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KILLER WHALE ATTACKS ON MINKE WHALES: PREY CAPTURE AND ANTIPREDATOR TACTICS

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ABSTRACT

We describe nine incidents of predation or attempted predation of minke whales (*Balaenoptera acutorostrata*) by mammal-hunting "transient" killer whales (*Orcinus orca*) in coastal waters of British Columbia, Washington, and southeastern Alaska. Pursuits of minke whales were characterized by prolonged chases on a straight heading at velocities of 15–30 km/h. In four of the nine cases the adult-sized minke whale gradually outdistanced the killer whales, which abandoned the high-speed pursuit after 0.5–1 h. In one case the minke beached itself and died. Four attacks were successful. In one instance a subadult minke was killed in open water following a chase. In two cases the fleeing minke entered a confined bay and was killed by the killer whales. One adult minke was taken after apparently attempting to seek cover beside a large sailboat. Minke whales made no attempt to physically defend themselves and were killed by repeated ramming or by asphyxiation. Although killer whales are capable of sprinting speeds greater than those of minke whales, it appears that adult minkes can maintain higher sustained

speeds and evade capture if sufficient space for an extended escape trajectory is available. Successful predation of minke whales in coastal waters is rare compared to pinnipeds and small cetaceans, the main prey of transient killer whales.

Key words: *Orcinus orca*, *Balaenoptera acutorostrata*, predator-prey interactions, transient killer whales, predator evasion, hunting strategy.

Killer whales (*Orcinus orca*) are known to prey on a wide variety of species, including baleen whales (Scammon 1874, Martinez and Klinghammer 1970, Jefferson *et al.* 1991). However, there are few data on the extent to which mysticetes are hunted by killer whales. Springer *et al.* (2003) recently suggested that baleen whales are the preferred prey of mammal-hunting killer whales in the North Pacific and that the depletion of whale stocks by commercial whaling caused killer whales to shift to preying on pinnipeds and sea otters (*Enhydra lutris*), resulting in a sequential collapse in the abundance of those populations. In contrast, Jonsgård (1968*a*, *b*) argued there is little evidence that killer whales routinely take healthy adult baleen whales, and suggested that it is probably difficult for them to do so under normal conditions. Corkeron and Connor (1999) proposed that predation pressure from killer whales is responsible for the migratory patterns seen in certain baleen whales, especially gray whales (*Eschrichtius robustus*) and humpback whales (*Megaptera novaeangliae*). Clapham (2001), however, remarked on how rarely killer whales have been seen attacking humpback whales despite many years of field study, and concluded that "there is little evidence that humpback whales are anything more than a very occasional target of killer whales anywhere."

Much of the uncertainty about the predator-prey relationship of killer whales and baleen whales results from the scarcity of observations of attacks and kills, and the lack of an ecological context in which to place such events. Most published accounts of attacks on baleen whales are anecdotal or incomplete (Jefferson *et al.* 1991) and involve killer whales of unknown population identity. Dedicated studies of predation by mammal-hunting killer whales are needed to determine the hunting tactics used to prey on baleen whales and to evaluate the relative success rates of such attacks compared to other prey.

Two sympatric ecotypes of killer whale, so-called "residents" and "transients," are found in coastal waters of British Columbia, Washington, and southeastern Alaska (Bigg 1982, Bigg *et al.* 1990, Dahlheim *et al.* 1997, Ford *et al.* 2000). Residents prey on salmon (*Oncorhynchus* spp.), other fish species, and squid, whereas transients feed on homeothermic prey, primarily pinnipeds and small odontocetes (Ford *et al.* 1998). Until recently, predation by transient killer whales on mysticetes in the region had rarely been observed. Only three attacks on mysticetes were seen in 186 predation events by transients documented by Ford *et al.* (1998) in waters of British Columbia and southeastern Alaska during 1973–1996. Those attacks involved an unsuccessful chase of a minke whale (*Balaenoptera acutorostrata*) and two attacks on gray whale calves. No mysticetes were involved in 138 attacks on marine mammals observed off southern Vancouver Island, British Columbia, by Baird and Dill (1995), or in 20 predation events by transients observed in southeastern Alaska by Matkin and Dahlheim (1995). Two kills of minke whales have been reported previously in British Columbia (Hancock 1965, Ford and Ellis 1999), but the killer whales involved were unidentified.

Here we describe recent observations of coordinated attacks by transient killer whales on minke whales in waters near Vancouver Island, British Columbia, and Glacier Bay, Alaska. These observations are noteworthy in that they add *B. acutorostrata* to the prey of known transient killer whales, document the escape tactics of minke whales under attack, and provide insights into the means by which killer whales capture, debilitate, and kill the species in coastal waters. Such detailed accounts of killer whale predation on minke whales or other mysticete species are rare, both regionally and globally (Jefferson *et al.* 1991, Guinet *et al.* 2000).

METHODS

Observations of predation were made during long-term studies of the life history and ecology of killer whales in British Columbia and Washington state (since 1973; Ford *et al.* 1998), and in the Glacier Bay-Icy Strait region of southeastern Alaska (since 1988; Matkin and Dahlheim 1995). Field studies were generally undertaken from small vessels (<10 m in length) and were confined to coastal waters up to 20 km from shore.

Accounts of predation events involving minke whales were compiled from notes, photographs, and video recordings collected concurrently or sequentially by multiple observers on small vessels or on shore. Transient killer whales were identified visually in the field or from photographs of unique natural markings, using the catalog in Ford and Ellis (1999) or a reference photo-identification catalog maintained at the Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, BC. In the following accounts of predation events, *chases* are defined as high-speed pursuits of minke whales by killer whales, and *attacks* are assaults involving physical contact. Speeds and distances were determined from GPS tracks or were estimated.

RESULTS

Nine predation events involving transient killer whales and single minke whales were documented during 1994–2004. Four resulted in the minke being killed and eaten, and one ended with the minke stranding in shallow water and dying without being attacked. In the other four cases the minke escaped. Chases and attacks involved groups of 2–13 transient killer whales and continued for 0.5 to more than 8.5 h before the minke was killed or escaped. A total of 33 individual killer whales were involved in these events, from a population of about 250 transient killer whales photo-identified in northern Washington state, British Columbia, and southeastern Alaska (Ford and Ellis 1999; J. Ford and G. Ellis, unpublished data). An account of each event is provided below, with additional details given in Table 1. Locations of predation events are shown in Figure 1.

