Short Note

Evidence that Killer Whale (*Orcinus orca*) Predation of Humpback Whales (*Megaptera novaeangliae*) Occurs in the West Indies

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Killer whales (Orcinus orca) are a cosmopolitan species in the Delphinidae family; however, sparse data exist regarding their life history in the Caribbean Sea (Forney & Wade, 2006; Bolaños-Jiménez et al., 2014, 2023; Jefferson et al., 2015). Killer whale sightings reported in the lower latitudes of the western North Atlantic (NA) Ocean indicate they occur year-round and far from shore. This is supported mostly by anecdotal observations but bolstered by 13 scientifically recorded observations collected during systematic research efforts (Bolaños-Jiménez et al., 2014, 2023). Indirect and anecdotal evidence suggest prey items are diverse and include cetaceans; however, the scientific community currently lacks a definitive picture of where or how these killer whales are foraging (Caldwell & Caldwell, 1969; Ottley et al., 1988). The collective catalog of killer whales photographed throughout the Caribbean Sea from all known encounters includes a sparse 35 individuals. Within this catalog, there are limited views of the unique identifying marks that are useful for confirming resightings among and between years or between geographically defined catalogs in other areas of the NA (J. Bolaños-Jiménez, pers. comm., 13 March 2024). The paucity of data leaves large knowledge gaps for all aspects of Caribbean killer whales' life history and their role within the ecology throughout the NA. Because killer whales are an apex predator across their collective global range (Forney & Wade, 2006), understanding and monitoring variations in abundance, occurrence, distribution, prey species, and social behaviors are of significant interest to marine managers tasked with mitigating biological and economic impacts to the species and its ecosystem(s).

North Atlantic humpback whales (*Megaptera novaeangliae*; NAHWs) are a medium-sized rorqual in the Balaenopteridae family. The number of individuals in the NA stock is estimated to be 35,000 based on data from population surveys in the 1980s and 1990s, representing a successful post-whaling recovery (Robbins et al., 2024). Their range extends between feeding areas in the higher latitudes and winter breeding and calving areas in lower latitudes, including the Caribbean Sea (Stevick et al., 2006). Calves arriving on the feeding grounds after their first migration have been documented with scars from killer whale dentition, indicating failed predation attempts along the migration route (Mehta et al., 2007; Koilpillai et al., 2022). This short note provides evidence of at least one location where killer whale predation occurs on NAHW neonates.

We documented killer whales targeting NAHW calves in their calving areas, specifically between the Turks and Caicos Islands and Puerto Rico in the eastern Caribbean (referred to in this short note as the "Taino Killer Whale" or KWT as a useful geographical reference mirroring the area of the West Indies once inhabited by indigenous populations of Taino people). We describe three separate events of KWT predation on NAHW calves, including direct observation of a predation event in progress where CATS tags (Customized Animal Tracking Solutions, Moffat Beach, Queensland, Australia; www.cats.is) were successfully deployed on two individuals with key roles in this event.

We conducted surveys of cetaceans from 2010 to 2021 during the winter occupancy of NAHWs; NAHWs are typically present from early January through the first week in May. These surveys were conducted from aerial, land, and/or vessel-based platforms. Surveys were conducted off Puerto Rico in 2010 through 2017. Systematic surveys were conducted among the Turks and Caicos Islands in 2016 and 2017, and off the Dominican Republic in 2021 (Figure 1). Permits were obtained from all

agencies responsible for overseeing marine mammal research in each country for all survey areas. All activities described herein were included on the permits, including deploying suction cup tags to the individual killer whales and humpback whales. It is noted that data collection stalled between 2018 and 2020: research was hindered by two hurricanes, an earthquake, and a pandemic. Details of the events described herein are limited to identifying at least one area in the NA where NAHW calves are being preyed upon by killer whales.

Data were collected for this study as part of a larger research effort examining the behavioral ecology of killer whale ecotypes, humpback whales, and the interactions between the two species in the same area, including (1) high-resolution digital photography by skilled observers in small vessels, on land platforms, and from fixed wing aircraft; (2) videography from CATS tags affixed temporarily with suction cups to a NAHW calf and an adult KWT; and (3) videography from an array of video cameras (e.g., GoPros or similar) attached to a 3-m pole and submerged during focal follows (for detailed method, see MacKay, 2015). Data were analyzed post-encounter for direct and indirect evidence of a recent attempted predation of NAHWs by KWTs. Data included in this analysis

