

## Short Note

# Acoustic Predator–Prey Reaction: Gray Whales' (*Eschrichtius robustus*) Acoustic Response to Killer Whales (*Orcinus orca*)

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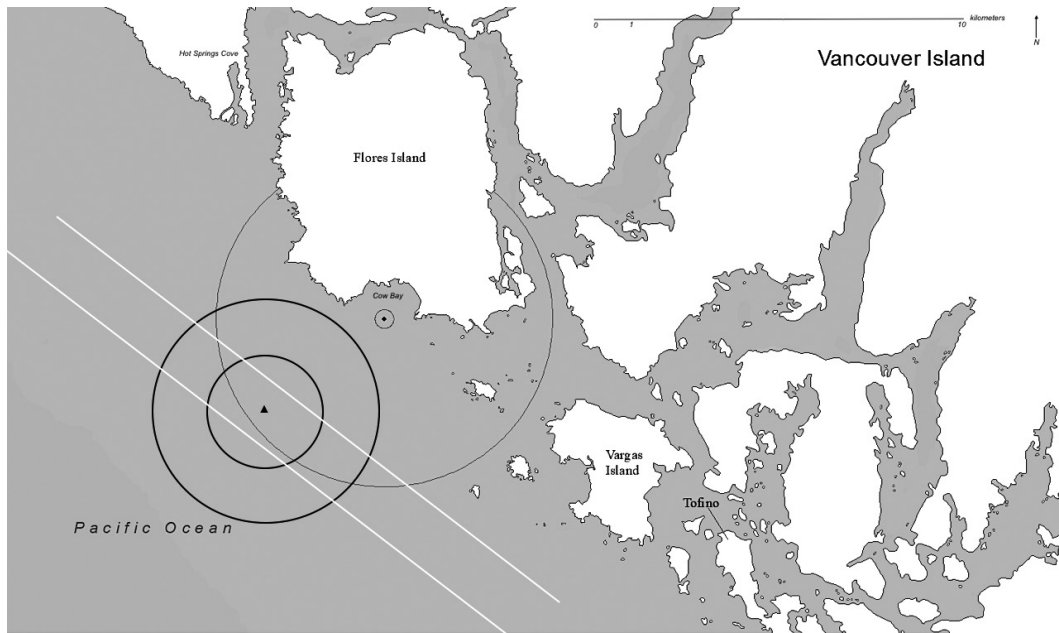
Killer whale (*Orcinus orca*) predation can have a significant effect on gray whale (*Eschrichtius robustus*) demographics and may be responsible for a large proportion of their natural mortality (Rice & Wolman, 1971; Ljungblad & Moore, 1983). Matkin & Durban (2011) state that in Unimak Pass, Alaska, mammal-eating Bigg's (formerly transient) killer whales remove between 5 to 50% of the calf production per year. Both fight and flight behaviours by gray whales have been noted in the presence of killer whales (Cummings & Thompson, 1971; Dahlheim, 1987; Ternullo & Black, 2002; Ford & Reeves, 2008); however, their acoustic response is less well-described. Playback experiments have shown that gray whales employ near to complete silence as a tactic in the presence of killer whale calls (Cummings & Thompson, 1971; Dahlheim, 1987; Dahlheim & Castellote, 2016). During presentation of recordings of natural and anthropogenic sounds to whales in San Ignacio breeding lagoons, the projection of Bigg's killer whale sounds resulted in the cessation in calling, an effect only replicated by the presence of an unfamiliar test tone (Dahlheim & Castellote, 2016). Furthermore, experiments conducted by Cummings & Thompson (1971) using the projection of killer whale "screams" to whales transiting Point Loma, San Diego, California (USA), during two consecutive southward migrations found just two gray whale phonations in recordings during playback periods ( $n = 36$ ), whereas 47 had been noted in control periods where random noise ( $n = 10$ ) or pure tones ( $n = 10$ ) were projected. In Monterey Bay, California, researchers who recorded migrating whales found they vocalised less, and were often silent, when transiting over deep ( $> 100$  m depth) water where the masking effects of ambient noise were reduced (Crane & Lashkari, 1996). It was speculated that reduced phonation in these cases affords lower detectability from killer whales. Silence was also noted during observations of killer

whales pursuing feeding gray whales in the northern Bering Sea (Ljungblad & Moore, 1983).