Event 1 began at 0730 on 12 July 1994, when two transient killer whales, the adult male T14 and adult female T13, were observed traveling west in Johnstone Strait, off northeastern Vancouver Island, British Columbia. At 0802, an adult-sized minke whale was spotted traveling west at a moderate pace 60 m ahead of the killer whales. By 0814, T13, swimming ahead of the male, gradually closed to within 30 m of the minke. At 0818 the killer whales suddenly accelerated towards the minke and a high-speed chase ensued. All three whales porpoised as they swam towards the west at speeds of 25–30 km/h. At 0825 the whales turned and

Table 1. Summary of details of chases and attacks by killer whales on minke whales documented in this report. General locations of predation events are shown in Figure 1. Start position is the geographical coordinates where an attack or chase began or was first seen. Distance covered refers to the distance traveled by the killer whales and minke during a chase. Identities of killer whales involved in predation events are from Ford and Ellis (1999) or from a catalog of identification photographs maintained at the Pacific Biological Station, Nanaimo, BC. Group composition is the number of mature males (♂), mature females (♀) and subadults of both sexes in each predation event.

Event no.	Date	Location	Start position	Incident	No. of killer whales	Killer whale identities	Killer whale group composition	Duration of chase or attack (h)	Distance covered (km)
1	12 Jul 1994	Johnstone Strait, BC	50°31′N, 126°38′W	Chase	2	T13, T14	1♂, 1♀	0.5	9
2	27 Jul 1996	Glacier Bay, AK	58°20′N, 135°57′W	Kill	13	T63, T64, T64A, T65, T65A, T65B, T72, T87, T88, T90, T93, T94, T97	4♂, 4♀, 5 subadult	1.5+	n/a
3	7 Sep 1998	Cormorant Channel, BC	50°37′N, 126°50′W	Chase	9	T18, T19, T19B, T29, T2B, T59, T59A, T60, T60B	1♂, 5♀, 3 subadult	0.5	11
4	15 Oct 2002	Ganges Harbour, BC	48°50′N, 123°28′W	Kill	4	T11, T11A, T12, T12A	2♂, 2♀	6.5+	7+
5	19 Aug 2003	Juan de Fuca Strait	48°26′N, 122°59′W	Chase	4	T18, T19, T19B, T19C	2♀, 2 subadult	1	15
6	2 Sep 2003	Blackfish Sound, BC	50°35′N, 126°42′W	Kill	4	T18, T19, T19B, T19C	2♀, 2 subadult	1.3	13
7	5 Sep 2003	Glacier Bay, AK	58°30′N, 136°05′W	Chase	2	T71, T71B	1♀, 1 subadult	0.7	15
8	1 Dec 2003	Juan de Fuca Strait	48°27′N, 123°02′W	Kill	6	T18, T19, T19B, T19C, T20, T21	1♂, 3♀, 2 subadult	1.3+	18+
9	28 Oct 2004	Shoal Harbour, BC	50°45′N, 126°30′W	Chase	2	T12, T12A	1♂, 1♀	8.5+	6+

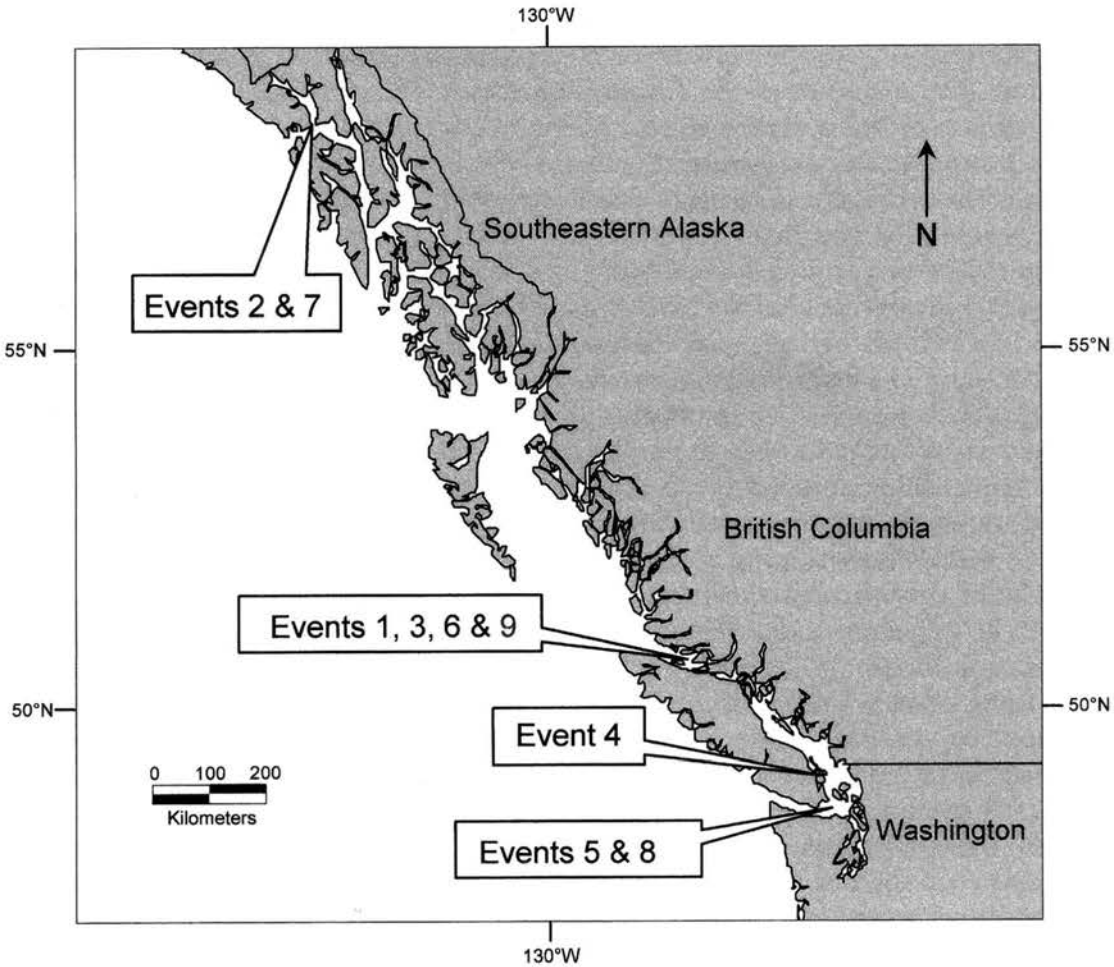

Figure 1. Locations of predation events involving minke whales and transient killer whales. See Table 1 and the text for further details.

continued porpoising towards the east, with T13 swimming 3–4 m from the minke and T14 about 15 m behind. By 0828 the minke had pulled ahead of the killer whales, with T13 45 m and T14 60 m behind the minke. The chase continued for another 16 min during which time the killer whales, especially the male, continued to fall behind the minke. At 0844 the killer whales ended the pursuit. During the 26 min chase, the whales traveled 9 km at an average speed of about 20 km/h.

