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Humpback whales interfering when mammal-eating killer whales attack other species: Mobbing behavior and interspecific altruism?

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Abstract

Humpback whales (*Megaptera novaeangliae*) are known to interfere with attacking killer whales (*Orcinus orca*). To investigate why, we reviewed accounts of 115 interactions between them. Humpbacks initiated the majority of interactions (57% *vs.* 43%; $n = 72$), although the killer whales were almost exclusively mammal-eating forms (MEKWs, 95%) *vs.* fish-eaters (5%; $n = 108$). When MEKWs approached humpbacks ($n = 27$), they attacked 85% of the time and targeted only calves. When humpbacks approached killer whales ($n = 41$), 93% were MEKWs, and ≥87% of them were attacking or feeding on prey at the time. When humpbacks interacted with attacking MEKWs, 11% of the prey were humpbacks and 89% comprised 10

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other species, including three cetaceans, six pinnipeds, and one teleost fish. Approaching humpbacks often harassed attacking MEKWs (≥55% of 56 interactions), regardless of the prey species, which we argue was mobbing behavior. Humpback mobbing sometimes allowed MEKW prey, including nonhumpbacks, to escape. We suggest that humpbacks initially responded to vocalizations of attacking MEKWs without knowing the prey species targeted. Although reciprocity or kin selection might explain communal defense of conspecific calves, there was no apparent benefit to humpbacks continuing to interfere when other species were being attacked. Interspecific altruism, even if unintentional, could not be ruled out.

Key words: humpback whale, interspecific altruism, killer whale, *Megaptera novaeangliae*, mobbing behavior, *Orcinus orca*, predation.

Anecdotes have been passed down for centuries about dolphins at sea coming to the aid of distressed conspecifics, as well as other species, including humans (Caldwell and Caldwell 1966, Connor and Norris 1982, Whitehead and Rendell 2015). However, more recent observations, including popular accounts (*e.g.,* Dolphin 1987, D'Vincent *et al.* 1989, Pitman and Durban 2009) and videos posted on the internet (Appendix S1), suggest that a baleen whale—the humpback whale (*Megaptera novaeangliae*)—also approaches marine vertebrates in distress, most notably, when they are being attacked by killer whales (*Orcinus orca*). This seems particularly maladaptive for the humpbacks because they themselves are attacked by killer whales (Whitehead and Glass 1985, Jefferson *et al.* 1991, Reeves *et al.* 2006, Ford and Reeves 2008, Saulitis *et al.* 2015).

It is generally accepted that, due to their enormous size, large whales have no significant natural predators except, possibly, mammal-eating killer whales (MEKWs *vs*. fish-eating forms; Jefferson *et al*. 1991, Reeves *et al.* 2006). The prevalence and overall ecological impact of MEKW predation on large whales, however, remains contentious and unresolved (*e.g*., Doak *et al.* 2006, Reeves *et al.* 2006, Springer *et al.* 2006, Trites *et al.* 2007).

Much of the uncertainty about killer whale predation on large whales is because attacks have been so rarely reported (Jefferson *et al.* 1991, Pitman *et al.* 2001, Springer *et al.* 2008, Ferguson *et al.* 2010). Although some have argued that this lack of observations is evidence that killer whales are *not* important predators of large whales (*e.g.*, Clapham 2001, Mizroch and Rice 2006), this "absence of evidence" could also be a legacy of 20th century industrial whaling (Tønnessen and Johnsen 1982, Clapham *et al.* 2008, Rocha *et al.* 2014), which means that most living humans have never experienced oceans that were not already depleted of large whales. Within this "shifted baseline" (Pauly 1995) nearly all large whale species are still in various stages of recovery, making it is impossible to assess the historical impact of MEKW predation on their populations (Doak *et al.* 2006, Kareiva *et al.* 2006, Springer *et al*. 2006, Pitman *et al.* 2015). Furthermore, by the time commercial whaling ended, any populations of killer whales that might have previously preyed upon large whales would almost certainly have either declined, become extirpated, or been forced to switch to alternative prey (Springer *et al.* 2003, Branch and Williams 2006, Doak *et al.* 2006; but see Wade *et al.* 2007 for an opposing view). Consequently, MEKW populations around the world could also be in various stages of recovery, albeit at a lagged and slower rate than large whales (Pitman *et al.* 2015). Only if and when these species recover will we have a chance to view predator/prey interactions as they once were (Kareiva *et al.* 2006).

For humpback whales, it is generally assumed that their most important nonhuman predators are MEKWs (Jefferson *et al.* 1991, Paterson and Paterson 2001, Ford and Reeves 2008). Until very recently, however, based on the relatively few documented attacks (Chittleborough 1953, Whitehead and Glass 1985, Dolphin 1987, Jefferson *et al.* 1991, Flórez-González *et al*. 1994, Ford and Reeves 2008), MEKW predation on humpbacks had been considered to be a rare (and almost never fatal) event and therefore of limited ecological impact (Jonsgård 1968, Jefferson *et al.* 1991, Clapham 2001, Mizroch and Rice 2006, Mehta *et al.* 2007, Ford and Reeves 2008).

There is, however, mounting evidence to suggest that killer whales may in fact regularly attack humpbacks, and that calves and juveniles are the main targets (Chittleborough 1953, Katona *et al.* 1980, Whitehead and Glass 1985, Jefferson *et al*. 1991, Paterson and Paterson 2001, Baird *et al.* 2006, Reeves *et al.* 2006, Ford and Reeves 2008, Saulitis *et al.* 2015). In three separate studies (Naessig and Lanyon 2004, Mehta *et al.* 2007, Steiger *et al.* 2008), images from humpback whale photo-identification catalogs compiled from various studies around the world were analyzed for MEKW tooth rake marks on the flukes and used to infer the prevalence of killer whale attacks (keeping in mind that marked whales represent only the survivors of such attacks, Clapham 2001). Although the frequency of rake-mark occurrences in some populations ranged as high as 20%–40%, in the largest study (Mehta *et al*. 2007) less than 7% of whales acquired additional rake marks after the first time they were photographed. Based on similar findings, all three studies concluded that killer whales regularly attacked humpback calves and juveniles but rarely adults (Naessig and Lanyon 2004, Mehta *et al.* 2007, Steiger *et al.* 2008). Furthermore, these attacks could result in significant calf mortality. When Gabriele *et al.* (2001) compared the number of individually identified humpback mothers with calves on their North Pacific breeding grounds, with those found later *without* calves in the feeding areas, calf mortality during the first year of life was estimated to be approximately 18% (15%–24%), although the specific causes or locations of that mortality could not be identified.

In addition to overt predation, even just the threat of MEKW attack could significantly influence behavioral decisions made by large whales, with potential population-level consequences (Creel and Christianson 2008, Wirsing *et al.* 2008). For example, many baleen whale species undertake extensive seasonal migrations between high-latitude feeding grounds and often prey-deficient, low-latitude breeding areas, but there is no consensus as to why they make these energetically costly movements (Stevick *et al.* 2002, Stern 2009). Some authors have suggested that migration allows calves to be born in lower latitudes where there are fewer killer whales and a reduced risk of predation (Corkeron and Connor 1999, Connor and Corkeron 2001; see also Cartwright and Sullivan 2009). Others (*e.g.,* Clapham 2001, Rasmussen *et al.* 2007), however, are not convinced that the threat of killer whale attack could provide the impetus for what is (or at least was, prior to the advent of global industrial whaling) arguably the largest seasonal movement of animal biomass on Earth. Observations from Western Australia also indicate that migrating humpback cows with calves take longer, more inshore routes compared to nonbreeders, presumably to reduce the risk of MEKW attack (Pitman *et al.* 2015). This suggests that the threat of predation could be influencing not only *why*, but *how* humpbacks migrate.

Clearly, MEKW predation, even if rarely observed and targeting mainly calves and subadults, represents a threat to humpbacks that is persistent, widespread, and perhaps increasing (Houghton *et al.* 2015, Pitman *et al.* 2015; see also Discussion). As such, humpbacks could be expected to show some specific antipredator behaviors,

and indeed some have been suggested. Ford and Reeves (2008) summarized the defensive capabilities of baleen whales faced with killer whale attack, and they identified two general categories of response. Balaenopterid rorquals (*Balaenoptera* spp.) use their high speed and hydrodynamic body shape to outrun killer whales and were classified as *flight* species. The generally more rotund and slower-swimming species—right whales (*Eubalaena* spp.), bowhead whale (*Balaena mysticetus*), gray whale (*Eschrichtius robustus*), and humpback whale—apparently rely on their bulk and powerful, oversized appendages (tail and flippers) to ward off attackers. This group was categorized as *fight* species. As part of their fight response, humpbacks have also been reported exhibiting group defense against killer whale attack (*e.g.,* Whitehead and Glass 1985, Dolphin 1987, D'Vincent *et al*. 1989), and humpback cow/calf pairs are sometimes accompanied by an escort that will also help defend the calf from attack (Chittleborough 1953, Pitman *et al.* 2015).

As is evident above, most reports describing humpback interactions with MEKWs have emphasized humpback defensive behaviors, but there is a growing body of evidence to suggest that humpback antipredator behavior may have evolved beyond just basic defense, possibly including humpbacks deliberately interfering when MEKWs are attacking other humpbacks and even other species. To investigate the nature and scope of these interactions, we reviewed published and unpublished sources and compiled observations of 115 separate encounters between humpbacks and killer whales from around the world. From these, we identified two general categories of interactions, with each species responding either offensively or defensively, depending on which species approached the other. Herein, we describe these interactions and discuss the adaptive and ecological significance of these behaviors for both species.

Methods

We compiled published and unpublished observations of interactions between humpback whales and killer whales, recorded over a 62 yr period (1951–2012), by at least 54 different observers from around the world. Nearly all of the observations were made either opportunistically (usually by passengers or naturalists on whale-watching boats), or by researchers studying killer whales or humpbacks (mainly photo-identification studies). Because the observations were recorded by scientists, naturalists, and laymen alike, they vary widely in accuracy, detail, and interpretation. The accounts are presented largely in their entirety in Appendix S2 and summarized in Table 1. For transparency, we have kept the accounts largely unedited and indicated in brackets any editorial comments or changes made for clarity. Collectively, we believe that these narratives offer new insights into the nature and prevalence of humpback/killer whale interactions (Bates and Byrne 2007).