Herein, we report the response in gray whale calling during migration and foraging in the presence of vocalising killer whales. We compare calling rate and call structure by gray whales when killer whale vocalisations are heard to periods when they are absent. The responses to the acoustic presence of Bigg's (mammal-eating) and resident (fish-eating) killer whales are additionally compared. Following previous research, the expectation is for acoustic silence by gray whales, particularly in the presence of Bigg's killer whales.

Recordings were made by an Autonomous Multichannel Acoustic Recorder (AMAR G3; JASCO Applied Science, [www.jasco.com/amar-specifications](http://www.jasco.com/amar-specifications)) with GeoSpectrum M8E-132 calibrated omnidirectional hydrophone (sensitivity  $-165$  dB V/ $\mu$ Pa, effective bandwidth 5 Hz to 150 kHz, gain of 6 dB) in Clayoquot Sound on the west coast of Vancouver Island. Migration recordings come from deployments timed for two northward (N1: 21 February to 25 April 2015, 1,510.6 h; N2: 7 March to 5 May 2016, 1,422.7 h) and one southward (27 September 2016 to 25 January 2017, 2,920.3 h) migration, with the AMAR positioned in the migration corridor (49.21028,  $-126.24667$ ; Figure 1), approximately 5 nmi from Siwash Point on the coast of Flores Island and in 51 m water depth. Summer foraging recordings were made in two consecutive summers (F1: 6 May to 14 September 2015, 3,138.9 h; F2: 30 May to 5 September 2016, 2,351.8 h) in Cow Bay on the south coast of Flores Island (49.25629,  $-126.15928$ ; Figure 1). This is a productive feeding bay in Clayoquot Sound, which is also used for nursing and weaning by gray whale cow–calf pairs.

The recordings were examined for acoustic co-occurrence of killer whales, both Bigg's and resident ecotypes, and gray whales. The range of



**Figure 1.** Offshore location of AMAR deployment for north- and southward migration (triangle at 49.21028, -126.24667) with estimated detection range of gray whale (*Eschrichtius robustus*) moans for most of the recordings (80% of the time; 3 km) and furthest extent (10% of the time; 6 km) marked with black circles. Killer whale (*Orcinus orca*) detection is approximately 900 m 80% of the time and 9 km 10% of the time for this period (unpub. data). The white lines parallel to the coast represent the migration corridor (Burnham et al., 2018). Inshore location of summer recordings made in Cow Bay (circle at 49.25629, -126.15928), with detection range denoted with grey circles, whereby the range of detection of moan calls 90% of the time (500 m) and 10% of the time (9 km), is shown (unpub. data). For killer whales, range detection of calls is approximately 700 m 90% of the time and up to a maximum of 8 km 10% of the time.

likely detection of calls from both species was estimated using ambient noise measures and call characteristics, including frequencies and average source levels, using Holt et al. (2009) for killer whales and Guazzo et al. (2017) for gray whales. The gray whale detection range was presumed to encompass that of the killer whales due to its lower-frequency call range. Likely detection ranges were estimated to represent the majority of the recording time (80 to 90%) as well as the furthest reaches (10%), which represented periods where ambient noise was at its least. The detection range of gray whale moan calls for most of the migration recordings (80% of the time) were estimated to be within 3 km, with furthest extent (10% of the time) to be 6 km. Killer whale call detection range during these winter recordings was approximately 900 m most of the time (80%) and 9 km for 10% of the recordings. For summer recordings from Cow Bay, the gray whale detection range was reduced to 500 m (in 90% of recordings) with a maximum extent up to 9 km for moan calls. For the same period, the killer whale call detection range was estimated to be approximately 700 m for most of the recordings from

Cow Bay (90%) up to 8 km for 10% of the time (Whale Research Lab, unpub. data, 2015-2017; Burnham et al., 2016, 2018; Figure 1). Data were manually inspected by aural and visual analysis of spectrograms (256-point Hann window FFT with 50% overlap). In addition, the recordings were subjected to automated detection software that logged killer whale clicks and whistles (Mahoney et al., 2014; Mouy et al., 2015). A minimum of every fifth day (20%) of recordings was manually inspected for the presence of gray and killer whale calls. Additional recordings were scrutinised if killer whales were found to encompass the full encounter, sometimes several hours in length, and where killer whale calls were identified by the auto-detector. The total amount inspected for northward migration was 1,183.13 h or 39.12% pooling data from 2015 and 2016; southward migration was 604.5 h or 20.7%; and foraging periods were 5,065.31 h or 37.34%, again pooling 2015 and 2016.

