Aquatic Mammals 2021, *47*(2), 196-205, DOI 10.1578/AM.47.2.2021.196

Observations of Killer Whale (*Orcinus orca*) Feeding Behavior in the Tropical Waters of the Northern Mozambique Channel Island of Mayotte, Southwest Indian Ocean

Maeva Terrapon,[1,2] Jeremy J. Kiszka,[3] and Jeanne Wagner[4,5]

[1]*Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, UK*
E-mail: mt208@st-andrews.ac.uk
[2]*MEGAPTERA, 23 Rue Alexandre Dumas, 75011 Paris, France*
[3]*Department of Biological Sciences, Coastlines and Oceans Division, Institute of Environment, Florida International University, 3000 NE 151st Street, North Miami, FL 33181, USA*
[4]*Université de la Réunion, Avenue René Cassin 15, CS 92003, 97744 Saint Denis Cedex 9, La Réunion, France*
[5]*Parc Naturel Marin de Mayotte, Centre d'Affaire de l'Aéroport, 97615 Pamandzi, Mayotte, France*

Abstract

Very little is known about the foraging ecology of killer whales (*Orcinus orca*) in tropical oceans and on how these large apex predators affect prey communities. In most tropical waters, the presence of killer whales is unpredictable, and most information on their ecology is inferred from opportunistic records. This is particularly the case in the Indian Ocean where limited information is available. Between 2002 and 2017, killer whales were opportunistically encountered around the Mozambique Channel island of Mayotte in the eastern Comoros Archipelago (southwest Indian Ocean). A total of 15 killer whale sightings collected by various local experts were compiled and used to describe observed feeding events. Twenty-seven distinct individuals from four separate groups were identified by photo-identification, highlighting short-term site fidelity (minimum 7 days) to this area. Feeding was observed on seven occasions, and recorded prey included two species of elasmobranchs (*Centroscymnus coelolepi* and *Mobula* spp.) and two species of cetaceans: a humpback whale (*Megaptera novaeangliae*) calf and a pantropical spotted dolphin (*Stenella attenuata*). This study represents the first account of killer whales foraging on a combination of marine mammals and elasmobranchs in tropical waters, and describes the first presumed predation on a humpback whale calf in the southwest Indian Ocean.

Key Words: killer whale, *Orcinus orca*, Indian Ocean, elasmobranchs, humpback whale, *Megaptera novaeangliae*, pantropical spotted dolphin, *Stenella attenuata*, feeding ecology, tropical ecosystems

Introduction

Killer whales (*Orcinus orca*) are distributed globally and are apex marine predators that feed on a wide range of prey, including marine mammals (Baird & Dill, 1995; Pitman et al., 2001, 2015; Best et al., 2010), elasmobranchs (Fertl et al., 1996; Pyle et al., 1999; Reyes & García-Borboroglu, 2004; Visser, 2005), teleosts (Similä et al., 1996; Ford & Ellis, 2006; Guinet et al., 2007), sea turtles (Pitman & Dutton, 2004; Fertl & Fulling, 2007; Elwen & Leeney, 2011), and seabirds (Condy et al., 1978; Straneck et al., 1983; Pitman & Durban, 2010), as well as on a combination of several other taxa (Visser et al., 2008; Reisinger et al., 2011). Worldwide, several populations have been differentiated genetically, morphologically, and ecologically, sometimes displaying highly specialized foraging behaviors (Guinet & Bouvier, 1995; Ford et al., 1998, 2011; Pitman & Ensor, 2003; Foote et al., 2009; de Bruyn et al., 2013).

Most existing information on the feeding ecology and behavior of killer whales comes from high-latitude regions when these animals can be studied continuously due to their coastal occurrence and high site fidelity (Ford et al., 1998; Saulitis et al., 2000; de Bruyn et al., 2013). In contrast, little is known of the ecology of killer whales in tropical waters (25° N to 25° S) where information on their presence and diet is scarce and generally reported opportunistically due to the rare occurrence of this species. The most reported prey item in the literature for killer whales in low latitudes are humpback whale (*Megaptera novaeangliae*) calves, predated upon despite the protection from their mothers in their breeding ground, particularly in Hawaii (Baird et al., 2006), off the Pacific

coast of Colombia (Flórez-González et al., 1994), and in Eastern (Paterson & Paterson, 2001) and Western (Pitman et al., 2015) Australia. Other large whales, such as neonate blue whales (*Balaenoptera musculus*; Pitman et al., 2007), Bryde's whales (*Balaenoptera edeni*; Bolaños-Jiménez et al., 2014), and sperm whales (*Physeter macrocephalus*; Reeves et al., 2006) have also been recorded as killer whale prey in tropical waters. A variety of other prey has been recorded in tropical waters, including small delphinids and medium-sized odontocetes (Bolaños-Jiménez et al., 2014; Pitman et al., 2015), large teleosts (Weir et al., 2010), cephalopods (Baird et al., 2006), and sea turtles (Pitman & Dutton, 2004; Bolaños-Jiménez et al., 2014). Overall, there is limited information on the prey of killer whales in tropical oceans. More specifically, it is unknown whether killer whales feed on a range of species or if they tend to specialize on specific taxa as shown in several coastal populations in temperate waters (Ford et al., 1998; Visser, 2005; Jourdain et al., 2020).

In the tropical western Indian Ocean, killer whale sightings are uncommon and have been reported in only a few locations such as in Somalia and in the Seychelles (Gambell et al., 1975; Ballance & Pitman, 1998; Hermans & Pistorius, 2008). The sole record of killer whale predation in the Indian Ocean describes foraging events in Sri Lanka on three species of cetaceans, including *B. musculus*, *P. macrocephalus*, and *Mesoplodon* spp. (Gemmell et al., 2015). Opportunistic observations of killer whale predation off the island of Mayotte, located in the northeastern Mozambique Channel, are compiled in the present study to increase the current knowledge on the occurrence and feeding ecology of killer whales in this region. This is the first study documenting multiple killer whale sightings and feeding events in the western tropical Indian Ocean.

