Aquatic Mammals 2025, *51*(5), 38-55, DOI https://doi.org/10.1578/AM.51.5.2025.38

Killer Whale (*Orcinus orca*) Acoustic Responses to Naval Sonar

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Abstract

Regulators and navies need to estimate the effects of underwater noise, such as naval sonar, on cetaceans. In this study, we investigated acoustic responses of four killer whale (*Orcinus orca*) groups exposed to naval sonar in experiments that contained one or three exposure sessions. Using DTAGs, we compared group acoustic behaviour before, during, and after exposure sessions. Groups feeding and acoustically active prior to exposure ($n = 2$) significantly changed call rate and call overlap, and increased the maximum frequency of their calls during 1 to 2 kHz or 6 to 7 kHz sonar exposures. One group that switched from feeding to travelling prior to exposure also changed its call rate. In one session, there was a noticeable increase in call rate timed closely to sonar transmissions, with high call overlap and the production of highly frequency-modulated calls. During the remaining two sessions in which whales were calling but not feeding prior to exposure, there were no significant changes in calling behaviour, although high-frequency whistles were recorded in one case when a calf briefly separated from its group. The results from these case studies indicate that vocal responses, concurrent with changes from feeding to travel, reflect changes in the animals' behavioural state, though, as of yet, undetermined effects of behavioural context likely influence acoustic responses to sonar. Further data will be needed to advance our understanding of the drivers behind vocal adjustments in different noise and behavioural contexts.

Key Words: behavioural response, call rate, call overlap, noise, high-frequency whistles, killer whale, *Orcinus orca*

Introduction

Concern has increased over the effects of underwater noise on cetaceans since anthropogenic activities, particularly military sonar exercises, have been linked to deleterious and sometimes lethal effects such as mass strandings of beaked whales (e.g., Frantzis, 1998; Balcomb & Claridge, 2001; National Marine Fisheries Service [NMFS], 2005; D'Amico et al., 2009) and habitat avoidance by killer whales (*Orcinus orca*; Kuningas et al., 2013). Such concerns gave rise to behavioural response studies that may be fully observational or include controlled exposure experiments to determine responses to short-term sonar exposures (e.g., Miller et al., 2012; Southall et al., 2016, 2024; Harris et al., 2017). The nature, magnitude, and type of behavioural responses observed in such studies appears to often be influenced by the behavioural and environmental context of exposed individuals (Ellison et al., 2012; Miller et al., 2012)—for example, observed responses may include interruption of functional behaviours such as feeding (Goldbogen et al., 2013; Sivle et al., 2016), changes in diving (Tyack et al., 2011; Sivle et al., 2012; DeRuiter et al., 2013b; Stimpert et al., 2014; Miller et al., 2015; Wensveen et al., 2015), changes in horizontal movement to avoid the sound source (Antunes et al., 2014; Miller et al., 2015; Wensveen et al., 2017, 2019), and changes in acoustic behaviour (e.g., Miller et al., 2000, 2012; Tyack et al., 2011; Melcón et al., 2012).

Changes in acoustic behaviour as a response to sonar include both increases and decreases in sound production rates. For example, odontocetes have been reported to cease click production—either associated with cessation of echolocation-based feeding (Isojunno et al., 2016) or as an adapted acoustic crypsis response, possibly to avoid detection by an external threat (Tyack et al., 2011; Wensveen et al., 2019). On the other hand, at least some social delphinids were found to increase sound production rates (Rendell & Gordon, 1999; DeRuiter et al., 2013a) and/or produce sounds resembling the sonar stimuli (DeRuiter et al., 2013a; Alves et al., 2014; Casey et al., 2024).

Public concern over the effects of sonar on killer whales arose when visual observations suggested responses to navy sonar exercises (WWF Norway, 2001; NMFS, 2005). A retrospective analysis of sighting data during sonar exercises in Norway suggested that killer whales abandoned the area when prey availability was low but likely not when it was high, supporting a role of environmental context in responses to sonar signals in this species (Kuningas et al., 2013). Controlled exposure experiments showed prolonged avoidance responses of killer whales away from a sonar source but with high inter- and intra-individual variation, suggesting response thresholds vary with a range of contextual and individual-specific variables (Miller et al., 2014). Given their social and vocal nature, we might expect killer whale behavioural responses to external stimuli to be reflected in changes in acoustic signalling as shown for other social delphinids (e.g., DeRuiter et al., 2013a). For example, we might hypothesise that calling rates would increase as part of the social component of group-level avoidance (Miller et al., 2014) or, alternatively, that calling decreases after cessation of foraging due to lack of functional benefit of calling while travelling as a group (Samarra & Miller, 2015).