Gray whale calls were identified and classified according to descriptions by Dahlheim (1987). Core call types include class 1 knocks, here distinguished by the presence of frequency

modulation (1a) or not (1b); class 2 sweeping tones; class 3 moans; and class 4 rumbles. Classes 5 and 6 represent acoustic byproducts of subsurface exhalations (Dahlheim, 1987) and, as such, are not considered further in this analysis. Also, calls described as possible “motherese” were included. The term *motherese* is used here for communicative calls thought to be made exclusively between a cow and her calf. These call types were originally noted in the breeding lagoons in Mexico and include class 7 complex tonal growls, class 8 grunt-like “uggs,” class 9 roar-like tones, class 10 grunt-like rumbles, and class 11 rattle sounds (Ollervides, 2001; Charles, 2011). The number of calls per call type per hour determined call rate. For each call, parameters of low and high frequency (Hz), extent of harmonics, frequency range, peak frequency (where most of the energy is focused), and length (s) were derived using Raven Pro Interactive Sound Analysis software. This allows for examination of changes in call structure, by type, in the presence of killer whales.

Killer whale presence was determined using the automated detector output and was confirmed manually as outlined in Burnham et al. (2016). Echolocation clicks were not used as a reliable indicator of killer whale presence, with encounters defined by the presence of whistles or other pulsed or tonal calls. Designation of calls to ecotype was done using reference to calling known to distinguish resident and Bigg’s killer whales (Ford, 1984, 1987, 1991).

A total of 3,455 h of data were manually analysed, of which 111 h showed killer whale acoustic presence (Tables 1 & 2). From this, a total of 16,611 calls were noted, with 2,384 of these in the presence of killer whale calling. During those periods of killer whale acoustic presence, the overall average gray whale call use and rate increased for class 1 knocks (class 1a, kw present  $\bar{x} = 0.68$  call/h, absent  $\bar{x} = 0.35$  call/h; 1b, kw present  $\bar{x} = 1.13$  calls/h, absent  $\bar{x} = 0.36$  call/h) and for class 3 moans (present  $\bar{x} = 4.83$  calls/h, absent  $\bar{x} = 3.33$  calls/h), and decreased for class 2 sweeping tones (present  $\bar{x} = 0.23$  call/h,

absent  $\bar{x} = 0.45$  call/h), predominantly upsweeps, though differences were seen for foraging and migratory periods when considered separately (Table 2). When considering the general response, the use of modulated knock calls increased significantly in the presence of killer whales (Mann-Whitney U,  $p = 0.033$ ) as did overall average call number/h (Mann-Whitney U,  $p = 0.039$ ). Knock calls (both classes 1a and 1b) were the most affected in playback experiments in breeding lagoons, with increased use and greater repetition in call structure when an acoustic stimulus was presented (Dahlheim, 1987; Dahlheim & Castellote, 2016). No significant differences in calling rate were seen when comparing calling in the acoustic presence of Bigg’s or resident killer whale ecotypes, with calling rate typically higher in the presence of the mammal-eaters. This trend does not agree with the results of playback studies (Cummings & Thompson, 1971; Dahlheim, 1987; Dahlheim & Castellote, 2016) or natural observations (Ljungblad & Moore, 1983).

The more useful comparison may be made between responses in different behavioural settings. Killer whales were heard most during the northward migration. These encounters also afforded a comparison between the Bigg’s and resident ecotype (Table 1). Significant decreases were heard in the call rate of upsweeps (Student’s  $t$  test,  $t(482.396) = -4.876$ ,  $p < 0.001$ ) and moans (Student’s  $t$  test,  $t(163.666) = -8.206$ ,  $p < 0.001$ ; Mann-Whitney U,  $p < 0.001$ ) when killer whales were present during northward migration. Moans are dominant during this time, exceeding 83% of calls, with knock and upsweep calls making up the rest of the vocal repertoire approximately equally (Burnham et al., 2018). Therefore, the decreased use of moan calls resulted in a significant change in overall calling rates by gray whales in the presence of killer whales (Mann-Whitney U,  $p < 0.001$ ; Table 2). There was no significant difference in acoustic reaction when comparing the mammal- and fish-eating killer whale ecotypes during this time, both instilling decreased calling from gray whales. This agrees with findings from previous studies (Cummings & Thompson, 1971; Crane & Lashkari, 1996).

**Table 1.** Acoustic presence of killer whales (in hours of recording) for each deployment period, with the number of encounters identified to ecotype shown. The hours of killer whale presence are from the total hours of recordings that were manually inspected: 765 h for north migration, 615 h for south migration, and 2,073 h for summer foraging. Killer whale calls were marked as present-absent only.