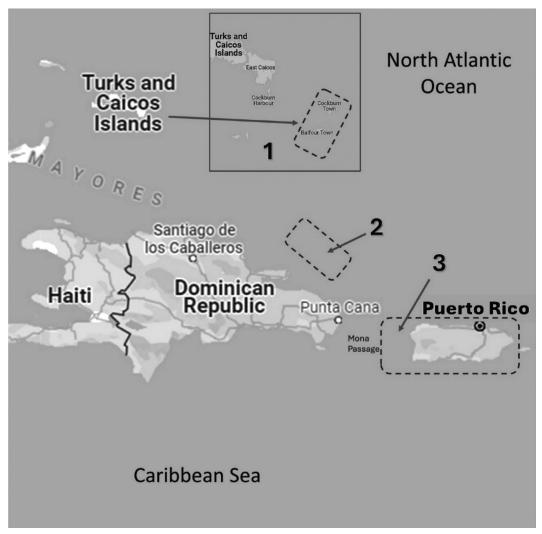


Figure 1. A map of the study area of the Taino Killer Whale (*Orcinus orca*) ecotype in the Greater Antilles of the Caribbean Sea between 2010 and 2021. Boxed areas represent approximate locations of surveys across all study years: (1) the area around the Turks Islands of Salt Cay and Grand Turk, Turks and Caicos Islands; (2) the area of the Silver Bank and Navidad Bank, Dominican Republic; and (3) the area around Puerto Rico, including Mona Passage.

were records of direct behavioral observations, digital images of the events, and video recorded during any observed interaction between NAHW mothercalf pairs and KWTs. Behavioral data recorded via videography, high-resolution photography, and/or direct visual observations of NAHWs and KWTs were categorized using ethograms and entered onto data sheets. Post-encounter analysis of KWT images include photo-identification of individuals by examining the following physical characteristics: morphology (body shape and size), pigmentation (shape, position, and size of saddle patches and eye patches), unique markings (scars, abrasions, and other injuries in various stages of healing), and dorsal fin (size and shape) (Evans & Yablokov, 1978; Dahlheim, 1997; Mehta et al., 2007; McInnes et al., 2024). Injuries to a NAHW calf noted via direct observation by skilled, experienced observers, or captured on still or video images, were analyzed for characteristics consistent with killer whale predation attempts previously documented in other areas (Naessig & Lanyon, 2004; Steiger et al., 2008; Elwen et al., 2014; McCordic et al., 2014; MacKay et al., 2016, 2019).

The three confirmed predation events of KWT hunting NAHW calves encountered during the study were documented in 2013, 2014, and 2021. In 2013, KWTs were photographed from a small aircraft during an encounter with a group of NAHWs between Puerto Rico and the Dominican Republic (Event #1). In 2014, a NAHW calf was photographed from a small boat above and below the surface with recent injuries (Event #2). Analysis was conducted to determine the probable cause of the injuries to the calf. In 2021, a successful KWT predation event on a NAHW calf (i.e., calf was consumed), clearly evident by directly observing the killer whales attempting to acquire the calf from the mother, was videoed underwater with two CATS tags, videoed aerially with a helicopter-mounted gyroscopic camera, and photographed with a DSLR camera from a small vessel. Also, observations with an unaided eye off the Dominican Republic were recorded on datasheets augmented by real-time narration into a voice recorder (Event #3). Event #3 data collection began while the event was already in progress. Analysis included broad- and fine-scale coding of acoustics (vocalizations and percussive activity detected on the videos) and behaviors for KWTs and NAHWs, with observations of apparently coordinated efforts by two groups of KWTs in their attack until the event's conclusion that ended with consumption of the NAHW calf (MacKay & Seger, unpub. data, 2021). Specifics of the three events are detailed below:

 Event #1 (Figure 2) – KWTs were observed during an attack on NAHWs during an aerial, line-transect survey from a small fixed-wing aircraft over Mona Passage, the channel separating western Puerto Rico and the island of Hispanola, on 1 May 2013. The pilot discontinued the transects and began circling the group for approximately 15 min. There were no other groups of NAHWs or KWTs visible for the duration of the focal follow. At least ten KWTs were observed in direct contact with three NAHWs (a mother-calf pair and another adult) approximately 5 km northwest of Isla Desecheo, an island 22 km west of Aguadilla, Puerto Rico. The KWTs were observed maintaining an outside perimeter of three to five NAHW adult body lengths around the NAHW mother-calf pair, maintaining direct contact with the NAHW mother-calf pair, targeting the calf with direct contact, and separating the other adult NAHWs from the mother-calf pair by at least ten NAHW adult body lengths for the duration of the focal follow. It is unknown if the adult NAHW with the mother-calf pair was an escort (presumed male) or a female without a calf. The KWTs were observed making numerous, aggressive moves toward the NAHW mother-calf pair, such as swimming directly at the mother at high speed and appearing to make contact, and appearing to ram the pair from the side. These behaviors elicited tail throws at the KWTs from the NAHW mother. Less surface activity was observed near the other adult NAHW: however, indications of subsurface interactions (splashing, indistinct movement) were noted by the observers. Observations lasted less than 15 min, and the outcome of Event #1 was not observed.