Event 2 began at 1735 on 27 July 1996, when observers aboard a 20-m sailboat near Glacier Bay, Alaska, observed a group of 13 transient killer whales in close high-speed pursuit of an adult-sized minke whale. As the transients and minke drew near to the boat, the minke slowed and approached closely alongside the boat as if it was attempting to hide from the attacking whales. At this point, the transients caught up to the minke, and the adult male T63 began ramming it repeatedly from beneath. Individual transients positioned themselves in front of the minke to block its forward path and prevent it from diving. On two occasions, a humpback whale approached to within 50 m of the scene of the attack. Each time, T63 left the minke and rammed the side of the humpback several times. The humpback responded by rolling over and thrashing its tail flukes towards the killer whale, which then returned to the minke attack.

The attack continued until 1900, when the minke disappeared beneath the surface and probably sank to the bottom in 40 m of water. The killer whales continued to mill and dive at the site of the kill until observations ended at 2040. Oil and bits of blubber at the surface indicated that the transients were feeding on the carcass. On 30 July a minke carcass, presumably that of the animal killed three days earlier, was observed near the site of the kill, floating with stomach and intestines protruding from a hole in its ventral side. Bite and teeth rake marks were visible on the tail flukes and other parts of the body, and much of the skin had been peeled off.

Event 3 involved a group of nine transient killer whales that was first encountered moving west in Blackfish Sound, British Columbia, at 1430 on 7 September 1998. At 1610, the whales, which were spread over about 1 km^2 and traveling at 5–6 km/h, suddenly began swimming towards Cormorant Channel at a speed of 20–25 km/h in pursuit of an adult-sized minke whale. The minke was initially observed porpoising 100 m ahead of the lead killer whales, and it gradually pulled away over the course of the chase. Female killer whales were closest to the minke, and the single mature male was swimming at the rear of the procession. At 1640, the killer whales abandoned the pursuit and returned to their original slow pace. The chase involved a straight trajectory and covered a total distance of 11 km in 30 min.

Event 4 began at 0930 on 15 October 2002, when residents of Ganges, Saltspring Island, British Columbia, observed a group of four killer whales chase a minke whale into Ganges Harbour, a narrow bay 3.5 km long by 0.5–1.0 km wide. The whales involved in the chase were later identified as the transient female T11, her mature son T11A, the female T12, and her mature son T12A (Table 1). When the approximately 9-m minke reached the head of the bay, it became grounded in shallow water adjacent to the harbor's breakwater. The tide was moderately low (1.75 m above datum) at the time, and the killer whales seemed reluctant or unable to approach closer than 10–20 m to the minke, which lay passively in 1 m of water.

By 1300 the tide had risen sufficiently to allow the female killer whales to swim up to the minke and initiate an attack. The larger males remained 10–30 m away in deeper water. The killer whales moved slowly and deliberately. Over the next 20 min, the two female killer whales took turns swimming up to the minke, which was oriented towards the shore with its tail in deeper water. The female T11 bit or butted the peduncle area of the minke on two occasions, and struck it once with its flukes. At 1321 T11 approached and seized the minke's tail flukes with her teeth, and by pushing forward pivoted the minke's body into deeper water. The minke then swam slowly ahead for 10 m, at which point its rostrum hit an adjacent rock breakwater and the whale stopped. The female killer whales continued taking turns slowly approaching the minke about every 2 min for the next 32 min. On five occasions T11 rammed her rostrum into the minke's left side, but T12 did not strike the whale. At 1354 the minke, which by now was fully afloat (tide 3.3 m above datum), began swimming parallel to the breakwater. The female killer whales immediately drew alongside and T11 appeared to grasp the minke's left pectoral fin in its mouth and pull the whale into deeper water.

The activity levels of the killer whales intensified once they left the shore and headed towards the outer bay, and the two males became full participants in the attack. The killer whales swam tightly on each side of the minke, or positioned themselves directly in front of the whale to impede its travel, prevent it from diving, and steer it away from shallow water. Over the next hour the killer whales, particularly the males, rammed the ventral side of the minke at least 16 times. On

three occasions, either a male or female killer whale rode up on the minke's rostrum and forced its head underwater. Underwater acoustic monitoring during the latter phase of the attack indicated that the transients where very vocal. The minke weakened considerably over the course of the assault, and was last seen alive at the surface at 1450. The killer whales then began a series of dives at the location the minke disappeared, evidently feeding on the carcass. Water depth at this location was 15 m. At 1511 blood and a 75-kg piece of the minke's throat appeared at the surface. At 1517 a killer whale was sighted with minke skin and blubber in its mouth. The killer whales were still milling and diving at the same location, apparently while continuing to feed, when observations ended at 1645.

The following morning, the floating carcass of the minke was observed at the entrance to Ganges Harbour. The carcass was floating ventral side up and its stomach, inflated by gases from decomposition, protruded from the whale's throat. Most of the skin had been removed from the ventral surface and the tongue was missing, but little blubber or other tissue appeared to have been consumed. It was not possible to determine the condition of the carcass' dorsal surface. The four killer whales involved in the attack were observed at 1300 on this day to kill and apparently consume a Dall's porpoise at a location 30 km distant.[1]

Event 5 took place on 19 August 2003 when, at 1950, a group of four transient killer whales (T18, T19, T19B, T19C) was observed initiating a high-speed chase of an adult minke whale on Salmon Bank, off southern San Juan Island, Washington. When initially observed, the distance between the minke and the transients was only 50–80 m, but this gradually increased over the course of the 1-h chase. The whales swam on a straight course to the southeast at speeds of 15–30 km/h. The subadult male T19B (born in 1995) led the pursuit, with the other members of the group following 100–300 m behind. By 2045 the chase had covered 15 km and the minke was 800–900 m ahead of the transients. At 2050 the killer whales aborted the chase and slowed to 10 km/h, while the minke continued to flee at high speed.

