate from feeding grounds in higher latitudes to breeding and calving grounds in lower latitudes (Clapham and Mayo 1987; Mattila et al. 1989; Corkeron and Connor 1999; Charif et al. 2001; Robbins et al. 2001; Barco et al. 2002). Silver Bank, off the Dominican Republic, is the location of the main aggregation of North Atlantic humpback whales, with smaller aggregations on Navidad Bank and in Samaná Bay (Mattila et al. 1994; Betancourt et al. 2012). Some North Atlantic humpback whales migrate past the large aggregation off the Dominican Republic to waters around Puerto Rico (Martin et al. 1984; Mattila and Clapham 1989; Mattila et al. 1989) and the Lesser Antilles (Mitchell and Reeves 1983; Mattila and Clapham 1989).

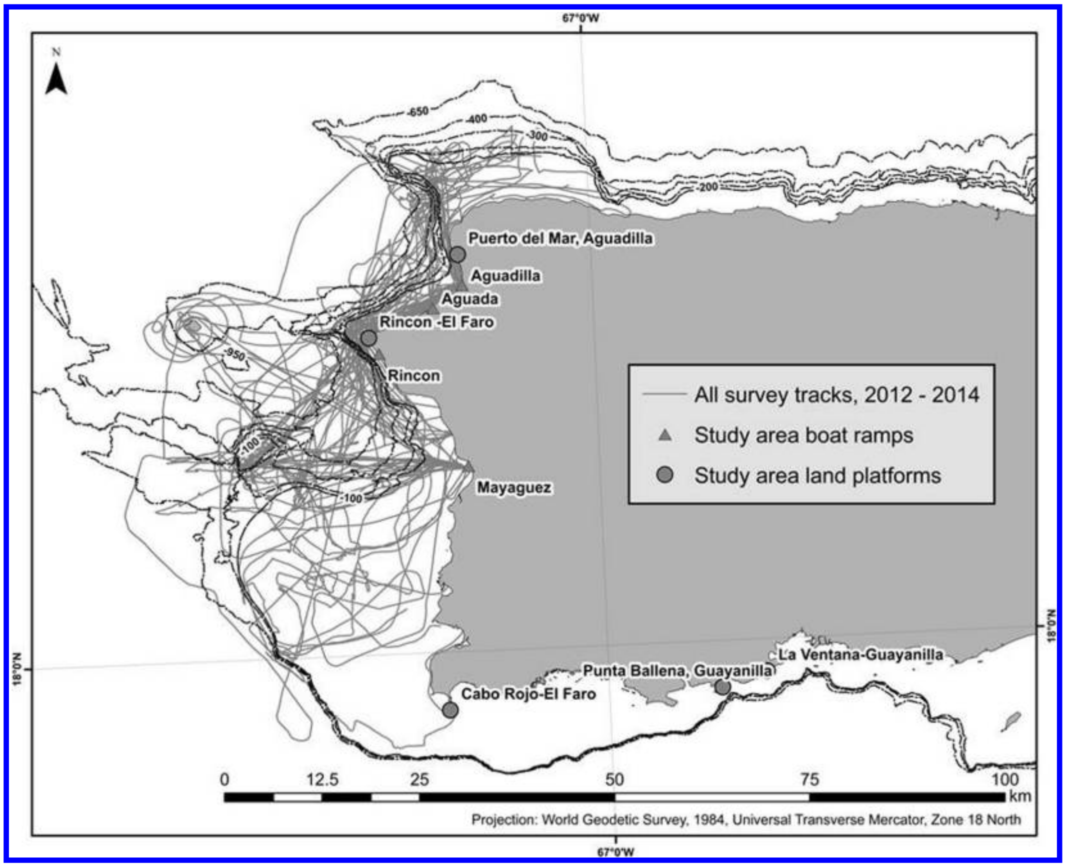
Mona Passage is an underwater canyon between the west coast of Puerto Rico and the island of Hispaniola. The variation along the canyon provides relatively shallow areas, as well as deep gorges (Brink 2007). Mona Passage has varying slopes of 10°–50° extending from 20–30 km wide, 140 km long, and 2–3.5 km deep (Mondziel

Received 20 September 2015. Accepted 22 April 2016.

M.M. MacKay. Department of Marine Biology, Texas A&M University at Galveston, Pelican Island, Galveston, TX 77553, USA; Marine and Coastal Ecology Research Center, Pipe Creek, TX 78063, USA.
B. Würsig. Department of Marine Biology, Texas A&M University at Galveston, Pelican Island, Galveston, TX 77553, USA.
C.E. Bacon. Marine and Coastal Ecology Research Center, Pipe Creek, TX 78063, USA.
J.D. Selwyn. HoBi Lab, Department of Life Sciences, Texas A&M University – Corpus Christi, Corpus Christi, TX 78412, USA.
Corresponding author: Mithriel M. MacKay (email: Mithriel@Marine-Eco.org).

 Published at www.nrcresearchpress.com/cjz on 7 May 2016.

Fig. 1. Boat survey tracks in Mona Passage between 2012 and 2014.



et al. 2010). The deepest part of the canyon is greater than 1000 m, with reefs and seamounts (submarine mountains with the summit below the surface) scattered throughout the canyon, creating shallow areas (Brink 2007). The west coast of Puerto Rico (included in Mona Passage) has a coastal shelf that extends as follows from key locations: (*i*) approximately 0.5 km between Aguadilla (at the northwest tip) and Mayagüez (center of the west coast), and (*ii*) 15 nm/27 km surrounding the southwest corner of the island at Cabo Rojo (Schuchert 1936; Brink 2007; United States Geological Survey Simrad EM-1002 survey from the National Oceanic and Atmospheric Administration ship *Nancy Foster*, 2007 survey).

Humpback whale mothers with calves show a preference for shallow, coastal areas (Smultea 1994; Félix and Haase 2001; Ersts and Rosenbaum 2003; Franklin et al. 2011; Craig et al. 2014; Martinez et al. 2015). Dyads have been observed nearshore; competitive groups show a bias for deeper waters past the shelf break (Whitehead and Moore 1982; Mattila and Clapham 1989; Mignucci-Giannoni 1998; Félix and Haase 2001; Swartz et al. 2002; Frantzis et al. 2004; Félix and Haase 2005; Kaschner et al. 2006). There have been investigations that examine the possibility that humpback whales are using the song for spacing between males on the breeding grounds (Frankel et al. 1995; Mercado et al. 2007, 2008).