Killer whales produce sounds that are generally divided into clicks, whistles, and burst-pulsed calls (Ford, 1989). Their clicks are short, broadband pulses primarily used for echolocation (Barrett-Lennard et al., 1996; Au et al., 2004; Simon et al., 2007b). Killer whale whistles are tonal sounds produced during socialising, presumably for short-range communication (Thomsen et al., 2001, 2002). Although most whistles have varied frequency contours, some are stereotyped and shared by different groups, providing a community-level means of recognition (Riesch et al., 2006; Riesch & Deecke, 2011). Several, but not all, populations also produce high-frequency whistles, generally with the entire frequency contour above 20 kHz (Samarra et al., 2010; Filatova et al., 2012; Simonis et al., 2012; Trickey et al., 2014; Andriolo et al., 2015), but the context of their use remains unknown. The burst-pulsed calls (hereafter referred to as calls) of killer whales are the most common social sounds produced (Ford, 1989) and consist of a series of pulses, which are emitted at high rates such that they sound and appear tonal in spectrogram analyses (Watkins, 1967). Calls have stereotyped frequency contours, allowing for their division into discrete categories (Ford, 1989). Calls that cannot be clearly arranged into discrete categories and are not repetitive are termed "variable," while "aberrant" calls represent versions of a stereotyped call with a highly modified or distorted structure (Ford, 1989).

Stable social units produce unique repertoires of discrete calls suggesting that calls function in group recognition and to maintain pod cohesion (Ford, 1991; Strager, 1995; Yurk et al., 2002; Filatova et al., 2007). On the other hand, little is known about the function of variable and aberrant calls in killer whales (Ford, 1989; Rehn et al., 2007). Discrete call types are generally not exclusively associated with specific behavioural categories (but see Saulitis et al., 2005; Simon et al., 2006); however, call type usage changes depending on behavioural context (e.g., different behavioural categories: Ford, 1989; Saulitis et al., 2005; Simon et al., 2007a; different feeding behaviours: Van Opzeeland et al., 2005; following calf birth: Weiß et al., 2006; mixed-group encounters: Weiß et al., 2007; Filatova et al., 2013). Similarly, the production of variable and aberrant calls increases in multi-group social encounters (Weiß et al., 2007). During these multi-group encounters, the number of overlapped calls can also increase—to the point of impairing call type identification (Ford, 1989). During high arousal and excited contexts, which often involve apparent altercations and rough play, discrete call types tend to be of shorter duration and higher pitch than normal (Ford, 1989). Ford (1989) suggests that variations in emotional state of the sound-producing whale result in such structural changes in discrete calls. "Excitement" calls, characterized by a high number of frequency modulations, are also commonly observed in such contexts (Ford, 1989). Thus, killer whales clearly modify their vocal behaviour as a response to different social, behavioural, and environmental contexts.

Herein, we use data collected during Phase 1 (between 2006 and 2009) of the 3S Behavioural Response Study (Miller et al., 2011) to investigate killer whale vocal behaviour before, during, and after controlled sonar exposure experiments. Expert scoring of responses of killer whales to these sonar exposures revealed numerous changes in behaviour, including avoidance movement responses, changes in dive profile and group spacing/synchrony, cessation of foraging, and mother–calf separation (Miller et al., 2012). Changes in vocal behaviour were also scored but not quantified (Miller et al., 2012). Informed by the expert scoring process, our goal in this study was to quantify if and how vocal behaviour changed when killer whales were exposed to sonar in those experiments, specifically focusing on (1) call rate and overlap, (2) call frequency and duration, and (3) high-frequency whistle production. We focused on these metrics and signal types deliberately due to the preliminary findings of the expert scoring process and the knowledge that killer whales change at least some of these vocal features in response to different contexts.