Killer whale communities, at least within the continental shelf zone of much of the North Pacific (Ford *et al.* 1998, Ford 2011) and in Antarctica (Pitman and Ensor 2003), comprise sympatric populations of mammal- and fish-eating prey specialists ("ecotypes"). Distinguishing among these ecotypes clearly has important implications for understanding their interactions with humpbacks. In the text and table, Bigg's killer whales (Ford 2011; often referred to as "transient killer whales" or "transients"), refers to a mammal-eating ecotype from the eastern and central North Pacific. "Residents" and "offshores" are fish-eating ecotypes from the same area. Similarly, in Antarctica, in addition to mammal-eating killer whale ecotypes (type A and large type B [B1]), there is at least one fish-eating form (type C) from eastern Antarctica

Table 1. Summarized observations of interactions between humpback whales and killer whales (see Appendix S2 for complete accounts). Individual events where killer whales initially approached humpbacks or other species, and then other humpbacks subsequently approached those killer whales, are treated as separate events and are indicated by the same event numbers followed by "a," "b," and "c."

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
(a) Killer whales approached humpbacks													
1	Humpback(s) without calf	3	1	MEKW	A	U							KW jumped on head and tail of HB
2	Humpback(s) without calf	10–12	3	MEKW	A	N	x	x		x			KW attacking HB on feeding grounds; attacked threesome may have included a calf
3	Humpback(s) without calf	17		MEKW	U	N				x			KWs attacking or perhaps testing scattered HB
6	Humpback(s) without calf	6	1	FEKW	T	N		x	x	x		5	Resident KWs (identified by G. Ellis) harass[?] lone adult male HB for 5 min
10	Humpback(s) without calf	5		MEKW	A	Y							KWs apparently killed and ate what appeared to be a juvenile HB (possibly a calf)
13	Humpback(s) without calf	6	1	MEKW	T	N				x		5	Transient KWs; one female "tests" adult HB, then leaves

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Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
14	Humpback(s) without calf	3	1	MEKW	A	N				x			Juvenile HB wounded on wintering ground
16a	Humpback(s) without calf	15	3	MEKW	A	N						90	Transient KWs attacked 3 HB, smaller animal possibly a calf; see #16b
21	Humpback(s) without calf	4	1	MEKW	A	N						20	Unsuccessful attack by KW on a subadult HB
28	Humpback(s) without calf	10	1	MEKW	T	N		x	x	x		2	2 largeType B KWs from a group of 10 briefly harass an adult HB
58b	Humpback(s) without calf		1	MEKW	A	N							KWs attack juv HB from #58a (HB possibly a calf of #58c)
30	Humpback(s) with calf	5	2	MEKW	A	U							KWs attack HB calf (with mother) on breeding ground - outcome unknown

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Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
31	Humpback(s) with calf	4–5	3	MEKW	A	N	x			x			KWs attack 3 HBs (2 adults, 1 calf), an apparent HB escort drove off KWs
32	Humpback(s) with calf	6	2	UnE	U	N						12	KWs (ecotype unknown) spent 12 min as close as 15 m to HB cow with calf; no responses
33	Humpback(s) with calf	2	3	MEKW	A	N						20	KWs targeted HB calf; 2 HB adults flanked calf, KWs left
34	Humpback(s) with calf	10	3	MEKW	A	U		x		x		26+	KWs attack 3 HBs (2 adults, 1 calf); result of attack unknown
35	Humpback(s) with calf	1	2	MEKW	A	N				x			KW (1) attacks cow/calf HB; unsuccessful
36	Humpback(s) with calf	7	3	MEKW	A	Y							KWs attack 3 HBs (2 adults, 1 calf); calf reportedly killed

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Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
37	Humpback(s) with calf	2	3	MEKW	A	N				x			KWs attack 3 HBs (2 adults, 1 calf); unsuccessful
38	Humpback(s) with calf	5–6		MEKW	A	U							In response to KW attack, 13–16 HB form rosette with calves in the middle
39a	Humpback(s) with calf	15	2	MEKW	A	N				x			Large type B KWs attack HB cow/calf; other HBs chased off KWs; see #39b
40	Humpback(s) with calf	5	2	MEKW	A	N				x		20	Transient KWs harassed HB calf w/cow, near a group of feeding HBs
41	Humpback(s) with calf	10	2	MEKW	A	U				x		390+	10 KWs harass cow/calf HB for over 6.5 h next to oil platform; outcome unknown
42	Humpback(s) with calf	7	2	MEKW	A	N							Transient KWs apparently attack HB calf after a sea lion kill; displaced by cow HB

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Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
43	Humpback(s) with calf	2	3	MEKW	A	N				x			KWs attack HB calf with mother and companion on breeding ground; whalewatchers break it up
44	Humpback(s) with calf		5	UnE	T	N						10	4 adult HBs huddle to protect 1 calf; KWs depart after circling 10 min
45	Humpback(s) with calf	6	2	MEKW	A	N		x		x			KWs harass HB calf; cow apparently drives them off
46	Humpback(s) with calf	2	2	MEKW	T	N				x			KWs approach HB cow/calf; cow apparently drives them off
47	Humpback(s) with calf	7		MEKW	A	N						45+	3 adult HBs successfully defend a HB calf from attacking KWs

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Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
48a	Humpback(s) with calf	6	1	MEKW	A	U						150+	6 KWs attack apparent calf HB; 13 + 2 HBs join calf and KWs leave (see also #48b)
49a	Humpback(s) with calf	30–40	4	FEKW	U	N		x	x	x		45+	35 small type B Antarctic KWs (fish-eaters?) moved in among group of HBs; HBs initially agitated but no incidents (see #49b)
(b) Humpbacks approached killer whales													
4	Humpback(s) without calf			MEKW	A	U					> 1 mile (1.6 km)		HBs come from "over a mile away" to aid another HB attacked by KWs
15	Humpback(s) without calf	18	2	FEKW	U	N						60+	2 HBs follow 18 fish-eating KWs for at least 2 h without incident in AK
29	Humpback(s) without calf	50–70	2	FEKW	U	N							Single HB follows KW group (Antarctic small type B, fish-eaters?); foraging together?

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Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
48b	Humpback(s) without calf	6	15	MEKW	A	N		x					6 transient KWs attack and injure HB calf (see #48a); 13 + 2 HB "swam up to injured calf"; KWs leave
58c	Humpback(s) without calf		2	MEKW	A	N				x			2 adult HB come to defense of juvenile HB in #58b; possibly a calf of one of the adults
16b	Humpback(s) with calf	15	3	MEKW	A	N						30	Transient KWs attacking 3 HBs (#16a) joined by 3 other HBs and appeared to drive KW away
39b	Humpback(s) with calf	15	3	MEKW	A	N	x						3 adult HBs drove off large type B KWs that were attacking HB cow/calf pair; see #39a

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Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
49b	Humpback(s) with calf	35	6	FEKW	U	N							HBs w/calves joined agitated group from #49a; group dispersed without incident while small type B KWs stayed among them
51	Gray whale	4	1	MEKW	A	N							KWs attack (test?) GW briefly; humpback swims close by; no interaction
52	Gray whale	5–6	1	MEKW	A	N	x		x	x		33+	Transient KWs attack GW calf w/cow; HB appears to help calf escape
53	Gray whale		>5	MEKW	A	N		x					Transient KWs attack GW calf w/cow; 5 + HB come in to drive off KWs

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Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
55	Gray whale	11	16	MEKW	A	Y	x	x	x	x	3.5 mile (5.6 km); 3.6 mile (6.7 km); 4.1 mile (7.6 km)	437+	Transient KWs kill gray whale calf; 2 HBs present, and at least 14 others join in and apparently interfere with attack and feeding by KWs
56	Minke whale	13	1	MEKW	A	Y				x			Transient KWs chase MW to boat; a demonstrative HB approaches but MW killed
57	Dall's porpoise	2	1	MEKW	A	N	x	x				8+	Transient KWs chase DP; HB follows bellowing
58a	Steller sea lion		1	MEKW	A	Y							Juv HB approaches KWs attacking SSL; SSL presumably killed (see #58b, c)

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Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
59	Steller sea lion	5–6	9	MEKW	A	U	x	x	x	x	1.8 km	105	KWs attacking SSL when HBs including a cow/calf pr intrude; "excited" HBs stay 4+ h
65	Steller sea lion	4	2	MEKW	A	Y		x		x			Transient KWs kill SSL; 2 HBs (adult male + adult female) approach and tail slash
66	Steller sea lion	10	7	MEKW	A	Y	x	x				60	Transient KWs kill SSL; up to 7 HB move in close and follow KWs
67	Steller sea lion	10	1	MEKW	A	Y						39+	KWs attacking SSL "approached" by HB; SSL "very likely" killed
68	Steller sea lion	16	1	MEKW	A	Y			x	x			KWs attack and kill a SSL: HB makes a "big fuss" in an apparent "rescue attempt"

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Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
70	Steller sea lion	4	3	MEKW	A	Y		x		x			3 HBs joined 4 KWs that had just killed a SSL; HBs agitated
73	California sea lion	7	8	MEKW	A	Y						105+	Transient KWs kill CSL; "2 + 2 + 2 + 2" HBs "in area"
77	California sea lion	8	2	MEKW	A	U	x			x	2 miles (3.2 km)		Transient KWs attack CSLs; HB approach from 2+ miles, "swatting KW w/ their flukes"
78	California sea lion	pod	2	MEKW	A	Y		x			several hundred m		KWs kill CSL; 2 HBs approached kill site from "several hundred meters," bellowing
80	California sea lion	7	2	MEKW	A	Y						15	Transient KWs taking CSLs; 2 HBs surface in the middle of the KWs
82	California sea lion	5–6	3	MEKW	A	U						82	Transient KWs kill CSL; 2 + 1 HBs approach and stay over an hour

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Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
86	California sea lion	8	7	MEKW	A	Y	x					29	Transient KWs carrying juvenile SL; 2 HB "actually chasing" and "harass" KW; 2 + 1 + 2 more HB arrive
87b	Weddell seal	10	2	MEKW	U	N		x	x	x			Large type B KWs; a pr of HB joins pair of HB from #87a during possible WS attack
89	Crabeater seal	10	2	MEKW	A	N	x	x					Large type B KWs attack CS on ice; pair of HBs from #87a appear to follow then interfere with attack
90	Harbor seal	5	1	MEKW	A	Y						44	Transient KWs attack and apparently kill a HS; single HB approaches then departs

(Continued)

Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
92	Harbor seal	6	2	MEKW	A	Y					200 m		Transient KWs attacking a HS approached by 2 HBs
94	Northern elephant seal	5	1	MEKW	A	Y	x					58+	Transient KWs kill NES - HB shows up and chases KWs
96	Ocean sunfish	6–7	3	MEKW	A	U	x	x			>300 m	36+	Transient KWs attacking a sunfish are "mobbed" by 3 HBs
97	Unidentified prey	8–12	2	MEKW	A	Y						26	Transient KWs vocalizing with unidentified kill; pair of HB approach and may have scattered KWs
99	Unidentified prey	6	1	MEKW	A	Y						74+	Transient KWs "killed something?"; " 1 HB close by"

(Continued)

Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
100	Unidentified prey	6	7	MEKW	A	Y	x					18+	Transient KWs "killed something"; joined by up to 7 HB, several of which follow the KWs
102	Unidentified prey	6	7	MEKW	A	Y	x						Transient KWs "killed something"; 2 + 3 + 2 HB join and follow KWs
104	No prey observed	5–6	2	MEKW	U	U		x				73	Transient KWs, possibly with prey, approached by 2 HB, which stayed with them over 1 h
105	No prey observed	11	11	MEKW	U	U	x					124	2 + 3 + 6 HBs following 5 + 6 KWs; HBs "friendly" with boat
107	No prey observed	5	4	MEKW	U	U	x						"5 KWs followed by 4" HB
108	No prey observed	4	3	MEKW	U	U							HBs approach transient KWs that were "playing, jumping"

(Continued)

Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
(c) Approaching whale(s) unknown													
5	Humpback(s) without calf	12–14	1	MEKW	U	U		x	x			45	Agitated HB surrounded by transient KWs; [KWs possibly after other prey?]
7	Humpback(s) without calf	3	1	MEKW	T	U							Transient Kws "harass" 1 HB
8	Humpback(s) without calf	2	1	MEKW	U	N							Two KWs "harassing" HB; possible test or attack
9	Humpback(s) without calf	4	1	MEKW	T	U							Transient KWs "harass" 1 HB
11	Humpback(s) without calf	5	>1	MEKW	T	U							Transient KWs "harass" HBs
12	Humpback(s) without calf	3	1	UnE	U	N							3 KWs passed within 25 m of 1 HB with no interaction
17	Humpback(s) without calf	4–5	1	MEKW	A	N		x	x	x			KWs attacked lone HB - attackers apparently repelled
18	Humpback(s) without calf	3–4	2	MEKW	U	U				x		60+	3–5 KWs circled pr of adult HBs for over 1 h; HB tail-slapping

(Continued)

Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
19	Humpback(s) without calf	12	4	MEKW	U	N	x	x				30+	Group of HB charge at group of KWs and scatter them
20	Humpback(s) without calf	4–5	4	MEKW	U	U				x			4–5 KWs in immediate area of tight group of 4 tail-slapping HBs
22	Humpback(s) without calf	4–5	3	UnE	U	U		x					Agitated HBs (2 adult male and 1 unidentified) swim away from group of milling KW
23	Humpback(s) without calf	8	1	UnE	U	U			x	x			"Harassed" HB adult apparently repels KW with appendage slaps
24	Humpback(s) without calf	4	>1	MEKW	U	U							4 KWs "with HBs"
25	Humpback(s) without calf	3	3	MEKW	U	U							Transient KWs; no interaction recorded
26	Humpback(s) without calf	5	3	UnE	U	U							No specifc interaction recorded

(Continued)

Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
27	Humpback(s) without calf	8	1	MEKW	U	U			x	x		180+	8 KWs spent over 3 h with agitated HB
50	Humpback(s) with calf	15	5	UnE	U	N	x					30+	HBs chasing KWs for 30 min; HB cow/calf broke off early
54	Gray whale	15	7	MEKW	A	Y							15 KWs at GW kill; "3 + 4 HBs" present
60	Steller sea lion	4	1	MEKW	A	Y						65+	KWs attacking SSL with a lone male HB acting "protective" of SL
61	Steller sea lion	6	4	MEKW	A	Y		x	x	x		50	Transient KWs kill SSL; HBs demonstrative around carcass, touch it with flippers
62	Steller sea lion	4	2	MEKW	A	U		x		x			KWs attacking SSL; 2 adult male HBs converge, "agitated" they stay close to SL

(Continued)

Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
63	Steller sea lion	8	3	MEKW	A	Y						60+	Transient KWs kill SSL; 2–3 HB "corralled" by adult male KW during kill
64	Steller sea lion	6	1	MEKW	A	U			x	x			Transient KWs attacking SSL; lone HB possibly slashing at KWs (or prey) with flippers and flukes
69	Steller sea lion	3	7	MEKW	A	Y	x	x	x	x	1/2 mile (0.8 km)	30+	Transient KWs kill SSL; agitated HBs closely follow and possibly "harass" KWs
71	California sea lion	3	5	MEKW	A	Y						102+	Several HB "near" as transient KWs attack CSLs; kill and eat one; no interactions noted
72	California sea lion	6	2	MEKW	U	N				x		40+	Transient KWs appear to be hunting CSLs; possible "interference" by pair of HB

(Continued)

Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
74	California sea lion	3	3	MEKW	A	Y							Transient KWs attack CSL; 3 HB (including cow/calf) "interacted with" KW
75	California sea lion	3	2	MEKW	A	Y						109+	Transient KWs kill CSL; 2 HB "'involved, curious?"
76	California sea lion	5	>1	MEKW	A	Y		x					Transient KWs kill CSL; HB "interfering" with KW and carcass
79	California sea lion	15	12	MEKW	A	N						69	Transient KWs chasing SLs; at least 5 HBs "present"
81	California sea lion	6	4	MEKW	A	U						63+	Transient KWs chasing SLs; 4 HBs "present"
83	California sea lion	6	4	MEKW	A	Y							Transient KWs kill CSL; "2 + 2 HB in area"
84	California sea lion	6	2	MEKW	A	Y						46+	Two HBs in among transient KWs for at least 46 min as they attack and kill a CSL

(Continued)

Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
85	California sea lion	12	3	MEKW	U	U						9+	Transient KWs with 3 HBs and CSLs present; no interactions recorded
87a	Weddell seal	10	2	MEKW	U	N		x	x	x			Large type B KWs; WS possibly seeking refuge among 2 + 2 HB (see #87b)
88	Weddell seal	11	2	MEKW	A	Y	x	x	x	x	1/4 mile (0.4 km)		Large type B KWs attack WS; one of a pair of "protective" HBs takes seal up on its chest; 3 WS kills
91	Harbor seal	4	1	MEKW	A	Y	x			x		60+	Transient KWs attack and presumably kill HS; adult male HB taking tail swipes at seal?
93	Northern elephant seal	10	2	MEKW	A	Y							HBs apparently turned toward hunting transient KWs; no interaction seen

(Continued)

Table 1. (Continued)

Event no. (from Appendix)	Species interacting with killer whales	No. of killer whales	No. of humpback whales	Killer whales			Humpback whale behavior				Travel distance(s)	Duration of interaction (min)	Comments[d]
				Ecotype[a]	Behavior[b]	Prey killed?[c]	Pursued killer whales	Bellow	Flipper slap or slash	Fluke slap or slash			
95	Ocean sunfish	15	5-6	MEKW	A	U							Transient KWs apparently ate a sunfish; "associated" with 5–6 HB
98	Unidentified prey	3		MEKW	A	Y							Transient KWs "eating something"; reportedly "test" an HB
101	Unidentified prey	4–5	3	MEKW	A	Y		x					Transient KWs diving on prey slick; 3 HB swimming around perimeter
103	Unidentified prey	3	4	MEKW	A	Y						68+	Transient KWs "killed something" and 4 HB have "excited interaction" with them
106	No prey observed	5	2	MEKW	U	U	x						Two HBs chasing transient KWs briefly

[a]MEKW: mammal-eater, FEKW: fish-eater, UnE: undetermined ecotype.
[b]A: Attack, T: Test, U: Unknown.
[c]N: No, Y: Yes, U: Unknown.
[d]KW: killer whale; HB: humpback whale.

and another possible fish-eater (small type B [B2]) found in Antarctic Peninsula waters (Pitman and Ensor 2003, Durban *et al.* 2016). The killer whales listed in Table 1 were classified as mammal-eating killer whales (MEKWs) if they were identified in the Appendix S2 accounts as "transients;" if they were attacking a marine mammal at the time of the observation, or if the encounter occurred in tropical or subtropical waters. Killer whales in lower latitudes tend to have unspecialized diets that include marine mammals (Baird *et al.* 2006). Killer whales were classified as fish-eating ecotypes if they were identified as such by experienced observers or from photo-identification matches to known types. Killer whales that could not be categorized were classified as "ecotype unknown."

From the accounts in Appendix S2, we classified interactions between humpbacks and killer whales based on which species approached the other (*i.e.*, which species initiated the interaction) or as "unknown" if a determination could not be made (*i.e.*, the interaction was already in progress when the observer arrived) or was unrecorded (Table 1). Based on our interpretation of the duration and intensity of the approaches and the specific comments in the Appendix S2 accounts, we further categorized MEKW approaches to humpbacks as either a "test" (sometimes described in the narratives as a brief harassment), an attack, or unknown. Tests usually lasted 5 min or less and often were little more than a brief pass-by; attacks lasted more than 5 min and involved direct contact with the targeted species.

When possible, humpbacks were also noted as being either with or without a calf. If a calf was not specifically identified, humpbacks were recorded "without calf," although small calves may have been overlooked and larger calves can be difficult to distinguish from other adults. The sex of individual humpback whales was sometimes determined, either genetically (through the analysis of tissue biopsies or sloughed skin) or from photographs of the genital area. An animal was also inferred to be female if it was closely and consistently attended by a calf at some time.

The term "escort" is usually used to indicate an adult male humpback that accompanies a female with a calf on the breeding grounds (Herman and Antinoja 1977, Tyack and Whitehead 1983, Clapham 2000). However, as is clear from the accounts in Appendix S2 and Pitman *et al*. (2015), cow/calf pairs are sometimes accompanied by another humpback also during migration and on the feeding grounds. Therefore, although deviating somewhat from current usage, for this paper we define "escort" as any humpback that accompanies a humpback cow/calf pair anytime or anywhere, including on the breeding or feeding grounds, or during migration. "Group size" for killer whales and humpbacks refers to the total number of individuals directly involved in an individual interaction and within one humpback body length (*ca.* 15 m) of other conspecifics at some time during the interaction.

"Bellowing" is the term we use for the very loud exhalations humpbacks make when they are excited (Whitehead and Glass 1985, Dolphin 1987). These sounds are variously referred to in Appendix S2 as "trumpeting," "trumpet blowing," "wheezing blows," "snorting," "exhaling loudly," *etc*. "Mobbing behavior" is defined as one or more humpbacks approaching MEKWs and doing one or more of the following: charging or chasing after the MEKWs, bellowing, and/or slapping or slashing their flipper or tail. As an additional cue, when humpbacks were mobbing, MEKWs actively fled from them or avoided them. Unless otherwise indicated, numbered references in the text (usually in parentheses) refer to the specific numbered events in Appendix S2 and Table 1.

Results

Appendix S2 (summarized in Table 1) provides details of 108 encounters between killer whales and humpback whales; six of these encounters (Appendix S2: #16, 39, 48, 49, 58, 87) included a further 1–2 interactions with additional groups of humpbacks, which were treated as separate events, giving a total of 115 interactions. Although these events were recorded at widely scattered locations around the world (Fig. 1), by far the majority was recorded in the eastern North Pacific Ocean including Monterey Bay, California (48 interactions; 42% of total) and Southeast Alaska (27 interactions; 23%).

