The Killer Whale in the Caribbean Sea: An Updated Review of Its Ecology, Exploitation, and Interactions with Fisheries

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Abstract

The killer whale (Orcinus orca) is a cosmopolitan cetacean distributed worldwide. Extensive studies have described its ecology and behavior across multiple polar and temperate regions. On the other hand, there is limited information on the distribution, ecological roles, and abundance of killer whales in tropical and subtropical regions. Herein, we build on previous work to update information on the spatiotemporal distribution, exploitation, and natural history of killer whales in the Caribbean Sea. We also document new records on their interaction with other species and human activities. We collated 385 records from the literature, online biodiversity information systems, the Internet (social networks and video-hosting websites), and citizen science-based initiatives. Records included sightings (87.3%), intentional captures (10.6%), bycatch (0.3%), and strandings (1.8%). Data primarily originated from research projects/activities (57%) and citizen science-based initiatives (43%). Records were distributed in the eastern Caribbean (39.5%), the southern Caribbean (19.7%), the Greater Antilles (19.2%), the Bahamian Region (13.0%), Central America (6.8%), and eastern Florida (1.8%). Killer whales were recorded year-round, but most data were reported between March and August (59.6%). The scarcity of records in Central America could reflect true lower densities in the region, lower observation

effort, or a combination of the two. Because of the paucity of data, this study supports the growing importance of citizen-science initiatives to document the occurrence and ecology of this species in the Caribbean. Our dataset also confirms the occasional and widespread occurrence of killer whales throughout the Caribbean Sea. Potential low densities and limited predictability of their occurrence hinder dedicated research on this species.

Key Words: western tropical Atlantic, occurrence, feeding ecology, exploitation, bycatch, killer whales, *Orcinus orca*

Introduction

Cetacean diversity in the Caribbean Sea is high, including at least 31 cetacean species (Ward & Moscrop, 1999; Ward et al., 2001; Debrot et al., 2013; Lucke et al., 2014), which accounts for one-third of the world's cetacean biodiversity. However, knowledge of the ecology of cetaceans in the region is limited; and for most species, their occurrence, distribution, and movement patterns remain poorly understood (Ward et al., 2001; Lucke et al., 2014; Luksenburg, 2014). This lack of information is largely due to the paucity of systematic surveys in the region, despite more extensive efforts in recent years (2012 to 2022), mainly in the eastern Caribbean (Gandilhon et al., 2012; Debrot et al.,

2013; Mannocci et al., 2013; Geelhoed et al., 2014; Van Canneyt et al., 2018) and the Greater Antilles (MacKay et al., 2016, 2019; Stevick et al., 2018). The lack of data is probably due to the high costs and limited capacity of most states from the region to carry out dedicated research as most of them are among the "low-income" and "lower-middle-income" classifications (World Bank, 2022).

During the last decade, the increased quality and availability of digital cameras and equipped mobile phones has led to an increase in new image data through "citizen-based science" initiatives (Andrachuk et al., 2019; Garcia-Soto et al., 2021). The growing documentation of opportunistic sightings of wildlife species by nonspecialists, coupled with increased data sharing on social networks (e.g., Facebook, Instagram, TikTok) and video-hosting websites (e.g., YouTube), has created an important source of potentially valuable information for cetacean biologists and conservationists. In cetaceans, for example, citizen sciencebased initiatives have contributed to improving the knowledge of ecology, distribution, and densities of several species in British Columbia, Canada (Harvey et al., 2018), the strait of Sicily, Italy (Alessi et al., 2019), and Chile (García-Cegarra et al., 2021). In the Caribbean Sea, citizen-science data were used to model the habitat preferences of the pantropical spotted dolphin (Stenella attenuata; Barragán-Barrera et al., 2019; Courtin et al., 2022) and the migratory movements of humpback whales (Megaptera novaeangliae; Stevick et al., 2018; www.happywhale.com).

The killer whale (Orcinus orca) is a cosmopolitan cetacean distributed worldwide, capable of extensive movements (Jefferson et al., 2015). Satellite telemetry and photo-identification methods suggest that some individuals can travel over 8,000 km (Guerrero-Ruiz et al., 2005; Matthews et al., 2011; Durban & Pitman, 2012). Most research on the biology and ecology of killer whales has been carried out in polar and temperate waters across the globe (Ferguson et al., 2010; Durban et al., 2016; Reeves et al., 2017), whereas information on the behavior, occurrence, and natural history of this species is generally lacking in tropical and subtropical regions (Bolaños-Jiménez et al., 2014; Terrapon et al., 2021).