Methods

Data Collection and Experiments

The data analysed herein were collected as part of the 3S Behavioural Response Study in which controlled exposure experiments were conducted with killer whales in 2006, 2008, and 2009 in Vestfjord and off Vesterålen, northern Norway (Miller et al., 2011). During these experiments, killer whales were tagged with suction cup-attached digital archival tags (DTAGs; Johnson & Tyack, 2003), containing two hydrophones to record sound at a sampling rate of 96 or 192 kHz, a pressure sensor, and a three-axis magnetometer and accelerometer that provided underwater movement data (for further methodological details, see Miller et al., 2011). Each tag record identifier was formatted as "ooYY_XXXz" for which "oo" stands for *Orcinus orca*, "YY" stands for the year of the deployment (e.g., 06 represents 2006), "XXX" represents the Julian day of the year when the deployment started, and "z" represents the deployment order of that day, with "a" and "s" representing the first deployments of the day.

During experimental exposure sessions, killer whales were exposed to a sequence of 1 to 2 kHz hyperbolic upsweep sonar signals, 6 to 7 kHz hyperbolic upsweep signals, or 2 to 1 kHz hyperbolic downsweep signals transmitted by a towed sound source. Due to the short duration of some of the tag deployments, the entire period from tag attachment to start of the first exposure session was considered baseline behaviour. Each individual sonar pulse had a duration of 1 s and was transmitted every 20 s. The exposure periods started with a 10-min ramp-up period during which the source level was increased from 152 dB re 1 µPa m (1 to 2 kHz sessions) or 158 dB re 1 µPa m (6 to 7 kHz sessions) to the maximum level of 214 dB re 1 µPa m (1 to 2 kHz sessions) or 199 dB re 1 µPa m (6 to 7 kHz sessions) (for further details, see Miller et al., 2011). In 2006 only, the sonar pulses were transmitted every 10 s during the ramp-up period. Before ramp-up, the source vessel adjusted its course to approach the tagged killer whale until the source–whale distance was 1 km, after which point the course of the source vessel was fixed. Transmission ceased 5 min after passing the closest point of approach to the whale, or if an early shutdown was triggered by very close encounters (< 100 m). This protocol resulted in exposure sessions (each including a ramp-up and a full-power period) that lasted 30 to 59 min. Two experiments contained just one exposure session, and two contained three sonar exposure sessions (Table 1), with a minimum of 1 h between sessions.

Data Analysis

The acoustic record of each tag was aurally and visually inspected using *Adobe Audition*, Version 2.0 (Blackmann-Harris window; FFT = 2,048 or 4,096 for 96 and 192 kHz sampling rates, respectively; 90% overlap), and the beginning and end time of each call detected was marked. Each call was assigned a quality from 1 (poor) to 3 (high). High-quality calls were those with a high perceived signal-to-noise ratio, had clear fundamental frequency contours, and were clearly audible. High-quality calls were assumed to be produced by the tagged killer whale or by whales in its immediate vicinity and were subsequently used for further analyses. This may introduce bias towards higher source level calls; however, this criterion was used to ensure that analysed sounds were more likely to be produced by the tagged whale or a nearby whale. All high-quality, high-frequency whistles detected were also marked and used for subsequent analyses.

We first used a before-during-after design to test for vocal responses to the sonar. We selected three metrics: (1) *call rate*, defined as the number of high-quality calls per minute; (2) *minimum number of overlapped calls per minute*, which included high-quality calls with any of their duration overlapped by at least one other call (of medium or high quality); and (3) *minimum number of highly overlapped calls per minute*, which included high-quality calls with 50% or more of their duration overlapped by at least one other call (of medium or high quality). When calls overlapped, we marked as many separate calls as possible; however, as it was not always possible to distinguish all overlapped calls, our measure is a minimum estimate. For each exposure session, these three metrics were calculated in 1-min bins during exposure and for periods of the same duration immediately before and after the exposure, hereafter referred to as the pre- and post-exposure phases, respectively. Due to the short duration of some tag deployments, this meant that the period considered as post-exposure of one session could overlap with the pre-exposure of the next session. To test for differences in call rate, minimum number of overlapped calls per minute, and