Methods

Mayotte (45° 10' E, 12° 50' S) is a French island of the Comoros Archipelago in the northern Mozambique Channel (Figure 1) and was recently recognized as an Important Marine Mammal Area (IMMA) (International Union for Conservation of Nature [IUCN] Marine Mammal Protected Areas Task Force, 2019), with over 20 cetacean species recorded from this area among the 33 species identified in the western Indian Ocean (Kiszka et al., 2010). The island is surrounded by a 197-km barrier reef, which delimits the second largest closed coral lagoon in the world, with an area of 1,200 km^2 and an average depth of 20 m (Quod et al., 2000). The diversity of marine habitats around Mayotte and its surrounding islets is substantial and includes deep oceanic waters with many submarine canyons in close proximity to the steep slope of the barrier reef (Quod et al., 2000).

Killer whale sightings in Mayotte were collected between 2002 and 2017 from a range of boat-based opportunistic platforms, including humpback whale photo-identification surveys conducted during the austral winter (July to October) by local cetacean experts and whale-watching operators. The effort was focused on areas of known cetacean presence around the island, both inside and outside of the lagoon. Information on the exact location and time of the sighting (defined as an uninterrupted time spent with a group of killer whales), duration, group size, and behaviors were collected. If a feeding event (confirmed kill and ingestion, at least partially) was observed, the type of prey and behavior were recorded from the boat or from underwater observations. Prey species identification was subsequently carried out by one of the authors (JK or JW) using photographs or videos, particularly for elasmobranchs (JK). Whenever possible, photographs were collected for photo-identification purposes to identify how many different killer whale individuals were involved in these feeding events. Individuals were identified from images of the right and left sides of their dorsal fin and eye patches, both of which are described as distinctive features for this species (Bigg, 1982; Visser & Mäkeläinen, 2000). Individuals were grouped into four age and sex categories: (1) adult males (easily recognizable by their characteristically high and triangular dorsal fin), (2) adult females (assessed mature by their large size, their curved dorsal fin, and/or the presence of a calf in close proximity), (3) calves (young individual [< 3 y old] in very close proximity to its presumed mother), and (4) juveniles (individuals of unknown age and sex not confirmed as mature adults) (as per Olesiuk et al., 1990).

Results

Sightings

A total of 15 killer whale sightings were recorded between 2002 and 2017 in the waters of Mayotte (Table 1). All sightings occurred outside of the lagoon in relatively deep waters (mean depth = 700 m; SD = 335; Figure 1). Over 11 of these sightings, 27 different distinct individuals from four different groups were identified from good quality photographs that included at least one clear distinctive feature (dorsal fin or eye patch) for a given individual (the photo-identification catalogue is available in the "Supplementary Material" section of the *Aquatic Mammals* website: https://www.aquaticmammals-journal.org/index.php?option=com_content&view=article&id=10&Itemid=147). No photographs were taken during sightings #1, 2, 4, and 12 (Table 1). Group size varied from two to ten individuals (mean = 6.1; SD = 2.6). Only one sighting occurred before 2011. In general, annual sightings were rare. Only