Event #2 (Figure 3) - A NAHW mothercalf-escort group was observed 8 km west of Rincón, Puerto Rico, on 26 March 2014. Subsurface visibility was estimated to be 25 m. The mother and calf were sighted by blows 3 km from the vessel. The pair remained at the surface and did not appear to be traveling. We approached the group and observed an escort initially positioned five adult body lengths from the mother-calf pair. The mother-calf-escort group made close approaches (less than 15 m) to our stationary vessel numerous times. Video of scarring and fluke identification features were collected. The mother and escort had no visible injuries. The calf had (1) obvious, fresh injuries (2 to 4 d healing) along the dorsal ridge extending the length of the peduncle to the fluke and (2) a fluke torn from the leading edge toward the trailing edge near the right distal (lateral)

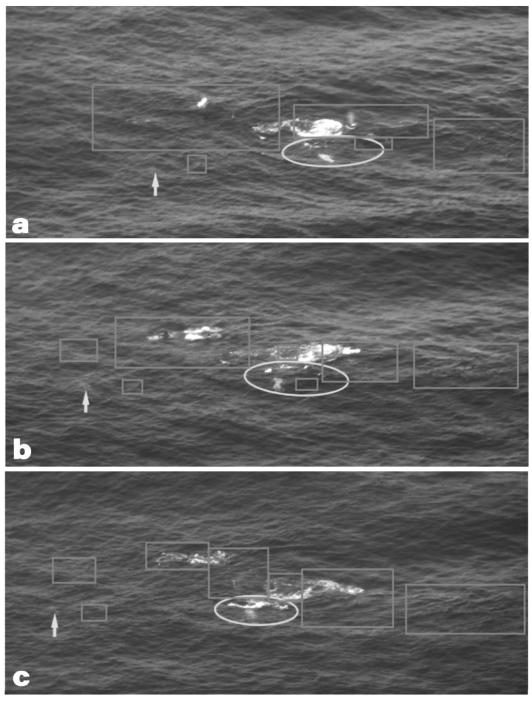


Figure 2. A group of at least ten Taino Killer Whales (KWTs) interacting with three North Atlantic humpback whales (*Megaptera novaeangliae*; NAHWs). Images were captured from a fixed wing aircraft on 1 May 2013 between Puerto Rico and the Dominican Republic during an aggressive interaction: (a) NAHW calf on its mother's back, (b) the calf sliding off its mother's back, and (c) the calf beside the mother. Boxes indicate locations of KWTs above and below the surface. Ellipses indicate locations of the NAHW mother–calf pair. Large patches of white water indicate tail throws observed from the NAHW mother aimed at the KWT. Arrows indicate submerged left flipper of an adult NAHW.

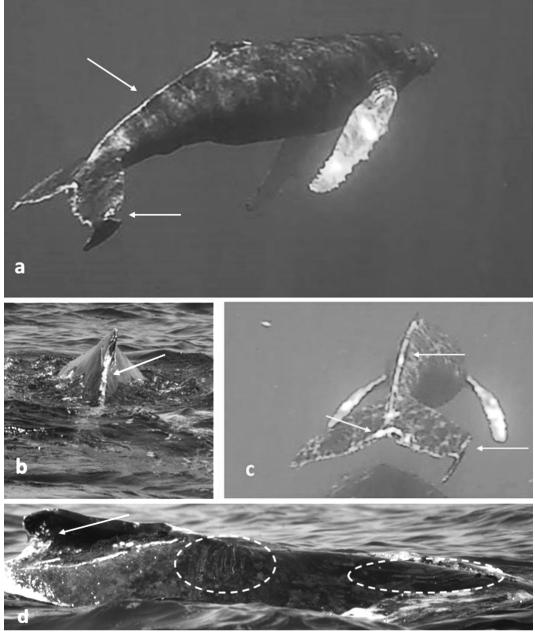


Figure 3. A NAHW calf with views of injuries indicated by white arrows documented on 26 March 2014, consistent with a recent killer whale attack between western Puerto Rico and the Dominican Republic: (a) injuries on the latero-caudal dorsal ridge and leading edge of right fluke, underwater and perpendicular view; (b) fresh injury to dorsal ridge from above the water's surface; (c) same as (a) but from underwater and inclusive of the torn fluke from leading edge to trailing edge near the right distal (lateral) tip; and (d) rake marks indicated by dashed ovals and fresh injury to dorsal fin (white arrow). (Photographs taken by Mithriel M. MacKay under National Marine Fisheries Permit #15682)