Table 1. Summary of all tag deployments on killer whales (*Orcinus orca*) with controlled exposure experiments used in this study. Note that the tag record identifier has the format "ooYY_XXXz" for which "oo" stands for *Orcinus orca*, "YY" stands for the year of the deployment (e.g., 06 represents 2006), "XXX" represents the Julian day of the year when the deployment started, and "z" represents the deployment order of that day, with "a" or "s" representing the first deployment. Exposure sessions are presented in consecutive order. Note that two exposure sessions did not have a post-exposure period due to early tag detachment from the whale. The tags with exposure sessions without post-exposure were marked with a †. Tag on and tag off times are given in UTC time. For each exposure session, the duration (in minutes and seconds [mm:ss]), the sonar signal type (as 1 to 2 kHz [upsweep], 6 to 7 kHz [upsweep], or 2 to 1 kHz [downsweep]), and the number of sonar pings transmitted (see text for further details on the sonar signals used) are indicated. The total number of calls and high-frequency whistles across the entire duration of each deployment are also indicated, with details on how many of those signals were detected in each phase of the exposure in brackets (pre-exposure [pre]; during [dur]; post-exposure [post]). For those exposure sessions without post-exposure data, the number of calls and high-frequency (hf) whistles are marked as "NA."

Date (d/mo/y)	Tag ID	Tag on/ tag off time (h:min)	Deployment duration (h)	Age/ sex class	Sonar exposure start/ end time (h:min)	Sonar exposure duration (min:s) (type; no. of pings)	No. calls (pre; dur; post)	No. hf whistles (pre; dur; post)
13/11/2006	oo06_317s†	13:32/14:32	1.2	Adult male	14:10/14:43	33:01 (1-2 kHz; 129)	16 (10; 0; NA)	21 (21; 0; NA)
23/11/2006	oo06_327s	12:42/18:07	5.4	Adult female	13:36/14:10	34:01 (6-7 kHz; 129)	346 (70; 93; 0)	0 (0; 0; 0)
28/5/2008	oo08_149a	09:01/00:44	15.7	Adult female	12:48/13:40	52:41 (6-7 kHz; 156)	94 (1; 13; 0)	22 (4; 0; 0)
					14:56/15:46	50:01 (1-2 kHz; 151)	(0; 0; 0)	(0; 0; 0)
					22:38/23:08	30:21 (6-7 kHz; 91)	(9; 12; 19)	(0; 11; 7)
24/5/2009	oo09_144a†	09:02/21:50	11.9	Adult male	14:13/14:47	34:01 (1-2 kHz; 103)	838 (95; 368; 0)	109 (29; 0; 0)
					16:15/17:14	59:01 (6-7 kHz; 178)	(0; 0; 0)	(0; 0; 0)
					21:13/21:51	38:01 (2-1 kHz; 115)	(0; 0; NA)	(0; 0; NA)

minimum number of highly overlapped calls per minute across the different phases (pre-exposure, exposure, and post-exposure), we used non-parametric Kruskal-Wallis tests. For exposures with more than two phases (i.e., including pre-, during, and post-exposure), significant differences across experimental phases were then tested with Dunn's *post-hoc* tests to determine which pairwise comparisons differed.

Subsequent to these tests, we conducted in-depth analyses of the exposure sessions for which differences in calling behaviour were found (oo06_327s/6 to 7 kHz and oo09_144a/1 to 2 kHz upsweep) to understand if such differences were accompanied by changes in the characteristics of the calls produced. First, spectrograms of all detected high-quality calls produced in the pre-exposure, exposure, or post-exposure phases were generated in *MATLAB* (spectrogram parameters: FFT = 2,048 or 4,096 for 96 and 192 kHz sampling rates, respectively; overlap = 87.5%; window function = Hann; frequency resolution = 46.9 Hz; time resolution = 2.67 ms). Measurements of start, mid, end, minimum, and maximum frequency of the fundamental frequency contour, which corresponded to the first harmonic, as well as duration, were manually

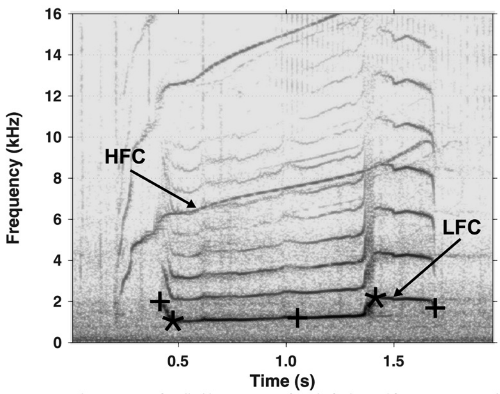


Figure 1. Example spectrogram of a call with measurements from the fundamental frequency contour at the start, mid, and end frequency (crosses), and at the minimum and maximum frequency points (asterisks). Measurements were only made from the low-frequency component (LFC) of calls, even in the case of calls that also had an overlapping high-frequency component (HFC).

extracted from the spectrograms (Figure 1). Only the low-frequency component was measured as high-frequency components do not consistently appear due to their higher directionality (Miller, 2002). Call frequency and time characteristics were compared between the pre-exposure and exposure periods using Mann-Whitney U-tests, with a Bonferroni correction for multiple comparisons.