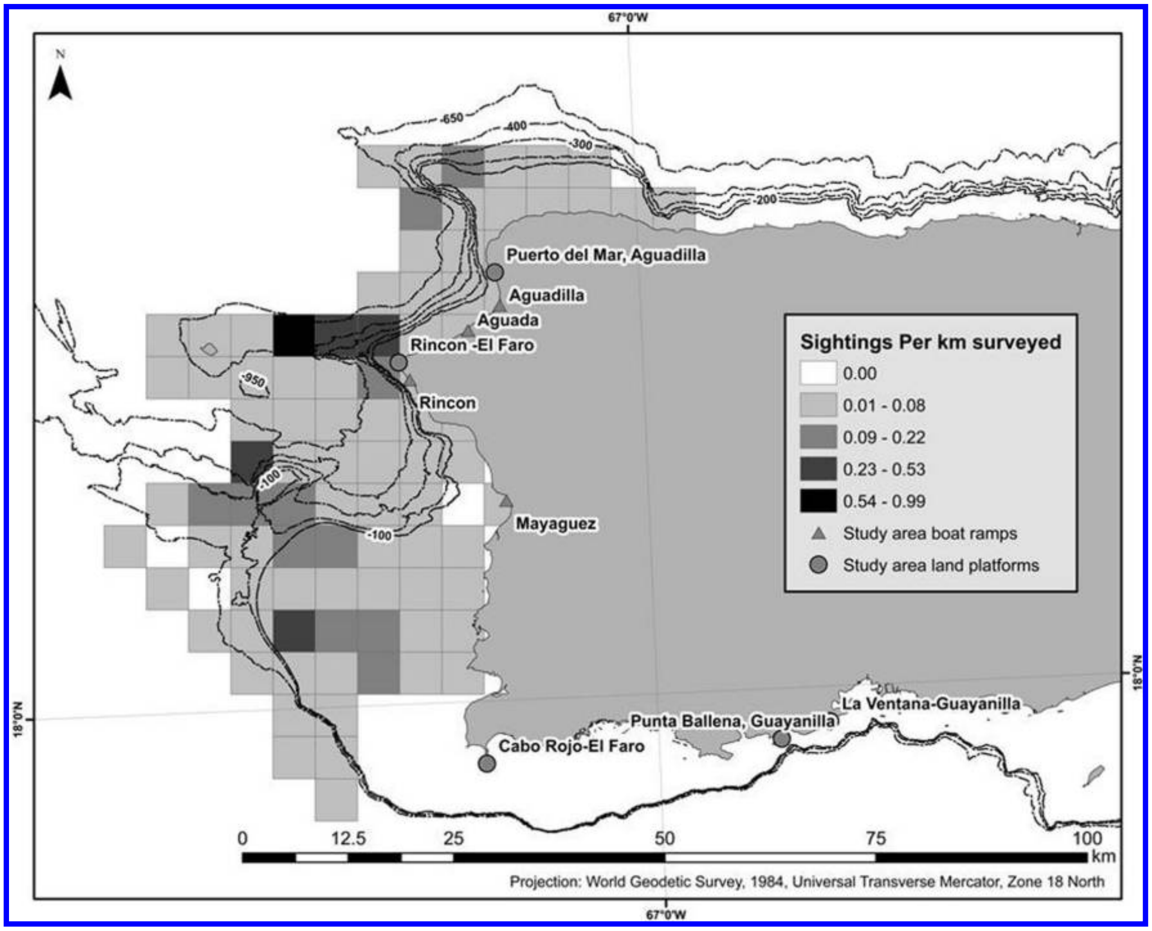
A long-term study has been conducted off the Abrolhos Bank, Brazil, the location of the largest wintering area for humpback whales in the western South Atlantic (Martins et al. 2001). A spatial analysis was examined in the context of distance from shore and depth within the archipelago, as concern for the outcome of interaction between humpback whales, including mother–calf pairs occurring near shore, in support of a management plan for tourism operations. Data collected between 1992 and 1998 were used to determine baseline occurrence patterns and demonstrated bias for areas defined by depth and distance from shore among group association types. The concerns for the humpback whales wintering in the subtropical area of the Abrolhos are similar to the interactions between anthropogenic activity and whales off Puerto Rico; therefore, a similar baseline study is needed to identify areas where whales are aggregating during winter months.

This study provides information regarding the occurrence patterns of North Atlantic humpback whales in a low-density area (off western Puerto Rico) decades after the last systematic studies have been conducted (Mattila 1984; Mattila et al. 1989, 1994; Clapham et al. 1992; Clapham and Mattila 1993; Stevick et al. 2003). We examined humpback whale group types as categorical dependent variables to determine if there is an association with bathymetric features consistent with what has been observed in other areas that may lead to an explanation of occurrence patterns in Mona Passage. The current status of North Atlantic humpback whales is a success story of recovery after whaling; therefore, bathymetric features in the study area, often associated with fishing and recreational activities, are of particular interest to this investigation as we anticipate the National Marine Fisheries Service and the Puerto Rico Department of Natural and Environmental Resources will find this information useful for marine management strategies.

Materials and methods

Data were gathered from shore, vessel (by visual and hydrophone listening aids), airplane, and (or) stationary bottom mounted underwater listening devices. We selected a single methodology (detailed below) per day to maximize data collection of humpback whale group type throughout the season in a location where weather, the size of the study area, and the low density of whales necessitated more than any single means to a robust data set. Group type included mother with calf (M–C pair), mother–calf–escort (M–C–E group), dyads, competitive groups (focal female and two or more males), singletons, and the number of groups of singers per year between 2012 and 2014. If one or both individuals in a dyad were singing, then they

Fig. 2. North Atlantic humpback whale (*Megaptera novaeangliae*) sightings per unit effort from 2012 to 2014.



were counted as a single group of dyads; therefore, singers may be underestimated.

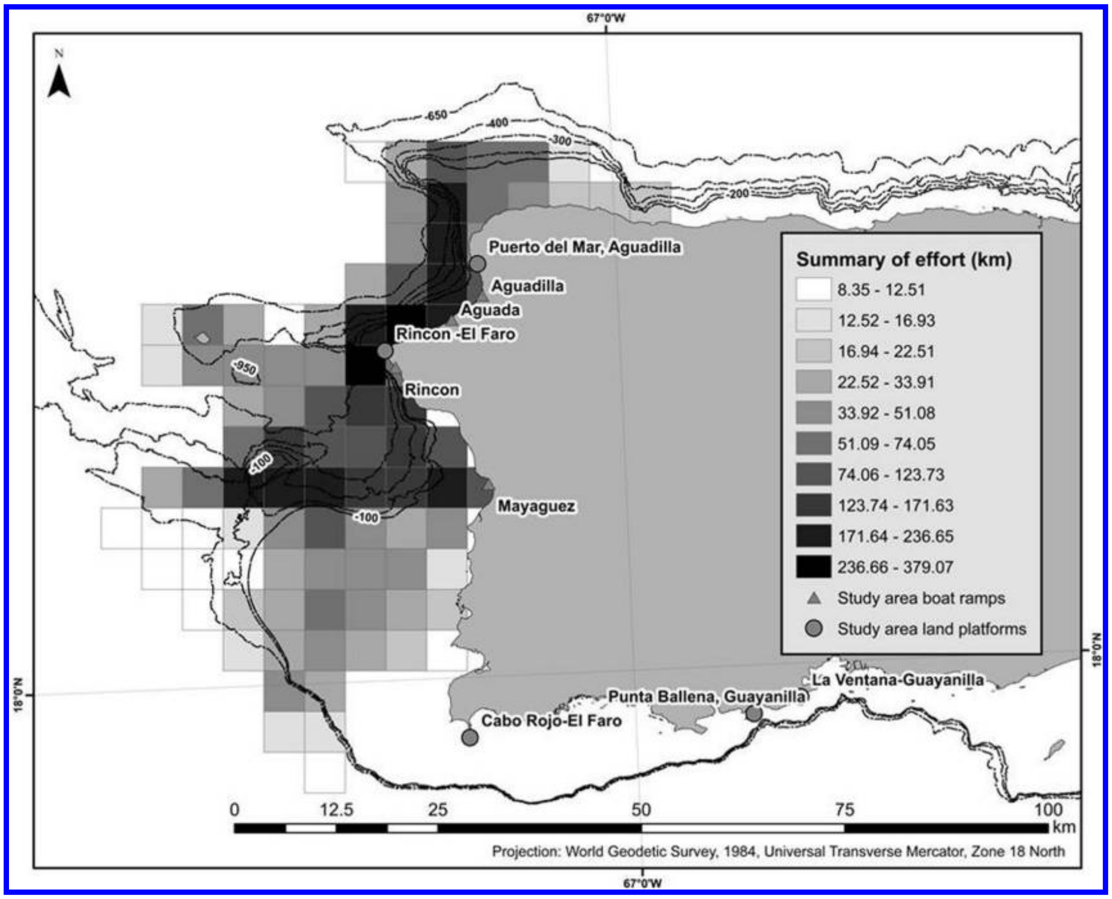
Shore-based observations

Cliffs overlooking the survey area were selected in locations where humpback whales had been sighted during previous surveys (Mattila 1984; Mignucci-Giannoni 1998; Mercado et al. 2007, 2008), and where anecdotal information (fishermen, residents, fisheries biologists) indicated humpback whales were sighted. The west and southwest coasts were selected as a matter of practical feasibility and efficiency for a small team. Observations were conducted from shore-lining cliffs at four locations in 2011, two locations in 2012, and a single platform in the 2013 and 2014 seasons (Fig. 1). The land station was reduced to one site when it became apparent that sighting humpback whales from a cliff would be possible from a single location, at Parque El Faro, Rincón. The survey team consisted of observers using reticle binoculars and unaided eye for sampling. A theodolite was used to collect horizontal and vertical angles to a group of humpback whales, and then converted into GPS coordinates using the program Mysticetus (Entiat River Technologies, Preston, Washington, USA; available from http://www.mysticetus.com). When a group of humpback whales was sighted, scanning was suspended and a focal follow was initiated until the humpback whale(s) were no longer sighted or data collection was deemed to be complete.

