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REVIEW

Distribution, feeding habits and morphology of killer whales *Orcinus orca* in the Caribbean Sea

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ABSTRACT

1. Killer whales *Orcinus orca* are found in all oceans of the world, but most of our knowledge on the species comes from studies conducted at higher latitudes. Studies on killer whales in the Caribbean have been scarce.
2. We compiled 176 records of killer whales from the Caribbean, including 95 previously unreported records and 81 records recovered from the literature, consisting of 27 capture or kill records, 4 stranding records and 145 sighting records.
3. Our results indicate that killer whales are widespread in the Caribbean Sea and can be found year-round in the region. Mean group size was 3.7 animals. A diversity of prey items was recorded, including sea turtles and marine mammals and possibly fish. We cannot exclude ecotype or morphotype-specific dietary specialization in the Caribbean population. A preliminary morphological analysis of 10 characters in 52 individuals from 21 different groups suggests that Caribbean killer whales do not represent any of the four Antarctic and subantarctic types, type 1 from the northwest Atlantic, or 'resident' and 'transient' killer whales from the northwest Pacific. Some Caribbean killer whales share a combination of characters typical of type 2 in the North Atlantic, whereas others share those typical of 'offshore' killer whales in the northwest Pacific. The significance of this is unclear. Comparison of Caribbean killer whales to previously described morphotypes and ecotypes is hampered by the lack of detailed, quantitative data on variation within other types, as well as by the lack of comparisons of genetic diversity.
4. Our study adds to the growing knowledge of the diversity of killer whales worldwide but underscores that additional research is warranted in the tropics.

INTRODUCTION

The killer whale *Orcinus orca* has a worldwide distribution and is most commonly found in coastal, temperate waters with high marine productivity (Forney & Wade 2006, Taylor et al. 2008, Ford 2009). For most parts of their geographical range, little is known about their biology, abundance and taxonomy, which hinders proper assessment of their conservation status (Anonymous 2008a). Most of our knowledge on the species comes from studies conducted in the North Atlantic (Foote et al. 2009, 2011), Pacific Ocean (Bigg et al. 1987, 1990, Ford et al. 1994, 1998, 2000, Baird 2000, Krahn et al. 2004, Baird et al. 2006), Antarctica (Pitman & Ensor 2003, LeDuc et al. 2008, Pitman et al. 2011) and New Zealand waters (Visser 2007).

The killer whale is recognized as a single species (Rice 1998, Wilson & Reeder 2005, Taylor et al. 2008). Recently, several ecotypes or distinguishable populations have been identified in the north-western Pacific Ocean, north-eastern Atlantic Ocean, New Zealand and Antarctica, differing in morphology, prey preference, social structure and distribution pattern (Ford et al. 1998, Baird 2000, Pitman & Ensor 2003, Visser et al. 2007, Taylor et al. 2008, Pitman et al. 2011). Recent molecular genetics and phylogeographic studies support the view that several ecotypes and populations have unique evolutionary histories, and some may qualify as full species or subspecies (LeDuc et al. 2008, Morin et al. 2010, Anonymous 2011, Foote et al. 2013a). The killer whale, as a single taxonomic unit, is classed as data deficient by the International Union for Conservation of Nature (Taylor et al. 2008). At a local level, some stocks are considered to be under threat, including the killer whales in New Zealand waters (Hitchmough et al. 2007). The so-called Southern Residents of the North Pacific are currently listed as endangered (Anonymous 2008b).

Very little information is available about the occurrence, zoogeography, ecology and morphology of killer whales in the Caribbean Sea. A few records, mostly from St Vincent and the Grenadines, were detailed by Reeves and Mitchell (1988) and Katona et al. (1988). All phylogenetic analyses of killer whales to date lacked samples from the Caribbean Sea (Hoelzel et al. 2002, Morin et al. 2010). This makes it difficult to determine whether killer whales in the Caribbean belong to one or more known ecotypes or might represent another, previously undescribed, ecotype or subpopulation. Regional subpopulations of killer whales can be small and highly specialized, and therefore vulnerable to habitat deterioration and overexploitation (Taylor et al. 2008). A better understanding of the distribution, morphology, ecology and natural history of killer whales in the Caribbean may shed further light on their evolutionary ecology, taxonomy and current status, and will help to set research priorities.

Here we synthesize all known records of killer whales in the Caribbean Sea, add new records based on photographic

evidence and reliable observations, relate these records to the species' spatial and temporal distribution, and present new information on its natural history and morphology.

METHODS

Study area

The study area consisted of the Caribbean Sea and the Atlantic Ocean adjacent to the West Indies. For the analysis of distribution, we divided the area into four subregions which grossly corresponded to the Caribbean ecoregions as described by Spalding et al. (2007): Greater Antilles (including Cuba, Cayman Islands, Dominican Republic, Haiti, Jamaica and Puerto Rico), Eastern Caribbean (Anguilla, Antigua and Barbuda, Barbados, Dominica, Leeward Dutch Antilles, French Antilles, Grenada, Montserrat, St Kitts and Nevis, St Lucia, St Vincent and the Grenadines, U.S. Virgin Islands, British Virgin Islands); Southern Caribbean (Aruba, Bonaire, Colombia, Curaçao, Trinidad and Tobago, Venezuela) and Western Caribbean (Belize, Costa Rica, Guatemala, Honduras, Nicaragua, Panamá and the Caribbean side of the Yucatán Península; Fig. 1).