Interactions between humpbacks and killer whales were usually agonistic and sometimes protracted, but which species behaved offensively, and which defensively, depended largely on the ecotype of the killer whales involved, and which species initially approached the other. Humpback whales interacted almost exclusively with mammal-eating killer whales (MEKWs) *vs.* fish-eating forms: of the 115 killer whale groups observed interacting with humpbacks, 108 (94%) were identified to type, and these included 95% MEKWs and 5% known or suspected fish-eaters (Table 1).

Overall, humpbacks approached MEKWs more often than MEKWs approached humpbacks: of 103 interactions, MEKWs approached humpbacks 27 times (26%), humpbacks approached MEKWs 38 times (37%), and the approaching species was unknown 38 times (37%). When the approaching species was known (n = 65), humpbacks initiated 58% of these interactions and MEKWs 42%. Among the 43 humpback/killer whale interactions for which the approaching species was not known, 38 (88%) included groups of MEKWs and 5 (12%) involved unidentified killer whale types.

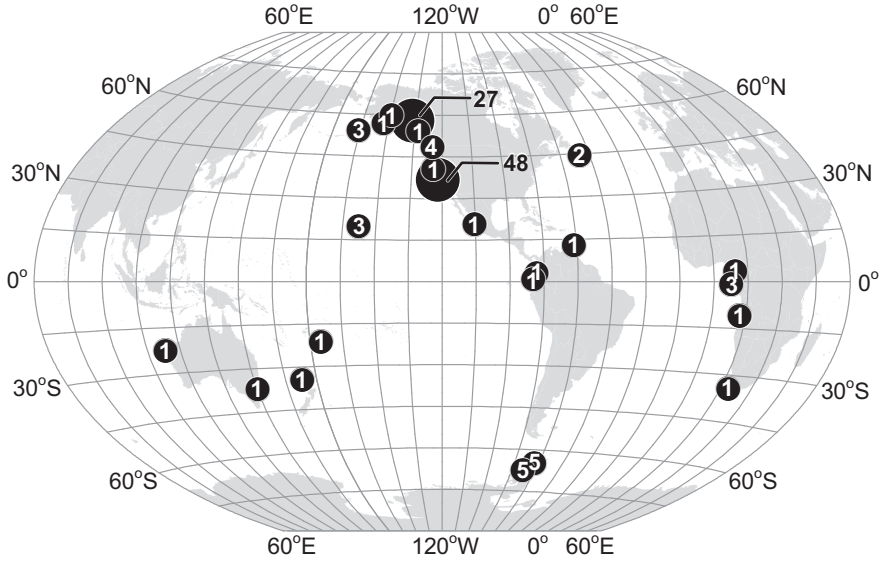

Figure 1. Locations and numbers of recorded interactions between humpback and killer whales described in Appendix S2 and summarized in Table 1; the number in each circle is the number of interactions from the general area.

Below we describe the behavioral responses of humpbacks and killer whales during their interactions based on which was the approaching species. We also provide some quotes from Appendix S2 from people who observed these interactions.

Killer Whales Approached Humpbacks

Killer whale groups that approached humpbacks (n = 31) were almost exclusively MEKWs (at least 27 groups; 87%). The remainder comprised fish-eaters (6%, n = 2) and unidentified types (6%, n = 2; Table 1). Among the identified ecotypes, MEKWs comprised 93% of the total. On the two occasions when fish-eaters approached humpbacks, the interactions were relatively benign: (1) a group of "resident" killer whales apparently "harassed" a lone adult male humpback for 5 min before leaving it (#6), and 2) suspected fish-eaters in Antarctica (type B2; Pitman and Durban 2010, Durban *et al.* 2016) caused a group of humpbacks to become briefly agitated. Other humpbacks converged on the site, but then the killer whales traveled with the humpbacks for a while afterward without incident (#49).

When MEKWs approached humpbacks (n = 27), no other potential prey species were observed, although it is possible that small prey, such as a pinniped, could have been overlooked (see, for example, #87). Humpback calves were present during at least 17 (63%) of the approaches, and MEKWs attacked during at least 16 (94%) of those. In at least 12 of the 16 (75%) attacks with a calf present, it was reported (or suspected) that the calf was specifically targeted (#30, 33, 34, 36, 37, 39, 40, 42, 43, 45, 47, 48), and in the other four cases, calves were likely targeted as well (#31, 35, 38, 41).

When MEKWs attacked humpbacks and no calf was reported, there was, nonetheless, evidence that younger animals were in fact targeted in most and perhaps all cases. On the 10 occasions when MEKWs approached humpbacks and a calf was not reported, 7 resulted in attacks of which at least 6 (86%) appeared to target nonadults, including two possible calves (#2, 16), two single juveniles (#14, 58), a possible juvenile (#10), and a lone subadult (#21). The remaining attack was on an animal of unknown age (#1). During the three MEKW approaches when no humpback calves were seen and no attack was reported, MEKWs were described as "testing" or "harassing" (*i.e.*, possibly attacking) humpbacks of unknown age on one occasion (#3), and on two other occasions MEKWs approached single humpbacks that were identified as adults (#13, 28), engaged them briefly, and then left.

Although interaction times were infrequently noted, when MEKWs approached humpbacks the interaction lasted longer if the humpback was with a calf. Six interactions with calves present lasted 20, 20, 26+, 45+, 150+, and 390+ min (#33, 40, 34, 47, 48, and 41, respectively). When MEKWs approached humpbacks and calves were definitely not present, typically there was a brief bout of bellowing or surface-active behavior by the humpback(s), and the MEKWs moved on (#13, 28; these two interactions lasted an estimated 5 and 2 min, respectively).

Although MEKWs purportedly killed one humpback calf (#36) and possibly another (#10; neither kill was confirmed), no adult humpbacks were reported killed or seriously wounded during any of the interactions. Observers sometimes reported seeing exposed flesh, minor bleeding, or bits of skin and blubber floating on the surface during some of the attacks (#2, 3, 34, 47), but there was no evidence to suggest that any adult humpbacks sustained life-threatening wounds.

Humpbacks Approached Killer Whales

The killer whales that humpbacks approached were almost exclusively mammal-eating forms: among the groups identified to ecotype, 38 of the 41 (93%) were MEKWs; the remaining three (7%) were known or suspected fish-eaters (Table 1).

Humpback approaches to fish-eating killer whales were relatively uneventful. In Alaska, humpbacks followed a group of known fish-eaters for over 2 h without incident (#15); in Antarctica, a lone humpback followed a group of suspected fish-eaters (#29). Also in Antarctica, suspected fish-eaters caused a group of humpbacks to become agitated, and several nearby humpbacks moved in among them, but nothing happened and the humpbacks dispersed (#49b).

Although infrequently noted, the distance humpbacks traveled to approach MEKWs was sometimes considerable. The six observer accounts that included estimated travel distances included: 200 m, >300 m, "several hundred meters," >1 mile (>1.6 km), *ca*. 1.8 km, and 2 miles (3.2 km; #92, 96, 78, 4, 59, and 77, respectively). On another occasion (#55), one humpback observed among a group of attacking MEKWs had been photographed feeding 2.7 h earlier, 3.5 nmi (6.5 km) away; a second had been photographed feeding 2.5 h earlier, 3.6 nmi (6.7 km) away, and a third humpback among this group had been photographed feeding 6.1 h earlier, 4.1 nmi (7.6 km) away. During each of these events, the MEKWs were attacking or feeding on prey when the humpback(s) arrived. The killer whale prey included a harbor seal (*Phoca vitulina*), an ocean sunfish (*Mola mola*), a California sea lion (*Zalophus californianus*), a humpback (no calf reported), a Steller sea lion (*Eumetopias jubatus*), another California sea lion, and a gray whale calf, respectively.

When humpbacks approached MEKWs (n = 38), at least 87% were attacking or feeding on prey at the time, and at least three of the other five MEKW groups may also have been with prey. Two groups (#87, 99) were suspected of having prey, and in one event (#108) MEKWs were "playing, jumping," which they often do after a kill (Ford and Ellis 1999, Matkin *et al.* 1999; Table 1). When humpbacks approached attacking MEKWs, among the prey identified (n = 29) were at least 10 species of large marine vertebrates, including humpbacks (17%) and other species (83%), the latter including four cetaceans, at least five pinnipeds, and one teleost fish. During an additional 43 interactions between MEKWs and humpbacks when the approaching species was not known, at least 23 (56%) of the MEKW groups were reported attacking or feeding on eight different prey species (including other humpbacks). Overall, humpbacks interacted with MEKWs that were attacking a total of 11 different prey species: other humpbacks (n = 6; two with calf, four without); gray whales (n = 5), common minke whale (*Balaenoptera acutorostrata*; n = 1), Dall's porpoise (*Phocoenoides dalli*; n = 1), Steller sea lions (n = 13), California sea lions (n = 14), Weddell seals (*Leptonychotes weddellii*; n = 1), crabeater seals (*Lobodon carcinophaga*; n = 1), harbor seals (n = 3), northern elephant seals (*Mirounga angustirostris*; n = 2), ocean sunfish (n = 2), and unidentified (but nonhumpback) prey (n = 7; Table 1, Fig. 2). In summary, when humpbacks interacted with attacking MEKWs (*i.e.*, humpbacks approached killer whales or the approaching species was unknown), and the prey were identified (n = 56), 11% were humpbacks and 89% were species other than humpbacks.