An additional 36.7 h of recordings from nine DTAGs deployed on killer whales between 2005 and 2009 (for details, see Samarra & Miller, 2015), during which sonar experiments were not conducted, were used to establish a baseline catalogue of killer whale discrete call types recorded in the study area. Calls were classified into types by aural and visual inspection, and were matched whenever possible to existing call types described in the literature for Norwegian killer whales (Strager, 1993; Van Opzeeland et al., 2005; Shapiro, 2008). In cases where calls did not fit into any of the previously determined types described in the literature, a new call type was assigned if at least three examples of that type existed in the dataset (for details of call classification and types assigned, see Selbmann et al., 2021). Otherwise, the calls were classified as variable or aberrant. Aberrant calls represented versions of a stereotyped call with a highly modified or distorted structure such as those with added frequency modulations. Variable calls could not be separated into clearly defined structural categories. Call types and subtypes produced during pre-exposure were compared to those produced during exposure to investigate changes in calling behaviour. During data analysis, the production of a set of highly frequency-modulated calls (≥ 5 inflection points; i.e., a change from positive to negative or negative to positive slope of the contour) in one exposure session in 2009 (oo09_144/1 to 2 kHz upsweep) was noticed in apparent close synchronization to the sonar pulses. We investigated this vocal response specifically by measuring the interval between the start of sonar transmission and the start of each highly frequency-modulated call in this particular session.

The rate of high-frequency whistle production was also calculated before, during, and after sonar exposure, and differences across the different phases (pre-exposure, exposure, and post-exposure) were tested using Kruskal-Wallis tests. All statistical tests were performed using *R*, Version 3.2.2 (The R Foundation for Statistical Computing, Vienna, Austria; https://www.R-project.org), applying Bonferroni corrections to adjust the significance level to account for multiple comparisons.

Results

A total of eight exposure sessions were conducted on four tagged killer whale groups (Table 1), resulting in approximately 34 h of acoustic recordings. Tag oo06_317s was deployed on an adult male that was part of a group of 50 to 80 whales that were feeding on herring. The group stopped feeding soon after tag attachment and switched to travelling behaviour. Tag oo06_327s was deployed on an adult female, often associated with a small animal, in a group of 70 to 80 whales feeding on herring, including all age/sex classes. Both deployments, oo06_317s and oo06_327s, were conducted in the winter herring grounds when killer whales can be found in large aggregations. Tags oo08_149a and oo09_144a were deployed in spring, in inshore and offshore waters, respectively. Tag oo08_149a was deployed on an adult female in a group of seven animals (one newborn calf, two juveniles, two males, and two females) that were reported to possibly have predated on a minke whale (*Balaenoptera acutorostrata*) prior to tagging, although this was not confirmed. In the pre-exposure period, the whales milled in shallow water near the mouth of a fjord. Tag oo09_144a was deployed on an adult male in a group of 15 killer whales, including calves, that were feeding presumably on herring during pre-exposure (for more details on all deployments, see Miller et al., 2011).

A total of 1,294 high-quality calls were extracted from across the entire duration of all deployments; however, call production differed substantially across deployments, with oo06_327s and oo09_144a accounting for most calls recorded (Table 1). These vocally active deployments were on killer whales that were feeding prior to the first exposure session (Miller et al., 2011). Similarly, high-frequency whistle production varied between tagged individuals, with oo09_144a also accounting for most high-frequency whistles recorded and oo06_327s registering no such whistles (Table 1). All exposure sessions included pre-, during, and post-exposure data except the exposure of tag oo06_317s and the third exposure of tag oo09_144a, which lacked post-exposure data due to premature detachment of the tags.