Until 2014, information on the occurrence and exploitation of killer whales in the Caribbean Sea was limited to whaling records from the southeastern Caribbean, particularly in St. Vincent and the Grenadines (Caldwell et al., 1971; Caldwell & Caldwell, 1975; Price, 1985; Fielding, 2010; Fielding & Kiszka, 2021). Additional records came from a review of the sightings and intentional takes by the former "American pelagic" whaling fleet

that operated in the North Atlantic (1851 to 1894; Reeves & Mitchell, 1988) and a literature review by Katona et al. (1988) of records collected in the central-western Atlantic.

Over the past two decades, there has been an increase in published reports on the distribution and behavior of killer whales from tropical and subtropical regions (Weir et al., 2010; Rankin et al., 2013; Bolaños-Jiménez et al., 2014; Pitman et al., 2015; Whitt et al., 2015; Testino et al., 2019; Denkinger et al., 2020; Vargas-Bravo et al., 2020; Castro Azofeifa, 2021; Iñíguez-Bessega et al., 2021; Kiszka et al., 2021; Terrapon et al., 2021). For most of these published studies, however, sample sizes are usually small, and most records are based on opportunistic, occasional sightings or stranding events detected during research surveys or reported by third parties.

Herein, we provide an update on the first review of the distribution, ecology, and morphology of Caribbean killer whales (Bolaños-Jiménez et al., 2014). We reviewed the most recent published and gray literature, and new unpublished records (e.g., sighting, stranding, and catch records) from various sources (e.g., systematic surveys, citizen science-based data, multiple online sources) to further advance knowledge on the ecology, spatiotemporal distribution, and threats of killer whales in the Caribbean Sea.

Methods

The region of interest for this review is the Caribbean Sea (Figure 1), which was further divided into six ecoregions (modified from Spalding et al., 2007, and Bolaños-Jiménez et al., 2014): (1) the Bahamian region, (2) the Greater Antilles, (3) the eastern Caribbean, (4) the southern Caribbean, (5) Central America, and (6) eastern Florida. Following Jefferson et al. (2009) and Bolaños-Jiménez et al. (2014), information on killer whale occurrence in the study area was collated by reviewing the literature and online biodiversity information systems (OBIS SEAMAP: www.observation.org, www.obsenmer.org) and from reports submitted directly to the authors and collaborators by interested parties (i.e., experienced observers, whale watchers, local nongovernmental organizations, citizen science-based initiatives). We also included searches of posts on social media (e.g., Facebook, Instagram, Twitter, TikTok), video-hosting websites (e.g., YouTube), and reports from citizen science-based initiatives. The records were classified as sightings, strandings, intentional takes (i.e., "takes" defined as sightings that resulted in the intentional kill of at least one individual), and incidental captures (or bycatch).

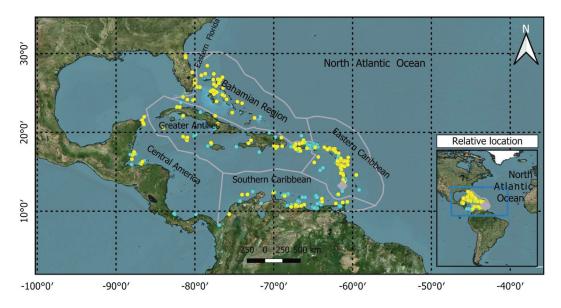


Figure 1. Map of the Caribbean Sea indicating the regionalization (ecoregions modified from Spalding et al., 2007, and Bolaños-Jiménez et al., 2014) and the sources of the dataset. Light blue dots: records published in Bolaños Jiménez et al. (2014) (n = 176; 1866 to 2012). Yellow dots: new records (n = 209; May 1851 to January 2023). The gray diamond indicates 35 take events involving at least 83 individuals landed in Barrouallie, St. Vincent and the Grenadines, for which coordinates are not available. (Basemap: Bing; https://www.microsoft.com/en-us/maps)

The records were classified also as originated by (1) scientific projects or activities and (2) citizen science-based initiatives. Scientific projects or activities included gray or published literature, research surveys, reviews of logbooks from whaling ships operating in the 19th and 20th centuries in the North Atlantic and the Caribbean Sea, online biodiversity information systems, and records available in field notebooks from researchers. Citizen science included any multimedia material shared on social media or uploaded to video-hosting websites, as well as records provided by organized initiatives from the public, naturalists, whale watchers, and so on.