Vessel surveys, acoustics, and photo-identification

Boat effort from a small vessel was concentrated in the mornings, preceding the effects of the trade winds, allowing for 4–6 h per day and 1–3 days per week. Beaufort sea state along the west coast and away from shore varied greatly from day to day; the departure location, distance from shore surveyed, and area surveyed were largely dictated by weather. In general, Beaufort sea state above 4, swell over 4 feet (ft; 1 ft = 30.48 cm), and rain were criteria for terminating boat effort. Observation effort began immediately when the boat was launched from the ramp, terminating effort when the boat returned to the ramp. The boat was motored towards a predetermined "listening point", changing heading if a humpback whale was spotted before reaching that location. Predetermined listening points are locations outside of the bay from where the boat was launched, or a location where humpback whale singing had been detected multiple times on previous excursions. The boat motors were shut off and we deployed a H2c hydrophone (AFAB Enterprises, LLC DBA, Aquarian Audio Products, Anacortes, Washington, USA) or similar, with a preamp and digital recorder to listen for singing humpback whales. If the singer was estimated to be within detection range of our directional hydrophone, then a custom-made directional hydrophone (modeled, with modifications, after Whitehead and Gordon 1986; Weilgart and Whitehead 1997; Whitehead et al. 1998; Douglas et al. 2005) was lowered into the water on a pole to determine the compass bearing to the singer. If more than one singer was detected, we noted the direction and estimated distance of singers, and then focused our effort to the closest individual. The directional hydrophone brought us closer to the location of the singer where the team waited for a whale to surface. If humpback whale singing was not detected, then the boat was moved to another predetermined listening point. Observers remained on effort; data were collected for humpback whale groups on the surface and while transiting between listening points. A waypoint was marked with a GPS and mapped in real time in the program Mysticetus to denote the location of humpback whale groups. Photographs of flukes, dorsal

Fig. 3. Summary of effort: boat track lines between 2012 and 2014 summarized into 5 km² blocks.



fins, and scars of all individuals in each group were obtained whenever possible. High-resolution images were captured with a digital single-lens reflex camera (Nikon D7000 with Sigma 50–500 mm and Nikkor 55–300 mm lenses) fitted with a video camera (GoPro2 or Midland XTC 100). If humpback whales approached our boat upon surfacing, then underwater video cameras (GoPro2, GoPro Hero 3, Midland XTC 100) fastened to a PVC (polyvinyl chloride) pole were lowered into the water to capture fluke photos and identifying markings subsurface. Fluke photos were entered in iMatch5 software along with metadata that included date, time, location, and identification of all humpback whales in the same group. Images of dorsal fins were obtained in addition to, or in lieu of, fluke photos whenever possible. Photographs were compiled into a catalog and submitted to the repository for North Atlantic humpback whales (Allied Whale Project, College of the Atlantic, Bar Harbor, Maine, USA) to acquire available age and sex history for previously sighted whales.

This study was not aimed at an abundance estimate that would require a systematic survey of the area of interest; therefore, methods did not include line transects. Instead, our goal was to find whales in a low-density area and attempt to determine if they were occurring in areas overlapping with human activity. Line transects would have limited our ability to see humpback whales over a large area; therefore, modifications were made to the methods during the first two seasons to locate whales and maximize the number of sightings throughout the survey area. To maximize sightings, acoustic detection using a directional hydrophone was used to lead the team to singers. Locations where we were likely to see whales became more apparent with each season; therefore, the team would head in the direction of locations where humpback whales were known to aggregate and where acoustic detection pointed to singers. To minimize bias, the team initiated effort at the boat ramp and continued effort until returning to the boat ramp.

Table 1. Total number of effort hours (543:29:07) and effort days (n = 165 days) across each platform for each year in the study of North Atlantic humpback whales (*Megaptera novaeangliae*).

	Research effort hours		Total number of days		
Year	Land platform (h:mm:ss)	Boat platform (h:mm:ss)	Aerial recon flights	Land effort	Boat effort
2011	129:52:20	0	0	26	0
2012	76:14:09	62:05:30	5	19	16
2013	59:40:36	90:26:29	4	21	22
2014	37:49:35	87:20:28	4	15	33
Total	303:36:40	239:52:27	13	81	71

Aerial surveys

Aerial surveys were employed as a means of reconnaissance during times when humpback whales were particularly difficult to locate (when movement patterns shifted within and between years), sea state was favorable for aerial observations but not for boat and land observations, fishermen reported multiple sightings of humpback whales in an offshore location, and to get a periodic overview of the study area. A Cessna Skyhawk II (high-wing, single engine) and pilot were chartered beginning in 2012. The plane had four seats accommodating the pilot, two observers (right wing and left wing), and a data recorder and observer. The duration of each aerial survey was between 1 and 2 h, which allowed for enough flight time to scan a majority of the study area with sufficient coverage to determine the location of humpback whales in a single flight. The pilot was directed to maintain an altitude of at least 457 m (1500 ft) over the survey area to avoid harassment (Würsig et al. 1985, 1989; Richardson et al. 1995). When a whale was sighted, the observer

Table 2. Summary of first and last arrival of North Atlantic humpback whales (*Megaptera novaeangliae*) in the study area by year.

	Acoustic detection		Visual detection		
Study year*	First	Last	First	Last	Peak season
2007	No data	30 Apr. 2007	No data	No data	Unknown
2008	19 Jan. 2008	20 May 2008	No data	No data	Unknown
2009	No data	No data	No data	No data	Unknown
2010	19 Jan. 2010	27 Apr. 2010	No data	No data	Unknown
2011	29 Dec. 2010	14 May 2011	20 Jan. 2011	2 Mar. 2011	Unknown
2012	23 Nov. 2011	23 Apr. 2012	13 Feb. 2012†	28 Mar. 2012	27 Feb. – 13 Mar.
2013	2 Jan. 2013	16 May 2013	23 Jan. 2013	18 Apr. 2013	27 Feb. – 13 Mar.
2014	26 Dec. 2013	29 Apr. 2014	17 Jan. 2014	17 Apr. 2014	24 Feb. – 10 Mar.

*Years prior to 2011 are only loggers with no visual surveys. Digital spectrogram recorders were the first to detect whales by song, as they were placed in Mona Passage before land and boat work began each year.

†In March 2012, detection of whales was improved by adding a hydrophone deployed from the boat. In January 2013, a directional hydrophone was added to the methods.

Table 3. Summary of seasonal occurrence of North Atlantic humpback whales (*Megaptera novaeangliae*) by groups during 2011–2014 surveys.

Year	No. of individuals*	No. of groups‡	No. of M–C groups	No. of M–C–E groups	No. of competitive groups	Total no. of individuals in competitive groups	No. of singletons	No. of pairs†	No. of mixed-species groups	Total no. of humpbacks in mixed-species groups
2011	63	36	8	0	3	9	12	13	0	0
2012	19	12	4	0	0	0	5	3	0	0
2013	145	78	1	2	5	22	28	38	4	11
2014	104	71	4	6	0	0	46	13	2	6
Total	331	197	17	8	8	31	91	67	6	17
% Total individuals			10.3	7.3	4.1	9.4	27.5	40.5	6	5.1
% Total groups			8.6	4.1	4.06		46.2	34.0	3.05	

Note: M–C, mother–calf; M–C–E, mother–calf–escort.

*Individual counts are exclusively humpback whales.

†Excludes M–C pairs.

‡Singers were represented in 2012 by 1 group, in 2013 by 9 groups, and in 2014 by 14 groups.

obtained a declination angle using a Suunto clinometer. The altitude and GPS location of the plane at the time of the sighting were entered into the database using a GlobalSat BT 358 GPS unit (live feed) in conjunction with the program Mysticetus, thereby creating a waypoint overlaying a bathymetric map of the area in real time.