Records

Killer whale records were obtained from published and unpublished reports dating from May 1866 to November 2012. A request for information (in particular for sightings accompanied by photographs or video footage) was sent out in early 2009 to three international Internet discussion fora on marine mammals (the discussion list of the Group of Experts for the Implementation of the Marine Mammal Action Plan for the Wider Caribbean Region, under the auspices of the Secretariat of the Specially Protected Areas and Wildlife Protocol of the Cartagena Convention; the discussion list of the Dutch Caribbean Cetacean Network; and CBI-Latam, the Latin American Network of Non-Governmental Organizations for Conservation of Cetaceans) and to colleagues working on marine mammals in the Caribbean Sea. We searched the Internet for pictures and video footage of killer whales and reviewed the digital

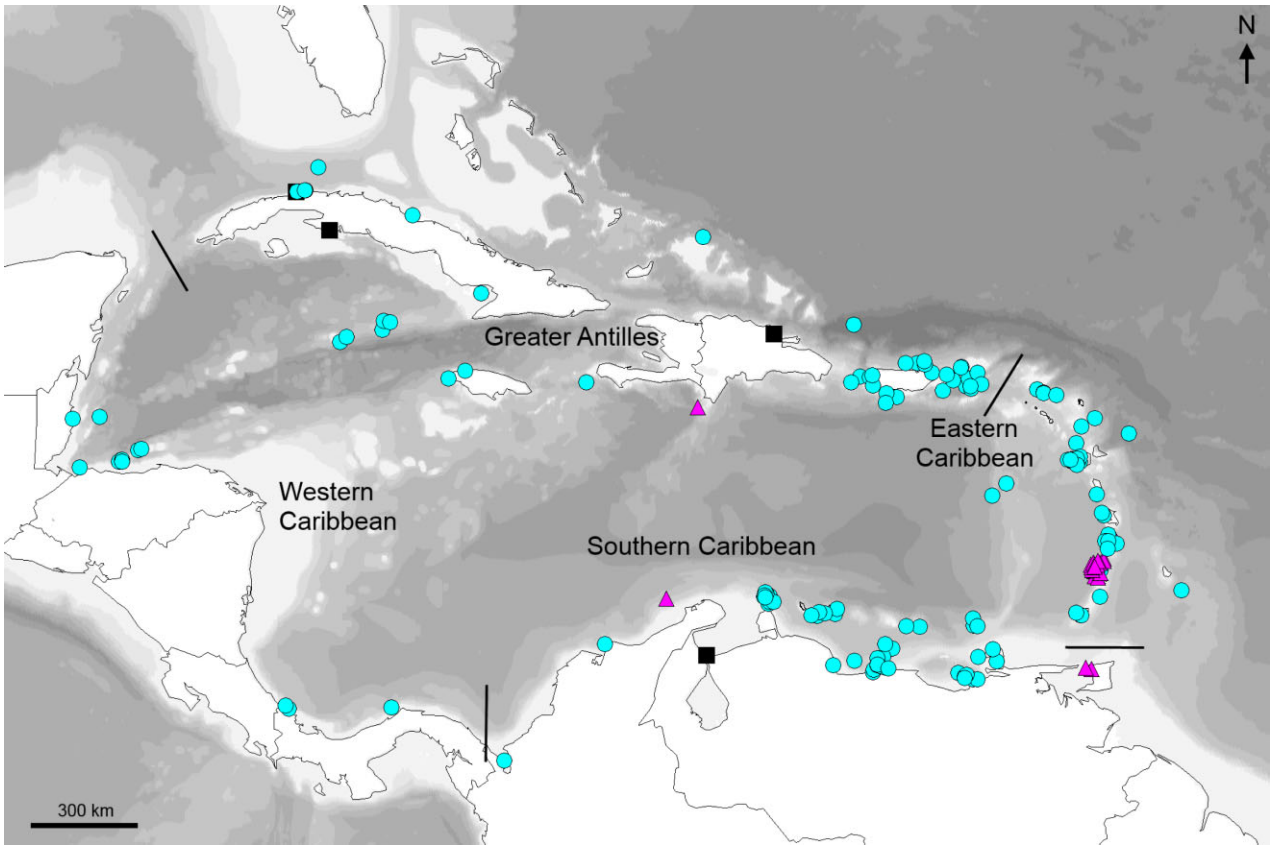

Fig. 1. Distribution of killer whale records ($n = 169$) in the Caribbean region (1866–2012). Circles represent sightings ($n = 138$), squares represent strandings ($n = 4$) and triangles represent captures ($n = 27$). Black lines indicate the limits between the four named subregions.

versions of regional newspapers. Whenever possible, we contacted the journalists and original observers (see Acknowledgements). Records were divided into three categories: captures or takes (either intentional or accidental), strandings and sightings. All captured killer whales were determined to have been killed. Following Katona et al. (1988), records of killer whales on different days were treated as unique, even if locations were not far apart. All of the records are summarized in Appendix S1. The data set, pictures, videos and related information have been uploaded to the Ocean Biogeographic Information System–Spatial Ecological Analysis of Megavertebrate Populations of Duke University (OBIS-SEAMAP, http://seamap.env.duke.edu/dataset/1012; Halpin et al. 2006).

Zoogeography

The distribution of the sighting and capture records was assessed in terms of the following variables: (i) spatial distribution; (ii) depth distribution (500 m depth bins); (iii) seasonal distribution (spring: 1 March–31 May, summer: 1 June–31 August, autumn: 1 September–30 November, and winter: 1 December–28 February); and (iv) tropical temporal distribution (dry season, January–April; rainy season, May–December). Depth at the location of sightings was obtained from nautical charts or from Google Earth v. 5.1 and from the General Bathymetric Chart of the Oceans Digital Atlas system (Anonymous 2012) at a resolution of 30 arcseconds. Kruskal–Wallis tests and Mann–Whitney *U*-tests were used to assess differences in the number of sightings between seasons.