Event 6 involved the same group of four transients as Event 5. At 1610 on 2 September 2003, the group was observed moving west at 6 km/h in Blackfish Sound, off northeastern Vancouver Island, British Columbia. At 1712 the whales suddenly reversed their course and took chase after an adult minke whale. The whales swam at high speed in the center of the Sound, porpoising as they surfaced, with T19B in the lead and the other three killer whales 0.5–1 km behind. As they continued in a straight line to the east they entered Parson Bay, a 1 km wide by 2 km long bay off the north side of Blackfish Sound. The chase ended at 1759, when the killer whales cornered the minke at the head of the bay and started attacking it. The chase had covered 13 km in 47 min, at an average speed of 17 km/h. Over the next 39 min the transients prevented the minke's escape by swimming tightly against its sides, while alternately ramming the animal from below (a minimum of eight times) and sliding up on its back and head to force it underwater. The minke was last seen alive when it was pushed under the surface a final time at 1838. From this time until observations ended at 2100, the whales made repeated dives at this location while presumably feeding on the carcass.

At 0930 the next morning the same killer whales were found in Parson Bay, still feeding on the minke. The carcass was afloat when observers arrived at the scene, but

[1] Personal communication from Mark Malleson, 812 Wharf St., Victoria, BC V8W 1T3, Canada, 22 October 2002.

the whales took it underwater shortly thereafter. Most of the minke's skin, blubber, throat area, and tongue were gone, but little other flesh had been consumed. The transients continued to feed on the carcass until they left the bay at 1325.

Event 7 took place on 5 September 2003 in Sitakaday Narrows at the entrance to Glacier Bay, Alaska. At 1045 a pair of transient killer whales, the female T71 and her subadult offspring T71B, was encountered swimming at high speed approximately 400 m behind an adult-sized minke whale. Over the next 30 min the minke porpoised at an average speed of 20 km/h in a straight line out of the Narrows. At 1130 the minke slowed and turned to the southeast. By this time, the transients had abandoned the chase and were no longer visible.

Event 8 was observed in Juan de Fuca Strait, Washington, on 1 December 2003. At 1100, shore-based observers sighted a group of killer whales traveling at a fast pace off southwestern San Juan Island, Washington, and guided a research boat to the whales' position. The whales maintained a consistent course at high speed, until the research boat intercepted them at 1215, 18 km from where they were first sighted (mean speed = 14.4 km/h). At this time the whales slowed, and it became evident that they were in the process of attacking a subadult minke whale (approximately 5 m long). The six transient whales surrounded the minke and, despite little evidence of a violent assault, the minke disappeared from the surface and apparently succumbed within 5 min. The transients dove repeatedly at the site of the kill (water depth 50 m) until observations ended at 1600. The presence of oil at the surface indicated that the whales were likely feeding on the carcass.

Event 9 took place near Echo Bay, British Columbia, on 28 October 2004. At approximately 0950 an adult minke whale was seen entering Cramer Pass from the north, being pursued at high speed by two adult killer whales, the female T12 and her son T12A. At 1000 the minke turned and swam through the narrow (<150 m) entrance to Shoal Harbour, a shallow 2.5 km long bay. T12, which was approximately 500 m behind the minke, followed it into Shoal Harbour, and T12A followed several minutes later. The minke proceeded to the far end of the bay, vigorously drove itself onto the gently sloping beach, and remained stranded over the next 8.5 h. Although the water was initially too shallow for the killer whales to approach, a rising tide eventually allowed T12 to swim up to the minke. She passed over the minke's flukes on several occasions and bit them once, but did not ram the whale. While T12 approached the minke, the male T12A remained in the deeper portion of the bay, 200–500 m distant. As the tide rose, the minke pushed itself farther up on the beach. On four occasions, both killer whales left the bay and returned approximately 30 min later. When observations ended at nightfall (1830 h), the minke whale was still in the shallows and the killer whales were milling in the bay. The next morning the killer whales were absent and the minke was dead, lying within 10 m of where it beached. The minke was a 7.7 m long female, with superficial contusions and abrasions on its tail flukes and ventral surface mostly resulting from contact with the beach.

Discussion

Cetaceans under attack by killer whales employ various antipredator tactics depending on species and circumstance. Large cetaceans may physically defend themselves, seek refuge nearshore, adopt cryptic behaviors, or attempt to flee from the predators (Morejohn 1968, Baldridge 1972, Arnbom *et al.* 1987, Jefferson *et al.* 1991, Dahlheim and Heyning 1999, Pitman *et al.* 2001). In the predation events

documented here, the minke whale responded to pursuit by transient killer whales by fleeing on a highly directional heading at speeds of 15–30 km/h. In four unsuccessful chases, the killer whales pursued the minke whale for 0.5–1.0 h before aborting the pursuit after falling several hundred meters behind the intended prey. All unsuccessful chases involved adult-sized minke whales. During three chases, the fleeing minke entered a confined bay or harbor, where it was entrapped and killed by the transients (two occasions) or became stranded and died (once). Two successful attacks took place in open waters: one involved a subadult minke that was evidently unable to outrun the pursuing killer whales, and in the other case the adult minke was killed after apparently attempting to seek cover beside a large sailboat.