Effect of trade winds on surveys

Boat effort and observations from land were affected by the trade winds and accompanying increase in Beaufort sea state that occurred most afternoons, with some degree of variability between and within seasons. It became clear that data collection should largely be limited to morning hours (typically from first light to noon each day) and an attempt to distribute data collection over all daylight hours was abandoned during the 2012 season. In 2014, a single land platform, vessel surveys, and occasional aerial reconnaissance continued to be the standard operating procedure for data collection. Observations through the end of April 2014 are included in these analyses.

Mapping and statistics

Geographic information system (GIS) mapping technology was used to analyze sightings per kilometre surveyed (SPKS) and kernel density estimate (KDE) with respect to bathymetry. Maps were generated using existing data sets from the National Centers for Environmental Information (available from http://ngdc.noaa.gov; griddeddata = 3 arc seconds). Kernel density estimators were derived using standard methods and a bandwidth of 5 km for effective discrimination within the study area. Within the data set, SPKS were calculated. In this study, SPKS is defined by sightings in each 5 km^2 block (Fig. 2) surveyed between 2012 and 2014 by boat. The summary of effort map (Fig. 3) represents raw track lines summarized into grid cells (5 km^2 blocks) for a visual representation of distance covered by boat over the study area between 2012 and 2014.

We sought to test whether group type (i.e., M–C or singleton) could be explained by various bathymetric variables. The independent bathymetric variables used were bathymetric depth, Euclidean distance from the shelf edge, and slope of the seafloor. These variables were transformed based on the Box–Cox transformation to normalize the data (Box and Cox 1964) and to reduce the influence of extreme values, thereby improving the models' ability to converge. Collinearity of independent variables was tested using Kendall's τ due to variables not being from a bivariate normal distribution (Hollander et al. 2013). Problems of collinearity between independent variables were assessed using the variance inflation factor (VIF) that indicates likely problems with collinearity with values greater than 10 (O'Brien 2007). Because the dependent variables are categorical (group assignment), we used a multinomial logistic regression to test the probability of each group type being present given the independent variables. An exhaustive search of models was performed with all possible additive and interactive models using the three independent variables. The best model was chosen based on minimization of Akaike' information criterion (AIC) (Akaike 1974). This analysis was performed using the polytomous package implemented in R version 3.1.1 (Arppe 2012; R Core Team 2014).

Results

Effort and sightings

Between 11 January 2011 and 1 May 2014, 543.5 h were dedicated to research effort from land and boats (303.6 h from land, 240.9 h from boat) (Table 1, Fig. 1). North Atlantic humpback whales in 197 groups (n = 331) were sighted over the study period between winter 2011 and 2014 (Tables 2 and 3, Fig. 4). Fluke identification photos were difficult to capture, as deep dives were not typical, in favor of "no

Fig. 4. Distribution of 197 groups of North Atlantic humpback whales (*Megaptera novaeangliae*) (2011 and 2014) in Mona Passage.

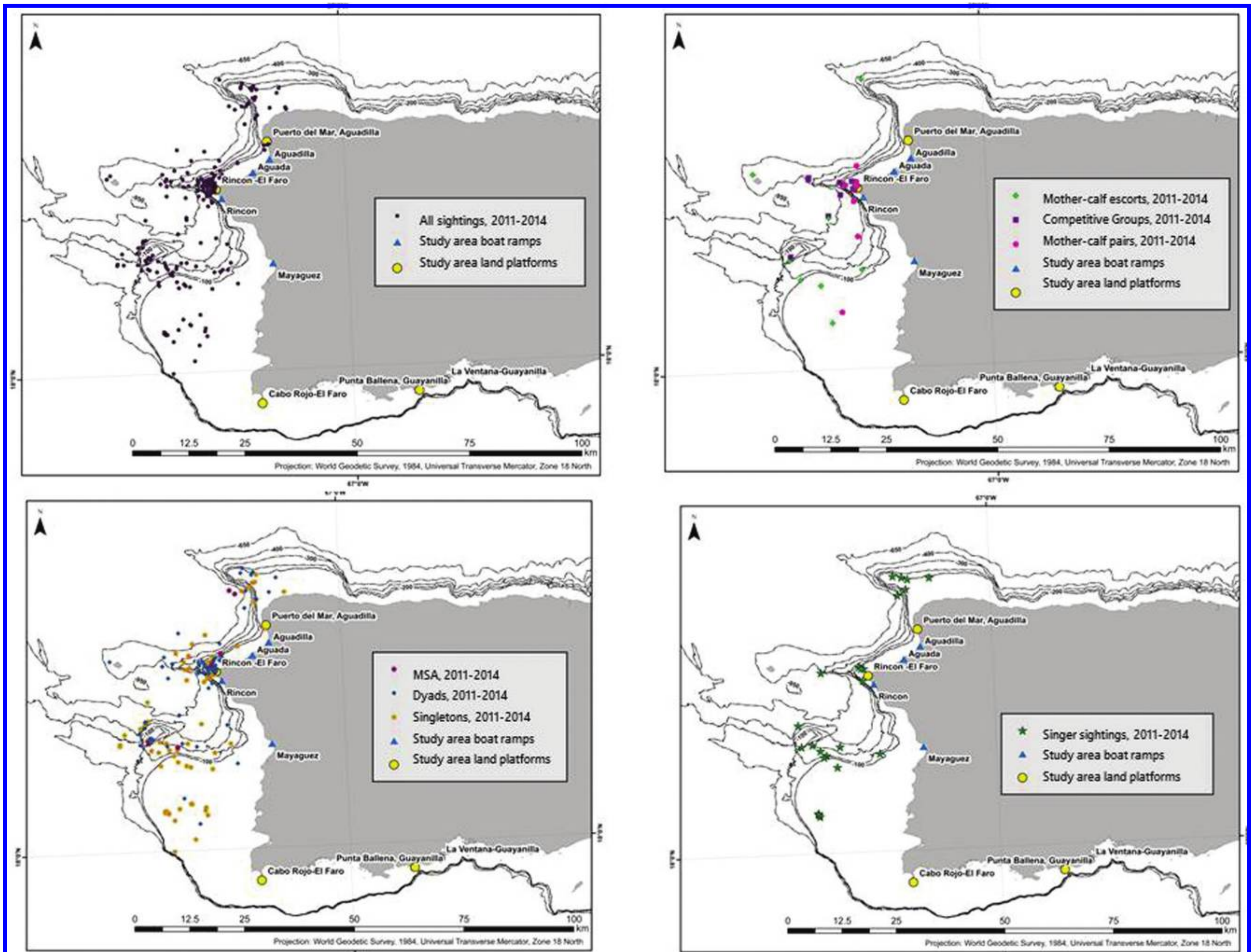
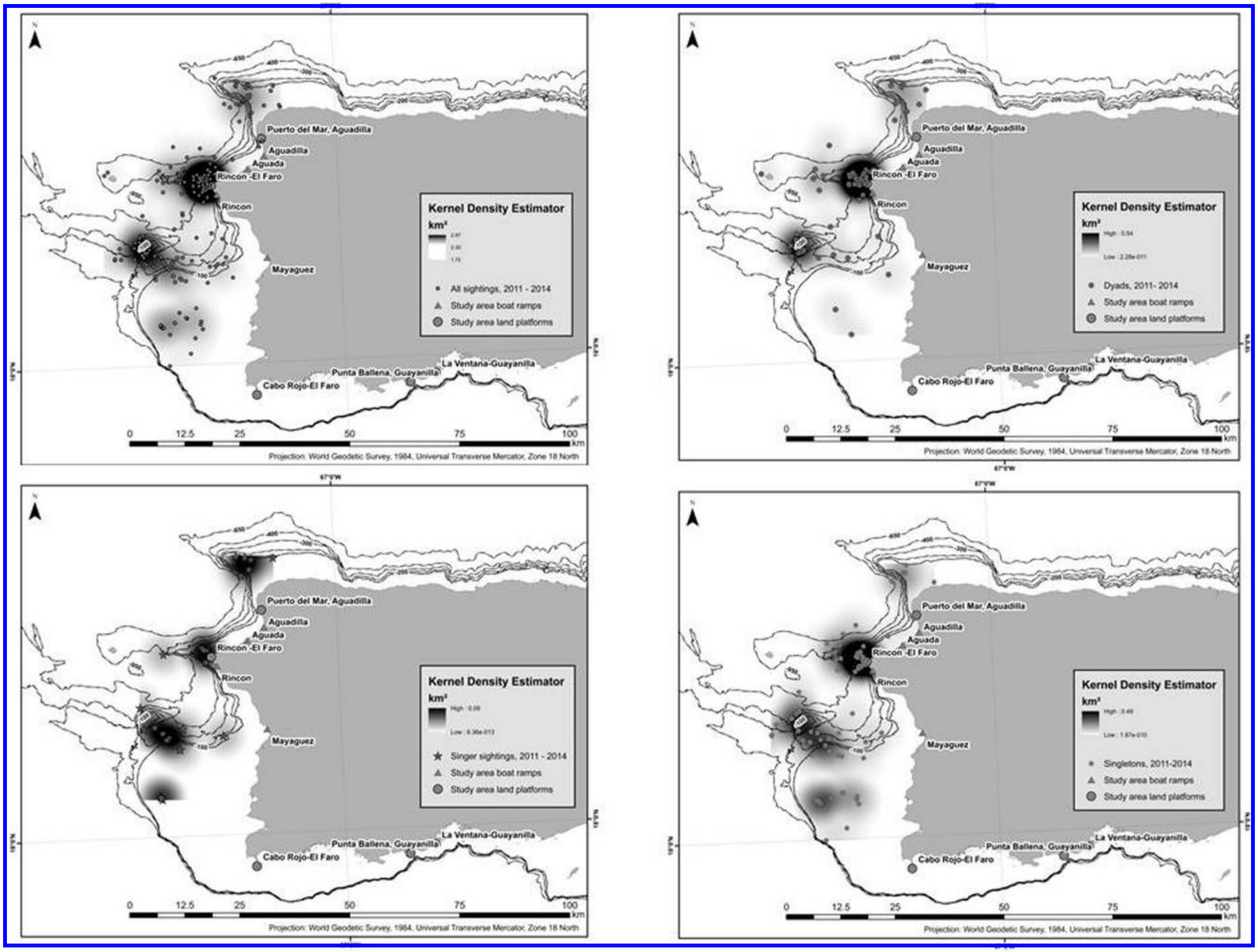