The sex of humpbacks that approached MEKWs was determined for 15 individuals from nine events and included both males and females (one male was recorded twice; see below). Among humpbacks that approached attacking MEKWs, the sex was known for five individuals from three events: a single male and a single female

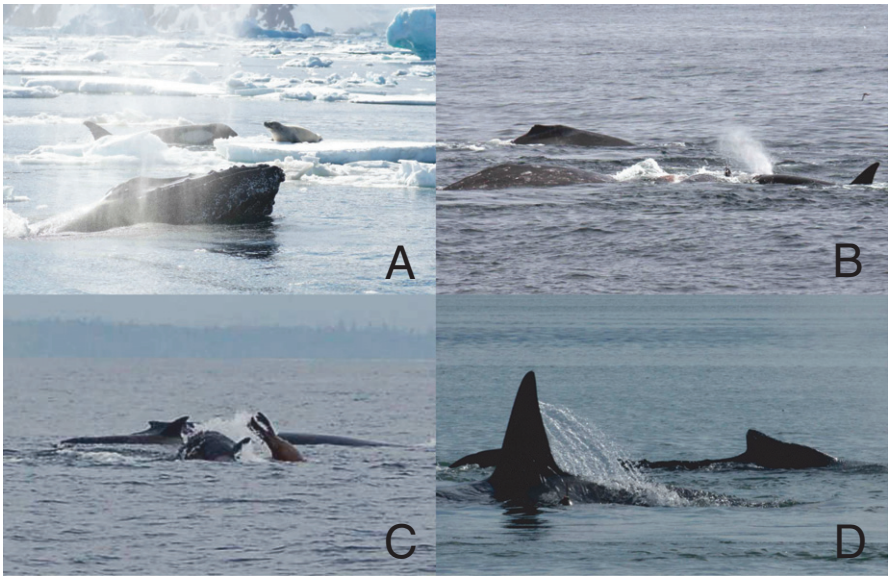

Figure 2. Examples of humpback whales interacting with mammal-eating killer whales attacking various prey species: (A) large type B killer whales attacking a crabeater seal hauled out on an ice floe with an agitated (bellowing) humpback in the foreground; January 2009, Western Antarctic Peninsula, Appendix S2 account #89; photo by J. Durban; (B) Bigg's killer whales attacking a gray whale calf (gray whale mother on left; wounded calf in center) with a humpback whale in the background; May 2012, Monterey Bay, CA, #55; photo E. Robinson courtesy Monterey Bay Whale Watch; (C) Bigg's killer whales attacking a Steller sea lion with humpback in the immediate background; 21 August 2010, Vancouver Island, Canada, #67; photo by R. Frank; (D) Bigg's killer whales attacking a harbor seal (below trailing edge of killer whale dorsal fin; the seal has a transmitter mounted on its head) and a humpback in the background; June 2005, Glacier Bay, AK, #91; photo by M. de Roos.

(apparently initially unassociated) responded to an attack on a Steller sea lion (#65); an adult female with two adults of unknown sex approached MEKWs that were with a Steller sea lion kill (#70), and an adult female with 2–6 adult humpbacks of unknown sex, and an adult male with three other adult humpbacks of unknown sex approached MEKWs that killed a gray whale calf (#55). The sex of an additional 10 humpbacks from six events where the approaching species was not known included eight males and two females: two single males interacted with MEKWs attacking a Steller sea lion (#60) and a harbor seal (#91); at least two of four humpbacks present at a Steller sea lion attack (#61) were males; two previously unassociated males each responded to an attack on a Steller sea lion (#62); an adult male and another adult of unknown sex interacted with MEKWs at a Steller sea lion kill (#69); and one of a pair of humpbacks at a Weddell seal attack in Antarctica (#88) was genetically identified as a male. In addition, on at least two occasions, cow/calf pairs were among other humpbacks that approached during MEKW attacks on a Steller sea lion (#59) and a California sea lion (#74), respectively. The single male in event #60 was also photo-identified as one of the two males in event #62; both events involved MEKW attacks on single Steller sea lions in Icy Strait, Alaska, one in September 1988 and one in September 2003—15 years apart!

When humpback whales interacted with MEKWs, they generally showed the same behavioral responses regardless of whether they approached MEKWs, or MEKWs approached them (*i.e.*, the same behaviors were used offensively and defensively), and regardless of whether the MEKWs were harassing or attacking them, their calves, other humpbacks, or other species of marine animals (Table 1). The most commonly reported behaviors for humpbacks interacting with MEKWs, regardless of the approaching species ($n = 103$), included: slapping their flukes at the surface ("lob-tailing") or slashing them from side-to-side (37 interactions; 36%), bellowing (26%), pursuing behavior (21%), and flipper slapping (14%). When humpbacks pursued MEKWs ($n = 22$), regardless of the initially approaching species, they were variously described as just following the killer whales (#52, 55, 57, 59, 66, 69, 88, 89, 91, 100, 102, 104, 107), chasing them (#2, 39, 50, 55, 86, 94, 96, 105), or charging at them (#19, 31, 55, 77). We categorized as "mobbing behavior" (see Discussion) whenever humpbacks used any of these behaviors offensively (*i.e.*, whenever humpbacks approached attacking MEKWs, or when the approaching species was not known and humpbacks were interacting with MEKWs attacking a third species or another humpback). Based on these criteria, humpbacks exhibited mobbing behavior during at least 31 out of 56 (≥55%) interactions with attacking killer whales.

Observers sometimes reported that approaching humpbacks appeared to affect the outcome of the attack, and were reportedly responsible for the escape of at least two humpbacks (#16, 39), two gray whales (#52, 53), probably a Weddell seal (#87), and an unrecorded number of sea lions (#53). When humpbacks approached MEKWs attacking humpbacks ($n = 5$; two with calves), four of the attacks were unsuccessful and the outcome of the other was unknown. Furthermore, the approaching humpbacks were described as coming to the aid (#4) or defense (#58) of the attacked whales, and in two other cases (#16 and 39) they reportedly drove off the attackers. When humpbacks approached MEKWs that were attacking pinnipeds ($n = 18$), the prey was killed on at least 13 (72%) occasions. It was not always possible to determine exactly when the pinniped died, but on at least five of those occasions (#65, 73, 78, 86, 92) the prey was probably already dead when the humpback(s) arrived.

What follows are quotes from Appendix S2 by three different observers, which offer some insights into the behaviors of humpbacks that approached attacking MEKWs.

"We observed the harassment of a humpback whale by [about 15] killer whales once; during the attack, other humpback whales rapidly converged on the attackers and appeared to drive the killer whales away" (#16).

[After being attacked by a group of approximately 15 killer whales, a humpback cow/calf pair joined a trio of humpbacks] "and for the next few minutes we could see what clearly looked like the three Humpback whales chasing off the Orcas! The Orcas left the scene completely, all the time with the three Humpbacks behind them" (#39).

"[W]e had traveled quite a distance to observe a group of killer whales attacking a gray whale mother and calf pair and out of NOWHERE, a humpback whale came trumpeting in followed by another and then another until we had about 5 or more humpbacks in the immediate area. It was strange because during the entire journey with several observers on effort, not a single humpback whale had been observed. It seemed quite clear that the KW/gray whale interaction had attracted the humpbacks, though I cannot say whether it was motivated by curiosity, playfulness or an act of benevolence. The result however was that the gray whale cow/calf pair was able to escape. [On other occasions] I also personally observed several sea lions surviving predation attempts as a result of humpback whales distracting killer whales" (#53).

Additional Biological Observations

The overall median number of MEKWs present during each individual interaction with humpbacks was six ($n = 97$; range 1–17), and the median was the same regardless of whether they approached humpbacks ($n = 26$; range 1–17), or humpbacks approached them ($n = 33$, range 2–16). The overall median group size for the total number of humpbacks present in each interaction was 2 ($n = 92$; range 1–16), also regardless of whether they approached MEKWs ($n = 36$; range 1–16), or MEKWs approached them ($n = 23$; range 1–3).

The duration of interactions between humpbacks and attacking MEKWs was variable but often protracted and ranged from 15 to 437+ min (Table 1). Using data only from sightings observed from start to finish, humpback/MEKW interactions lasted an average of 59 min ($n = 10$, range 15–124). Longer events, however, were rarely observed in their entirety, usually because observers arrived after the event was already in progress or departed before it was over. If we also include events where the approaching species was unknown, there were 13 partially-observed interactions that lasted 60 min or longer. The longest occurred during a gray whale calf kill where humpbacks were present for a minimum of 437 min (#55).

When lone humpback cow/calf pairs were attacked ($n = 6$), the mother was sometimes able to drive off the MEKWs by herself (#35, 42, 45, 46; killer whale group size during these attacks was 1, 7, 6, and 2, respectively). When humpback cow/calf pairs were accompanied by an escort, the escort at times appeared to defend the calf as vigorously as the mother, although even their combined efforts apparently were not always successful (#36). Escorts were reported accompanying cow/calf pairs on the feeding grounds (#33, and probably 58), on the breeding grounds (#34, 37, 43), and on migration (#31, 36).

Attacking MEKWs often tried to separate the humpback calf from its mother (#34, 43, 45, 47), and the humpbacks took specific countermeasures. A lone mother raised her calf out of the water on her back and head (#46). Mothers and escorts sometimes responded by flanking the calf (#33, 36, 43, and probably 58), and during one attack, a mother and an escort flanked a calf and partly raised it out of the water with their flippers (#33). If there were more than two adult humpbacks present, they sometimes surrounded the calf or calves (#38, 44).

In addition to mothers and escorts protecting calves from attacking MEKWs, other unassociated humpbacks in the area sometimes assisted in driving away the attackers (#4, 16, 39, 48, 49). For example, "in a harassment observed in 1988 in Chatham Strait [Alaska], humpbacks came from over a mile away to the aid of the victim" (#4). In another, 15 MEKWs attacked the smaller of three humpback whales, and an hour into the attack, three other humpbacks "rapidly converged on the attackers and appeared to drive the killer whales away" (#16). In an encounter in Antarctica, a humpback cow/calf pair under attack swam in among three adult humpbacks and the trio apparently chased off the killer whales (#39). In another case, killer whales were attacking a humpback calf, and 30 min later 13 humpbacks "swam up to the injured calf" and the killer whales left the area (#48).

Overall, regardless of the approaching species, a minimum of 38 prey animals were reported killed during the humpback/killer whale interactions, including humpback whales (two calves/juveniles; kill(s) likely but not confirmed), gray whales (2; including at least one calf), minke whale (1), Steller sea lions (10), California sea lions (10), Weddell seal (1), harbor seals (3), northern elephant seals (2), and unidentified prey (7). One, possibly two ocean sunfish were attacked and probably killed, also. When

humpbacks interacted with MEKWs that were attacking other humpbacks ($n = 17$), the fate of the prey was recorded 7 times (41%) and there were no kills. These included two groups with calves and five without. The fate of the prey was unrecorded 10 times (59%). When humpbacks interacted with MEKWs that were attacking nonhumpback prey ($n = 53$), the fate of that prey was recorded 44 times (83%): of those 36 (82%) were killed, and at least 8 (18%) were seen (or suspected) to escape (#51, 52, 53, 57, 72, 79, 87, 89).