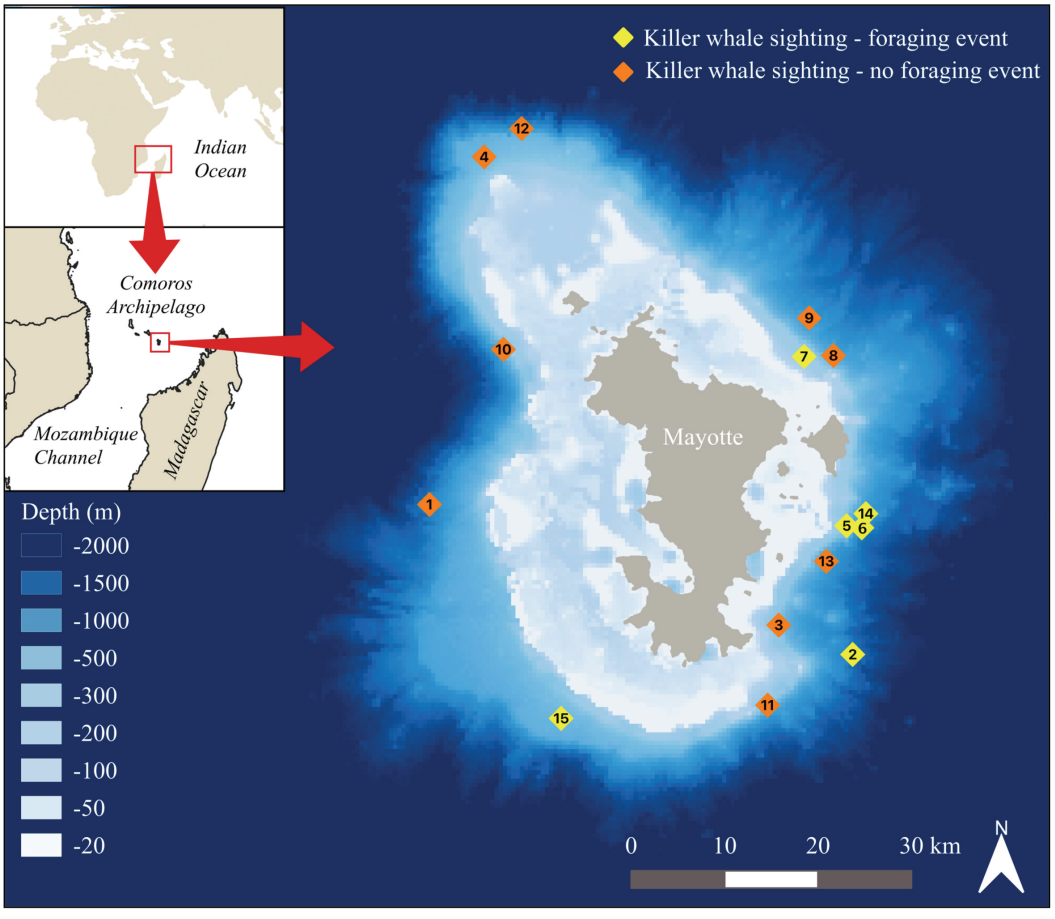

Figure 1. Study area, including all locations of killer whale (*Orcinus orca*) sightings around Mayotte between 2002 and 2017. Numbers represent the associated sighting number from Table 1. Feeding events on marine mammals occurred in sightings #2 and 15; all other feeding events involved elasmobranchs.

one sighting was recorded each year in 2002, 2011, 2014, 2016, and 2017. In contrast, ten sightings occurred in August 2015 over 14 d, including a group of six individuals resighted together on four different occasions over 9 d (sightings #6, 9, 10, and 13; Table 1). Two individuals, believed to be a mother–calf pair, were also sighted together on five different occasions over a 9-d period (sightings #5, 7, 9, 10, and 13). Overall, group composition varied and included a diverse combination of adult males, adult females, calves, and juveniles. No individual was resighted interannually.

Feeding Events

A total of seven feeding events were observed, including three during which underwater photographs were collected (Table 1; Figure 2). Prey identified included three species of elasmobranchs and two species of cetaceans.

On 11 March 2011, a group of four killer whales (sighting #2) was observed during a whale-watching tour with a group of about 20 pantropical spotted dolphins (*Stenella attenuata*) off the southeastern coast of Mayotte, off the reef slope (Table 1). The killer whales, including two presumed adult females and two juveniles, started chasing the dolphins and separated an individual from the group. They remained in close proximity to the isolated dolphin until one of the females attacked it from below. Several minutes later, all individuals surfaced together with the dolphin partially consumed (Figure 2A). After the predation event (unknown duration), the killer whales exhibited slow travel as their main behavior.

On 21 August 2015, two groups of killer whales were observed off the east side of Mayotte (sightings #5 and 6) each engaged in a feeding event. The first group of four killer whales,

Table 1. Sightings of killer whales (*Orcinus orca*) in Mayotte between 2002 and 2017, including feeding events if observed. Italicized latitudes/longitudes were missing from original data sources and were approximated based on available information.

Sighting number	Date (d/mo/y)	Location around Mayotte	Latitude/ longitude	Duration (min)	Approx. depth (m)	Minimum group size	Prey observed	Observed behavior	Source / observer
1	8/5/2002	West	*12° 50.76' S 44° 53.16' E*	N/A	1,000	10	No	N/A	J. J. Kiszka
2	11/3/2011	SE	*12° 59.64' S 45° 18.24' E*	N/A	1,300	4	Pantropical spotted dolphin (*Stenella attenuata*)	Foraging	N. Bertrand, August 2015
3	14/10/2014	SE	*12° 57.90' S 45° 13.86' E*	N/A	350	2	No	Surface resting, curious about boats	M-J. Douiri, September 2015
4	17/8/2015	North/ NW	*12° 30.18' S 44° 56.40' E*	N/A	500	N/A	N/A	N/A	J. Wagner
5	21/8/2015	East	12° 51.84' S 45° 17.68' E	175	400	4	Portuguese dogfish (*Centroscymnus coelolepi*)	Zigzag travelling, foraging, surface activity (tail slaps, breachs), curious about boats, subgroups	J. Wagner; A. Eynard, September 2015
6	21/8/2015	East	*12° 52.14' S 45° 18.78' E*	N/A	1,000	8	Mobulid ray (*Mobula* spp.)	Foraging	J. Wagner
7	24/8/2015	East	12° 45.79' S 45° 18.83' E	120	150	4	Reef manta rays (*Mobula alfredi*) or mobula rays (*Mobula* spp.)	Zigzag travelling, foraging, curious about boats	J. Wagner; V. Torte, September 2015
8	24/8/2015	East	*12° 41.94' S 45° 17.10' E*	60	800	7	No	Travelling, social interactions	J. Wagner
9	26/8/2015	East to North	*12° 39.72' S 45° 15.66' E*	120	1,000	8	No	Travelling in tight formation, curious about boats, surface activity (tail slaps)	M. Terrapon
10	27/8/2015	NW	*12° 41.58' S 44° 57.54' E*	60	500	8	No	Same group as 26/8/2015, travelling	M. Terrapon
11	28/8/2015	South/ SE	*13° 2.64' S 45° 13.20' E*	90	300	2	No	1-h-long vocalizations (mostly static), travelling, boats avoidance	M. Terrapon, J. Wagner
12	29/8/2015	North	*12° 28.50' S 44° 58.62' E*	N/A	900	N/A	N/A	N/A	J. Wagner
13	30/8/2015	East	*12° 54.12' S 45° 16.68' E*	90	800	9	No	Zigzag travelling, travelling in line formation, boats avoidance	M. Terrapon
14	6/11/2016	East	*12° 51.30' S 45° 19.02' E*	240	1,000	6	Unidentified shark (> 2 m)	Travelling, surface activity (breaches close to boats), feeding	D. Pelourdeau, November 2016
15	18/8/2017	South	*13° 3.42' S 45° 0.96' E*	240	500	7	Humpback whale (*Megaptera novaeangliae*) calf	Surface activity (breaches close to boats), feeding	D. Pelourdeau, August 2017