Fig. 5. Kernal density estimates of North Atlantic humpback whales (*Megaptera novaeangliae*) in Mona Passage between 2011 and 2014.



Published by NRC Research Press

Table 4. Model selection based on minimizing Akaike's information criterion (AIC) in the study of North Atlantic humpback whales (*Megaptera novaeangliae*).

Model no.	Depth	Slope	ED	Depth × slope	Depth × ED	Slope × ED	Depth × slope × ED	AIC	ΔAIC
4	X		X					538.56	0.00
3			X					539.67	1.11
10	X	X	X					547.11	8.55
5	X		X		X			548.23	9.68
6		X	X					550.33	11.78
11	X	X	X	X				553.68	15.12
12	X	X	X			X		554.66	16.11
13	X	X	X		X			556.83	18.28
7		X	X			X		557.56	19.00
14	X	X	X	X	X	X	X	579.34	40.78
9	X	X		X				596.48	57.92
8	X	X						601.96	63.41
2		X						606.05	67.49
1	X							608.17	69.61

Note: Xs within the table indicate inclusion in the model. Multiple effects are included additively with interactive effects shown in separate columns. ED is the Euclidean distance from the shelf edge. ΔAIC is the difference between the AIC of the model and the best model.

Table 5. Table of the results of the best model based on minimizing Akaike's information criterion in the study of North Atlantic humpback whales (*Megaptera novaeangliae*).

Independent variable	M–C	Dyad	M–C–E	Competitive group	Singleton	Singer
ln(Depth)	<u>0.512</u>	<u>1.236</u>	1.205	<u>1.641</u>	1.092	0.625
(Euclidean distance)$^{1/4}$	1.024	1.098	1.153	1.161	<u>1.258</u>	<u>0.262</u>

Note: Numbers indicate coefficients of the change in odds with increasing depth or Euclidean distance. Underlined values are significant at $\alpha = 0.10$. M–C, mother–calf; M–C–E, mother–calf–escort.

fluke dives" when humpback whales arched their bodies to move below the surface without raising their flukes above the surface.

Patterns of area use

SPKS and KDE were mapped for boat effort between 2012 and 2014 (Figs. 4 and 5). Each map indicates the number of groups sighted in areas corresponding to the four bathymetric features (Figs. 4 and 5). SPKS confirm the KDE associating groups with the bathymetric features. KDEs indicated that sightings were clustered near four bathymetric features in Mona Passage (Fig. 5):

1. Bajo de Sico, which is a seamount offshore from Mayagüez midway down the west coast),
2. Los Rabos, which is a ledge in the shape of a tail extending from the northwest corner of the main island,
3. Rincón, which is a ledge extending out from the point of land from the west coast,
4. Cabo Rojo, which is a shelf extending out as far as 20 km from the southwest corner of the main island.

Singletons and dyads (non-M–C pairs) were found associated with all four bathymetric features, over and along the edge of each feature (Figs. 4 and 5). Competitive groups were associated with bathymetric features near Rincón (Figs. 4 and 5). M–C pairs were sighted close to the point at Rincón, whereas M–C–E groups were more likely to be offshore (Figs. 4 and 5). A Mann–Whitney *U* test resulted in a *p* value of 0.0003 (test statistic 2.000), rejecting the null hypothesis that there was no significant difference in the distance from shore of M–C pairs and M–C–E groups (mean distance from shore of M–C pairs = 2.69 km; mean distance from shore of M–C–E groups = 18.04 km) (Figs. 4 and 5).

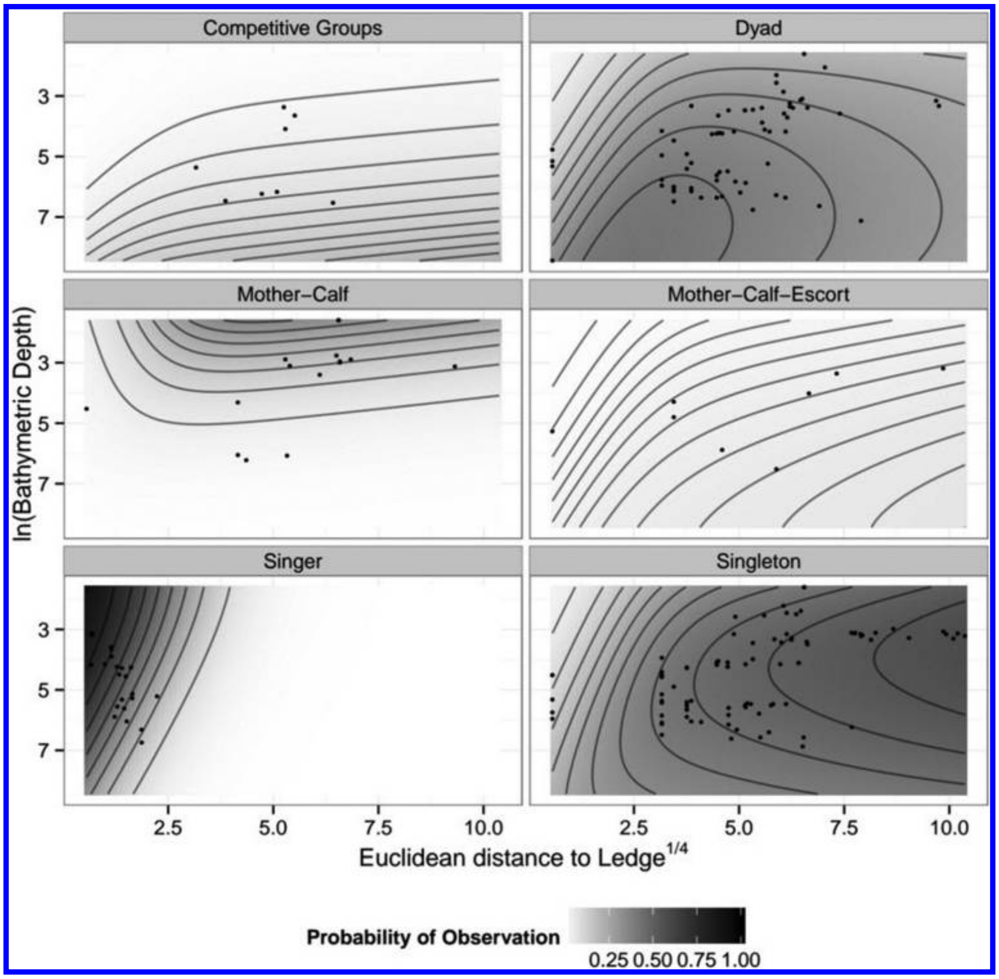
Although there was evidence of significant correlations between all three independent variables, the VIF values indicated no undue influence of collinearity on the model occurred owing to these correlations (Kendall's $\tau = -0.391$ to 0.536, all $p < 0.05$, VIF = 1.36 to 1.68). Based on an exhaustive search, the best model explained observed grouping using the additive effect of Euclidean distance from the shelf edge and depth (Table 4). This model found a significant decrease in the odds of observing a M–C pair at increasing depths (odds = 0.512, $p = 0.0062$). Additionally, we found a significant increase in the odds of observing singleton males (odds = 1.258, $p = 0.0021$) and significant decrease in singing males (odds = 0.262, $p < 0.001$) with increasing Euclidean distance from the shelf edge. The odds of observing dyads and competitive groups were found to have marginally significant increases with increasing depth (odds = 1.24, $p = 0.074$ and odds = 1.64, $p = 0.084$, respectively). The odds of observing other groups were not significantly affected by either depth or Euclidean distance from the shelf edge (Table 5, Fig. 6).