Observer Comments

Some observers were clearly puzzled about why humpbacks would approach attacking MEKWs, and a number of possible explanations were included in the accounts. For example, it was suggested that the humpbacks might have been merely curious (#53, 75, 89), and others suggested that the humpbacks were also trying to kill or injure the prey that the MEKWs were attacking, by swatting them with their flippers or flukes (#61, 64, 65, 91). Although humpbacks in some of the accounts reportedly struck killer whale prey with their flippers or flukes, including in one case when the prey was apparently already dead (#65), it was unclear whether this contact was intentional, or at least in some cases, whether the purported contact actually occurred. For example, "three adult humpbacks participated {in a Steller sea lion kill} by lobtailing on or near the sea lion 15 times, making physical contact with it a minimum of 10 times" (#61). However, after a careful review of the video that this account was based on, RLP has concluded that the humpbacks remained in close proximity to the sea lion and were swatting only when the killer whales made close passes, and that there was no confirmed contact with the carcass.[2]

The following is an example of observer confusion as to whether humpbacks were attempting to strike the prey with their appendages or were targeting the killer whales. "It definitely looked like the humpback was slashing, with its pectoral fins, at the {Steller} sea lion. We were astonished and thought at the time that the humpback was participating in the kill. I remember noticing that the pectoral fin slashes were 'late,' a few beats behind as the Steller swam on the surface alongside the humpback, with orcas following. . .It's quite possible that the humpback was actually slashing at the orcas following the sea lion. Perhaps the animal wasn't late with its slashes, it might have been right on time!" (#64).

Other observers specifically stated that the aggressive behavior of the humpbacks was in fact directed at the attacking killer whales and not their prey (#19, 58, 68, 77, 86). According to one: "I remembered thinking that humpbacks can be fearsome if necessary. The trumpeting noise and quick forceful movements, directly at the Orcas, was impressive" (#19). Another wrote that the humpbacks were "swatting killer whales with their flukes!" (#77). Despite the numerous accounts of humpbacks slapping or slashing their appendages in the presence of attacking killer whales ($n = 38$; Table 1), there were no confirmed reports of humpbacks actually striking MEKWs, although it could have happened (*e.g.*, #55, 59). And finally, some observers interpreted the humpbacks' behavior as attempts to rescue, guard or protect the prey (#52, 53, 55, 60, 68, 88).

[2]Based on this same video footage, some of the co-authors (VBD, CMG, DRM, and JLN) thought that the humpbacks were actually attempting to strike the sea lion with their flukes. Links to the video are listed in Appendix S1.

Discussion

It is clear from these results that killer whales and humpback whales regularly approached each other but for entirely different reasons. Killer whales that approached humpbacks were almost exclusively mammal-eating forms (*vs*. fish-eaters), and they appeared to be looking for calves or juveniles to attack (see also Pitman *et al.* 2015, Saulitis *et al.* 2015). When humpbacks approached killer whales, they were selective about the type of killer whale that they interacted with and the circumstances: 93% of the killer whale groups that they approached were MEKWs, and at least 84% (and perhaps 100%) of those were attacking or feeding on prey at the time (Fig. 2). Although the threat of injury to an approaching adult humpback was probably minimal (see below), these interactions did come at a cost to the humpbacks. In addition to disruption of their normal behaviors (*e.g.*, feeding, resting, socializing), they sometimes traveled distances >2 km to approach killer whales. They often responded vigorously and aggressively and sometimes for extended periods of time: interactions regularly lasted >1 h and up to almost 7 h. Particularly puzzling was the fact that when humpbacks approached attacking MEKWs, and the species of prey was identified ($n = 33$), 85% of the time it was a species other than a humpback whale, but the approaching humpbacks often continued their interactions or harassment regardless of the prey species. Below, we discuss the adaptive significance and implications of these interactions for both species, and we comment on how and why humpbacks may be willing to confront MEKWs, even when they were attacking species other than humpbacks.

Survival of the Biggest

Our review supports previous conclusions that healthy adult humpback whales, because of their much larger size, sometimes combative nature, and robust appendages (see below), are probably immune to killer whale predation (Whitehead and Glass 1985, Jefferson *et al*. 1991, Mehta *et al*. 2007, Ford and Reeves 2008, Steiger *et al.* 2008, Pitman *et al.* 2015). Even lone humpbacks sometimes deliberately approached and interacted with groups of 10 or more MEKWs that were attacking various prey species (Table 1), and when MEKWs approached adult humpbacks without calves, the MEKWs left almost immediately. This confirms that any putative absence of predation pressure on humpback whales by MEKWs (Clapham 1996, 2001; Clapham and Mead 1999; Mehta *et al.* 2007) pertains only to healthy adult humpbacks, which presumably allows them to approach attacking MEKWs largely with impunity.

Although adult humpbacks may be safe from MEKW predation, subadults, juveniles, and especially calves are vulnerable to attack, and this probably applies to all species of large whales (Melnikov and Zagrebin 2005; Reeves *et al.* 2006; Ford and Reeves 2008; Pitman *et al.* 2007, 2015; Barrett-Lennard *et al.* 2011). As Scammon (1874) commented about killer whales, "it is but rarely these *carnivora* of the sea attack the larger Cetaceans, but chiefly prey with great rapacity upon their young."

Armed Response

The humpback whale is, to our knowledge, the only cetacean that deliberately approaches attacking MEKWs and can drive them off, although southern right whales (*Eubalaena australis*) may also group together to fend off MEKWs attacking

other right whales (Sironi *et al.* 2008). The adult humpback's enormous body size certainly contributes to its apparent invulnerability, but there are other, larger whale species that are not known to deliberately approach MEKWs. We suggest that the evolution of the humpback's massive pectoral flippers may have given it an advantage over killer whales and perhaps altered the balance of power in their interactions.

Humpback flippers (Fig. 3) can measure up to 5 m long, one third of their total body length (Woodward *et al.* 2006), and can weigh over 1 ton (1,016 kg, Tomilin 1967). Although they are by far the largest cetacean flippers, both relatively and absolutely, they are quite flexible and maneuverable, and humpbacks can wield them adroitly (Edel and Winn 1978). Furthermore, in addition to sheer impact power, each flipper has a knobby leading edge often encrusted with large, sharp, sessile barnacles (*Coronula* spp.) that can tear the flesh of their opponents (Pierroti *et al*. 1985, Ford and Reeves 2008). These formidable appendages provide protection at the anterior end of the whale, and, when used in concert with the flukes, afford humpbacks with fore and aft, offensive and defensive weaponry—a capability that is unique among living baleen whales. When humpbacks are agitated by killer whales, they appear to randomly flail their flippers and flukes without specifically targeting individual attackers. Nevertheless, killer whales appear to recognize the danger and normally remain "at arm's-length" when interacting with humpbacks (RLP, personal observation)

Various other functions have been suggested for the humpback's over-sized flippers, including prey herding, visual and acoustic signaling, temperature regulation, "coital clasping" during mating, and increased swimming proficiency and maneuverability (Edel and Winn 1978, Fish and Battle 1995, Woodward *et al.* 2006). These massive flippers can be especially important during the breeding season, when adult

Figure 3. A mother humpback whale and newborn calf photographed off Baja California, Mexico, Oct 2009. When necessary, the mother will use her massive pectoral flippers to defend her small calf from attacking predators, especially killer whales. Photo: M. Lynn, NOAA, Southwest Fisheries Science Center.

male humpbacks participate in aggressive contests for access to breeding females. During these bouts, vying males engage in charging behavior, flipper- and tail-slapping, and bellowing (Tyack and Whitehead 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985)—the same behaviors that both sexes use during aggressive interactions with killer whales (Pitman *et al.* 2015, this study). Regardless of the initial evolutionary impetus for enlarged flippers in humpback whales, or any additional functions they may have acquired over time, it is clear that they currently have important survival value as weaponry against killer whales and for calf protection, and they may also be a major reason why humpbacks are able to confront and drive off MEKWs.

Humpback Whale Antipredator Behaviors

Among the *fight* baleen whale species described by Ford and Reeves (2008; see Introduction), mothers with calves will often seek refuge in their physical environment when they are attacked. This includes gray whales and right whales moving into shallower waters (Ford and Reeves 2008, Sironi *et al.* 2008, Barrett-Lennard *et al.* 2011), and bowhead whales using sea ice as protection from killer whales (Nerini *et al.* 1984, Philo *et al*. 1993). Although humpback mothers and calves also retreat to shallow waters when threatened (Pitman *et al.* 2015) or around structures such as boats (#37) or oil platforms (#41), they appear to require less shelter overall, which Ford and Reeves (2008) suggested might be due to the proficiency of adult humpbacks in fending off attacking MEKWs.

In addition to mothers retreating to shallow waters, the *fight* species described by Ford and Reeves (2008) also share a number of other behavioral responses to attacking MEKWs. For example, southern right whales respond with tail- and flipper-slapping when attacked and have been reported to strike killer whales with their flukes (Ford and Reeves 2008, Sironi *et al.* 2008). Right whales also exhibit group defense with nearby whales coming in to help defend calves from attacking killer whales. There are also reports of right whales protecting a calf from attack by using their bodies to enclose the calf in a circle or "rosette," with their heads pointed in and tails out (Ford and Reeves 2008, Sironi *et al.* 2008).

Cooperative defense by humpbacks during killer whale attacks has, however, received relatively little attention. Clapham (2000) made no mention of it in his comprehensive review, but more recently Ford and Reeves (2008) listed several instances when humpback mothers and calves were attacked by MEKWs, and nearby humpback adults approached and acted aggressively toward the killer whales (Fig. 4; see also Whitehead and Glass 1985, Dolphin 1987, D'Vincent *et al.* 1989). According to Ford and Reeves (2008), the approaching humpbacks sometimes "displayed apparently defensive or protective behaviour" as they positioned themselves closely around the calves.

From the Appendix S2 accounts, we identified two separate humpback responses to MEKWs attacking other humpbacks: (1) when (apparently) unassociated humpbacks approached other humpbacks that were being attacked (*e.g.*, Fig. 4), and (2) when one or more escorts traveling with a cow/calf pair responded aggressively toward attacking MEKWs. As examples of the former, on one occasion four adult humpbacks "grouped tightly" around a calf, and the circling MEKWs left after 10 min (#44). On another occasion, humpbacks near Hawaii formed a rosette (heads in, tails out) around an unspecified number of calves to shield them from attacking

Figure 4. In the Aleutian Islands, Alaska, 17 Bigg's killer whales (in the background) attacked a large humpback calf accompanied by its mother and an escort in July 2003; three other adult humpbacks joined in and helped drive off the killer whales. (This record arrived too late to be included in Appendix S2). Photo: © Flip Nicklin/Minden Pictures.

MEKWs (#38). The latter and Acevedo-Guitiérrez (2009) are, to our knowledge, the only reports of rosette-formation by humpback whales.

Herman and Antinoja (1977) first used the term "escort" to describe a whale accompanying a mother/calf pair on the breeding grounds, and they suggested that escorts might have a protective role. Herman and Tavolga (1980) subsequently suggested that the escort might also be a male waiting for the female to come into estrus. Later work confirmed that escorts on breeding grounds are almost always males and the current consensus is that their main function is to mate with the escorted female if the opportunity arises (Clapham 2000). Although the protective role of escorts have been dismissed (*e.g.,* Darling 2001), there have been numerous recent observations from Ningaloo, Western Australia, of escorts accompanying cows with calves during migration to the breeding grounds and vigorously defending the calf when killer whales attack (Pitman *et al.* 2015, see also Chittleborough 1953). Combined with some of the Appendix S2 accounts (*e.g.*, #34, 36, 37, 43), these observations suggest that calf defense by humpback escorts is a temporally and spatially widespread antipredator measure. Future research that identifies the relatedness of humpback escorts to the mothers and calves that they accompany, and the duration of their associations, will be important for further understanding the social and antipredator roles of the escort.