Morphology

Photographs (published and unpublished) of killer whales from different areas of the Caribbean were used to compare morphological characteristics. In all cases, photographic material was available for only one side of each individual, making it impossible to assess symmetry or asymmetry in some characteristics. Whenever possible, multiple photographs of the same animals were used to assess characteristics. Only characteristics that could be viewed laterally during surface activities were chosen for the analysis, consisting of the eye patch, the dorsal fin, the saddle patch and the dorsal cape. Photographs of calves and juveniles were excluded from the analysis, except for those showing the eye patch, which has been demonstrated to show consistency over time (Visser & Mäkeläinen 2000).

Ten characteristics were scored. (1) The shape of the eye patch was placed in one of nine categories described by Visser and Mäkeläinen (2000). (2) The position of the anterior margin of the eye patch relative to the blowhole was determined (anterior to, at, or posterior to the blowhole). (3) The orientation of the eye patch was determined by comparing an imaginary line through the long axis of the eye patch with the body axis (Evans et al. 1982, Visser & Mäkeläinen 2000). (4) The relative length of the eye patch was expressed as a percentage of the distance between the posterior end of the blowhole and the anterior margin of the dorsal fin (based on Visser & Mäkeläinen 2000). (5) The position of the tip relative to the base of the dorsal fin was categorized as follows: (i) anterior to the anterior setting of the dorsal fin, (ii) at the anterior setting of the dorsal fin, (iii) between the anterior and posterior settings of the dorsal fin, (iv) at the posterior setting of the dorsal fin, and (v) beyond the posterior setting of the dorsal fin (Bigg et al. 1987). This character was included because it is known to differ among ecotypes in the north-western Pacific and Antarctica (Baird 2000, Pitman et al. 2011), although there is individual and age-related variation in this character (I. Visser, pers. comm.). (6) The shape of the tip of the dorsal fin was noted (rounded or pointed; Bigg et al. 1987, Ford et al. 2000). (7) The distinctiveness of the saddle patch was noted (faint, intermediate or conspicuous; Baird et al. 2006, Riesch et al. 2012). (8) The shape of the saddle patch was scored based on the categories defined by Evans et al. (1982). (9) The presence or absence of a conspicuous dorsal cape was noted (Evans et al. 1982). (10) The shape of the forehead was noted (bulbous, as in type D killer whales, or non-bulbous; Pitman et al. 2011).

RESULTS

Records

We collected 176 records of killer whales, of which 81 (46%) were obtained from the literature and 95 (54%) are new reports. The records included 27 captures or kills (15%), four strandings (2%) and 145 sightings (82%; Fig. 1).

Captures

Documented captures of killer whales in the Caribbean Sea include intentional captures by whaling ships in the 19th century ($n = 2$), captures in cetacean fisheries in St Vincent and the Grenadines ($n = 22$, see Table 1), captures in Trinidad and Tobago ($n = 2$, Ottley et al. 1988, see Table 1) and the killing of a juvenile killer whale in Colombia in retaliation for depredation on the bait and captures in longline fisheries (Álvarez-León 2002; see Table 1). Most (63%) of these captures occurred during the spring and summer months. Capture data for the cetacean fisheries in St Vincent and the Grenadines are available for the period 1968–2011 and represent 85% (56 individuals) of the total number of captured individuals in the study area. All reported kills of killer whales in these fisheries were made

Table 1. Capture records for killer whales in the Caribbean region from 1866 to 2012; all captured animals were determined to have been killed

Date	Country	*N* (killed)	Latitude	Longitude	Comments	Reference
28 May 1866	Dominican Republic	1	17.500	–71.833	One killer whale and one pilot whale taken at the same time	Reeves & Mitchell 1988
30 Apr 1884	St Lucia	1	14.117	–60.933		Reeves & Mitchell 1988
1925?	Trinidad & Tobago	1	10.642	–61.513	Skull and pictures held at the National Museum & Art Gallery, Port of Spain	Reeves & Mitchell 1988, di Sciara *In Litt.*
13 May 1968	St Vincent	3	13.550	–61.200	Three were taken from a group of six	Caldwell & Caldwell 1969, 1975
May 1968	St Vincent	3	13.483	–61.200		Caldwell & Caldwell 1975
11 Jul 1968	St Vincent	3	13.250	–61.333	Three were taken from a group of eight. One male (6 m long) had heavily worn teeth	Caldwell et al. 1971, Caldwell & Caldwell 1975
4 Jun 1969	St Vincent	4	13.433	–61.300		Caldwell et al. 1971
May 1971	St Vincent	3	13.217	–61.350		Caldwell & Caldwell 1975
Jul 1971	St Vincent	9	13.283	–61.367		Caldwell & Caldwell 1975
Jun 1972	St Vincent	1	13.150	–61.362		Caldwell & Caldwell 1975
Jan 1973	St Vincent	1	13.200	–61.458		Caldwell & Caldwell 1975
May 1974	St Vincent	1	13.083	–61.367		Caldwell & Caldwell 1975
19 Apr 1982	St Vincent	1	13.067	–61.433		Price 1983
16 Aug 1982	St Vincent	2	13.033	–61.350		Price 1983
1986	Colombia	1	12.490	–72.658	4.4-m juvenile, killed in retaliation for depredating on bait and captures in longline fisheries	Álvarez-León 2002
10 Jun 1987	Trinidad & Tobago	1	10.674	–61.666	One female, of a pod of 15 individuals, entangled in drift gillnet and cut up. Remains of unidentified sea turtle found in stomach	Ottley et al. 1988, Vidal et al. 1994
1 Jul 1994	St Vincent	2	13.3.225	–61.417		This paper
7 Apr 1996	St Vincent	5	13.3.152	–61.275	All five whales in the group killed	Sutty, unpublished data
1 May 2000	St Vincent	3	13.3.152	–61.283	All three whales in the group killed	Sutty, unpublished data
5 Nov 2007	St Vincent	1	13.3.233	–61.500		Fielding 2010 and pers. comm.
1 Sep 2008	St Vincent	2	13.3.300	–61.517		Fielding 2010 and pers. comm.
13 Sep 2008	St Vincent	3	13.3.383	–61.533		Fielding 2010 and pers. comm.
7 Nov 2008	St Vincent	1	13.3.433	–61.467		Fielding 2010 and pers. comm.
21 Nov 2008	St Vincent	3	13.3.383	–61.433		Fielding 2010 and pers. comm.
19 Dec 2008	St Vincent	2	13.3.383	–61.367		Fielding 2010 and pers. comm.
20 Dec 2008	St Vincent	1	13.3.483	–61.350		Fielding 2010 and pers. comm.
14 Jun 2011	St Vincent	1	13.3.317	–61.433		This paper