Figure 2. Feeding events observed in Mayotte: (A) pantropical spotted dolphin (*Stenella attenuata*) remains on 11 March 2011, (B) Portuguese dogfish (*Centroscymnus coelolepi*) on 21 August 2015, (C) large mobulid (*Mobula* spp.) on 24 August 2015, and (D) humpback whale (*Megaptera novaeangliae*) calf on 18 August 2017. (*Photo credits:* N. Bertrand, A. Eynard, V. Torte, and Lagon Aventure)

including a mother–calf pair and two individuals of unknown sex (either females or immature males), were observed off the reef slope (approximately 400 m deep) carrying a 1.2- to 1.5-m-long Portuguese dogfish (*Centroscymnus coelolepi*; Figure 2B; sighting #5). The shark, brought to the surface by one of the individuals of unknown sex, appeared dead and mostly intact. The adult female was observed from underwater pushing the shark with her rostrum while her calf circled around it. At about the same time, a second group that was composed of a minimum of eight other killer whales, including three adult males, was observed further offshore, 1 to 2 km away (sighting #6). The killer whales were seen predating on a large mobulid ray (*Mobula* spp.), but no further details are available.

On 24 August 2015, off the east coast with an approximate water depth of 150 m, four killer whales (sighting #7) (identified as the same individuals seen on 21 August 2015; i.e., sighting #5) were observed from both the surface and underwater predating on a large mobulid ray (*Mobula* spp.) on at least two occasions (two different feeding events) during a 2-h sighting. During the underwater observation, the ray was handled by a single individual and was either dead or in tonic immobility (Figure 2C). This large (at least 1.5 m in disk width) ray was shared and eaten by all the individuals of the group. Simultaneously, another group of a minimum of seven killer whales (including the same three males seen on 21 August 2015; i.e., sighting #6) was observed further offshore (sighting #8), 3 km east of the

first sighting, for about an hour. They were travelling south and socializing, including potential reproductive behavior between a male (penis visible while surfacing) and two females. No predation was observed. Several individuals from the two groups of killer whales observed on 21 and 24 August 2015 were resighted together afterward (sightings #8, 9, 10, 11, 12, and 13), suggesting they were all part of the same large group.

On 6 November 2016, six killer whales were observed east of Mayotte offshore (sighting #14) where several whale-watching operators were present. The group was observed for a total duration of 4 h, and a variety of behaviors were recorded, including travelling, socializing, and predation on an unidentified carcharhinid shark (> 2 m), which was brought to the surface after a long dive.

On 18 August 2017, a group of at least seven killer whales was observed for a duration of about 4 h in the south of Mayotte, beginning relatively close to the reef slope and ending further offshore (sighting #15). The animals were exhibiting active surface behaviors (breach, tail slap) and were subsequently observed feeding on a recently dead humpback whale calf. The predation event was not observed, but feeding was confirmed from underwater videos (Figure 2D). Up to three killer whales were observed pulling sections of blubber from the dead calf at the same time, while the other individuals remained at a distance. The ventral part of the humpback whale calf mostly faced the surface, and killer whales fed on it from the top looking down. The skin and blubber on the dorsal and ventral part of the whale were almost entirely consumed by the killer whales.

Discussion

Globally, the occurrence of killer whales is relatively rare in tropical waters (Forney & Wade, 2006), and few sightings have been reported in Mayotte in the past 15 y, despite a substantial amount of effort spent on the water by both researchers and whale-watching operators (Kiszka et al., 2010, 2011, 2012; Van Bressem et al., 2015). However, although no effort data are available, the occurrence of 12 (80%) of the sightings from 2015 to 2017 has been atypically higher. These data also highlight the importance of opportunistic sighting data collection programs involving local stakeholders (in our case, whale-watching operators) to document the occurrence and prey preferences of elusive species such as killer whales.

Observations of predation events off Mayotte mostly occurred on the east coast of the island where whale-watching operators primarily carry out their activity. While the paucity of data collected prevents conclusive characterization of the breadth and level of specialization of killer whales occurring in this region, the variety of prey recorded in Mayotte contributes to the general observation that killer whales have a relatively broad diet in tropical waters compared to temperate waters (Baird et al., 2006; Alava & Merlen, 2009; Weir et al., 2010; Bolaños-Jiménez et al., 2014). Killer whales in other tropical regions have previously been reported to feed on various taxa, including cetaceans, cephalopods, large teleosts, and sea turtles (Baird et al., 2006; Bolaños-Jiménez et al., 2014). This study highlights that killer whales in the northern Mozambique Channel can feed on a variety of taxa, including cetaceans and elasmobranchs. At other tropical locations in the eastern Pacific (e.g., Galápagos, Costa Rica), killer whales are also known to feed on various taxa, including elasmobranchs (Fertl et al., 1996; Alava & Merlen, 2009), baleen whales (Pitman et al., 2007; Alava et al., 2013), and sea turtles (Denkinger et al., 2020).