For flight to be an effective antipredator tactic, fleeing minke whales must be able to sustain a higher swimming velocity for a longer period than their predators. Killer whales are the fastest of the odontocetes, capable of sprinting speeds of 45 km/h (Williams 2002). Minke whales are among the fastest mysticetes, but have only been recorded to reach sprinting speeds of approximately 30 km/h (Williams 2002). Although killer whales may have an initial speed and acceleration advantage, the observations reported here suggest that adult minke whales have superior endurance and can outpace killer whales in a prolonged chase. Transients appeared to be able to match the speed of a fleeing minke for the first 10–30 min of the chase, but then gradually fell behind and abandoned the pursuit after 30–60 min. Smaller, subadult minkes may not be able to sustain a velocity sufficient to outdistance pursuing killer whales (*e.g.*, event 8). As full-grown minkes are longer than killer whales, they likely have a larger turning radius and slower turning rate (Domenici 2001) than their smaller predators. Thus, maintaining a constant flight heading, as observed in the chases documented here, would be a more effective evasion tactic than attempting to avoid capture by making frequent or sudden turns (Weihs and Webb 1984, Domenici 2001). Successful predator evasion by minke whales likely also depends on early detection of pursuing killer whales and having sufficient open water for an extended escape trajectory. Transient killer whales typically hunt in silence, evidently to avoid detection by potential prey (Barrett-Lennard *et al.* 1996, Deecke *et al.* 2005). High-speed flight from transients was a successful escape tactic even when chases were initiated at ranges as close as 30 m (*e.g.*, event 1).

Although fleeing minke whales entered a bay or harbor in three of the nine chases, it is not clear that this was a deliberate antipredator tactic. Minke whales seldom deviated from their flight trajectories, and it appeared that their course inadvertently took the animals into these locations. Once in a confined bay, however, minke whales appeared to seek refuge from pursuing killer whales by beaching themselves in the shallows. While beaching may have temporarily prevented the whale's death, it was not ultimately a successful tactic in the instances described here or in previously reported cases (Pike and MacAskie 1969, Lowry *et al.* 1987, Guinet *et al.* 2000). Apparent attempts by minkes to seek shelter under or beside boats to avoid attack were also unsuccessful (event 2 and Hall 1986).

When transient killer whales were able to catch up to and surround a fleeing minke whale, the prey did not make any attempt to physically defend itself from attack. No defensive actions other than attempts to escape have been noted in previous accounts of killer whale attacks on minke whales (Hancock 1965, Hall 1986, Lowry *et al.* 1987, Guinet *et al.* 2000). This submissive behavior contrasts with the vigorous defensive responses to attacks observed in certain other mysticete species. Rolling, thrashing the water's surface with flukes and flippers, and slashing flukes at attacking killer whales are defensive measures that have been noted in

humpback whales (Chittleborough 1953, Whitehead and Glass 1985, Florez-Gonzalez *et al.* 1994), southern right whales (*Eubalaena australis*; Cummings 1985, Payne 1995), bowhead whales (*Balaena mysticetus*; Eschricht 1866, Mitchell and Reeves 1982, Finley 1990), and gray whales (Ternullo and Black 2002; N. A. Black;[2] J. Ford and G. Ellis, unpublished data). As these species are the slowest of the mysticetes (Reeves and Leatherwood 1985, Clapham and Mead 1999, Williams 2002), they are likely incapable of escaping killer whales by high-speed flight and thus resort to these alternative antipredator tactics. On the other hand, species in the genus *Balaenoptera* are all fast swimmers (Gambell 1985, Yochem and Leatherwood 1985, Bose and Lien 1989, Fish 2002, Williams 2002) and appear to respond to killer whale attacks in a manner similar to that seen in minke whales. Although detailed observations are rare, high-speed flight and a lack of physical defense are characteristic of documented attacks by killer whales on fin whales (*B. physalus*; Vidal and Pechter 1989), blue whales (*B. musculus*; Cotton 1944, Tarpy 1979), and Bryde's whales (*B. edeni*; Silber *et al.* 1990).

The tactics used by transient killer whales to capture and kill minke whales were generally similar to those previously described for killer whale predation on large cetaceans (see review by Jefferson *et al.* 1991). Although killer whales may intentionally herd prey towards shore in order to entrap them in confined waters (Jefferson *et al.* 1991, Ford *et al.* 1998), in the chases we observed the transient killer whales lagged too far behind the fleeing minke whale to have any apparent influence on its direction of flight. Once transients caught up to a minke whale, they attacked it by ramming and swimming onto its back to impede respiration, tactics that have been reported previously in predation on minke whales and other large cetaceans (Silber *et al.* 1990, Jefferson *et al.* 1991, Goley and Straley 1994, Pitman *et al.* 2001). We observed no attempt by the killer whales to remove flesh from a minke whale while it was alive, although this has been noted in attacks on larger mysticetes (Tarpy 1979, Whitehead and Glass 1985, Silber *et al.* 1990) and sperm whales (Pitman *et al.* 2001). As has often been reported in observations of predation on mysticetes (Jefferson *et al.* 1991), only the skin, tongue and a small portion of the minke whale's blubber was typically consumed. More substantial amounts of blubber and other flesh were taken from the carcass when feeding was protracted (event 6).

Several well-documented accounts of killer whale predation on marine mammals note that females and subadults were active particpants throughout attacks, but mature males had little or no involvement (Arnbom *et al.* 1987, Silber *et al.* 1990, Jefferson *et al.* 1991) or only participated during final stages of attacks (Pitman *et al.* 2001, Pitman *et al.* 2003). In other reports, males were fully involved in the attacks (*e.g.*, Hancock 1965, Whitehead and Glass 1985). In the minke whale chases we observed, adult males, when present, tended to trail behind or were gradually outpaced by mature females and subadults during high speed pursuits. When chases resulted in minke whales becoming stranded on shore, adult males milled offshore while females continued the attack in the shallows. When minke whales were surrounded by transients in deeper water, adult males participated equally with females in physically attacking and killing the prey.