tip. Rake marks consistent with killer whale dentition were visible on the calf's anterior dorsal fin posterior to the blowhole. Additional bite marks were noted closer to the fluke notch, on either side of the midline. The calf's dorsal fin injury was irregular and flanked by longitudinal scrapes that were consistent with killer whale biting and scraping. Analyses of these injuries using photographs and videos suggested an attempted KWT predation on this calf and were consistent with scarring attributed by other researchers to killer whale attacks on cetaceans (Naessig & Lanyon, 2004; Mehta et al., 2007; Steiger et al., 2008; McCordic et al., 2014; Koilpillai et al., 2022). The authors concede that false killer whales (Pseudorca crassidens) have similar dentition to KWTs; however, reported sightings of false killer whales are rare in the survey area even among the anecdotal reports of cetacean sightings and research efforts (Swartz et al., 2002; Merten & Rodríguez-Ferrer, 2014; Rodriguez-Ferrer et al., 2018). False killer whales typically target a variety of fish and cephalopods as prey items, and there are no data available documenting a large whale as a prey species in any population (Stacey et al., 1994; Odell & McClune, 1999; Baird, 2017). We concluded that Event #2 was an attempted predation event by killer whales given the geographical context of historical killer whale and false killer whale data, and additional sightings of KWTs in the area reported by fishermen (MacKay, unpub. data, 2014-2021).

Event #3 (Figure 4) – The R/V OceanXplorer, a ship equipped for offshore scientific research, set out in March 2021 to locations off the Dominican Republic where KWTs were expected to be hunting NAHWs. Targeted areas for this cruise were based on previous analysis of more than a decade of temporal and spatial data of NAHW mothercalf occurrence and behaviors, anecdotal data of KWT occurrence, spatial analysis of anthropogenic activities, bathymetric data, and research data (MacKay, 2015; MacKay et al., 2016, 2019; MacKay, unpub. data, 2010-2020). A small vessel (less than 7 m) and a helicopter were launched for concurrent surveys from the ship on 5 March 2021, off the northern coast of the Dominican Republic near Silver and Navidad Banks. The aerial team alerted the small vessel team of a mixed species group that included KWTs and a NAHW mother-calf pair. The small vessel changed course to the location provided by

aerial observers where a predation event, already in progress, was identified. Tagging efforts, photographic data collection, and behavioral data collection were initiated from the small vessel. The helicopter collected limited aerial video data before departing the area to return to the ship. The entire focal follow lasted 3 h, 15 min. It included the following details (all timestamps in local time of GMT-4/Atlantic Standard Time):

- 09:57 Small vessel arrived at predation event.
- 10:06 CATS tag attached to back of adult female KWT using 3-m pole with methods replicated from Stimpert et al. (2012) and Seger (2016).
- 10:23 CATS tag attached to back of NAHW calf (Figure 4).
- 11:08 Calf tag stopped recording data as tag had been knocked off during predation event at the time of the kill, floated to the surface, and was recovered by small vessel team.
- 13:13 KWT tag stopped recording video data; acoustic data collection continued for several hours as tag stayed on animal overnight and was recovered the next day.
- 13:15 Focal follow concluded at end of predation event after the calf was consumed.

Analysis of all unaided-eye observations, as well as video and photographic data, elucidated several notable events in the focal follow. A group of seven or eight KWTs attempted to acquire the NAHW calf from the mother's back. A second KWT group (9 to 10 individuals) were observed joining the hunt approximately 35 min after the start of our focal follow, expanding the number of KWTs to 16 to 18 individuals. The combined KWT group included four adult males, two mother-calf pairs, and approximately ten adult females. They performed complex, coordinated, responsive movements that strongly suggested they hunted together previously (MacKay & Seger, unpub. data, 2021). The group of killer whales attempted to separate the NAHW calf from the mother by pushing the calf from one side over the other side of the mother's back. Eventually, the calf was



Figure 4. An adult female KWT (top) and a NAHW calf (bottom right) tagged during a predation event in the Greater Antilles. CATS tags (https://cats.is/cats-cam) recorded video, acoustic, and global positioning tracking data. The two CATS units stayed attached to both individuals throughout the event. The calf's tag was dislodged at the time of the kill. The KWT tag remained on until after this event, including while the NAHW calf was consumed by the KWT group. The KWT tag was located and retrieved the next day. (Research activities were conducted under the Dominican Republic Government permit issued in February 2021.)

separated long enough, pulled down, and did not resurface. The video analysis from the CATS tags clearly shows the calf being consumed by killer whales at depth and away from the mother.

Detailed descriptions of identifying physical characteristics of the KWTs and mothercalf NAHWs were possible. Photographs and video often included physical characteristics of all body surfaces of each individual KWT in this predation event. Individuals were identified and entered into a catalog. Two groups of KWTs were identified using differences in saddle patch and eye patch shape and color (Evans & Yablokov, 1978; Dahlheim, 1997; Mehta et al., 2007; McInnes et al., 2024). These characteristics confirm visual (unaided eye) observations from the small vessel of noted distinctions between the first group observed by the aerial and small vessel teams and the second group observed by the small vessel team when it joined the hunt.