All confirmed records that included the date and GPS coordinates were added to the database. When GPS coordinates were not provided but the observers indicated the distance to the coast and/or a reference point, we estimated approximate coordinates and added them to the database (Katona et al., 1988; Jefferson et al., 2009). The coordinates were entered into the freely available geographical information system *QGIS*, Version 3.22 (QGIS.org), to visualize the spatial distribution of records. Other information for each record included the source and origin of the record, group size and composition (e.g., presence of calves, females, or juveniles), and links to social media. The identification of

each record was evaluated and then coded with one of two confirmation codes (modified from Jefferson et al., 2009):

- Confirmed Records that included videos, photographs, or the explicit description of diagnostic characters and/or validation by another knowledgeable cetologist.
- Rejected Records lacking availability of diagnostic characters and that were of doubtful accuracy. These records were not included in the analysis.

All the new records included in this review were evaluated and validated by the lead author (JBJ) before being added to the dataset. Any published information on the occurrence, ecology, and exploitation of killer whales in the Caribbean region was also compiled. Whenever possible, interactions with other species (i.e., sea turtles, fish, other cetaceans) were also documented. Interactions with boats and fishing gear were recorded as well. We defined "interaction" as any approach to or swimming at the sides of the whales to either a recreational boat, a fishing boat, nets, fishing aggregating devices, or fishing lines.

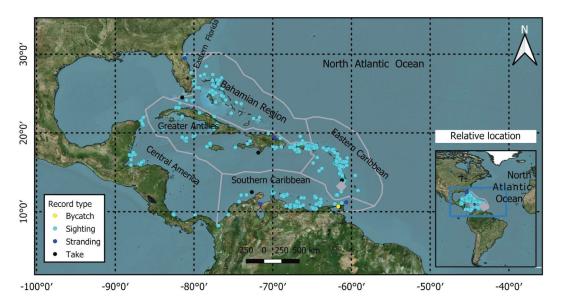


Figure 2. Killer whale records in the Caribbean Sea, May 1851 to January 2023, classified by record type. The gray diamond indicates 35 take events involving at least 83 individuals landed in Barrouallie, St. Vincent and the Grenadines, for which coordinates are not available. (Basemap: Bing; https://www.microsoft.com/en-us/maps)

Results

We compiled 385 records of killer whales in the Caribbean Sea covering the period May 1851 to January 2023. Of these, 176 records were previously published in Bolaños-Jiménez et al. (2014), and 209 are new records (Figure 1). Records included sightings (87.3%), intentional takes (10.6%), bycatch (0.3%), and strandings (1.8%) (Figure 1). Historical, intentional takes included three by whaling ships: one off Isla Beata, Dominican Republic, on 28 May 1866; one off St. Lucia on 30 April 1884; and one off the Florida Keys in 1921 (Katona et al., 1988; Reeves & Mitchell, 1988). In addition, 35 direct takes involving at least 83 individuals were documented in St. Vincent and the Grenadines and two in St. Lucia. A female was incidentally caught in a gillnet in the Gulf of Paria, Trinidad and Tobago, in 1987 (Ottley et al., 1988; Bolaños-Jiménez et al., 2014). The origin of the records included scientific research (57%) and citizen-science initiatives (43%).

Spatial Distribution

Reports of killer whales were distributed in the eastern Caribbean (39.5%), the southern Caribbean (19.7%), and the Greater Antilles (19.2%), with only 13.0, 6.8, and 1.8% for the Bahamian region, Central America, and eastern Florida, respectively (Figure 3). Most of the records were from the French West Indies (18.4%), Venezuela (13.0%),

the Bahamas Archipelago (12.5%), St. Vincent and the Grenadines (10.6%), and Puerto Rico (7.8%) (Table 1).