Reasons for such differential roles of the sexes in predation of large cetaceans are unclear, although Pitman *et al.* (2003) suggest that the larger size of males

[2] Personal communication from N. A. Black, Monterey Bay Whale Watch, P. O. Box 52001, Pacific Grove, CA 93950, U.S.A., 16 November 2004.

compared to females may be an "ecological sex trait" that enables predation of a wider range of prey sizes than would be possible if both sexes were of uniform size. We agree that the marked sexual dimorphism in the species may be responsible for these differential roles, but propose that it is more likely due to physical constraints resulting from this dimorphism, at least in the minke whale chases and attacks described here. Mature male and female killer whales typically reach lengths of 8.2 m and 7.0 m, respectively, and males may attain a mass more than 2 tonnes greater than females (Heyning and Dahlheim 1988, Dahlheim and Heyning 1999). The pectoral flippers of males are up to 2 m in length, or almost 20% of body length, compared to 11%–13% of body length in the smaller females. The dorsal fin of males may be 1.8 m tall, more than double the 0.7 m tall dorsal fin of females (Heyning and Dahlheim 1988). The larger body size and appendages of adult males are likely to have a negative impact on their speed and maneuverability compared to females. To reach and sustain high swimming speeds such as those observed during minke whale chases, killer whales, like other small to medium sized cetaceans, adopt a porpoising mode of swimming. Although this is the most efficient means of high-speed swimming, the energy required for leaping increases rapidly with body size (Au and Weihs 1980). As a result, males would experience an increased energy cost compared to the smaller females in a prolonged chase. Drag from appendages represents a significant component of the overall resistance experienced by cetaceans moving through water (Fish 1993). The disproportionately large pectoral flippers and dorsal fin of adult male killer whales would further add to the drag and thus the energy burden they face during high speed swimming compared to that of females and subadults. Maneuverability decreases with body size in aquatic vertebrates (Domenici 2001), potentially making males less agile during high speed chases and attack. Finally, our observations suggest that the larger size of mature males prevented them from venturing into shallow waters to attack beached minke whales, a constraint that was less evident among females.

If large body and appendage sizes reduce the hunting proficiency of mature male killer whales in some circumstances, they may be less inclined to participate in chases and attacks as fully as females and subadults. An analogous situation appears to exist among African lions, where the larger size of males reduces their speed and agility compared to females, and makes them conspicuous when attempting to stalk wary prey (Schaller 1972). As a result, males are comparatively ineffective hunters and seldom participate in hunts until the prey is killed by females in the group (Schaller 1972, Scheel and Packer 1991, Stander 1992).

Transient killer whales hunt most marine mammal species found regularly in the region, but the importance of each species in their diet differs considerably (Ford *et al.* 1998). Prey choice by transients, as in other predators, is likely influenced by a variety of factors including prey encounter rates, predator group size, probability of success, risk of injury to the attackers, and prey profitability (Schaller 1972, Stephens and Krebs 1986, Scheel 1993, Bowen *et al.* 2002). Potential prey specialization by different transient individuals or groups does not seem to be a significant factor (Ford *et al.* 1998). Predation on minke whales in our study area appears to be a relatively rare occurrence. The four successful minke kills described here represent only 1.2% of 325 marine mammal kills by transient killer whales documented over the past 30 yr in British Columbia, Washington, and southeastern Alaska (Baird and Dill 1995; Matkin and Dahlheim 1995; Ford *et al.* 1998; J. Ford, G. Ellis and D. Matkin, unpublished data). Six of the nine predation events involving minke whales took place during 2002–2004, suggesting a possible recent increase in predation rates on this species. If so, the

reason for this increase is unclear. Although no reliable population estimates are available for minke whales in the region, the species is not as common in inshore waters as the other marine mammal species routinely preyed upon by transient killer whales (Dorsey *et al.* 1990, Calambokidis and Baird 1994, Ford *et al.* 1998). There has been no obvious change in minke whale abundance over the course of our studies.

The most important prey of transient killer whales in the region is the harbor seal (*Phoca vitulina*), which is also the most abundant marine mammal species (Calambokidis and Baird 1994, Baird and Dill 1996, Ford *et al.* 1998, Olesiuk 1999, Jeffries *et al.* 2003, Angliss and Lodge 2004, Carretta *et al.* 2004). Small groups of transients (typically three to four individuals) appear to have little difficulty hunting harbor seals, as indicated by high success rates and generally short durations between prey detection and a kill taking place (Baird and Dill 1996, Ford *et al.* 1998). In one study off southern Vancouver Island, the estimated energy intake from harbor seal predation was more than sufficient to meet the requirements of transient groups foraging in that area (Baird and Dill 1996). Other significant prey in the diet of transient killer whales, though less important than harbor seals, are Steller sea lions (*Eumetopias jubatus*), California sea lions (*Zalophus californianus*), harbor porpoises (*Phocoena phocoena*), and Dall's porpoises (*Phocoenoides dalli*) (Matkin and Dahlheim 1995, Ford *et al.* 1998). Successful kills of these species appear to require larger transient group sizes on average than kills of harbor seals and, with the exception of harbor porpoises, chases and physical attacks are often lengthy with a comparatively high rate of failure (Ford *et al.* 1998). The relatively scarce minke whale appears to be an even more demanding species to hunt successfully. High-speed chases of >30 min duration are typical of minke whale pursuits, and the probability of an unsuccessful outcome is high. In addition, when a minke whale is killed only a small portion of the animal is usually consumed. Overall, it appears that minke whales play a relatively minor role in the diet of transient killer whales in coastal waters of the northeastern Pacific.

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Literature Cited

Angliss, R. P., and K. L. Lodge. 2004. Alaska marine mammal stock assessments, 2003. U.S. Department of Commerce, NOAA Technical Memo NMFS-AFSC-144. 230 pp.

Arnbom, T., V. Papastavrou, L. S. Weilgart and H. Whitehead. 1987. Sperm whales react to an attack by killer whales. Journal of Mammalogy 68:450–453.

AU, D., AND D. WEIHS. 1980. At high speeds dolphins save energy by leaping. Nature 284:548–550.

BAIRD, R. W., AND L. M. DILL. 1995. Occurrence and behaviour of transient killer whales: Seasonal and pod-specific variability, foraging, and prey handling. Canadian Journal of Zoology 73:1300–1311.

BAIRD, R. W., AND L. M. DILL. 1996. Ecological and social determinants of group size in transient killer whales. Behavioral Ecology 7:408–416.

BALDRIDGE, A. 1972. Killer whales attack and eat a gray whale. Journal of Mammalogy 53:898–900.

BARRETT-LENNARD, L. G., J. K. B. FORD AND K. A. HEISE. 1996. The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. Animal Behavior 51:553–565.

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.

BIGG, M. A., P. F. OLESIUK, G. M. ELLIS, J. K. B. FORD AND K. C. BALCOMB, III. 1990. Social organization and genealogy 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):383–405.

BOSE, N., AND J. LIEN. 1989. Propulsion of a fin whale (*Balaenoptera physalus*): Why the fin whale is a fast swimmer. Proceedings of the Royal Society of London B 237:175–200.