Discussion

Between 2011 and 2014, humpback whales in Mona Passage aggregated in four hotspots associated with four distinct bathymetric features (Figs. 4 and 5). In 2013, humpback whales were found predominantly off the northwest coast between Rincón and Aguadilla. In 2014, humpback whales were observed predominantly off the southwest coast between Bajo de Sico and Cabo Rojo. In all years, humpback whales aggregated along similar bathymetric features (Figs. 4 and 5).

Because the pilot study in 2011 was conducted exclusively from land, KDE are likely biased towards a higher probability of sighting groups near Rincón (the primary observation platform from land). We can assert this bias does not affect the outcome where whales are associated with this particular feature extending from Rincón three ways. First, data collected from our vessel platform affirm the association with this bathymetric feature. Secondly, we are not attempting to quantify the number of groups that are in the area; therefore, a higher probability does not negate the finding that humpback whales are associated with this feature. Finally, SPKS maps revealed clusters of humpback whales associated with the same four bathymetric features, including separate analysis of each group association type. Because SPKS represent observations from the boat and all analyses support the associations with bathymetric features indicated by the models, we conclude that the results are an accurate representation of humpback whale aggregations associated with bathymetric features.

Fig. 6. Contour plot of the results of the multinomial linear regression model for North Atlantic humpback whale (*Megaptera novaeangliae*) group association types with depth and Euclidean distance from the shelf ledge. Points represent observed groups, whereas contours represent the changing probability of observing each group type with black being high probability of observation and white being low probability of observation.



M–C pairs were sighted almost exclusively near the point at Rincón and, interestingly, when M–C pairs were accompanied by an escort, groups were found offshore (Fig. 4). The data supported a preference for shallow water by mothers with calves. M–C pairs were clustered near the point at Rincón and absent in other nearshore, shallow areas or over seamounts in Mona Passage. It is not a surprise that M–C pairs were sighted nearshore in shallow areas (Fig. 4), as this was consistent with observations in other winter habitats of humpback whales, including Brazil (Martins et al. 2001), Hawai'i (Smultea 1994; Cartwright et al. 2012), the Galápagos (Félix and Haase 2001), Australia (Franklin et al. 2011), and other areas in the West Indies (Whitehead and Moore 1982; Mattila 1984; Mignucci-Giannoni 1998). The few data collected for GPS waypoints of M–C–E groups are not sufficient to test if depth or Euclidean distance to a ledge were predictors for the location of this group type through modeling. We were able to demonstrate there is a significant difference from shore between M–C pairs and M–C–E groups, suggesting the presence of an escort is important for mothers offshore. M–C pairs were found nearshore in shallow water and distance from shore increased for all other group types of humpback whales.

Singletons were found clustered on the three shelves, and 10 singletons were sighted on top of the shallow shelf in the south (Cabo Rojo) (Fig. 4). The models predicted that singletons can be found farther from the shelf edge and depth was not a predictor for location of this group type. The top of plateaus, away from edges, may be where singers rest. North Atlantic humpback whales cluster on top of seamounts, and this may require obtaining age and sex of individuals through biopsy in addition to observations of behaviors.

Only eight competitive groups were sighted during the four seasons. Seven groups were sighted near Rincón and a single one over Bajo de Sico. The reason for the location of these sightings may be as simple as males of competitive groups potentially seeking out receptive females, and receptive females are likely to be in one of the three aggregations along the ledges and shelves. Competitive groups were more likely to be found in deeper water. Competitive groups were sighted off Rincón along a ledge extending from the point into deeper water away from the coastal shelf. M–C pairs favored shallow water along the coastal shelf at the same point off Rincón; however, competitive groups did not have a calf in any group and the location of competitive groups near Rincón may not be related to the presence of M–C pairs (Fig. 4).

Singers were sighted consistently on ledges associated with seamounts and including the drop-off at the edge of the shelf off Cabo Rojo (Fig. 4). The statistical model predicts that singers are found more frequently close to the shelf, which is consistent with our perception in the field. Singers may be gaining some advantage off ledges related to the song, including sound traveling farther or hearing themselves sing (Whitehead and Moore 1982). We noted pairs of singers in which one individual was noticeably smaller than the other, as well as an echo reverberating off the ledges while singers were broadcasting. Furthermore, there may be an acoustic advantage created by ledges to increase the efficiency of singing and to thereby maximize the potential for other humpback whales to detect that song (Frankel et al. 1995; Mercado and Frazer 1999). Mona Passage contains seamounts that provide ledges where North Atlantic humpback whales aggregate.

The data collected for this study cannot predict if there is an acoustic advantage for whales singing off ledges; however, the presence of singers associated with ledges indicate that future studies should include the approximate size and age (calf, subadult, adult) of individuals and an acoustical assessment of ledges where males sing. It may eventually be possible to predict the location of singers on winter grounds, and if and how subadults are taking advantage of the area away from the primary aggregation. Singers were the only group type with a strong association to shelf edges, implying that there is not an acoustic advantage for receivers near the same geological feature. It would be interesting to examine the bathymetric features off Madagascar, where depth and distance from shore are associated with group types (Ersts and Rosenbaum 2003), in addition to other winter grounds for Euclidean distance to shelves by group type, to determine if similar patterns of singers near ledges are found.

Dyads were also associated with bathymetric features in Mona Passage (Fig. 5) and the model predicts a strong trend towards finding dyads in deeper water. It may be that the dyads are singers vocalizing near the shelf or a pair transiting to a competitive group together, similar to singers in Hawai'i (Darling et al. 2006). This group type should be observed more closely over the next several seasons and the data divided into locations such as "dyads singing", "dyads traveling", and "dyads resting". We are intrigued by the composition of dyads. We were able to confirm some dyads consisted of two singers. A better understanding of the sex and class of each individual within dyads will be helpful to understanding the importance of physical surroundings for humpback whales migrating to the area off Puerto Rico.

Although North Atlantic humpback whale prewhaling abundance is unknown, the International Whaling Commission is in general agreement that humpback whales have recovered to approximately 54% of prewhaling global abundance estimates (Bettridge et al. 2015). As North Atlantic humpback whales continue to recover from whaling and greater numbers migrate to the West Indies, the possibility of competing with humans for resources, including space in areas used for wintering humpback whales, will also increase. The bathymetric features with which North Atlantic humpback whales are associated off Puerto Rico's west coast are the same areas used for recreational and commercial purposes. Activities that place humans in the same areas with humpback whales will occur more frequently as the number of North Atlantic humpback whales (Corkeron 1995; Lundquist et al. 2012) continues to increase overall, and as the humpback whales increase nearshore. Predicting where North Atlantic humpback whales cluster on winter grounds may enable managers to suggest or enforce minimization of interactions between humans and whales in areas where recreational and commercial activities overlap. This is especially important as North Atlantic humpback whales are presently considered for delisting as Endangered by the U.S. National Marine Fisheries Service, enabling managers to better plan for how best to protect this species because an increase in numbers are anticipated.