on an opportunistic basis during hunts of the short-finned pilot whale *Globicephala macrorhynchus* (Caldwell et al. 1971, Fielding 2010). Some of these records were pooled by month in the original source (e.g. Caldwell & Caldwell 1975), so it was not possible to determine how many capture events were involved.

Strandings

A total of four stranding events were recorded, each involving one individual. Two strandings were recorded in Cuba in 1910 and 2004 (Blanco Domínguez 2011). One individual stranded in the Dominican Republic in 1871 (Katona et al. 1988), and one individual stranded in Venezuela on 25 January 1979 (Rodríguez et al. 1993).

Sightings

Killer whales have been sighted in the Caribbean since the mid-19th century, though no records exist between 1895 and 1964. There were 145 sightings of killer whales in the Caribbean Sea. Of these, 13 (9%) were recorded during dedicated research surveys (Boisseau et al. 2006, Rinaldi et al. 2006, Magileviciute 2007, Ridoux et al. 2010, Luksenburg 2014). One male was resighted in Honduras in August 2007, six years after it was first recorded in August 2001 (Magileviciute 2007).

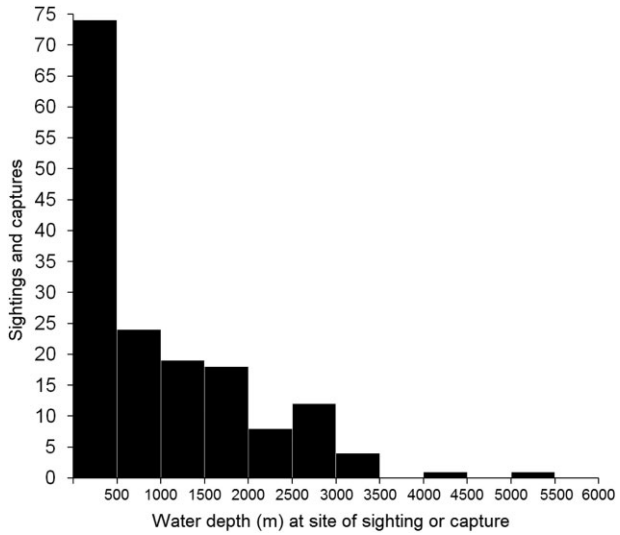

Fig. 2. Distribution of Caribbean killer whale sightings and captures ($n = 161$) in relation to water depth at site of sighting or capture (depth bins of 500 m).

Zoogeography

Killer whales were found most frequently in the Eastern Caribbean ($n = 71$), followed by the Southern Caribbean ($n = 54$), Greater Antilles ($n = 38$) and Western Caribbean ($n = 13$; Fig. 1).

The water depth at the location of the sightings and capture records ranged from 18 m to 8396 m. The majority of killer whales were sighted in waters less than 1000 m deep ($n = 97$, 60%; Fig. 2). Almost all killer whales were sighted in waters less than 3000 m deep ($n = 155$, 96%). There was one sighting in water of 8396 m deep. Killer whales were observed in both neritic and oceanic waters.

Killer whales were recorded (seen and captured) in all months of the year; the highest number was in April ($n = 21$, 15%) and the lowest in September ($n = 4$, 3%; Fig. 3). Spring had the highest number of records ($n = 48$, 35%), followed by summer ($n = 31$, 22%), autumn ($n = 31$, 22%) and winter ($n = 29$, 21%). The number of sightings did not vary significantly in seasonal distribution (Kruskal–Wallis test; $h = 3.29$, d.f. = 3, $P = 0.35$) or tropical temporal distribution (Mann–Whitney U-test; $P = 0.54$). During the rainy season, 86 records were made (62%), compared with 53 records during the dry season (38%).

Morphological characteristics

Photographs of 46 adult individuals (27 males, 19 females) and six calves or juveniles from 21 different groups were available for analysis. Seven characters were variable within the sample (Figs 4 and 5). Three further characters did not vary among the sampled individuals. In all whales where a saddle patch could be discerned, the patch was narrow and closed (Fig. 5). All animals lacked a conspicuous dorsal cape, and all lacked the bulbous head shape typical of sub-antarctic type D killer whales. No clear associations were apparent among the states of variable characters, although sample sizes were too small for meaningful statistical analysis.

Natural history

Killer whales were observed in groups ranging from one to 25 animals; the mean group size was 3.7 (standard deviation = 3.9). The majority of the records (81%) were of groups of 1–5 individuals, but one group of 25 individuals was seen. There was no correlation between group size and water depth (Spearman product–moment correlation $r = 0.08$, $P = 0.32$).