The tag was dislodged from the NAHW calf's back while it was being drowned, and it

surfaced as the calf was being consumed. The tag's camera continued to record from the surface while pointed downward and positioned over the KWTs as they consumed the NAHW calf. This allowed confirmation of a successful hunt and thorough documentation subsurface of how these KWTs acquire and consume NAHW calves, at least for this example (MacKay & Seger, unpub. data, 2021).

The observations described herein provide confirmation that KWTs hunt and consume NAHW calves in the Greater Antilles of the Caribbean Sea. Anecdotal evidence has been available that NAHW calves are killer whale prey items; however, the location along the NAHW migration route where neonates are targeted and consumed previously eluded researchers. A comprehensive review of the data collected from available resources, including from citizen scientists, had not included an observed predation of NAHWs by KWTs (Bolaños-Jiménez et al., 2023). Our group conducted hundreds of research effort hours before this direct observation of a single event that included KWTs hunting and consuming a NAHW calf (Event #3), which supports the suggestion that this region is a hunting area for killer whales.

There are several important discussion points from these three events that extend beyond identifying the Greater Antilles as a location for KWT predation of NAHWs. Population dynamics of Caribbean killer whales remain unknown, and observations are sparse. The literature puts forth the hypothesis that there are few observations of killer whales because they occur in small numbers over a large expanse and are highly mobile within their range (Mitchell & Reeves, 1988; Clapham, 2001; Forney et al., 2006; Bolaños-Jiménez et al., 2009, 2014; Durban & Pitman, 2012). We agree with previous research that killer whale numbers on winter NAHW calving areas probably do not rival group sizes in the higher latitudes; however, we posit that more than "a few" killer whales are needed to explain the number of NAHW calves observed with physical indications of attempted predation by killer whales in the estimated population of 35,000 in the NAHW stocks (McCordic et al., 2013; Robbins et al., 2024). Calf survival rate estimates exclude neonatal survival rates and include a calculated birth rate interval that cannot account for the number of neonates that do not survive the first migration to be counted. It follows that neonatal NAHW consumption by killer whales in the Caribbean is not possible to enumerate without dedicated, expansive surveys in areas far offshore as indicated by previous observations (Bolaños-Jiménez et al., 2009, 2014; MacKay, unpub. data, 2014-2020), leaving open the possibility that low estimates are a direct result of the challenges of observing killer whales rather than because they are rare occurrences in the Caribbean.

It is interesting to note that the areas in the eastern Caribbean with tourism aimed at encounters with NAHWs do not report sightings of killer whales in the largest aggregations of their winter areas. Spatial and temporal "fringes" (low density areas at the outer limits of winter aggregations) of the NAHW breeding grounds may offer mothers with calves threat reductions from the energetic behaviors of breeding groups while providing an opportunity for predation by KWTs. The long-distance migration of NAHWs must offer an advantage toward the success of the species, yet the risk to energy-depleted nursing mothers and dependent neonates is difficult to weigh in the context of the current body of knowledge of their life history. Speculation includes the possibility that pregnant females migrate to lower latitudes to give birth as a strategy for predator avoidance by killer whales resident on their feeding grounds (see published

discussion between Corcoran & Connor [1999] and Clapham [2001]). We weigh into this discussion by agreeing that predator avoidance does not explain seasonal migration of NAHWs because killer whales are now confirmed to hunt NAHW neonates in at least the Greater Antilles and are likely a recurring pressure. We deviate from the assertion that killer whales would be observed hunting NAHW calves where the aggregation is dense, such as the Silver Bank, because that strategy does not appear to align with KWTs hunting NAHW calves in our study. KWTs seem to prefer to acquire calves in the deep, offshore waters while mother-calf pairs are separated from other NAHW groups, and toward the end of the season as NAHWs migrate with neonates. We concede this remains speculation until more predation events are observed and that our data (published and unpublished) are enough to argue that if killer whale predation is also occurring on the breeding grounds or along the migration routes, then predator avoidance is not a key evolutionary strategy for the migration function. A better understanding of predators, such as killer whales and their ecotypes that target NAHW calves, will contribute to understanding the advantages or pressures that drive NAHW annual migrations and will better predict effects of natural and anthropogenic impacts.

Describing KWT ecotype(s) is currently limited to morphology, diet, vocal repertoire, body shape, pigment patterns, and behaviors (Foote & Nystuen, 2008; de Bruyn et al., 2013; Mäkeläinen et al., 2014; Moura et al., 2014, 2015; MacKay & Seger, unpub. data, 2021). Our observations of KWTs are similar to those in body shape and size of the NA Type 1 and Type 2 ecotypes described in higher latitudes (Bolaños-Jiménez et al., 2014; Mäkeläinen et al., 2014; Kiszka et al., 2021). We observed and photographed differences in the pigment patterns of saddle patches and eye patches that facilitated confirmation of the two groups that came together to successfully hunt and consume the NAHW calf reported in Event #3. NAHW neonates may represent an important seasonal prey item as part of a varied diet for KWTs, they may indicate more than one killer whale ecotype occupies offshore Caribbean waters, or they may indicate seasonal migration to the Caribbean by killer whales with a broad range yet to be determined. We anticipate that further analysis of our data will be useful in determining whether KWTs are reproductively separate from other populations in the Gulf of Mexico, Caribbean Sea, northern latitudes, and eastern NA winter areas by comparing physical characteristics and attempting to match individuals to local catalogs.