The Other "Killer Whales"

In addition to MEKWs, other species in the cetacean subfamily Globicephalinae (*i.e.*, "blackfish"), including false killer whales (*Pseudorca crassidens*) and pilot whales

(*Globicephala* spp.), are also known or suspected predators of other cetaceans, including calves of large whales, and humpbacks have at times shown similarly aggressive responses toward them also.

False killer whales have been known to attack large whales, including sperm whales (*Physeter macrocephalus*, Palacios and Mate 1996) and humpbacks (Dolphin 1987, Naessig and Lanyon 2004), and reportedly killed and ate a humpback calf in Hawaii (Mazzuca *et al.* 1998). Hoyt (1983) reported "an apparently aggressive episode between humpbacks and false killer whales" in Hawaii: "Snorkeling in the water, [Graeme] Ellis was watching five false killers quietly share a fish when 'a humpback came out of nowhere, charged into the middle of them and scattered them like bowling pins.' The false killers were emitting high-pitched squeaks as they sped away."

Pilot whales have also been known to act threateningly toward large whales—this includes short-finned pilot whales (*G. macrorhynchus*) interacting with sperm whales (Weller *et al.* 1996) and long-finned pilot whales (*G. melas*) with humpbacks (Ciano and Jørgensen 2000). In addition, Siebert (2009) describes an account of a pod of 40–50 short-finned pilot whales attacking a pair of gray whales off Baja California, Mexico, and a nearby humpback came in and drove off the attackers. Although it is unclear if this was an actual predation attempt by the pilot whales or just harassment, the humpback appeared to recognize them as a potential threat and showed the same aggressive responses that some humpbacks have shown to attacking MEKWs.

Where Do Attacks Occur?

There have been a number of speculations about where (geographically) MEKWs attack humpback whales, *i.e.*, where do the calves acquire their tooth rake marks. The three areas considered are the feeding grounds, the breeding grounds, or along the migratory corridors that link them, and all have been suggested as likely venues.

Clapham (2000) noted that although as many as 33% of the humpbacks in the western North Atlantic had killer whale tooth rake marks on their flukes, during two decades of humpback research in the Gulf of Maine there had been few killer whale sightings and no reported attacks on humpbacks, and that during 16 seasons of field work on the West Indies breeding grounds, no killer whales had ever been sighted (but see #30). From this it was concluded that calves were probably attacked mainly while en route to high-latitude feeding grounds during their first migration (Clapham 2000, 2001; Mehta *et al.* 2007). McCordic *et al*. (2014) reported significant differences in tooth-rake marks among populations of humpbacks sampled from five different feeding grounds in the North Atlantic, and because nearly all North Atlantic humpbacks breed in the West Indies, they concluded that attacks probably occurred either during migration or on the feeding grounds. When Steiger *et al.* (2008) analyzed tooth rake marks on humpbacks in the eastern North Pacific, they concluded that calves were attacked mainly on the breeding grounds. More recently, Pitman *et al*. (2015) documented MEKWs attacking humpback neonate calves during their northbound migration to breeding grounds off northwestern Australia, and estimated that at least dozens were taken annually.

Assuming that humpback calves wean only after they are large enough to defend themselves against killer whales, they are probably vulnerable to attack anytime and anywhere that they still accompany their mother. Since calves

normally stay with their mothers for about 1 yr (one entire migratory cycle; Clapham and Mayo 1990), this suggests that attacks could potentially occur anywhere within their migratory range, and our records confirm this: humpback calves have been attacked on or near breeding grounds in the West Indies (#30), Colombia (#34), Ecuador (#43), Hawaii (#10, 38), Tonga (#37), South Africa (#35), and West Africa (#41); on the feeding grounds in Alaska (#33, 40, 42, 46, 47), California (#44, 48), and Antarctica (#39), and during migration off Australia (#31, 36, see also Pitman *et al.* 2015).

It is still not clear where the majority of these attacks occur because the feeding and breeding grounds of humpbacks both offer advantages and disadvantages for both predator and prey. On the high-latitude feeding grounds, MEKWs are much more abundant (Forney and Wade 2006), but humpback calves there will have grown considerably larger by the time they reach those areas and would be more challenging to kill. By contrast, MEKWs are much less common on the low-latitude breeding grounds, where humpback calves are much smaller and more vulnerable to predation. Perhaps, as suggested by the disparate results and conclusions from the different rake-mark studies cited above, important attack areas may vary with region.

Do Humpbacks Respond to Killer Whale Attack Vocalizations?

Another question concerns how humpbacks were able to detect attacking MEKWs that were sometimes over 1 km away. We propose that they were responding to acoustic cues—cues from the MEKWs and not their prey.

Unlike fish-eating killer whales, MEKWs in the North Pacific, and probably globally, are mostly silent when they hunt, presumably because their mammalian prey species all have acute hearing capabilities (Barrett-Lennard *et al.* 1996; Deecke *et al.* 2005, 2011; Riesch and Deecke 2011). For example, it has been shown that when gray whales, harbor seals, belugas (*Delphinapterus leucas*), and sperm whales are exposed to playback calls of MEKWs, they respond with various antipredator behaviors (Cummings and Thompson 1971, Fish and Vania 1971, Deecke *et al.* 2002, Curé *et al.* 2013). Humpbacks in the eastern Atlantic also appear to avoid MEKW vocalizations (Curé *et al*. 2015).

Once MEKWs have detected potential prey, however, they often become vocally active, during and after attacks (Morton 1990, Guinet 1992, Goley and Straley 1994, Barrett-Lennard *et al.* 1996, Deecke *et al.* 2005, Ford *et al*. 2005, Deecke *et al.* 2011, Riesch and Deecke 2011). As Reeves *et al.* (2006) suggested, "active sound processing presumably becomes allowable, and perhaps functionally important, once contact with the prey has been established." The reason(s) for vocalizing in this context is not currently understood, but it could be important for coordinating attack behavior, or for calling in other killer whales—either to assist in the attack, to share in the kill, or for socializing (Deecke *et al.* 2005).

We suggest, therefore, that when humpback whales approached attacking MEKWs, they were responding to the attackers' vocalizations. Four observations support this notion: (1) MEKWs and fish-eating killer whales occur sympatrically in the NE Pacific, and presumably elsewhere. They have type-specific vocalizations (Ford and Fisher 1982, Riesch and Deecke 2011), which humpbacks should be able to distinguish (Deecke *et al.* 2002); (2) humpbacks approached MEKWs (*vs*. fish-eaters) in the large majority of cases (93%; $n = 41$), and when they did, at least 84% ($n = 32$) of the MEKW groups were already attacking or feeding on various prey species; (3)

although infrequently reported in Appendix S2, the distances that some of the humpbacks traveled when they approached killer whales were obviously well beyond the visual range of humpbacks. For example, on four occasions humpbacks reportedly traveled 1.6 and 7.6 km before approaching MEKWs that were attacking a humpback whale, a gray whale, a Steller sea lion, and a California sea lion (#4, 55, 59, 77, respectively); and (4) on two occasions, observers with hydrophones specifically recorded MEKWs vocalizing at an attack site before the humpbacks arrived (#90, 97).

As additional evidence that humpbacks can recognize and respond to MEKW vocalizations, at least in a defensive way, Curé *et al.* (2015) showed that humpbacks in the eastern Atlantic displayed strong negative reactions (*i.e.*, immediate changes in feeding behavior, diving patterns, avoidance behavior, *etc.*) in response to playbacks of MEKW vocalizations (recorded in the North Pacific). We do not have any information on how often humpbacks may actively avoid vocalizing MEKWs, and the Curé *et al.* (2015) sample size ($n = 8$) may have been too small to record the full range of humpback responses to their playbacks.

Little is known about nonsong vocalizations of humpback whales (Silber 1986, Clapham 2000, Dunlop *et al.* 2008, Zoidis *et al.* 2008, Wild and Gabriele 2014), including whether or not they have an alarm call; if they do, it would be difficult to explain why they responded when other species were being attacked. Furthermore, it seems unlikely that humpbacks would respond to acoustic signals from nonhumpback prey. On at least three occasions (#58, 59, 66), however, observers with hydrophones reported that humpbacks among attacking MEKWs made "a variety of sounds" underwater and that they regularly bellowed when they interacted with killer whales (Table 1; see also Whitehead and Glass 1985, Dolphin 1987). The purpose of the bellowing is unknown—it may only indicate a heightened level of excitement, or it could signal aggression. As mentioned previously, humpback males on the breeding grounds often bellow loudly during aggressive, competitive interactions with other males (Tyack and Whitehead 1983), but during interactions with killer whales and depending on how far this sound carries through the water, bellowing or other vocalizations could also serve as signals to summon or alert other humpbacks in the area. Therefore, we infer that humpbacks were reacting to calls of attacking killer whales and not to the calls of their prey, which meant that approaching humpbacks probably did not know which species of prey was being attacked until they arrived at the scene.

Although we assume that approaching humpbacks were responding primarily to MEKW vocalizations, once among the MEKWs, humpbacks showed various responses depending on the circumstances and, possibly, the demeanor of the individual humpback. If another humpback was being attacked, the approaching humpback (s) always acted aggressively towards the MEKWs, sometimes driving them off. But when a species other than a humpback was being attacked, the approaching humpback(s) showed a range of responses, including: moving away, staying on the periphery of the action as if curious, or aggressively confronting the attackers. This could be due to individual responses reflecting differences in, for example, sex, size, age, reproductive status, kinship, individual history with killer whales, or personality of the approaching humpback (*e.g.*, Briffa and Weiss 2010, Highfill and Kuczaj 2010). Another possibility, testable through play-back experiments, is that the variation in the humpback responses could also reflect changes in the vocal behavior of the killer whales: if humpbacks are attracted to attack vocalizations of killer whales, then if

MEKWs stop vocalizing when humpbacks approach, it might prevent humpbacks from interfering.