Confirmed prey items included leatherback turtles *Dermochelys coriacea*, unidentified sea turtles and marine mammals (pygmy sperm whale *Kogia breviceps* and an unidentified whale; Table 2). Marine mammal species that may have been attacked by killer whales include pantropical spotted dolphin *Stenella attenuata*, short-finned pilot whale and Bryde's whale *Balaenoptera brydei/edeni* (Table 2, Fig. 6), but predation could not be confirmed. Non-predatory association was recorded with sperm whales *Physeter macrocephalus*. The evidence for fish as prey items is indirect. There is one record of killer whales feeding on 'bonito' (Scombridae) thrown to them by fishermen in Panamá (Table 2). There is a further record of killer whales

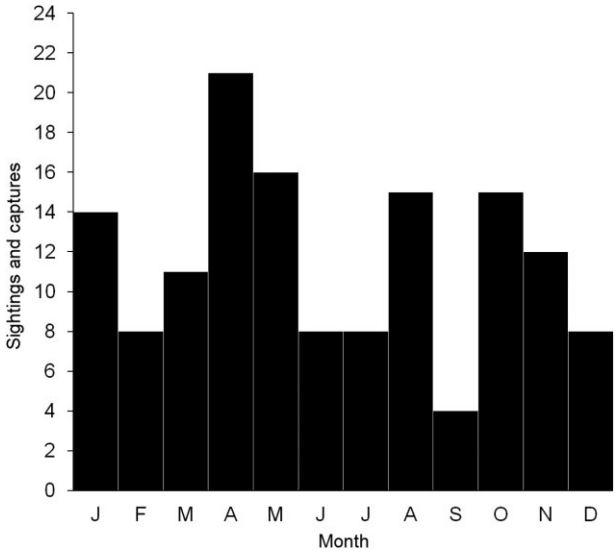

Fig. 3. Monthly distribution of killer whale sightings and captures throughout the Caribbean from 1866 to 2012 ($n = 139$).

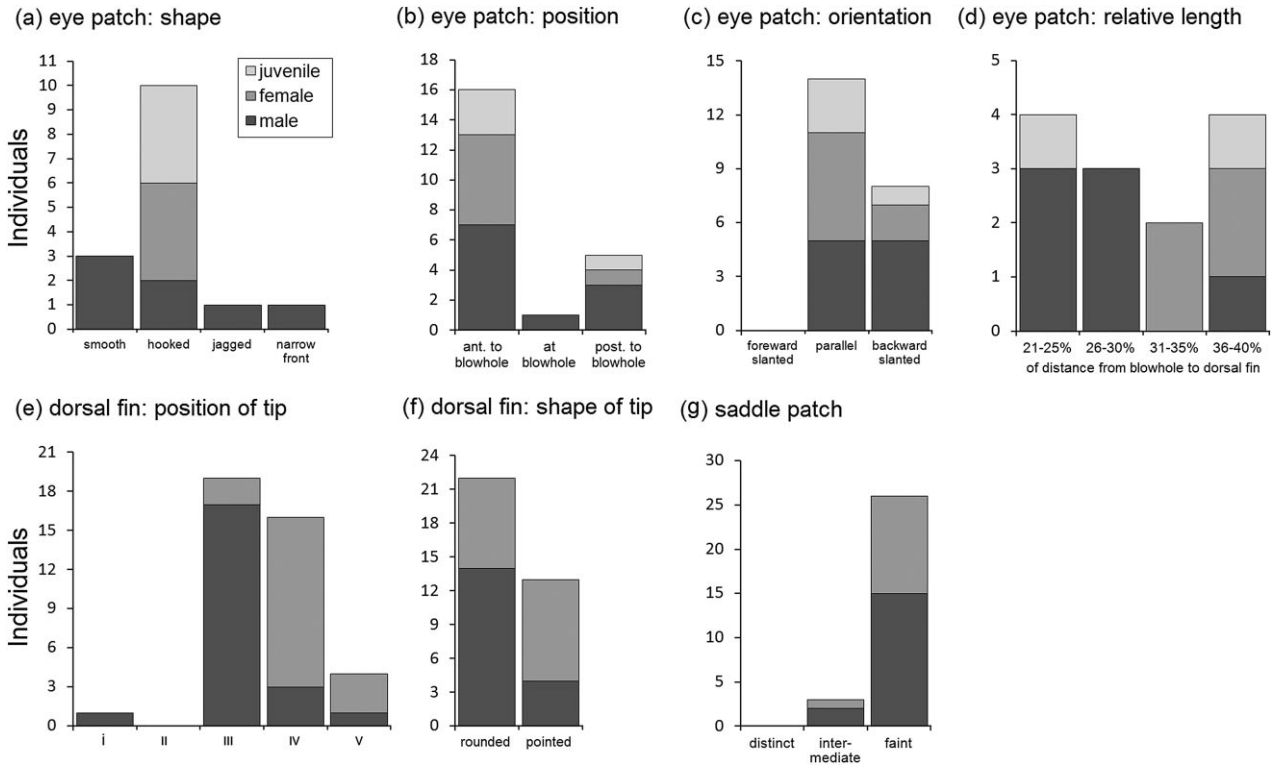

Fig. 4. Morphological variation in seven variable characters quantified in 46 adult and six juvenile killer whales in the Caribbean: (a) eye patch shape in 15 individuals belonging to 10 different groups (five of the nine categories did not occur and are not shown), (b) eye patch position in 22 individuals from 14 groups, (c) eye patch orientation in 22 individuals from 13 groups, (d) relative length of eye patch in 13 individuals from 10 groups, (e) position of tip of dorsal fin in 40 individuals from 19 groups (see Methods, Morphology, for definitions of categories), (f) shape of tip of dorsal fin in 35 individuals from 15 groups, (g) distinctiveness of the saddle patch in 29 individuals from 13 groups. No variation was found in the remaining three characters: the saddle patch was narrow and closed in all individuals, and none had a dorsal cape or a bulbous forehead. Ant., anterior; post., posterior.

in Aruban waters that appeared to be hunting fish (Luksenburg, pers. obs.). In an area favoured by local fishermen for its tuna *Thunnus* sp., wahoo *Acanthocybium solandri* and mahi-mahi *Coryphaena hippurus*, a group of five killer whales showed hunting behaviour (the individuals were scattered with up to 2 km distance between them and were swimming and diving in various directions but remained in the same area) for approximately one hour. Oil was observed on the water surface in the area, as well as numerous flying fish and tuna. Black-capped petrels *Pterodroma hasitata* were observed flying in the same area (as low as 10 cm above the water surface) and diving over the killer whales whenever they surfaced. Black-capped petrels are known to feed on squid, shrimp and fish (Haney 1987, Simons et al. 2006). Associations were also recorded with fishing lines and fish-aggregating devices and depredation was documented only in one case (see Table 1).