Killer whale predation on elasmobranchs is relatively uncommon, except in some coastal populations where elasmobranchs may constitute the bulk of their diet (Visser, 2005; Ford et al., 2011). The only shark identified in Mayotte as a prey of killer whales is a Portuguese dogfish, a deep-water demersal species occurring mostly between 128 and 3,700 m (Kiraly et al., 2003). This observation represents the first known occurrence of this shark species in the diet of killer whales. Other large carcharhinids, such as the white shark (*Carcharodon carcharias*), have been reported as prey of killer whales at multiple temperate locations (e.g., Eastern Pacific, South Africa), but the liver was the only consumed part of the animal (Pyle et al., 1999; Engelbrecht et al., 2019). Predation on mobulid rays observed around Mayotte could not be confirmed at the species level; however, pictures collected suggest that *Mobula japanica*, a relatively common species in the Mozambique Channel, could be the species involved (Kiszka et al., 2016). During one of the predation events, a killer whale was observed carrying a ray upside down. It is unclear if the ray was already dead or if it was in tonic immobility, or whether killer whales use this technique to catch and immobilize their prey. Killer whales feeding on mobulid rays (particularly giant manta rays [*Mobula birostris*]) has been recorded across multiple tropical and subtropical locations, including the Marquesas in French Polynesia (Gannier, 2002), Papua New Guinea (Visser & Bonoccorso, 2003), the Galápagos (Alava & Merlen, 2009; Denkinger et al., 2020), and off Rio de Janeiro, Brazil (Lodi & Hetzel, 1998).

Killer whale predation on marine mammals in the tropics is more commonly reported and generally involves small odontocetes (Pitman et al., 2001; Bolaños-Jiménez et al., 2014; Dunn & Claridge, 2014) or baleen whales (Jefferson et al., 1991; Flórez-González et al., 1994; Pitman et al., 2007, 2015; Gemmell et al., 2015). This study reports the first known occurrence of killer whales feeding on pantropical spotted dolphins and humpback whale calves in the western Indian Ocean. While adult humpback whales are not the primary target of killer whales worldwide, calves are targeted in all oceans, either in their breeding ground or during their first migration to their feeding ground (Clapham, 2000; Mehta et al., 2007; Steiger et al., 2008; Pitman et al., 2015). During previously described attacks on humpback whale calves, killer whales often target the throat and jaw of their prey. While the attack itself was not observed in this case, the remains of the calf on which the killer whales were feeding suggest individuals in Mayotte used a similar technique because the jaw of the dead calf was dislocated and the throat was entirely consumed.

Once captured, prey sharing among all group members was observed in both feeding events on cetaceans and on at least one of the predation events on rays. Prey sharing is commonly observed in this species, both with large (Guinet, 1992; Baird & Dill, 1995; Pitman & Durban, 2012; Ford, 2019) and small (Lopez & Lopez, 1985; Hoelzel, 1991; Pitman & Durban, 2012) prey. The subdivision of efforts within the group, with only a few individuals hunting at a time but sharing the prey with all group members, was also observed for a range of prey, including marine mammals (Silber et al., 1990; Guinet et al., 2000) and elasmobranchs (Fertl et al., 1996; Visser, 2005). Prey sharing between a female and a juvenile could also be important for the young individual to practice foraging tactics, particularly if prey are large or risky to capture (Hoezel, 1991; Guinet, 1992).

Predation on humpback whale calves remains rarely witnessed, but the prevalence of attacks can be inferred from the regular occurrence of killer whale tooth rake marks on the fluke of surviving individuals (Mehta et al., 2007; Steiger et al., 2008). However, such attacks are increasingly described in the literature (Paterson & Paterson, 2001; Baird et al., 2006; Pitman et al., 2015). While the increase in reporting may be the result of more people being "at the right place at the right time," it has also been suggested that the post-whaling recovery of baleen whales could be beneficial for killer whales by increasing the predictable availability of newborn calves in locations where other prey are scarce or unpredictable (Pitman et al., 2015).

The rarity of killer whales in the tropics largely precludes using dedicated systematic surveys to study them. Instead, opportunistic observations and regional collaborations will continue to be important to better assess the impact of killer whale predation on tropical ecosystems, including on recovering baleen whale populations. This study provides an initial insight on the presence and feeding ecology of killer whales in the waters of Mayotte and is a first step towards improving our understanding of killer whale behavior in the tropical southwestern Indian Ocean.

Acknowledgments

We would like to thank the generous data contributors who shared their killer whale sightings and photographs, and who are involved in several organizations, including Michel Vély, Mary-Jenny Douiri, and other volunteers from the NGO *MEGAPTERA*; Nils Bertrand from Sea Blue Safari; Donatien Pelourdeau from Lagon Aventure; the Parc Naturel Marin de Mayotte; and Katia Ballorain, Vincent Torte, and Alex Eynard. We also thank Robert L. Pitman for his comments on the first draft of the manuscript. This is Publication #238 from the Coastlines and Oceans Division at the Institute of Environment at Florida International University.

Literature Cited

Alava, J. J., & Merlen, G. (2009). Video-documentation of a killer whale (*Orcinus orca*) predatory attack on a giant manta (*Manta birostris*) in the Galápagos Islands. *Latin American Journal of Aquatic Mammals*, *7*(1-2), 81-84. https://doi.org/10.5597/lajam00139

Alava, J. J., Smith, K. J., O'Hern, J., Alarcón, D., Merlen, G., & Denkinger, J. (2013). Observations of killer whale (*Orcinus orca*) attacks on Bryde's whales (*Balaenoptera edeni*) in the Galápagos Islands. *Aquatic Mammals*, *39*(2), 196-201. https://doi.org/10.1578/AM.39.2.2013.196

Baird, R. W., & Dill, L. M. (1995). Occurrence and behaviour of transient killer whales: Seasonal and pod-specific variability, foraging behaviour, and prey handling. *Canadian Journal of Zoology*, *73*(7), 1300-1311. https://doi.org/10.1139/z95-154

Baird, R. W., McSweeney, D. J., Bane, C., Barlow, J., Salden, D. R., La'Ren, K. A., LeDuc, R. G., & Webster, D. L. (2006). Killer whales in Hawaiian waters: Information on population identity and feeding habits. *Pacific Science*, *60*(4), 523-530. https://doi.org/10.1353/psc.2006.0024

Ballance, L. T., & Pitman, R. L. (1998). Cetaceans of the western tropical Indian Ocean: Distribution, relative abundance, and comparisons with cetacean communities of two other tropical ecosystems. *Marine Mammal Science*,

14(3), 429-459. https://doi.org/10.1111/j.1748-7692.1998.tb00736.x

Best, P. B., Meÿer, M. A., & Lockyer, C. (2010). Killer whales in South African waters—A review of their biology. *African Journal of Marine Science*, *32*(2), 171-186. https://doi.org/10.2989/1814232X.2010.501544

Bigg, M. A. (1982). An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Report of the International Whaling Commission*, *32*, 655-666.