The acoustic repertoire and observed behaviors have not been characterized previously for the KWTs in the Caribbean Sea. The video, acoustic, and kinematic data from the CATS tags are currently under analysis and will result in the first opportunity to add these details to the description of this ecotype. While advancements in technology are expected to eventually answer many questions regarding the taxonomy, diet, and mobility of killer whale ecotypes globally, research efforts to survey areas offshore in the Caribbean remain cost prohibitive and logistically difficult. This confirmation of KWT predation of NAHW calves in the Greater Antilles adds an important piece of life history for both species. The impact and effective mitigation of natural and anthropogenic pressures from regional and global changes in their range require a great deal of resources in support of future research efforts aimed at this topic.

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Literature Cited

- Baird, R. W. (2017). False killer whales *Pseudorca crassidens*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 347-349). Academic Press.
- Bolaños-Jiménez, J., Fertl, D., & Iñíguez, M. (2009). Killer whale (Orcinus orca) occurrence in Venezuelan waters, 1982-2008. Latin American Journal of Aquatic Mammals, 7(1-2), 75-79. https://doi.org/10.5597/lajam00138
- Bolaños-Jiménez, J., Kiszka, J. J., Bouveret, L., Ferrer, G. R., Ramos, E. A., Henriquez, A., Luksenburg, J., Bernus, J., Briceño, Y., & Criollo, L. S. (2023). The killer whale in the Caribbean Sea: An updated review of its ecology, exploitation, and interactions with fisheries. *Aquatic Mammals*, 49(2), 184-194. https://doi.org/10.1578/AM.49.2.2023.184
- Bolaños-Jiménez, J., Mignucci-Giannoni, A., Blumenthal, J., Bogomolni, A., Casas, J. J., Henríquez, A., Iñíguez-Bessega, M., Khan, J., Landrau-Giovannetti, N., Rinaldi, C., Rinaldi, R., Rodríguez-Ferrer, G., Sutty, L., Ward, N., & Luksenburg, J. A. (2014). Distribution, feeding habits and morphology of killer whales (*Orcinus orca*) in the Caribbean Sea. *Mammal Review*, 44(3-4), 177-189. https://doi.org/10.1111/mam.12021
- Caldwell, D. K., & Caldwell, M. C. (1969). Addition of the leatherback sea turtle to the known prey of the killer whale, *Orcinus orca. Journal of Mammalogy*, 50(3), 636. https://doi.org/10.2307/1378803
- Clapham, P. J. (2001). Why do baleen whales migrate? A response to Corkeron and Connor. *Marine Mammal Science*, *17*(2), 432-436. https://doi.org/10.1111/j.1748-7692.1999. tb00887.x
- Clapham, P. J., & Mead, J. G. (1999). Megaptera novaeangliae. Mammalian Species, 4, 1-9. https://doi.org/10. 2307/3504352
- Corkeron, P. J., & Connor, R. C. (1999). Why do baleen whales migrate? *Marine Mammal Science*, 15(4), 1228-1245. https://doi.org/10.1111/j.1748-7692.1999.tb00887.x
- Dahlheim, M. E. (1997). A photographic catalog of killer whales, Orcinus orca, from the central Gulf of Alaska to the southeastern Bering Sea (NOAA Technical Report NMFS 131). U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. 58 pp.
- de Bruyn, P. N., Tosh, C. A., & Terauds, A. (2013). Killer whale ecotypes: Is there a global model? *Biological Reviews*, 88(1), 62-80. https://doi.org/10.1111/j.1469-185X.2012.00239.x
- Durban, J. W., & Pitman, R. L. (2012). Antarctic killer whales make rapid, round-trip movements to subtropical waters: Evidence for physiological maintenance migrations? *Biology Letters*, 8(2), 274-277. https://doi. org/10.1098/rsb1.2011.0875
- Elwen, S. H., Tonachella, N., Barendese, J., Collins, T., Best, P. B., Rosenbaum, H. C., Leeney, R. H., & Gridley, T. (2014). Humpback whales off Namibia: Occurrence, seasonality, and a regional comparison of photographic

catalogs and scarring. Journal of Mammalogy, 95(5), 1064-1076. https://doi.org/10.1644/14-MAMM-A-108