Mobbing Behavior in Humpback Whales

When a potential prey species detects a predator, the prey can show a range of responses, and although most animals seek to avoid predators and retreat to avoid detection, individuals of some species will, under certain circumstances, deliberately approach and even confront their predators (see review by Caro 2005). The resulting interaction typically falls into one of two general categories. *Predator inspection* is when a prey species approaches a predator, but maintains a safe distance and avoids direct interaction—it merely observes and sometimes follows the predator. *Mobbing behavior* (also known as "predator harassment") is when a prey species closely approaches, often harasses, and sometimes even attacks a predator, often while calling to alert or summon conspecifics (Curio 1978, Berger 1979, Dugatkin and Godin 1992). Whether the predator is inspected from a distance or harassed at close range normally depends on the level of vulnerability of the inspecting/mobbing animal or its brood (Berger 1979, Dugatkin and Godin 1992).

Predator inspection has been reported among a variety of fishes, birds, and terrestrial mammals, the latter including mainly ungulates, squirrels, and primates (Owings and Coss 1977, Curio 1978, Pitcher *et al*. 1986, Loughry 1988, Tamura 1989, FitzGibbon 1994, Caro 2005, Graw and Manser 2007). Although predator inspection can be dangerous and occasionally even fatal for the inspector (Sordahl 1990, Dugatkin and Godin 1992, FitzGibbon 1994), numerous overriding benefits have been proposed: it exposes the presence and location of a predator to conspecifics and kin; it lets stalking predators know that they have been detected, often causing them to move out of the area; it allows potential prey to monitor predator movements, and it may also provide an opportunity, especially for younger animals, to learn about predators (Curio 1978, Dugatkin and Godin 1992, FitzGibbon 1994, Caro 2005, Graw and Manser 2007).

Mobbing behavior is also a widespread antipredator response. Although especially common among birds, it is also found among insects, fishes, and terrestrial mammals (Curio 1978, Dugatkin and Godin 1992, Ostreiher 2003, Caro 2005). There have been numerous explanations proposed for this seemingly counterintuitive, and sometimes dangerous (*e.g.*, Denson 1979), antipredator strategy, but the consensus is that it serves many of the same functions suggested for predator inspection, *i.e.*, to alert stalking predators that they have been detected; to bring the predator to the attention of kin and other conspecifics, and to summon in others to assist in the mobbing and driving off the predator. The main difference between inspection and mobbing is in the level of engagement. Mobbing involves harassment at close range, often with the mobbers making bodily contact and sometimes even killing the predator (Caro 2005). The main benefit of mobbing (*vs*. inspecting) is that it can be more effective in driving off potential predators.

Although more difficult to observe in the marine environment, predator mobbing has been reported for a variety of marine mammal species. Among pinnipeds, Galápagos fur seals (*Arctocephalus galapagoensis*), Galápagos sea lions (*Zalophus wollebaeki*), and Australian fur seals (*A. pusillus doriferus*) have been reported to mob sharks (Barlow 1972, Trillmich 1996, Kirkwood and Dickie 2005). Steller sea lions have been reported "harassing" (possibly mobbing) killer whales on at least two separate occasions (Heise *et al.* 2003), although the specific details (including ecotype of killer

whales) were lacking. Matkin *et al.* (2007) reported six accounts of groups of 3–50 Steller sea lions approaching MEKWs and following them from distances of 50–100 m; in all but one case, the sea lions outnumbered the MEKWs, and on each occasion the MEKWs swam away from the sea lions.

Among cetaceans, mobbing behavior and possible predator inspection have previously been reported only for odontocetes (toothed whales and dolphins). Dolphins have been reported to mob sharks (Essapian 1953, Wood *et al.* 1970, review by Connor 2000) and possibly killer whales. For example, Saayman and Tayler (1979) described how three Indo-Pacific humpback dolphins (*Sousa chinensis*; length of adults <3 m) off South Africa broke from a group of 10 others and pursued an unidentified 4–5 m shark. The dolphins "forced" the shark into two separate coves before driving it off to the open ocean, after which the dolphins returned to their original group. Off Southern California, 14 adult bottlenose dolphins (*Tursiops truncatus*, 3–4 m) raced toward a white shark (<3 m). They rammed it, breached on it, and drove it toward the nearby beach before it disappeared.[3] Long-finned pilot whales were reported as possibly mobbing killer whales off Norway (Curé *et al.* 2012), and de Stephanis *et al.* (2015) described "mobbing-like" behavior by long-finned pilot whales toward killer whales in the Strait of Gibraltar. In New Zealand, small groups of dusky dolphins (*Lagenorhynchus obscurus*) were observed to approach killer whales and briefly swim around them before departing moments later at high speed (Srinivasan and Markowitz 2009) in what may have been an example of predator inspection.

We suggest that at least some of the humpback responses to attacking MEKWs were clear examples of mobbing behavior. When Curio (1978) described mobbing in birds, he stated that they "assemble around a stationary or moving predator (potentially dangerous animal), change locations frequently, perform (mostly) stereotyped wing and/or tail movements and emit loud calls." This description is almost identical to several of the Appendix S2 accounts that describe humpback whales fluke- and flipper-slapping, charging behavior, and bellowing during their interactions with attacking MEKWs. Although predator mobbing typically involves a smaller, more agile prey species harassing a larger predator, there are also cases of larger species mobbing smaller (usually pack-hunting) predators. For example, adult African elephants (*Loxodonta africana*), due to their extreme size and aggressive communal defense, are normally safe from predators, but their one important predator—the lion (*Panthera leo*)—can prey on elephant calves (Joubert 2006). When elephant calves are threatened, herd members will respond by mobbing (and sometimes killing) their considerably smaller attackers (McComb *et al*. 2011). Also, although mobbing species usually detect their predators visually, auditory cues from a predator are also known to elicit strong mobbing responses, especially among taxa that rely heavily on acoustic signals, including birds (McPherson and Brown 1981, Chandler and Rose 1988), and possibly, as we suggest above, humpback whales.

Altruism in Humpback Whales?

Reports of mobbing behavior by cetaceans have been rare, and the 31 accounts presented here are more than all previous reports, for all other cetacean species combined, and the first for a baleen whale. Not only was this behavior far from rare, but it occurred in widely scattered locations, across a wide range of years, and this raises

[3]Personal communication from Eric Martin, Manhattan Beach Roundhouse Aquarium, PO Box 1, Manhattan Beach, CA 90266, January 2015.

some interesting questions. Why, for example, would humpback whales deliberately interfere with attacking killer whales, spending time and energy on a potentially injurious activity, especially when the killer whales were attacking other humpbacks that may not be related, or even more perplexingly, as in the majority of cases reported, when they were attacking other *species* of prey? Mobbing presumably provides individual and/or inclusive fitness benefits and would be expected to persist if these benefits outweigh the costs. Below, we consider three possible drivers of mobbing behavior in humpbacks: kin selection, reciprocity, and altruism, and we discuss their possible fitness benefits.

Kin selection occurs only among related individuals; for unrelated individuals, reciprocity can occur if there is a stable social unit (Trivers 1971, Connor and Norris 1982). Many cetaceans live in stable social groups that include related individuals, which could allow for either kin selection or reciprocity, and some odontocete species are famously known for coming to the aid of threatened or injured conspecifics, as well as other species, including humans (Caldwell and Caldwell 1966, Connor and Norris 1982, Whitehead and Rendell 2015). A concise definition of altruism is: "a behavior that increases the recipient's fitness at the cost of the performers" (de Waal 2008). To date, purported altruism among cetaceans has been attributed almost exclusively to smaller odontocetes (Caldwell and Caldwell 1966, Connor and Norris 1982, Wang *et al.* 2013), but has also been reported for killer whales (Albert, Prince of Monaco 1898, Mikhalev *et al.* 1981) and sperm whales (Pitman *et al.* 2001, Whitehead 2003). The few instances of possible altruistic behavior among baleen whales have mostly involved individuals responding to calves or other associates that had been harpooned by whalers or were otherwise injured (Caldwell and Caldwell 1966, Deakos *et al.* 2010).

Although direct evidence for kin selection or reciprocity is generally lacking for humpbacks, they have several features that could promote the development of either, including some semblance of social structure as well as site fidelity. Humpbacks are usually characterized as occurring in small, unstable groups (Connor 2000, Clapham 2009), but some studies have found relatively stable associations on the feeding grounds that span different seasons (Weinrich 1991, Ramp *et al.* 2010) or even decades (Pierszalowski 2014), which could foster reciprocity. Maternally mediated philopatry among humpbacks could also allow for either reciprocity or kin selection. As mentioned previously, humpback calves typically stay with their mothers for about 1 yr (occasionally 2 yr; Clapham and Mayo 1990)—long enough for the calf to complete an entire migration circuit and learn their mother's feeding and breeding grounds (Weinrich 1998). After weaning, calves often exhibit maternally directed site fidelity (Clapham 1996, Baker *et al.* 2013, Barendse *et al.* 2013), with annual rates of return to their mother's feeding area up to 90% (Clapham 2000, Pierszalowski 2014). In addition, Baker *et al*. (2013) reported evidence of strong natal fidelity by humpbacks to their breeding grounds, although several feeding stocks sometimes mix within a single breeding area. This consistent evidence for site fidelity on the feeding and breeding grounds (Darling and Jurasz 1983; Baker *et al.* 1990, 2013; Weinrich 1991, 1998; Calambokidis *et al.* 2001; Weinrich *et al.* 2006; Witteveen *et al.* 2011) increases the likelihood that individual humpbacks are more related to, or long-term associates with, neighboring conspecifics than they are to individuals in the population at large, thus laying a foundation for either kin selection or reciprocity.

More often though, humpbacks approached MEKWs that were attacking prey species that were clearly not humpbacks (*e.g.*, a gray whale calf with its mother, a seal

hauled out on an ice floe, a sunfish), and although the humpbacks faced little risk of serious injury, they also gained no obvious benefits for their time and energy spent. However, if the net effect for mobbing humpbacks was an increase in their individual or inclusive fitness through kin selection or reciprocity, then this behavior could persist even if it inadvertently benefitted other species sometimes. This would be an example of what Norris and Dohl (1980) described as "'spillover' of an intraspecific pattern into the domain of more distant [*i.e.*, interspecific] relationships." We suggest that humpbacks providing benefits to other potential prey species, even if unintentional, could be a focus of future research into possible genetic or cultural drivers of interspecific altruism.

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Supporting Information

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Appendix S1. Links to video footage of humpbacks interacting with killer whales attacking various species of prey; numbers in parentheses refer to event numbers in Appendix S2 and in Table 1. All links accessed on 18 May 2016.

Appendix S2. Accounts of humpbacks interacting with killer whales. We have tried to retain as much of the original wording of these accounts as possible; any subsequent rewording, clarification or comments are included in brackets. The Appendix is arranged chronologically by the species of prey targeted by killer whales and, for humpbacks, whether or not they were with calves. The event numbers correspond to numbers provided in the text and in Table 1; mammal-eating killer whales in the Northeast Pacific are referred to as either "transients" or "Bigg's" killer whales; for information on Antarctic killer whale types see Pitman (2011) and Durban *et al.* (2016).