Bolaños-Jiménez, J., Mignucci-Giannoni, A. A., Blumenthal, J., Bogomolni, A., Casas, J. J., Henríquez, A., Iñíguez Bessega, M., Khan, J., Landrau-Giovannetti, N., Rinaldi, C., & Rinaldi, R. (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

Clapham, P. J. (2000). The humpback whale: Seasonal feeding and breeding in a baleen whale. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 173-196). University of Chicago Press.

Condy, P. R., Aarde, R. V., & Bester, M. N. (1978). The seasonal occurrence and behaviour of killer whales, *Orcinus orca*, at Marion Island. *Journal of Zoology*, *184*(4), 449-464. https://doi.org/10.1111/j.1469-7998.1978.tb03301.x

de Bruyn, P. J. 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

Denkinger, J., Alarcón, D., Espinosa, B., Fowler, L., Manning, C., Oña, J., & Palacios, D. M. (2020). Social structure of killer whales (*Orcinus orca*) in a variable low-latitude environment, the Galápagos Archipelago. *Marine Mammal Science*, *36*(3), 774-785. https://doi.org/10.1111/mms.12672

Dunn, C., & Claridge, D. (2014). Killer whale (*Orcinus orca*) occurrence and predation in the Bahamas. *Journal of the Marine Biological Association of the United Kingdom*, *94*(6), 1305-1309. https://doi.org/10.1017/S0025315413000908

Elwen, S. H., & Leeney, R. H. (2011). Interactions between leatherback turtles and killer whales in Namibian waters, including possible predation. *African Journal of Wildlife Research*, *41*(2), 205-209. https://doi.org/10.3957/056.041.0207

Engelbrecht, T. M., Kock, A. A., & O'Riain, M. J. (2019). Running scared: When predators become prey. *Ecosphere*, *10*(1). https://doi.org/10.1002/ecs2.2531

Fertl, D., & Fulling, G. L. (2007). Interactions between marine mammals and turtles. *Marine Turtle Newsletter*, *115*, 4-8.

Fertl, D., Acevedo-Gutierrez, A., & Darby, F. L. (1996). A report of killer whales (*Orcinus orca*) feeding on a carcharhinid shark in Costa Rica. *Marine Mammal Science*, *12*(4), 606-611. https://doi.org/10.1111/j.1748-7692.1996.tb00075.x

Flórez-González, L., Capella, J. J., & Rosenbaum, H. C. (1994). Attack of killer whales (*Orcinus orca*) on humpback whales (*Megaptera novaeangliae*) on a South American Pacific breeding ground. *Marine Mammal Science*, *10*(2), 218-222. https://doi.org/10.1111/j.1748-7692.1994.tb00264.x

Foote, A. D., Newton, J., Piertney, S. B., Willerslev, E., & Gilbert, M. T. P. (2009). Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. *Molecular Ecology*, *18*(24), 5207-5217. https://doi.org/10.1111/j.1365-294X.2009.04407.x

Ford, J. K. B. (2019). Killer whales: Behavior, social organization, and ecology of the oceans' apex predators. In B. Würsig (Ed.), *Ethology and behavioral ecology of odontocetes* (pp. 239-259). Springer. https://doi.org/10.1007/978-3-030-16663-2_11

Ford, J. K. B., & Ellis, G. M. (2006). Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Marine Ecology Progress Series*, *316*, 185-199. https://doi.org/10.3354/meps316185

Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R. S., & Balcomb III, K. C. (1998). Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology*, *76*(8), 1456-1471. https://doi.org/10.1139/z98-089

Ford, J. K. B., Ellis, G. M., Matkin, C. O., Wetklo, M. H., Barrett-Lennard, L. G., & Withler, R. E. (2011). Shark predation and tooth wear in a population of northeastern Pacific killer whales. *Aquatic Biology*, *11*(3), 213-224. https://doi.org/10.3354/ab00307

Forney, K. W., & Wade, P. (2006). Worldwide distribution and abundance of killer whales. In J. A. Estes, D. P. DeMaster, D. F. Doak, T. M. Williams, & R. L. Brownell, Jr. (Eds.), *Whales, whaling, and ocean ecosystems* (pp. 145-162). University of California Press. https://doi.org/10.1525/california/9780520248847.003.0012

Gambell, R., Best, P. B., & Rice, D. W. (1975). Report on the international Indian Ocean whale marking cruise 24 November 1973–3 February 1974. *Report of the International Whaling Commission*, *25*, 240-252.

Gannier, A. (2002). Cetaceans of the Marquesas Islands (French Polynesia): Distribution and relative abundance as obtained from a small boat dedicated survey. *Aquatic Mammals*, *28*(2), 198-210.