BOWEN, W. D., D. TULLY, D. J. BONESS, B. M. BULHEIER AND G. J. MARSHALL. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. Marine Ecology Progress Series 244:235–245.

CALAMBOKIDIS, J., AND R. W. BAIRD. 1994. Status of marine mammals in the Strait of Georgia, Puget Sound and the Juan de Fuca Strait and potential human impacts. Pages 282–303 *in* R. C. H. Wilson, R. J. Beamish, F. Aitkens and J. Bell, eds. Review of the marine environment and biota of Strait of Georgia, Puget Sound and Juan de Fuca Strait. Canadian Technical Report of Fisheries and Aquatic Sciences 1948.

CARRETTA, J. V., K. A. FORNEY, M. M. MUTO, J. BARLOW, J. BAKER AND M. LOWRY. 2004. U.S. Pacific Marine Mammal Stock Assessments: 2003. U.S. Department of Commerce, NOAA Technical Memo NOAA-TM-NMFS-SWFSC-358. 291 pp.

CHITTLEBOROUGH, R. G. 1953. Aerial observations on the humpback whale, *Megaptera nodosa* (Bonaterre), with notes on other species. Australian Journal of Marine and Freshwater Research 4:219–226.

CLAPHAM, P. 2001. Why do baleen whales migrate? A response to Corkeron and Connor. Marine Mammal Science 17:432–436.

CLAPHAM, P. J., AND J. G. MEAD. 1999. *Megaptera novaeangliae*. Mammalian Species 604:1–9.

CORKERON, P. J., AND R. C. CONNOR. 1999. Why do baleen whales migrate? Marine Mammal Science 15:1228–1245.

COTTON, B. C. 1944. Killer whales in South Australia. Australian Zoologist 10:293–294.

CUMMINGS, W. C. 1985. Right whales *Eubalaena glacialis* (Müller, 1776) and *Eubalaena australis* (Desmoulins, 1822). Pages 275–304 *in* S. H. Ridgway and R. Harrison, eds. Handbook of marine mammals. Volume 3. The sirenians and baleen whales. Academic Press, San Diego, CA.

DAHLHEIM, M. E., AND J. E. HEYNING. 1999. Killer whale *Orcinus orca* (Linnaeus, 1758). Pages 281–322 *in* S. H. Ridgway and R. Harrison, eds. Handbook of marine mammals. Volume 6. The second book of dolphins and the porpoises. Academic Press, San Diego, CA.

DAHLHEIM, M. E., D. K. ELLIFRIT AND J. D. SWENSON. 1997. Killer whales (*Orcinus orca*) of southeast Alaska: A catalog of photo-identified individuals. Day Moon Press, Seattle, WA.

DEECKE, V. B., J. K. B. FORD AND P. J. B. SLATER. 2005. The vocal behaviour of mammal-eating killer whales: Communicating with costly calls. Animal Behaviour 69:395–405.

DOMENICI, P. 2001. The scaling of locomotor performance in predator-prey encounters: From fish to killer whales. Comparative Biochemistry and Physiology Part A 131:169–182.

DORSEY, E. M., S. J. STERN, A. R. HOELZEL AND J. JACOBSEN. 1990. Minke whales (*Balaenoptera acutorostrata*) from the west coast of North America: Individual recognition and small-scale site fidelity. Report of the International Whaling Commission (Special Issue 12):357–368.

ESCHRICHT, D. F. 1866. On the species of the genus *Orca* inhabiting the northern seas. Pages 153–188 *in* Recent memoirs of the Cetacea. W. H. Flower, ed. Ray Society, London, UK.

FINLEY, K. J. 1990. Isabella Bay, Baffin Island: An important historical and present-day concentration area for the endangered bowhead whale (*Balaena mysticetus*) of the eastern Canadian Arctic. Arctic 43:137–152.

FISH, F. E. 1993. Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. Australian Journal of Zoology 42:79–101.

FISH, F. E. 2002. Speed. Pages 1161–1163 *in* W. F. Perrin, B. Würsig and H. G. M. Thewissen, eds. The encyclopedia of marine mammals. Academic Press, San Diego, CA.

FLOREZ-GONZALEZ, L., J. J. CAPELLA AND H. C. ROSENBAUM. 1994. Attack of killer whales (*Orcinus orca*) on humpback whales (*Megaptera novaeangliae*) on a South American Pacific breeding ground. Marine Mammal Science 10:218–222.

FORD, J. K. B., AND G. M. ELLIS. 1999. Transients: Mammal-hunting killer whales of British Columbia, Washington, and southeastern Alaska. UBC Press and University of Washington Press, Vancouver, BC, and Seattle, WA.

FORD, J. K. B., G. M. ELLIS, L. G. BARRETT-LENNARD, A. B. MORTON, R. S. PALM AND K. C. BALCOMB, III. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology 76:1456–1471.

FORD, J. K. B., G. M. ELLIS AND K. C. BALCOMB. 2000. Killer Whales: The natural history and genealogy of *Orcinus orca* in the waters of British Columbia and Washington. UBC Press and University of Washington Press, Vancouver, BC, and Seattle, WA.

GAMBELL, R. 1985. Sei whale *Balaenoptera borealis* Lesson, 1828. Pages 155–170 *in* S. H. Ridgway and R. Harrison, eds. Handbook of marine mammals. Volume 3. The sirenians and baleen whales. Academic Press, San Diego, CA.

GOLEY, P. D., AND J. M. STRALEY. 1994. Attack on gray whales (*Eschrichtius robustus*) in Monterey Bay, California, by killer whales (*Orcinus orca*) previously identified in Glacier Bay, Alaska. Canadian Journal of Zoology 72:1528–1530.

GUINET, C., L. G. BARRETT-LENNARD AND B. LOYER. 2000. Co-ordinated attack behavior and prey sharing by killer whales at Crozet Archipelago: Strategies for feeding on negatively-buoyant prey. Marine Mammal Science 16:829–834.

HALL, J. D. 1986. Notes on the distribution and feeding behavior of killer whales in Prince William Sound, Alaska. Pages 69–83 *in* J. Lockard and B. Kirkevold, eds. Behavioral biology of killer whales. J. Alan R. Liss, Inc., New York, NY.