Information on both morphological characters and their associations was obtained from four sightings of killer whales. (1) One female associating with sperm whales in Jamaica (early 2006) had a slightly backward-slanted eye patch of which the anterior margin was located anterior to the blowhole, a slightly backswept dorsal fin (position iv) with a pointed tip, and a faint saddle patch. (2) One male in Barbados (January 2007), which was observed killing a pygmy sperm whale, had a parallel-oriented eye patch of which the anterior margin was located anterior to the blowhole, a straight dorsal fin (position iii) with a rounded tip, and an intermediate saddle patch. (3) Two males possibly hunting fish in Aruba (April 2011) had backward-slanted eye patches of which the anterior margins were located posterior to the blowhole (behind the blowhole), straight dorsal fins (position iii) with rounded tips, and faint saddle patches (Fig. 5). A third male had a forward-slanted dorsal fin (position i), and a fourth female had a straight dorsal fin (position iii) with a rounded tip. (4) One male in Puerto Rico (October 2010) observed associating with fishing gear had a parallel-oriented eye patch of which the anterior margin was located posterior to the blowhole. Two males had straight dorsal fins (position iii) with rounded tips and

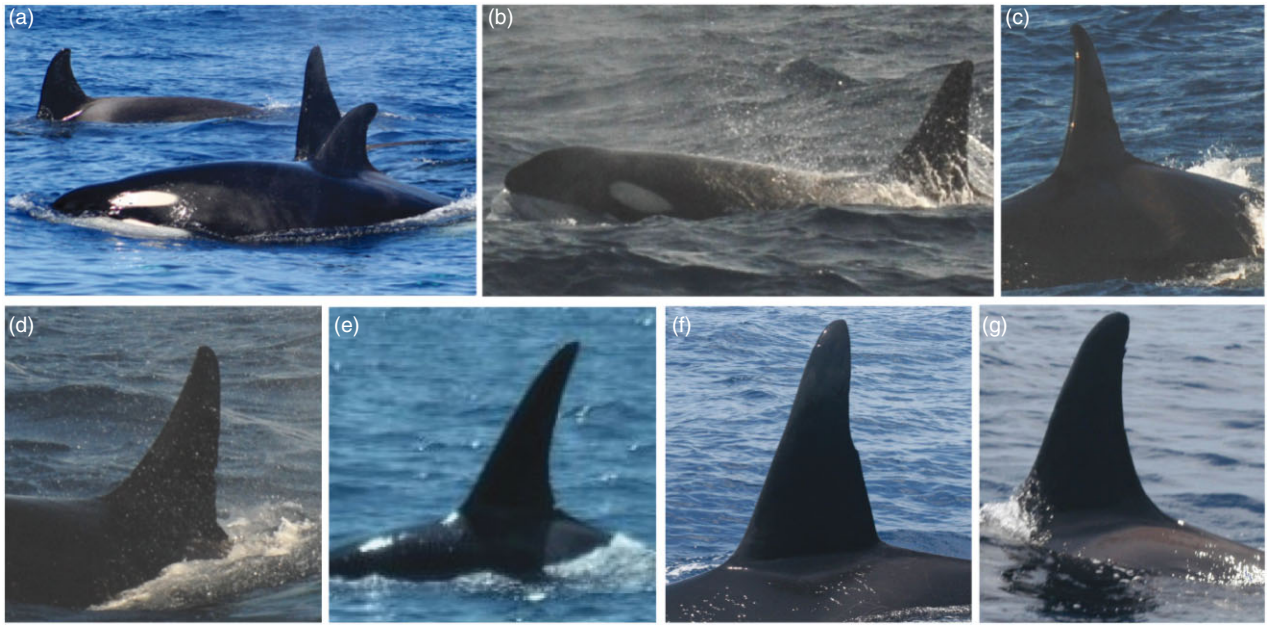

Fig. 5. Morphological variation in adult killer whales in the Caribbean: (a) parallel oriented eye patch, anterior margin of the eye patch before the blowhole (Guadeloupe 2006; photo: C. Rinaldi), (b) slightly backward-slanted eye patch, anterior margin of the eye patch after the blowhole, length 29% (Aruba 2011; photo: J.A. Luksenburg), (c) faint, narrow, closed saddle patch (Aruba 2011; photo: J.A. Luksenburg), (d) straight dorsal fin (position iii) with rounded tip (Aruba 2011; photo: J.A. Luksenburg), (e) backward-slanted dorsal fin (position v) with pointed tip (Aruba 2009; photo: G. Werleman), (f) straight dorsal fin (position iii) with pointed tip (Utila 2007; photo: S. Box), (g) straight dorsal fin (position iii) with rounded tip (Utila 2007; photo: S. Box).

faint saddle patches. A female in this group had a slightly backswept dorsal fin (position iv) with a pointed tip and intermediate saddle patch.

DISCUSSION

Until now, studies of the whaling operations in St Vincent and the Grenadines have been the most important source of information on the presence of killer whales in the Caribbean region (e.g. Caldwell & Caldwell 1969, 1975, Caldwell et al. 1971, Price 1983, 1985, Fielding 2010). The present study is the most comprehensive review of the presence of killer whales in this region. A limitation of this study was that sighting data were not collected systematically. Thus, the location of records reported here probably relates more to the distribution of human activities than to the relative abundance of killer whales themselves. Despite this limitation, our study documents the regular and widespread presence of killer whales in the Caribbean region. Killer whales were observed in all regions within the study area, in both neritic and oceanic waters, and in all months of the year. More detailed, systematic surveys are necessary to document the offshore distribution, relative abundance, habitat preference and prey preference of killer whales in the Caribbean region.