Behaviour	KW presence	Bigg’s	Resident	Unknown
Migration (north)	59	15	13	31
Migration (south)	24	--	--	24
Foraging	24	--	4	24

**Table 2.** The number of calls per call type that were heard (total) when killer whales were absent from the recordings (KW absent) and when they were acoustically present (KW present) during migration (north- and southward) and summer foraging. For summer recordings, the use of “motherese” call types were also quantified. The calls were identified either as transient or resident killer whales when possible. Those that were unidentified are represented in the KW present count. Mean calling rates (call/h) are also shown to compare calling in acoustic presence or absence of killer whales.

	Call class (rate)	Northward migration	Southward migration	Summer	“Motherese” call classes	Call number (rate)	
1a	Total	982	18	432	7	Total	47
	KW absent	912 (1.19/h)	17 (0.03/h)	245 (0.12/h)		KW absent	46 (0.02/h)
	KW present	70 (1.29/h)	1 (0.04/h)	187(0.18/h)		KW present	1 (0.04/h)
	Transient	19	0	0		Transient	0
	Resident	0	0	0		Resident	0
1b	Total	46	22	1,269	8	Total	163
	KW absent	43 (0.06/h)	22 (0.04/h)	1,147		KW absent	156 (0.08/h)
	KW present	3 (0.05/h)	0 (0.00/h)	122 (4.36/h)		KW present	7 (0.04/h)
	Transient	2	0	0		Transient	0
	Resident	0	0	0		Resident	0
2	Total	893	26	611	9	Total	108
	KW absent	876 (1.24/h)	21 (0.04/h)	607 (0.30/h)		KW absent	62 (0.03/h)
	KW present	17 (0.29/h)	5 (0.21/h)	4 (0.14/h)		KW present	46 (0.02/h)
	Transient	10	0	0		Transient	0
	Resident	0	0	0		Resident	0
3	Total	6,276	4,518	895	10	Total	80
	KW absent	6,159 (8.70/h)	4,120 (6.97/h)	869 (0.42/h)		KW absent	70 (0.03/h)
	KW present	117 (1.98/h)	398 (16.58/h)	26 (0.75/h)		KW present	10 (0.01/h)
	Transient	18	0	0		Transient	0
	Resident	29	0	0		Resident	0
4	Total	226	0	4			
	KW absent	224 (0.32/h)	0 (0.00/h)	4 (0.00/h)			
	KW present	2 (0.03/h)	0 (0.00/h)	0 (0.00/h)			
	Transient	0	0	0			
	Resident	0	0	0			

Generally, the opposite acoustic reaction was seen for southward migration, with a significant increase in calling rate (Mann-Whitney U,  $p = 0.009$ ) and the use of class 3 moan calls (Mann-Whitney U,  $p = 0.023$ ) in the acoustic presence of killer whales (Table 2). The changes in use of moan calls dominated the overall trend, being the main call (> 98%; Burnham et al., 2018) during this period. However, all other call types except for non-modulated knock calls (class 1b) also increased in rate. The comparison between ecotypes is not possible for southward migration as killer whale vocalisations were not positively identified to an ecotype (Tables 1 & 2).

The call structure of moan calls and upsweep class 2 calls were altered significantly in at least one parameter when produced in the acoustic presence of killer whales. For both call types, on

both north- and southward migration, the lowest frequency harmonic of the call was altered in conjunction with either the frequency range or focal formant of the call (Table 3). There is little employment of class 1b on migration in the presence of killer whales, with no calls in class 1a or 4 during southward migration when killer whales were heard.

The difference in call strategies between north- and southward migration may represent the different physiological state the whales are in and their vulnerability to predation. During the northward migration, gray whales are in a negative energy state and, thus, a strategy of reduced calling may be an anti-predation tactic while also avoiding energy use. The presence of vulnerable calves during this time may also strengthen this anti-predator reaction compared to other periods. During southward

**Table 3.** Changes of gray whale call parameters by call type in the presence of killer whale calls for north- and southward migration using a  $t$  test.  $t$  and  $p$  values are shown, with values in italics to highlight significance. Recordings were made approximately 5 nmi offshore from Flores Island, British Columbia. The number of calls per type in the presence (p) and absence (a) of killer whales are given in parentheses as (p, a).