Temporal Distribution

Killer whales were reported every month of the year (Figure 4), with the most records in August (n = 42) and April (n = 35), and the lowest in September (n = 13) and February (n = 17). No seasonal variation in occurrence was detected (Kruskal-Wallis, H = 56.6, p = 0.64).

Group Size

Estimates of minimum group size ranged from 1 to 25 individuals (Mean = 4.1, SD = 3.7, Mode = 1; Figure 5), and most of the groups (93.6%) had between one to 10 individuals. Solitary individuals were recorded in 28.1% of the cases. The minimum group size we found in this study is in the range of group size in other tropical regions (see Table 2).

Feeding Ecology

Information on the feeding ecology of killer whales in the Caribbean Sea remains scattered. A recent study combined the use of stable carbon and nitrogen isotope (δ^{13} C and δ^{15} N, respectively) analysis in killer whales' muscle tissues and whalers' perceptions in St. Vincent and the Grenadines (Kiszka et al., 2021). Bayesian stable isotope mixing models suggest that the

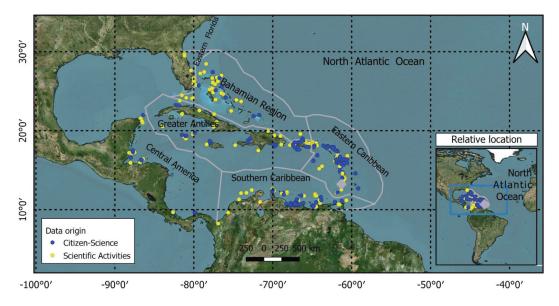


Figure 3. Distribution of killer whale records in the Caribbean Sea, May 1851 to January 2023, classified by the origin of the data. The gray diamond indicates 35 take events involving at least 83 individuals landed in Barrouallie, St. Vincent and the Grenadines, for which coordinates are not available. (Basemap: Bing; https://www.microsoft.com/en-us/maps)

diet of killer whales sampled in St. Vincent and the Grenadines is dominated by odontocete cetaceans (60.4%), including sperm whales (Physeter macrocephalus), short-finned pilot whales (Globicephala macrorhynchus), and smaller delphinids. Other prey, such as large pelagic sharks and teleosts, are probably consumed but in smaller proportions. Whalers' traditional knowledge from St. Vincent and the Grenadines confirmed that odontocetes are the main prey of killer whales in this region (Kiszka et al., 2021). The potential consumption of odontocete cetaceans such as sperm whales and short-finned pilot whales has also been reported opportunistically through observational evidence in the region (Bolaños-Jiménez et al., 2014). On 22 March 2019, a potential occurrence of predation of killer whales on sperm whales was observed off St. Vincent and the Grenadines (F. Vachon, pers. comm., 21 December 2022). While following a group of sperm whales and recording its sounds, a research team from Dalhousie University in Halifax, Nova Scotia, found a group of killer whales of which a male had a chunk of dark meat in his mouth. At the same time, a thick oil film was seen at the surface of the water but no samples were obtained so the species identification was not confirmed (F. Vachon, pers. comm.). Killer whales have also been observed (confirmed by photographs) catching and consuming pygmy sperm whales (Kogia breviceps; Bolaños-Jiménez et al., 2014) off Barbados. Probable predation has also been documented on Bryde's whales (*Balaenoptera edeni*; Bermúdez-Villapol & Sayegh, 2005) and leatherback sea turtles (*Dermochelys coriacea*; Oviedo et al., 2009).

Exploitation and Interactions with Other Species In the Caribbean, killer whales are only known to be directly targeted by humans at St. Vincent and the Grenadines and, to a lesser extent, off St. Lucia (Price, 1985; Fielding & Kiszka, 2021). Until 2014, St. Vincent captures were the main source of killer whale records in the region (Caldwell et al., 1971; Caldwell & Caldwell, 1975; Bolaños-Jiménez et al., 2014; Fielding & Kiszka, 2021). Recent research conducted in St. Vincent indicates that between 1947 and 2020, more than 109 killer whales were taken (Fielding & Kiszka, 2021).