HANCOCK, D. 1965. Killer whales attack and kill a minke whale. Journal of Mammalogy 46:341–342.

HEYNING, J. E., AND M. E. DAHLHEIM. 1988. *Orcinus orca*. Mammalian Species 304:1–9.

JEFFERSON, T. A., P. F. STACEY AND R. W. BAIRD. 1991. A review of killer whale interactions with other marine mammals: Predation to co-existence. Mammal Review 21:151–180.

JEFFRIES, S., H. HUBER, J. CALAMBOKIDIS AND J. LAAKE. 2003. Trends and status of harbor seals in Washington State. Journal of Wildlife Management 67:208–219.

JONSGÅRD, Å. 1968*a*. A note on the attacking behavior of the killer whale (*Orcinus orca*). Norsk Hvalfangst-Tidende 57:84–85.

JONSGÅRD, Å. 1968*b*. Another note on the attacking behavior of the killer whale (*Orcinus orca*). Norsk Hvalfangst-Tidende 57:175–176.

LOWRY, L. F., R. R. NELSON AND K. J. FROST. 1987. Observations of killer whales, *Orcinus orca*, in western Alaska: Sightings, strandings and predation on other marine mammals. Canadian Field-Naturalist 101:6–12.

MARTINEZ, D. R., AND E. KLINGHAMMER. 1970. The behavior of the whale *Orcinus orca*: A review of the literature. Zietschrift für Tierpsychologie 27:828–839.

MATKIN, D. R., AND M. E. DAHLHEIM. 1995. Feeding behaviors of killer whales in northern southeastern Alaska. Pages 246–253 *in* D. R. Engstrom, ed. Proceedings of the third Glacier Bay science symposium, 1993. National Park Service, Anchorage, AK.

MITCHELL, E. D., AND R. R. REEVES. 1982. Factors affecting abundance of bowhead whales *Balaena mysticetus* in the eastern Arctic of North America, 1915–1980. Biological Conservation 22:59–78.

MOREJOHN, G. V. 1968. A killer whale–gray whale encounter. Journal of Mammalogy 49:327–328.

OLESIUK, P. F. 1999. An assessment of the status of harbour seals (*Phoca vitulina*) in British Columbia. Fisheries and Oceans Canada, Canadian Stock Assessment Secretariat Research Document 99/33. 71 pp. Available from http://www.dfo-mpo.gc.ca/CSAS.

PAYNE, R. 1995. Among whales. Scribner, New York, NY.

PIKE, G. C., AND I. B. MACASKIE. 1969. Marine mammals of British Columbia. Fisheries Research Board of Canada Bulletin 171.

PITMAN, R. L., L. T. BALANCE, S. I. MESNICK AND S. J. CHIVERS. 2001. Killer whale predation on sperm whales: Observations and implications. Marine Mammal Science 17: 494–507.

PITMAN, R. L., S. O'SULLIVAN AND B. MASE. 2003. Killer whales (*Orcinus orca*) attack a school of pantropical spotted dolphins (*Stenella attenuata*) in the Gulf of Mexico. Aquatic Mammals 29:321–324.

REEVES, R. R., AND S. LEATHERWOOD. 1985. Bowhead whale *Balaena mysticetus* Linnaeus, 1758. Pages 305–344 *in* S. H. Ridgway and R. Harrison, eds. Handbook of marine mammals. Volume 3. The sirenians and baleen whales. Academic Press, San Diego, CA.

SCAMMON, C. M. 1874. The marine mammals of the northwestern coast of North America, together with an account of the American whale-fishery. Dover Publications Inc., New York, NY.

SCHALLER, G. B. 1972. The Serengeti lion: A study of predator-prey relations. University of Chicago Press, Chicago, IL.

SCHEEL, D. 1993. Profitability, encounter rates, and prey choice of African lions. Behavioral Ecology 4:90–97.

SCHEEL, D., AND C. PACKER. 1991. Group hunting behaviour of lions: A search for cooperation. Animal Behaviour 41:697–709.

SILBER, G. K., M. W. NEWCOMBER AND H. PÉREZ-CORTÉS M. 1990. Killer whales (*Orcinus orca*) attack and kill a Bryde's whale (*Balaenoptera edeni*). Canadian Journal of Zoology 68:1603–1606.

SPRINGER, A. M., J. A. ESTES, G. B. VAN VLIET, T. M. WILLIAMS, D. F. DOAK, E. M. DANNER, K. A. FORNEY AND B. PHISTER. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proceedings of the National Academy of Science 100:12223–12228.

STANDER, P. E. 1992. Cooperative hunting in lions: The role of the individual. Behavioral Ecology and Sociobiology 29:445–454.

STEPHENS, D. W., AND J. R. KREBS. 1986. Foraging theory. Princeton University Press, Princeton, NJ.

TARPY, C. 1979. Killer whale attack! National Geographic 155:542–545.

TERNULLO, R., AND N. BLACK. 2002. Predation behavior of transient killer whales in Monterey Bay, California. Pages 156–159 *in* Proceedings of the Fourth International Orca Symposium and Workshop, 23–28 September 2002, CEBC-CNRS, France. Available from http://www.cebc.cnrs.fr/Factua/Factua.html.

VIDAL, O., AND G. PECHTER. 1989. Behavioral observations on fin whale, *Balaenoptera physalus*, in the presence of killer whale, *Orcinus orca*. Fishery Bulletin, U.S. 87:370–373.

WEIHS, D., AND P. W. WEBB. 1984. Optimal avoidance and evasion tactics in predator-prey interactions. Journal of Theoretical Biology 106:189–206.

WHITEHEAD, H., AND C. GLASS. 1985. Orcas (killer whales) attack humpback whales. Journal of Mammalogy 66:183–185.

WILLIAMS, T. M. 2002. Swimming. Pages 1213–1222 *in* W. F. Perrin, B. Würsig and H. G. M. Thewissen, eds. The encyclopedia of marine mammals. Academic Press, San Diego, CA.

YOCHEM, P. K., AND S. LEATHERWOOD. 1985. Blue whale *Balaenoptera musculus* (Linnaeus, 1758). Pages 193–240 *in* S. H. Ridgway and R. Harrison, eds. Handbook of marine mammals. Volume 3. The sirenians and baleen whales. Academic Press, San Diego, CA.

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