Call class		Northward migration		Southward migration		
		$t$	$p$	$t$	$p$	
1a (70, 912)	Low freq.	-1.150	0.250	(1, 17)		
	High freq.	-0.861	0.392			
	Peak freq.	-1.189	0.238			
	Length	-2.798	<i>0.006</i>			
	Freq. range	-0.390	0.697			
1b (3, 43)	Low freq.	(0, 22)				
	High freq.					
	Peak Freq.					
	Length					
	Freq. range					
2 (17, 876)	Low freq.	-2.490	<i>0.013</i>	(5, 21)	5.307	< <i>0.001</i>
	High freq.	-1.718	0.091		5.424	< <i>0.001</i>
	Peak freq.	-2.096	<i>0.036</i>		1.554	0.133
	Length	-0.964	0.335		-0.271	0.794
	Freq. range	-0.325	0.745		0.061	0.952
3 (117, 6159)	Low freq.	2.256	<i>0.025</i>	(398, 4120)	-3.571	< <i>0.001</i>
	High freq.	3.157	<i>0.002</i>		12.383	< <i>0.001</i>
	Peak freq.	4.181	< <i>0.001</i>		-2.577	< <i>0.007</i>
	Length	2.132	<i>0.033</i>		0.561	0.104
	Freq. range	1.446	0.148		15.330	< <i>0.001</i>
4 (2, 224)	Low freq.	-1.386	0.184	(0, 0)		
	High freq.	-2.561	<i>0.020</i>			
	Peak freq.	-0.901	0.401			
	Length	1.571	0.180			
	Freq. range	-1.316	0.206			

migration, the use of moan calls increases significantly. The frequency extents and range of the harmonics are significantly altered (Table 3). This may reflect the use of alarm or warning calls as seen in other animals (Zuberbühler, 2009; Gill & Bierema, 2013; Suzuki, 2013) or represent information transfer of the type or proximity of threat, a phenomenon also well described for other species (Leavesley & Magrath, 2005; Templeton et al., 2005; Zuberbühler, 2009; Gill & Bierema, 2013; Suzuki, 2013; Cunningham & Magrath, 2017).

During foraging, calling behaviours differ from migration periods and have a higher use of within- and between-group vocalisation types such as classes 1 and 2 (Moore & Ljungbald, 1984; Whale Research Lab, unpub. data, 2015–2017). The presence of killer whales, however, did not instill a notable difference in rate or call type. While core call types were increased and “motherese” call types were decreased, none were statistically significant. The structure of modulated knock calls

showed significant changes in the presence of killer whales, with altered frequency ranges for call class 2, 3, 8, and 9 calls, often in conjunction with an adjusted lowest frequency extent (Table 4). There were no call class 4 or 7 calls heard when killer whales were acoustically present. “Motherese” calls were focused on in the recordings from Cow Bay (Table 2), showing decreased rate of use in the presence of potential predator threat. During the winter migration recordings, very few “motherese” calls were heard (north,  $n = 63$ ; south,  $n = 5$ ), with no calls from classes 7 through 11 heard when killer whale calls were present in the recordings.

Increased calling during foraging periods does not agree with previous studies; however, this is the first time a dedicated comparison between vocal behaviours in the acoustic presence of killer whales has been made, as well as the first study to consider the use of “motherese” calls during these times. The decreased use of “motherese,” and

**Table 4.** Changes of gray whale call parameters by call type in the presence of killer whale calls during summer foraging using a  $t$  test.  $t$  and  $p$  values are shown, with values in italics to highlight significance. Recordings were made in Cow Bay on the southern coast of Flores Island, British Columbia. The number of calls per type in the presence (p) and absence (a) of killer whales are given in parentheses as (p, a).

		Call class – Core		Call class – “Motherese”		
		$t$	$p$		$t$	$p$
1a (187, 245)	Low freq.	-4.754	< 0.001	7		
	High freq.	-3.206	0.002	(1, 46)		
	Peak freq.	-6.479	< 0.001			
	Length	3.623	< 0.001			
	Freq. range	-2.735	0.007			
1b (122, 1,147)	Low freq.	1.770	0.077	8	-6.000	< 0.001
	High freq.	0.689	0.491	(7, 156)	0.171	0.867
	Peak Freq.	1.153	0.250		-1.547	0.123
	Length	1.710	0.088		-0.353	0.724
	Freq. range	-0.704	0.501		7.237	< 0.001
2 (4, 607)	Low freq.	0.875	0.446	9	-3.997	< 0.001
	High freq.	-0.939	0.348	(46, 62)	4.312	< 0.001
	Peak freq.	1.052	0.293		0.138	0.890
	Length	0.026	0.979		-0.886	0.377
	Freq. range	-21.777	< 0.001		6.211	< 0.001
3 (26, 869)	Low freq.	2.239	0.025	10	0.538	0.602
	High freq.	3.667	< 0.001	(10, 70)	-0.883	0.378
	Peak freq.	-0.654	0.521		0.632	0.528
	Length	-3.485	0.003		0.117	0.907
	Freq. range	3.412	0.001		-1.185	0.237
4 (0, 4)						