Captures of killer whales occurred throughout the year but were more common during the spring and summer months. The killing of a juvenile killer whale in Colombia is the only case of retaliation known for the Caribbean Sea. Various authors have previously commented on the seasonal distribution of the species in the Caribbean. On the basis of five records from March to July, Reeves and Mitchell (1988) speculated that there might be one or more stocks during the summer in the Caribbean Sea. Katona et al. (1988) listed 14 dated records from the Caribbean, ranging from January to October, but noted that more data were necessary to interpret seasonal distribution. In Venezuela, Bolaños-Jiménez et al. (2009) recorded 18 killer whale sightings, of which 15 occurred between December and May. They concluded there was not enough information to speculate on any seasonality in the presence of killer whales in Venezuelan waters. In Honduras, Magileviciute (2007) suggested that the resighting of individual KW001-01W indicated the possibility of seasonal migration routes for this species in the waters off Utila Island. The absence of seasonal differences in the number of records with regard to the northern and tropical temporal distribution, as well as the opportunistic nature of records, preclude any interpretation on the probable origin or residence pattern of killer whales in the Caribbean Sea. Our results show that killer

Table 2. Summary of bio-ecological interactions of killer whales *Orcinus orca* in the Caribbean Sea, including predatory and non-predatory associations with other species

Date	Country	Group size	Association	Comments	Reference
28 May 1866	Dominican Republic	1	Pilot whale *Globicephala macrorhynchus*	One killer whale and one pilot whale taken at the same time	Reeves & Mitchell 1988
30 Apr 1884	St Lucia	1	Humpback whale *Megaptera novaeangliae*	Five humpback whales were seen at the same time as one killer whale was killed. No predation was documented	Reeves & Mitchell 1988
13 May 1968	St Vincent	6	Leatherback turtle *Dermochelys coriacea*	Remains of leatherback turtle found in stomach of three killed killer whales (adult female, subadult female, juvenile male)	Caldwell & Caldwell 1969
11 Jul 1968	St Vincent	3		One male (6 m long) with heavily worn teeth	Caldwell et al. 1971
≤1970	Puerto Rico	25	Unidentified whale species	25 killer whales attacking a large, unidentified whale	Erdman 1970
1986	Colombia	–	Longliners	Depredated on bait and captures, killed in retaliation	Álvarez-León 2002
10 Jun 1987	Trinidad	–	Unidentified sea turtle	Turtle remains found in stomach of one caught killer whale	Ottley et al. 1988
6 May 2002	Venezuela	–	Bryde's whale *Balaenoptera brydei/edeni*	Probable killer whale bite marks on a stranded Bryde's whale. Predation not confirmed	Bermúdez-Villapol & Sayegh 2005
29 May 2003	Aruba	–	Pilot whale *Globicephala macrorhynchus*	Probable killer whale bite marks on a stranded pilot whale. No predation confirmed	A. Henriquez, unpublished data
early 2006	Jamaica	5	Sperm whale *Physeter macrocephalus* and fishing gear	Some whales apparently interested in fishing gear but no depredation was documented	Pictures by S. Carvalho, courtesy C. O'Sullivan and C. Hanson
27 Jan 2007	Barbados	2	Pygmy sperm whale *Kogia breviceps*	Attacking and feeding on the pygmy sperm whale	Eastern Caribbean Cetacean Network newsletter, 27 Jan 2007; Ward, unpublished data; J. Pierce, pers. comm., 2012
15 Apr 2007	Venezuela	3	*Dermochelys coriacea*	Encircling and turning the turtle upside down. Turtle was last seen being dragged underwater, but consumption was not documented	Bolaños-Jiménez et al. 2009, Oviedo et al. 2009
20 Sep 2009	Puerto Rico	2–4	Fishing gear	No depredation observed	A.A. Mignucci-Giannoni, pers. obs. G. Rodríguez-Ferrer, pers. obs.
3 Nov 2009	Aruba	8–10	Unidentified species	Scattered blubber-like tissue observed in the vicinity of the sighting location	G. Werleman, pers. comm.
17 Oct 2010	Puerto Rico	8	Fishing gear	No depredation observed	A.A. Mignucci-Giannoni, pers. obs. G. Rodríguez-Ferrer, pers. obs.
14 Apr 2011	Aruba	5	Tuna *Thunnus* sp.	Hunting behavior of killer whales. Black-capped petrels *Pterodroma hasitata* hovering very low over the killer whales when they surfaced	J.A. Luksenburg, pers. obs.
22 Apr 2007	Venezuela	5	Fishing gear and bait	No depredation observed	Mazquiarán, pers. comm.
5 May 2007	Venezuela	3	Fishing gear	No depredation observed	Bolaños-Jiménez et al. 2009
5 Apr 2009	France (St Barthelemy)	1	Fishing aggregating device	No depredation observed	Natural Reserve St. Barth, Association Evasion Tropicale
25 Apr 2009	France (St Barthelemy)	1	Fishing aggregating device	No depredation observed	Nat. Res. St Barth, Association Evasion Tropicale
6 Sep 2009	France (St Barthelemy)	1	Fishing aggregating device	No depredation observed	Nat. Res. St Barth, Association Evasion Tropicale
8 May 2010	Panamá	1	Tuna, bonito, Scombridae	One killer whale observed feeding on fish thrown by humans	Tomás Cusatti, pers. comm.
30 Aug 2011	France (Martinique)	3	Sperm whale *Physeter macrocephalus* calf	No predation observed	J.M. Renaux
30 Nov 2011	Puerto Rico	6–7	Fishing gear	No depredation observed	A.A. Mignucci-Giannoni, pers. obs. G. Rodríguez-Ferrer, pers. obs.
11 Oct 2012	France (Martinique)	7	Pantropical spotted dolphin *Stenella attenuata*, small sea turtle	Animal remains floating on the water surface at the location of sighting. No predation observed	D. Delgrange, pers. comm.