Gemmell, G. L., McInnes, J. D., Heinrichs, S. J., & Wijeyeratne, G. S. (2015). Killer whale *(Orcinus orca)* predation on whales in Sri Lankan waters. *Aquatic Mammals*, *41*(3), 265-271. https://doi.org/10.1578/AM.41.3.2015.265

Guinet, C. (1992). Comportement de chasse des orques (*Orcinus orca*) autour des iles Crozet [Hunting behavior of killer whales (*Orcinus orca*) around the Crozet Islands]. *Canadian Journal of Zoology*, *70*(9), 1656-1667. https://doi.org/10.1139/z92-231

Guinet, C., & Bouvier, J. (1995). Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology*, *73*(1), 27-33. https://doi.org/10.1139/z95-004

Guinet, C., Barrett-Lennard, L. G., & Loyer, B. (2000). Co-ordinated attack behavior and prey sharing by killer whales at Crozet Archipelago: Strategies for feeding on negatively-buoyant prey. *Marine Mammal Science*, *16*(4), 829-834. https://doi.org/10.1111/j.1748-7692.2000.tb00976.x

Guinet, C., Domenici, P., de Stephanis, R., Barrett-Lennard, L., Ford, J. K. B., & Verborgh, P. (2007). Killer whale predation on bluefin tuna: Exploring the hypothesis of the endurance-exhaustion technique. *Marine Ecology Progress Series*, *347*, 111-119. https://doi.org/10.3354/meps07035

Hermans, A., & Pistorius, P. A. (2008). Marine mammal diversity in the remote waters of Aldabra atoll, southern Seychelles. *Atoll Research Bulletin*, No. 564. https://doi.org/10.5479/si.00775630.564.1

Hoelzel, A. R. (1991). Killer whale predation on marine mammals at Punta Norte, Argentina; food sharing, provisioning and foraging strategy. *Behavioral Ecology and Sociobiology*, *29*(3), 197-204. https://doi.org/10.1007/BF00166401

International Union for Conservation of Nature (IUCN) Marine Mammal Protected Areas Task Force. (2019). *Final Report of the Fifth IMMA Workshop: Regional Workshop for Western Indian Ocean and Arabian Seas*, Salalah, Sultanate of Oman. 60 pp.

Jefferson, T. A., Stacey, P. J., & Baird, R. W. (1991). A review of killer whale interactions with other marine mammals: Predation to co-existence. *Mammal Review*, *21*(4), 151-180. https://doi.org/10.1111/j.1365-2907.1991.tb00291.x

Jourdain, E., Andvik, C., Karoliussen, R., Ruus, A., Vongraven, D., & Borgå, K. (2020). Isotopic niche differs between seal and fish-eating killer whales (*Orcinus orca*) in northern Norway. *Ecology and Evolution*, *10*(9), 4115-4127. https://doi.org/10.1002/ece3.6182

Kiraly, S. J., Moore, J. A., & Jasinski, P. H. (2003). Deepwater and other sharks of the U.S. Atlantic Ocean Exclusive Economic Zone. *Marine Fisheries Review*, *65*(4), 1-64.

Kiszka, J., Quod, J-P., & Berggren, P. (2016). *Sharks and rays: A field guide to common elasmobranchs of East Africa*. Western Indian Ocean Marine Science Association.

Kiszka, J., Vely, M., & Breysse, O. (2010). Preliminary account of cetacean diversity and humpback whale (*Megaptera novaeangliae*) group characteristics around the Union of the Comoros (Mozambique Channel). *Mammalia*, *74*(1), 51-56. https://doi.org/10.1515/mamm.2010.003

Kiszka, J., Simon-Bouhet, B., Gastebois, C., Pusineri, C., & Ridoux, V. (2012). Habitat partitioning and fine scale population structure among insular bottlenose dolphins (*Tursiops aduncus*) in a tropical lagoon. *Journal of Experimental Marine Biology and Ecology*, *416*, 176-184. https://doi.org/10.1016/j.jembe.2012.03.001

Kiszka, J., Simon-Bouhet, B., Martinez, L., Pusineri, C., Richard, P., & Ridoux, V. (2011). Ecological niche segregation within a community of sympatric dolphins around a tropical island. *Marine Ecology Progress Series*, *433*, 273-288. https://doi.org/10.3354/meps09165

Lodi, L., & Hetzel, B. (1998). *Orcinus orca* (Cetacea; Delphinidae) em águas costeiras do Estado do Rio de Janeiro [*Orcinus orca* (Cetacea; Delphinidae) in coastal waters of the State of Rio de Janeiro]. *Bioikos*, *12*(1), 46-54.

Lopez, J. C., & Lopez, D. (1985). Killer whales (*Orcinus orca*) of Patagonia and their behavior of intentional stranding while hunting nearshore. *Journal of Mammalogy*, *66*(1), 181-183. https://doi.org/10.2307/1380981

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., Witteveen, B. H., & 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

Olesiuk, P. F., Bigg, M. A., & Ellis, G. M. (1990). Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission*, *Special Issue 12*, 209-243.

Paterson, R. A., & Paterson, P. (2001). A presumed killer whale (*Orcinus orca*) attack on humpback whales (*Megaptera novaeangliae*) at Point Lookout, Queensland. *Memoirs of the Queensland Museum*, *47*, 436.

Pitman, R. L., & Durban, J. W. (2010). Killer whale predation on penguins in Antarctica. *Polar Biology*, *33*(11), 1589-1594. https://doi.org/10.1007/s00300-010-0853-5

Pitman, R. L., & Durban, J. W. (2012). Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. *Marine Mammal Science*, *28*(1), 16-36. https://doi.org/10.1111/j.1748-7692.2010.00453.x

Pitman, R. L., & Dutton, P. H. (2004). Killer whale predation on a leatherback turtle in the northeast Pacific. *Pacific Science*, *58*(3), 497-498. https://doi.org/10.1353/psc.2004.0034

Pitman, R. L., & Ensor, P. (2003). Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *Journal of Cetacean Research and Management*, *5*, 131-139.