the shift of calls to lower frequencies and shorter lengths, suggests mothers and young become quiet in the presence of killer whales. The areas that cow-calf pairs frequent in Cow Bay may add to their acoustic hiding tactic, often staying close to breaking surf or hidden in kelp beds (Whale Research Lab, unpub. data, 1998-2018; Ford & Reeves, 2008; Wladichuk et al., 2010).

Resident fish-eating killer whales are strongly tied to the seasonal movements of their salmonid prey (Nichol & Shackleton, 1996), with their overwinter presence greater than expected from previous studies (also see Burnham et al., 2016). This ecotype frequently uses echolocation and often communicates within and between hunting groups (Ford 1987, 1991; Ford & Ellis, 1999). Conversely, mammal-eating Bigg's killer whales hunt with little to no calling. Vocalising is largely limited to surface-active and post-feeding behaviours (Ford, 1984; Morton, 1990; Guinet, 1992; Barrett-Lennard et al., 1996; Deecke, 2003; Deecke et al., 2005). The differences in prey preference and acoustic use between ecotypes might be expected to instill a different acoustic reaction in gray whales, but this was not the case where the comparison was possible during northward migration. The reaction to reduce calling may be precautionary, despite the killer whale not being a predatory threat. Taking a precautionary approach has been suggested by Crane & Lashkari (1996), who proposed the use of silence in areas where the presence of killer whales is expected to be high.

The continued use of calling in all cases demonstrates the importance of shared acoustic information to gray whales in each period of their life history. It may be that responses in this study balanced the cost and benefit of calling (Lima & Dill, 1990) and sharing information with conspecifics, especially if modifications of call parameters are required (Bradbury & Vehrencamp, 2011). It may also be that the calls used, and the modifications employed in the acoustic presence of killer whales, placed the acoustic energy of calls made below the frequency ranges where killer whales' hearing is most sensitive (Hall & Johnson, 1972; Szymanski et al., 1999; Miller, 2006; Branstetter et al., 2017). If this is true, the use of lower-frequency calls and sweeping tones, focused between 20 to 200 Hz, should be favoured over the knock-like calls of class 1 that have a wider and typically higher-frequency range (Dahlheim et al., 1984; Dahlheim, 1987; Burnham et al., 2018). However, these call types were reduced in the presence of killer whales, significantly so during the northward migration. The increased use of knock calls may indicate their use as an alert call, intended for conspecifics in closer range, though further work is needed to better tie call use and function. In this study, killer whale vocalisation harmonics were

present in spectrograms down to approximately 150 Hz, suggesting a significant overlap in the hearing and vocalising range of gray whales and killer whales.

Modifications in calling rate and call structure show plasticity in gray whale acoustic behaviours. Alterations in call parameters may be a method for gray whales to encode information through graded variation—perhaps used in concert with the call modification of increased note repetition within class 1 knock calls found in the playback study of Dahlheim & Castellote (2016). The difference in responses between the observations of this study and the experimental playback studies could be the context in which the recordings are made. Also, the sensitivity to a stimulus could vary due to an individual's age, reproductive status, and prior experience. Vulnerability of individuals to predation may be higher in breeding lagoons or when migrating with calves, or in areas of high presence of killer whales (e.g., Monterey Canyon [Goley & Straley, 1994; Crane & Lashkari, 1996] or Unimak Pass, Alaska [Barrett-Lennard et al., 2011; Matkin & Durban, 2011]). In these cases, silence may be the safest strategy.

The ability of killer whales to shape the behaviours of their prey has been well-documented, with changes in both swimming and calling behaviours noted (e.g., Fish & Vania, 1971; Dahlheim, 1987; Jefferson et al., 1991; Crane, 1992; Goley & Straley, 1994; Crane & Lashkari, 1996; Ford & Reeves, 2008; Baird, 2011; Matkin & Durban, 2011). This study adds to these examples; however, much work still remains to be done to understand the perception of predation risk over the life history stages of gray whales and how acoustics play into the anti-predator strategy and response.

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