Acknowledgements

We thank M. Lopez, J. Albrecht, B. Hurley, and the many research assistants and interns for their contribution to this project. We thank the anonymous reviewers for their thoughtful comments towards improving the manuscript. Photographs were taken under National Marine Fisheries Service (NMFS) permit No. 15682.

References

Arppe, A. 2012. Polytomous: polytomous logistic regression for fixed and mixed effects. R package version 0.1 4. Available from http://search.r-project.org/library/polytomous/html/polytomous.poisson.reformulation.html/.

Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans. Automat. Contr. **19**(6): 716–723. doi:10.1109/TAC.1974.1100705.

Barco, S.G., McLellan, W.A., Allen, J.M., Asmutis-Silvia, R.A., Mallon-Day, R., Meagher, E.M., Pabst, D.A., Robbins, J., Seton, R.E., Swingle, W.M., Weinrich, M.T., and Clapham, P.J. 2002. Population identity of humpback whales (*Megaptera novaeangliae*) in the waters of the U.S. mid-Atlantic states. J. Cetacean Res. Manage. **4**(2): 135–141. Available from http://uncw.edu/mmsp/documents/Barcoetal..pdf [accessed 14 April 2015].

Betancourt, L., Herrera-Moreno, A., and Beddall, K. 2012. Spatial distribution of humpback whales (*Megaptera novaeangliae*) in Samaná Bay, Dominican Republic. Paper SC/64/O12 presented to the IWC Scientific Committee, July 2012 (unpublished).

Bettridge, S., Baker, C.S., Barlow, J., Clapham, P.J., Ford, M., Gouveia, D., Mattila, D.K., Pace, R.M., III, Rosel, P.E., Silber, G.K. and Wade, P.R. 2015. Status review of the humpback whale (*Megaptera novaeangliae*) under the Endangered Species Act. U.S. Department of Commerce, NOAA Technical Memorandum NMFS NOAA-TM-NMFS-SWFSC-540. National Oceanic and Atmospheric Administration, NOAA Fisheries, Southwest Fisheries Science Center, Miami, FL. Available from http://www.fisheries.noaa.gov/pr/species/Status%20Reviews/humpback_whale_sr_2015.pdf.

Box, G.E.P., and Cox, D.R. 1964. An analysis of transformations. J. R. Soc. Ser. B Methodol. **26**(2): 211–252. Available from http://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.321.3819 [accessed 2 March 2016].

Brink, U. 2007. New bathymetric map of Mona Passage, northeastern Caribbean, aids in earthquake- and tsunami-hazard mitigation. US Geological Survey Sound Waves FY, **2007**(93): 1–13. Available from http://soundwaves.usgs.gov/2007/05/ [accessed 12 April 2015].

Cartwright, R., Gillespie, B., LaBonte, K., Mangold, T., Venema, A., Eden, K., and Sullivan, M. 2012. Between a rock and a hard place: habitat selection in female–calf humpback whale (*Megaptera novaeangliae*) pairs on the Hawaiian breeding grounds. PLoS ONE, **7**(5): e38004. doi:10.1371/journal.pone.0038004. PMID:22666432.

Charif, R.A., Clapham, P.J., and Clark, C.W. 2001. Acoustic detections of singing humpback whales in deep waters off the British Isles. Mar. Mamm. Sci. **17**(4): 751–768. doi:10.1111/j.1748-7692.2001.tb01297.x.

Clapham, P.J., and Mattila, D.K. 1993. Reactions of humpback whales to skin biopsy sampling on a West Indies breeding ground. Mar. Mamm. Sci. **9**(4): 382–391. doi:10.1111/j.1748-7692.1993.tb00471.x.

Clapham, P.J., and Mayo, C.A. 1987. Reproduction and recruitment of individually identified humpback whales, *Megaptera novaeangliae*, observed in Massachusetts Bay, 1979-1985. Can. J. Zool. **65**(12): 2853–2863. doi:10.1139/z87-434.

Clapham, P.J., Palsbøll, P.J., Mattila, D.K., and Vasquez, O. 1992. Composition and dynamics of humpback whale competitive groups in the West Indies. Behaviour, **122**(3–4): 182–194. doi:10.1163/156853992X00507.

Corkeron, P.J. 1995. Humpback whales (*Megaptera novaeangliae*) in Hervey Bay, Queensland: behaviour and responses to whale-watching vessels. Can. J. Zool. **73**(7): 1290–1299. doi:10.1139/z95-153.

Corkeron, P.J., and Connor, R.C. 1999. Why do baleen whales migrate? Mar. Mamm. Sci. **15**(4): 1228–1245. doi:10.1111/j.1748-7692.1999.tb00887.x.

Craig, A.S., Herman, L.M., Pack, A.A., and Waterman, J.O. 2014. Habitat segregation by female humpback whales in Hawaiian waters: avoidance of males? Behaviour, **151**: 613–631. doi:10.1163/1568539X-00003151.

Darling, J.D., Jones, M.E., and Nicklin, C.P. 2006. Humpback whale songs: do they organize males during the breeding season? Behaviour, **143**(9): 1051–1101. doi:10.1163/156853906778607381.

Douglas, L.A., Dawson, S.M., and Jaquet, N. 2005. Click rates and silences of sperm whales at Kaikoura, New Zealand. J. Acoust. Soc. Am. **118**(1): 523–529. doi:10.1121/1.1937283. PMID:16119371.

Ersts, P.J., and Rosenbaum, H.C. 2003. Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. J. Zoo. (Lond.), **260**(4): 337–345. doi:10.1017/S0952836903003807.

Félix, F., and Hasse, B. 2001. The humpback whale off the coast of Ecuador, population, parameters and behavior. Rev. Biol. Mar. Oceanogr. **36**(1): 61–74. Available from http://www.redalyc.org/articulo.oa?id=47936106 [accessed 10 April 2015].

Félix, F., and Hasse, B. 2001. The humpback whale off the coast of Ecuador, population, parameters and behavior. Rev. Biol. Mar. Oceanogr. **36**(1): 61–74. doi:10.4067/S0718-19572013000100016.

Frankel, A.S., Clark, C.W., Herman, L.M., and Gabriele, C.M. 1995. Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawai'i, determined using acoustic and visual techniques. Can. J. Zool. **73**(6): 1134–1146. doi:10.1139/z95-135.

Franklin, T., Franklin, W., Brooks, L., Harrison, P., Baverstock, P., and Clapham, P. 2011. Seasonal changes in pod characteristics of eastern Australian humpback whales (*Megaptera novaeangliae*), Hervey Bay 1992–2005. Mar. Mamm. Sci. **27**(3): E134–E152. doi:10.1111/j.1748-7692.2010.00430.x.

Frantzis, A., Nikolau, O., Bompar, J.-M., and Cammeda, A. 2004. Humpback whale (*Megaptera novaeangliae*) occurrence in the Mediterranean Sea. J. Cetacean Res. Manage. **6**(1): 25–28. Available from http://www.pelagosinstitute.gr/en/pelagos/pdfs/mediterranean_megaptera.pdf [accessed 10 April 2015].

Hollander, M., Wolfe, D.A., and Chicken, E. 2013. Nonparametric statistical methods. 3rd ed. John Wiley and Sons, Inc., Hoboken, N.J.

Kaschner, K., Watson, R., Trites, A.W., and Pauly, D. 2006. Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. Mar. Ecol. Prog. Ser. **316**: 285–310. doi:10.3354/meps316285.

Lundquist, D., Gemmell, N.J., and Würsig, B. 2012. Behavioural responses of dusky dolphin groups (*Lagenorhynchus obscurus*) to tour vessels off Kaikoura, New Zealand. PLoS ONE, **7**(7): e41969. doi:10.1371/journal.pone.0041969. PMID:22844536.