We documented 41 cases of intentional captures of killer whales from May 1866 to December 2022 in the Caribbean Sea, but these figures are with no doubt an underestimation (see the "Discussion" section). The first captures of killer whales in the region were traced back to the 19th century when American whaling ships caught whales in the Dominican Republic in 1866 and in St. Lucia in 1884 (Reeves & Mitchell, 1988). An additional capture was documented in 1986 along the Caribbean coast of Colombia, which represents the only case in which depredation on bait and fish catches was confirmed, and a killer whale was killed in retaliation (Álvarez-León, 2002;

Killer Whales in the Caribbean Sea

Table 1. Number and percentage of killer whale (Orcinus orca) records in the Caribbean Sea ordered by country or territory

Country	n	%
French West Indies	71	18.4
Venezuela	50	13.0
Bahamas Archipelago	48	12.5
St. Vincent and the Grenadines	42	10.9
Puerto Rico	30	7.8
Dutch West Indies	20	5.2
Cuba	14	3.6
Honduras	13	3.4
Cayman Islands	11	2.9
U.S. Virgin Islands	11	2.9
Dominican Republic	10	2.6
St. Lucia	8	2.1
United States	7	1.8
Belize	6	1.6
Colombia	6	1.6
Antigua and Barbuda	5	1.3
Dominica	5	1.3
Grenada	4	1.0
Jamaica	4	1.0
Mexico	4	1.0
Trinidad and Tobago	4	1.0
Haiti	3	0.8
British Virgin Islands	2	0.5
Costa Rica	2	0.5
Turks and Caicos	2	0.5
Anguilla	1	0.3
Barbados	1	0.3
Panama	1	0.3
Total	385	100.0

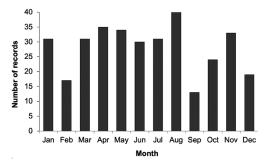


Figure 4. Monthly distribution of killer whale records in the Caribbean Sea between May 1851 and January 2023 (n = 345)

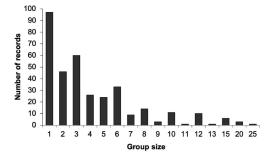


Figure 5. Group size frequency of killer whales in the Caribbean Sea between May 1851 and January 2023 (n = 345)

Region	N	Mean group size	SD	Reference		
Caribbean Sea	354	4.1	3.7	This work		
Hawaii	21	4.2	2.1	Baird et al., 2006		
Peru	25	4.3	3.5	Testino et al., 2019		
Peru	13	4.5	2.9	García-Godos et al., 2004		
Mexico (Eastern Tropical Pacific)	16	4.6	2.4	Vargas-Bravo et al., 2020		
West Africa	32	5.6	3.5	Weir et al., 2010		
Pacific coast of Costa Rica	31	3.4	2.6	Castro-Azofeifa, 2021		

Table 2. Summary of mean group size and standard deviation of killer whale group sizes in the Caribbean Sea and other tropical regions

Bolaños-Jiménez et al., 2014). The only case of bycatch was an entanglement of a young female in a gillnet in the Gulf of Paria, Trinidad and Tobago, on 10 June 1987 (Ottley et al., 1988).

In general, interactions of killer whales with other species and anthropogenic activities were documented on 106 occasions (27.5%). These interactions (n = 106) included intentional takes (40%), boats (30%), fishing gear (15%), other mammals (9%), fish species (5%), and sea turtles (1%).

Discussion

This review provides an update on available information on killer whales in the Caribbean Sea and includes records that more than double the first review published by Bolaños-Jiménez et al. (2014). The effort here provides more details on the species' ecology, natural history, exploitation, and interaction with other species and fisheries, contributing to improving the knowledge of this species in this tropical region and providing an additional foundation for informed conservation.

The proportion of records provided from citizenscience initiatives (including posts on social media) increased remarkably from 20% in the dataset (n = 176) published by Bolaños-Jiménez et al. (2014) to 43% when combining past and new records added here (n = 385), emphasizing the importance of the citizen-science programs when investigating rare and elusive species, particularly marine megafauna (Garcia-Soto et al., 2021).