Fig. 6. Wounds probably inflicted by killer whales on other marine mammals in the Caribbean Sea: (a) pilot whale *Globicephala macrorhynchus* in Aruba (photo: A. Henríquez), (b) Bryde's whale *Balaenoptera brydei/edeni* in Venezuela (photo: A. Sayegh, taken from Bermúdez-Villapol & Sayegh 2005).

whales are present year-round in the Caribbean, but it remains unclear whether they represent one or more resident populations, or perhaps multiple populations that visit the Caribbean at different times of the year. Studies using photo identification, genetics or telemetry are necessary to establish the movements of killer whales in the Caribbean.

This study documents that killer whales in the Caribbean are variable in a number of morphological characters that are known to differ among other, previously described populations and types. Characters include the position, orientation and relative length of the eye patch (Visser & Mäkeläinen 2000, Foote et al. 2009), the shape of the tip of the dorsal fin and its location in relation to the base of the dorsal fin (Bigg et al. 1987, Pitman et al. 2011), the shape of the saddle patch (Baird & Stacey 1988) and, to a lesser extent, the distinctiveness of the saddle patch (Baird et al. 2006, Riesch et al. 2012). However, the small size of our data set precludes a formal test to determine if there could be more than one morphotype present in the Caribbean Sea.

The killer whales in the Caribbean differed from all four described types of Antarctic and subantarctic killer whales. Thus, Caribbean killer whales (i) had closed saddle patches that were less distinct than those of Antarctic types A, B and C, (ii) lacked the conspicuous dorsal cape of types B and C, and (iii) had much larger eye patches than type D killer whales, as well as lacking their typical bulbous head shape (Pitman & Ensor 2003, Pitman et al. 2007, 2011).

Killer whales in West Africa were broadly similar to those in our study (Weir et al. 2010). However, detailed comparison between the two populations is not possible due to a lack of detailed and quantified data about the West African killer whales. Some killer whales in the Caribbean shared characteristics with those typical of type 2 in the North Atlantic: a backward-slanted eye patch, the anterior margin of the eye patch being located behind the blowhole, and a faint saddle patch (Foote et al. 2009). This combination of character states was observed in two of the 12 adult individuals from nine different groups for which all three characters could be scored. These two individuals may have been hunting tuna (J.A. Luksenburg, pers. obs.). In our data set, no killer whales possessed the conspicuous saddle patch typical of type 1 in the North Atlantic.

The three types of killer whale found in the north-east Pacific differ in morphology (Baird 2000). The Caribbean killer whales had overlapping character states only with the 'offshore' type, which is characterized by a rounded tip of the dorsal fin, a faint saddle patch and a parallel eye patch (Ford et al. 1994). This combination of character states was found in four adults (out of 10 individuals of eight different groups for which data on all three characters were available). One of these four adults had an intermediate saddle patch. Caribbean killer whales differed from the 'resident' and 'transient' types in the north-east Pacific by their faint saddle patch and from 'resident' killer whales also by their closed saddle (often open in 'resident' individuals; Baird & Stacey 1988, Baird et al. 2006). Killer whales in Hawaii have narrow, faint and closed saddle patches, similar to those observed in the Caribbean, but there is no further information on the morphology of that population (Baird et al. 2006). The comparison of Caribbean killer whales to previously described types is hampered by the lack of detailed, quantitative data on variation within other types and by the fact that Caribbean killer whales appear to be rather nondescript in their features.

Average group size of killer whales in the Caribbean (3.7) was similar to that in other tropical seas including those off the Bahamas (4.2, $n = 34$, Dunn & Claridge 2014), Hawaii (4.2, $n = 21$, Baird et al. 2006) and West Africa (5.6, $n = 32$, Weir et al. 2010). It was also similar to the group size of killer whales hunting seals in Scottish waters of the North Atlantic (5.5, Beck et al. 2012) and mammal-eating killer whales in the north-east Pacific (4.2, Baird & Dill 1995). In contrast, in the waters of Iceland in the North Atlantic, a mean group size of 14.8 was estimated for killer whales hunting herring *Clupea* sp. (Beck et al. 2012).

Our data on the diet of Caribbean killer whales indicate that it is most likely diverse, including sea turtles, marine mammals and possibly fish. Although Caribbean killer whales have not been directly observed feeding on fish, there are indications that fish could be part of their diet. The record of a male with heavily worn teeth in St Vincent (Tables 1 and 2) is suggestive of a fish-dominated diet. Severe apical tooth wear has also been observed in offshore killer whales in the north-eastern Pacific, a population believed to feed predominantly on sharks and large teleost fish (Krahn et al. 2007, Ford et al. 2011), and in type 1 killer whales in the North Atlantic, which feed predominantly on fish (Foote et al. 2009, 2013b). Diets of mainly salmon or marine mammals do not result in severe apical tooth wear (Foote et al. 2009, Ford et al. 2011). In the Bahamas, killer whales were only observed preying on marine mammals, but sample size was small (Dunn & Claridge 2014). Our results are similar to those of Weir et al. (2010), who reported a similarly broad range of prey items of killer whales in West African waters. It has been suggested that killer whales in the tropics are likely to be generalists (as opposed to more specialist killer whales in temperate regions; Baird et al. 2006). Our data, and those of Weir et al. (2010), are consistent with this hypothesis. However, we cannot exclude group-specific or morphotype-specific dietary specialization in killer whales in the Caribbean.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Summary of killer whale sightings, strandings and captures in the Caribbean Sea (1866–2012).