Martinez, E., Currie, J.J., Stack, S.H., Easterly, S.K., and Kaufman, G.D. 2015. Note on patterns of area use by humpback whales (*Megaptera novaeangliae*) in 2013 in Hervey Bay, Australia, with an emphasis on mother–calf dyads. Working paper SC/66a/SH2 submitted to the Scientific Committee of the International Whaling Commission, San Diego, Calif. Available from http://www.pacificwhale.org/sites/pacificwhale.org/files/SC_66a_SH_2.pdf.

Martin, A.R., Katona, S.K., Mattila, D., Hembree, D., and Waters, T.D. 1984. Migration of humpback whales between the Caribbean and Iceland. J. Mammal. **65**(2): 330–333. doi:10.2307/1381174.

Martins, C.C.A., Morete, M.E., Engel, M.H., Freitas, A.C., Secchi, E.R., and Kinas, P.G. 2001. Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground. Mem. Queensl. Mus. **47**(2): 83–90. Available from http://www.car-spaw-rac.org/IMG/pdf/Aspects_of_habitat_use_patterns_of_humpback_whales_in_the_Abrolhos_Bank_Brazil_breeding_ground.pdf [accessed 10 April 2015].

Mattila, D.K. 1984. Humpback whales in the Mona Passage, Puerto Rico: a summary. Report from the Center for Coastal Studies, Provincetown, Mass.

Mattila, D.K., and Clapham, P.J. 1989. Humpback whales, *Megaptera novaeangliae*, and other cetaceans on Virgin Bank and in the northern Leeward Islands, 1985 and 1986. Can. J. Zool. **67**(9): 2201–2211. doi:10.1139/z89-311.

Mattila, D.K., Clapham, P.J., Katona, S.K., and Stone, G.S. 1989. Population composition of humpback whales, *Megaptera novaeangliae*, on Silver Bank, 1984. Can. J. Zool. **67**(2): 281–285. doi:10.1139/z89-041.

Mattila, D.K., Clapham, P.J., Vásquez, O., and Bowman, R.S. 1994. Occurrence, population composition, and habitat use of humpback whales in Samana Bay, Dominican Republic. Can. J. Zool. **72**(11): 1898–1907. doi:10.1139/z94-258.

Mercado, E., III, and Frazer, L.N. 1999. Environmental constraints on sound transmission by humpback whales. J. Acoust. Soc. Am. **106**(5): 3004–3016. doi:10.1121/1.428120. PMID:10573910.

Mercado, E., III, Schneider, J.N., Green, S.R., Wang, C., Rubin, R.D., and Banks, P.N. 2007. Acoustic cues available for ranging by humpback whales. J. Acoust. Soc. Am. **121**(5): 2499–2502. doi:10.1121/1.2717495. PMID:17550148.

Mercado, E., III, Green, S.R., and Schneider, J.N. 2008. Understanding auditory distance estimation by humpback whales: a computational approach. Behav. Processes, **77**: 231–242. doi:10.1016/j.beproc.2007.10.007. PMID:18068910.

Mignucci-Giannoni, A.A. 1998. Zoogeography of cetaceans off Puerto Rico and the Virgin Islands. Caribb. J. Sci. **34**(3–4): 173–190. Available from http://manatipr.org/wp-content/uploads/2010/01/MigZoog98CJS.pdf [accessed 11 April 2015].

Mitchell, E.D., and Reeves, R.R. 1983. Catch history, abundance, and present status of northwest Atlantic humpback whales. Rep. Int. Whal. Comm. Spec. issue, **5**: 153–212.

Mondziel, S., Grindlay, M., Mann, P., Escalona, A., and Abrams, L. 2010. Morphology, structure, and tectonic evolution of the Mona Canyon (northern Mona Passage) from multibeam bathymetry, side-scan sonar, and seismic reflection profiles. Tectonics, **29**: 1–23. doi:10.1029/2008TC002441.

O'Brien, R.M. 2007. A caution regarding rules of thumb for variance inflation factors. Qual. Quant. **41**(5): 673–690. doi:10.1007/s11135-006-9018-6.

R Core Team. 2014. R: a language and environment for statistical computing. Version 3.1.1 [computer program]. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Richardson, W.J., Greene, C.R., Jr., Malme, C.I., and Thomson, D.H. 1995. Marine mammals and noise. Academic Press, San Diego, Calif.

Robbins, J., Bérubé, M., Clapham, P., Palsbøll, P., Stevick, P., and Mattila, D. 2001. Group composition and social dynamics of North Atlantic humpback whales (*Megaptera novaeangliae*) on their West Indies breeding grounds. Working paper SC/53/NAH4 submitted to the Scientific Committee of the International Whaling Commission, London, UK.

Schuchert, C. 1936. Historical geology of the Antillean–Caribbean region. J. Geol. **44**(7): 870–874. doi:10.1086/624488.

Smultea, M.A. 1994. Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. Can. J. Zool. **72**(5): 805–811. doi:10.1139/z94-109.

Stevick, P.T., Allen, J., Bérubé, M., Clapham, P.J., Katona, S.K., Larsen, F., Lien, J., Mattila, D.K., Palsbøll, P.J., Robbins, J., Sigurjónsson, J., Smith, T.D., Øien, N., and Hammond, P.S. 2003. Segregation of migration by feeding ground origin in North Atlantic humpback whales (*Megaptera novaeangliae*). J. Zool. (Lond.), **259**(3): 231–237. doi:10.1017/S0952836902003151.

Swartz, S.L., Martinez, A., Stamates, J., Burks, C., and Mignucci-Giannoni, A.A. 2002. Acoustic and visual survey of cetaceans in the waters of Puerto Rico and the Virgin Islands: February–March 2001. NOAA Tech. Mem. NMFS-SEFSC-463. National Oceanic and Atmospheric Administration, NOAA Fisheries, Southwest Fisheries Science Center, Miami, Fla. Available from http://docs.lib.noaa.gov/noaa_documents/NMFS/SEFSC/TM_NMFS_SEFSC/NMFS_SEFSC_TM_463.pdf [accessed 11 April 2015].

Weilgart, L., and Whitehead, H. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. Behav. Ecol. Sociobiol. **40**(5): 277–285. doi:10.1007/s002650050343.

Whitehead, H., and Gordon, J. 1986. Methods of obtaining data for assessing and modelling sperm whale populations which do not depend on catches. Rep. Int. Whaling Comm. Spec. Issue, **8**: 149–166.

Whitehead, H., and Moore, M.J. 1982. Distribution and movements of West Indian humpback whales in winter. Can. J. Zool. **60**(9): 2203–2211. doi:10.1139/z82-282.

Whitehead, H., Dillon, M., Dufault, S., Weilgart, L., and Wright, J. 1998. Non-geographically based population structure of South Pacific sperm whales: dialects, fluke-markings and genetics. J. Anim. Ecol. **67**(2): 253–262. doi:10.1046/j.1365-2656.1998.00187.x.

Würsig, B., Dorsey, E.M., Fraker, M.A., Payne, R.S., and Richardson, W.J. 1985. Behavior of bowhead whales (*Balaena mysticetus*) summering in the Beaufort Sea: a description. Fish. Bull. (Wash., D.C.) **83**: 357–377. Available from http://fishbull.noaa.gov/833/wursig.pdf [accessed 11 April 2015].

Würsig, B., Dorsey, E.M., Richardson, W.J., and Wells, R.S. 1989. Feeding, aerial and play behavior of the bowhead whale (*Balaena mysticetus*), summering in the Beaufort Sea. Aquat. Mamm. **15**(1): 27–37.

This article has been cited by:

1. Laurène Trudelle, Salvatore Cerchio, Alexandre N. Zerbini, Ygor Geyer, François-Xavier Mayer, Jean-Luc Jung, Maxime R. Hervé, Stephane Pous, Jean-Baptiste Sallée, Howard C. Rosenbaum, Olivier Adam, Jean-Benoit Charrassin. 2016. Influence of environmental parameters on movements and habitat utilization of humpback whales (Megaptera novaeangliae) in the Madagascar breeding ground. *Royal Society Open Science* **3**:12, 160616. [CrossRef]
2. Eduardo Mercado. 2016. Acoustic Signaling by Singing Humpback Whales (Megaptera novaeangliae): What Role Does Reverberation Play?. *PLOS ONE* **11**:12, e0167277. [CrossRef]