- Evans, W. E., & Yablokov, A. V. (1978). Intraspecific variation of the color pattern of the killer whale (*Orcinus orca*).
 In V. E. Sokolov & A. V. Yablokov (Eds.), *Advances in studies of cetaceans and pinnipeds* (pp. 102-115). USSR Academy of Sciences, Moscow, Russia. (In Russian)
- Foote, A. D., & Nystuen, J. A. (2008). Variation in call pitch among killer whale ecotypes. *The Journal of the Acoustical Society of America*, 123(3), 1747-1752. https://doi.org/ 10.1121/1.2836752
- Forney, K. A., Wade, P. R., & Estes, J. A. (2006). Worldwide distribution and abundance of killer whales. *Whales, Whaling, and Ocean Ecosystems,* 145, 162. https://doi. org/10.1525/california/9780520248847.003.0012
- Jefferson, T. A., Webber, M. A., & Pitman, R. L. (2015). Marine mammals of the world: A comprehensive guide to their identification (2nd ed.). Academic Press.
- Kiszka, J. J., Caputo, M., Méndez-Fernández, P., & Fielding, R. (2021). Feeding ecology of elusive Caribbean killer whales inferred from Bayesian stable isotope mixing models and whalers' ecological knowledge. *Frontiers* in Marine Science, 8, 648421. https://doi.org/10.3389/ fmars.2021.648421
- Koilpillai, H. A., Basran, C., Berrow, S., Broms, F., Chosson, V., Gowans, S., Jones, L., Kempen, R., Larsen, F., López Suárez, P., Magnúsdóttir, E., Massett, N., Prince, K., Rasmussen, M. H., Robbins, J., Sears, R., Simard, P., Simon, M., Whooley, P., & Wenzel, F., (2022). A tail of survival: Geographic distribution and severity of non-lethal attacks on North Atlantic humpback whales (Megaptera novaeangliae) by killer whales (Orcinus orca). Eckerd College.
- MacKay, M. M. (2015). Occurrence patterns and social behaviors of humpback whales (Megaptera novaeangliae) wintering off Puerto Rico, USA. Texas A&M University, Galveston.
- MacKay, M. M., Würsig, B., Bacon, C. E., & Selwyn, J. D. (2016). North Atlantic humpback whale (*Megaptera* novaeangliae) hotspots defined by bathymetric features off western Puerto Rico. Canadian Journal of Zoology, 94(7), 517-527. https://doi.org/10.1139/cjz-2015-0198
- MacKay, M. M., Bacon, C. E., Bouveret, L., Fossette, S., & Stevick, P.T. (2019). Humpback whale (*Megaptera novae-angliae*) intra/inter-seasonal exchanges between Puerto Rico and the southeastern Caribbean. *Animal Behavior* and Cognition, 6(2), 98-104. https://doi.org/10.26451/ abc.06.02.02.2019
- Mäkeläinen, P., Esteban, R., Foote, A. D., Kuningas, S., Nielsen, J., Samarra, F. I. P., Similä, T., van Geel, N. C. F., & Víkingsson, G. A. (2014). A comparison of pigmentation features among North Atlantic killer whale (Orcinus orca) populations. Journal of the Marine Biological Association of the United Kingdom, 94(6), 1335-1341. https://doi.org/10.1017/S0025315414000277
- McCordic, J. A., Todd, S. K., & Stevick, P. T. (2013). Differential rates of killer whale attacks on humpback whales in the North Atlantic as determined by scarification.

Journal of the Marine Biological Association of the United Kingdom, 94(6), 1311-1315. https://doi.org/10.1017/ S0025315413001008