Our results confirm that killer whales are widely distributed in the Caribbean Sea but in low densities such that it is not feasible to predict their presence at a local level, which is consistent with previous findings (Reeves & Mitchell, 1988; Bolaños-Jiménez et al., 2009, 2014). No seasonal trends in occurrence could be found, confirming that killer whales are present in the study area all year round. Reeves & Mitchell (1988) hypothesized that in the Caribbean Sea (1) one or more "stocks" of killer whales could summer either in

the Arctic or the tropics, (2) other stocks or populations that are nonmigratory might occur on a year-round basis, or (3) other unknown patterns of distribution in the Caribbean might occur. As recent research found that individual killer whales can travel more than 5,000 km and explore different ocean basins in a short period (i.e., Guerrero-Ruiz et al., 2005; Matthews et al., 2011; Durban & Pitman, 2012), we cannot confirm or exclude that the killer whale population that uses the waters of the Caribbean Sea is composed of a combination of nonmigratory individuals and/or individuals traveling from other parts of the Atlantic. Additional methods (e.g., population genetics/genomics, satellite telemetry, photo-identification, passive acoustics) will improve our understanding of the movements and population structure of killer whales in the Caribbean region and adjacent Atlantic waters.

The highest number of records in the French West Indies is mainly related to the existence of solid citizen-science initiatives in this region rather than a higher occurrence of killer whales. Citizen science also contributed remarkably to the detection of records in Puerto Rico and Venezuela (see Figure 3). Recent reviews on the occurrence of minke whales (Balaenoptera acutorostrata: Bolaños-Jiménez et al., 2021), false killer whales (Pseudorca crassidens; Alvarado-Hofmeister, 2021), and short-finned pilot whales (Valencia Cubillos, 2022) in the Caribbean Sea also identified a scarcity of records in Central American waters, emphasizing the need for increased research efforts, awareness, and local capacity building in this region. The disparity in research efforts and citizen science-based initiatives among territories and regions may thus have biased the proportion of detections in some countries and territories, but it is not clear from our data if the gap in Central America is due to a lower research effort, true low densities, or a combination of both.

In their earlier review, Katona et al. (1988) speculated that killer whale movements in the

Northwest Atlantic are linked to changes or movements in the local abundances of prey populations, mainly baleen whales. The authors also suggested that baleen whales wintering in the Caribbean Sea might be consumed by killer whales but that odontocete species could also be an important part of their diet, particularly after the large whales migrate back to their feeding grounds. This is, at least partially, consistent with recent studies on the feeding ecology of Caribbean killer whales, confirming that, at least in the eastern Caribbean, these animals primarily prey on odontocetes, including sperm whales, short-finned pilot whales, other smaller delphinids, and, to a lesser extent, on teleosts and large pelagic elasmobranchs (Kiszka et al., 2021). The relative importance of large baleen whales is unknown. However, all information combined strongly suggests that killer whales have a broad diet in the Caribbean region (Katona et al., 1988; Bolaños-Jiménez et al., 2014; Kiszka et al., 2021), thus contributing to the growing perception that killer whales in tropical regions are generalist feeders (Baird et al., 2006; Weir et al., 2010).

The exploitation of killer whales and other delphinids in St. Vincent and the Grenadines is likely to be the most important and direct threat, at least in the eastern Caribbean region. Fielding & Kiszka (2021) documented the take of at least 13,856 small cetaceans, including 109 killer whales, from 1947 to 2021. This number is an underestimation of the total number of killer whale catches as there are gaps in the collection of catch data during that period (Fielding & Kiszka, 2021). The systematic monitoring of killer whale catches will be critical to assess the magnitude of direct exploitation of this species and other small cetaceans.

Limited study and their probable low densities restrict our ability to predict if and where killer whales regularly occur in most Caribbean ecoregions, and dedicated research efforts will be hindered by our limited capacity to detect these animals at a rate that will allow us to improve our understanding of their movements, trophic interactions, and distribution. Our review emphasizes the need to further develop citizen-science initiatives, particularly in regions where records remain rare and poorly documented (e.g., the Central American coast of the Caribbean), to better assess the spatial and temporal distribution of Caribbean killer whales. Lastly, the combination of molecular, morphological/morphometric analysis and expanding the use of ecological tracers (e.g., stable isotopes, fatty acids, contaminants) will be critical for assessing the population identity, and the behavioral and evolutionary ecology of killer whales in this region. Future work should also include more detailed efforts to document

the potential presence of tropical ecotype(s) in the Caribbean Sea and, if such an ecotype exists, to describe its behavioral ecology.

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