Pitman, R. L., Ballance, L. T., Mesnick, S. I., & Chivers, S. J. (2001). Killer whale predation on sperm whales: Observations and implications. *Marine Mammal Science*, *17*(3), 494-507. https://doi.org/10.1111/j.1748-7692.2001.tb01000.x

Pitman, R. L., Fearnbach, H., LeDuc, R., Gilpatrick, J. W., Jr., & Ford, J. K. B. (2007). Killer whales preying on a blue whale calf on the Costa Rica Dome: Genetics, morphometrics, vocalisations and composition of the group. *Journal of Cetacean Research and Management*, *9*(2), 151-157.

Pitman, R. L., Totterdell, J. A., Fearnbach, H., Ballance, L. T., Durban, J. W., & Kemps, H. (2015). Whale killers: Prevalence and ecological implications of killer whale predation on humpback whale calves off Western

Australia. *Marine Mammal Science*, *31*(2), 629-657. https://doi.org/10.1111/mms.12182

Pyle, P., Schramm, M. J., Keiper, C., & Anderson, S. D. (1999). Predation on a white shark (*Carcharodon carcharias*) by a killer whale (*Orcinus orca*) and a possible case of competitive displacement. *Marine Mammal Science*, *15*(2), 563-568. https://doi.org/10.1111/j.1748-7692.1999.tb00822.x

Quod, J-P., Naim, O., & Abdourazi, F. (2000). The Comoros Archipelago. In C. Sheppard (Ed.), *Seas at the millennium: An environmental evaluation* (pp. 243-252). Pergamon Press.

Reeves, R. R., Berger, J., & Clapham, P. J. (2006). Killer whales as predators of large baleen whales and sperm whales. In J. A. Estes, D. P. DeMaster, D. F. Doak, T. M. Williams, & R. L. Brownell, Jr. (Eds.), *Whales, whaling, and ocean ecosystems* (pp. 174-187). University of California Press. https://doi.org/10.1525/california/9780520248847.003.0014

Reisinger, R. R., de Bruyn, P. J. N., Tosh, C. A., Oosthuizen, W. C., Mufanadzo, N. T., & Bester, M. N. (2011). Prey and seasonal abundance of killer whales at sub-Antarctic Marion Island. *African Journal of Marine Science*, *33*(1), 99-105. https://doi.org/10.2989/1814232X.2011.572356

Reyes, L. M., & García-Borboroglu, P. (2004). Killer whale (*Orcinus orca*) predation on sharks in Patagonia, Argentina: A first report. *Aquatic Mammals*, *30*(3), 376-379. https://doi.org/10.1578/AM.30.3.2004.376

Saulitis, E., Matkin, C., Barrett-Lennard, L., Heise, K., & Ellis, G. (2000). Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. *Marine Mammal Science*, *16*(1), 94-109. https://doi.org/10.1111/j.1748-7692.2000.tb00906.x

Silber, G. K., Newcomer, M. W., & Pérez-Cortés, M. H. (1990). Killer whales (*Orcinus orca*) attack and kill a Bryde's whale (*Balaenoptera edeni*). *Canadian Journal of Zoology*, *68*(7), 1603-1606. https://doi.org/10.1139/z90-238

Similä, T., Holst, J. C., & Christensen, I. (1996). Occurrence and diet of killer whales in northern Norway: Seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(4), 769-779. https://doi.org/10.1139/f95-253

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

Straneck, R., Livezey, B. C., & Humphrey, P. S. (1983). Predation on steamer-ducks by killer whale. *The Condor*, *85*(2), 255-256. https://doi.org/10.2307/1367268

Van Bressem, M-F., Simões-Lopes, P. C., Félix, F., Kiszka, J. J., Daura-Jorge, F. G., Avila, I. C., Secchi, E. R., Flach, L., Fruet, P. F., du Toit, K., Ott, P. H., Elwen, S., Di Giacomo, A. B., Wagner, J., Banks, A., & Van Waerebeek, K. (2015). Epidemiology of lobomycosis-like disease in bottlenose dolphins *Tursiops* spp. from South America and southern Africa. *Diseases of Aquatic Organisms*, *117*(1), 59-75. https://doi.org/10.3354/dao02932

Visser, I. N. (2005). First observations of feeding on thresher (*Alopias vulpinus*) and hammerhead (*Sphyrna zygaena*) sharks by killer whales (*Orcinus orca*) specialising on elasmobranch prey. *Aquatic Mammals*, *31*(1), 83-88. https://doi.org/10.1578/AM.31.1.2005.83

Visser, I. N., & Bonoccorso, F. J. (2003). New observations and a review of killer whale (*Orcinus orca*) sightings in Papua New Guinea waters. *Aquatic Mammals*, *29*(1), 150-172. https://doi.org/10.1578/016754203101024004 4

Visser, I. N., & Mäkeläinen, P. (2000). Variation in eye-patch shape of killer whales (*Orcinus orca*) in New Zealand waters. *Marine Mammal Science*, *16*(2), 459-469. https://doi.org/10.1111/j.1748-7692.2000.tb00938.x

Visser, I. N., Smith, T. G., Bullock, I. D., Green, G. D., Carlsson, O. G., & Imberti, S. (2008). Antarctic Peninsula killer whales (*Orcinus orca*) hunt seals and a penguin on floating ice. *Marine Mammal Science*, *24*(1), 225-234. https://doi.org/10.1111/j.1748-7692.2007.00163.x

Weir, C. R., Collins, T., Carvalho, I., & Rosenbaum, H. C. (2010). Killer whales (*Orcinus orca*) in Angolan and Gulf of Guinea waters, tropical West Africa. *Journal of the Marine Biological Association of the United Kingdom*, *90*(8), 1601-1611. https://doi.org/10.1017/S002531541000072X