- McInnes, J. D., Trites, A. W., Mathieson, C. R., Dahlheim, M. E., Moore, J. E., Olson, P. A., & Lester, K. M. (2024). Evidence for an oceanic population of killer whales (*Orcinus orca*) in offshore waters of California and Oregon. *Aquatic Mammals*, 50(2), 93-106. https://doi. org/10.1578/AM.50.2.2024.93
- Mehta, A. V., Allen, J. M., Constantine, R., Garrigue, C., Jann, B., Jenner, C., Marx, M. K., Matkin, C. O., Mattila, D. K., Minton, G., Mizroch, S. A., Olavarría, C., Robbins, J., Russell, K. G., Seton, R. E., Steiger, G. H., Víkingsson, G. A., Wade, P. R., & Clapham, P. J. (2007). Baleen whales are not important as prey for killer whales (*Orcinus orca*) in high-latitude regions. *Marine Ecology Progress Series*, 348, 297-307. https:// doi.org/10.3354/meps07015
- Merten, W., & Rodríguez-Ferrer, G. (2014). First stranding and sighting of the false killer whale (*Pseudorca crassidens*) off Puerto Rico. *Caribbean Journal of Science*, 48(1), 59-62. https://doi.org/10.18475/cjos.v48i1.a9
- Mitchell, E., & Reeves, R. R. (1988). Records of killer whales in the western North Atlantic, with emphasis on eastern Canadian waters. *Rit Fiskideildar*, 11, 161-193.
- Moura, A., Kenny, J., Chaudhuri, R., Hughes, M. A., Reisinger, R. R., de Bruyn, P. J. N., Dahlheim, M. E., Hall, N., & Hoelzel, A. R. (2015). Phylogenomics of the killer whale indicates ecotype divergence in sympatry. *Heredity*, 114, 48-55. https://doi.org/10.1038/hdy.2014.67
- Moura, A. E., Kenny, J. G., Chaudhuri, R. R., Hughes, M. A., Welch, A. J., Reisinger, R. R., de Bruyn, P. J. N., Dahlheim, M. E., Hall, N., & Hoelzel, A. R. (2014). Population genomics of the killer whale indicates ecotype evolution in sympatry involving both selection and drift. *Molecular Ecology*, 23(21), 5179-5192. https:// doi.org/10.1111/mec.12929
- Naessig, P. J., & Lanyon, J. M. (2004). Levels and probable origin of predatory scarring on humpback whales (*Megaptera novaeangliae*) in east Australian waters. *Wildlife Research*, 31(2), 163-170. https://doi.org/10.1071/ WR03086
- Odell, D. K., & McClune, K. M. (1999). False killer whale Pseudorca crassidens (Owen, 1846). In S. H. Ridgway & K. M. McClune (Eds.), Handbook of marine mammals. Vol. 6: The second book of dolphins and the porpoises (pp. 213-243). Academic Press.
- Ottley, T., Henry, C., Khan, A., Siung-Chang, A., & Sturm, M. (1988). Incidents involving whales in Trinidad waters during 1987. *Living World (Journal of the Trinidad and Tobago Field Naturalists' Club)*, 1987-88, 47.
- Reeves, R. R., & Mitchell, E. (1988). Killer whale sightings and takes by American pelagic whalers in the North Atlantic. *Rit Fiskideildar*, 11, 136-160.
- Robbins, J., Bérubé, M., Clapham, P. J., Mattila, D. K., Palsbøll, P. J., Asmutis-Silvia, R., Hill, A., Howes, L. J., Landry, S., Lonergan, S., Schulte, D., Tackaberry, J. E., Weinrich, M. T., & Pace III, R. M. (2024).

Before and after delisting: Population dynamics of North Atlantic humpback whales over two decades in the Gulf of Maine. *bioRxiv*, 2024-02. https://doi. org/10.1101/2024.02.04.577870

- Rodriguez-Ferrer, G., Reyes, R., Hammerman, N. M., & García-Hernández, J. E. (2018). Cetacean sightings in Puerto Rican waters: Including the first underwater photographic documentation of a minke whale (*Balaenoptera acutorostrata*). Latin American Journal of Aquatic Mammals, 13(1-2), 26-36. https://doi.org/10.5597/00246
- Seger, K. D. (2016). Ambient acoustic environments and cetacean signals: Baseline studies from humpback whale and gray whale breeding grounds. University of California, San Diego.
- Stacey, P. J., Leatherwood, S., & Baird, R. W. (1994). *Pseudorca crassidens. Mammalian Species*, 456, 1-6. https://doi.org/10.2307/3504208
- Steiger, G. H., Calambokidis, J., Straley, J. M., Herman, L. M., Cerchio, S., Salden, D. R., Urbán-R., J., Jacobsen, J. K., von Ziegesar, O., Balcomb, K. C., Gabriele, C. M., Dahlheim, M. E., Uchida, S., Ford, J. K. B., Ladrón de Guevara-P., P., Yamaguchi, M., & Barlow, J. (2008). Geographic variation in killer whale attacks on humpback whales in the North Pacific: Implications for predation pressure. *Endangered Species Research*, *4*, 247-256. https://doi.org/10.3354/esr00078

- Stevick, P. T., Allen, J., Clapham, P. J., Katona, S. K., Larsen, F., Lien, J., Mattila, D. K., Palsbøll, P. J., Sears, R., Sigurjónsson, J., Smith, T. D., Víkingsson, G., Øien, N., & Hammond, P. S. (2006), Population spatial structuring on the feeding grounds in North Atlantic humpback whales (*Megaptera novaeangliae*). Journal of Zoology, 270(2), 244-255. https://doi.org/10.1111/ j.1469-7998.2006.00128.x
- Stimpert, A. K., Mattila, D., Nosal, E. M., & Au, W. W. L. (2012). Tagging young humpback whale calves: Methodology and diving behavior. *Endangered Species Research*, 19(1), 11-17.
- Swartz, S. L., Martinez, A., Stamates, J., Burks, C., & Mignucci-Giannoni, M. M. (2002). Acoustic and visual survey of cetaceans in the waters of Puerto Rico and the Virgin Islands: February-March 2001 (NOAA Technical Memorandum NMFS-SEFSC-463). U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center.