Changes in Call Production During Experimental Sonar Exposures

Call rate changed significantly during the first sonar exposure session of deployments oo06_317s (1 to 2 kHz upsweep: $\chi^2 = 5.32$, $p = 0.02$), oo06_327s (6 to 7 kHz: $\chi^2 = 19.65$, $p < 0.001$), and oo09_144a (1 to 2 kHz upsweep: $\chi^2 = 23.80$, $p < 0.001$) (Table 2; Figure 2). On the other hand, call rate did not change significantly in response to sonar in deployment oo08_149a during the first ($\chi^2 = 5.41$; $p = 0.07$) and third ($\chi^2 = 0.10$; $p = 0.94$) exposures to 6 to 7 kHz (Table 2; Figure 2). During the second session of deployment oo08_149a, when the killer whales were exposed to 1 to 2 kHz sonar, the whales were silent throughout all phases.

In deployment oo06_317s, the killer whales did not produce any calls during exposure. However, their call rate was very low before exposure as well, with a total of 10 calls detected (Table 2). There was no post-exposure data in this deployment due to premature detachment of the tag. Therefore, no further analyses were conducted on this deployment. In the first exposure of deployment oo08_149a, the whales did not produce any calls during the post-exposure (Table 2), but this result was not statistically significant.

In deployment oo06_327s, the call rate recorded on the tag was not significantly different during exposure to 6 to 7 kHz (the only sonar type tested) relative to pre-exposure (Z = -0.55, adjusted-p = 1; Figure 2). However, high-quality calls were only recorded for the first 25 min of the 34-min-long exposure period, and the killer whales remained silent until the tag came off 4 h later (Table 2; Figure 3, top). Indeed, there was a significant decrease in call rate during post-exposure compared to pre-exposure (Z = -4.08; adjusted-p = 0.0001), and compared to during exposure (Z = 3.53; adjusted-p = 0.001) (Figure 2). There were also significant differences in the number of overlapped calls and a trend for differences in the number of highly overlapped calls per minute across the exposure phases (overlapped call rate: $\chi^2 = 9.80$, $p = 0.007$; highly-overlapped call rate: $\chi^2 = 5.68$, $p = 0.06$; Table 2). The number of overlapped calls per minute was significantly lower during post-exposure compared to during exposure (Z = 3.10; adjusted-p = 0.006), but not significantly different during exposure compared to pre-exposure (Z = 1.93; adjusted-p = 0.16) or between pre-exposure and post-exposure (Z = -1.17; adjusted-p = 0.72) (Table 2; Figure 2). However, these results should be interpreted with care because there were few instances of minutes with overlapped calls in the pre-exposure period.

The three most common call types in deployment oo06_327s during pre-exposure (N72.2, N73.1, and N77) accounted for 65 to 70% of calls recorded. During exposure, the same three call types in addition to N72.3 were the most commonly produced. N72.3 was produced more often during exposure than during pre-exposure (Figure 4, top). Call maximum frequency was on average ~0.4 kHz higher during exposure ($n = 27$ calls) than pre-exposure ($n = 37$ calls) (W = 219, adjusted-p = 0.01; Figure 5, top). There were no other significant differences in any of the call time and frequency parameters measured between the pre-exposure and exposure phases (duration: W = 490, adjusted-p = 1; start frequency: W = 417, adjusted-p = 0.11; end frequency: W = 332, adjusted-p = 1; mid frequency: W = 338, adjusted-p = 0.17; minimum frequency: W = 373, adjusted-p = 0.84; Figure 5, top).

In the first sonar exposure session of deployment oo09_144a, when killer whales were exposed to 1 to 2 kHz upsweeps, call rate increased from a mean of 2.79/min in pre-exposure to 10.82/min during exposure (Table 2), although this change in call rate was not statistically significant (Z = 1.64, adjusted-p = 0.31; Figure 2). Similar to what we observed in the 6 to 7 kHz session in deployment oo06_327s, in deployment oo09_144a, high-quality calls were detected during the first 16 min of the 34-min-long exposure period, and the whales remained silent throughout the post-exposure period, during subsequent exposure sessions, and for the remainder of the deployment (but note that there was no post-exposure data for the last exposure session on this tag due to premature detachment of the tag; Figure 3, bottom). Indeed, there was a significant decrease in the call rate in post-exposure compared to pre-exposure (Z = -3.16; adjusted-p = 0.005), and compared to during exposure (Z = 4.80; adjusted-p < 0.001) (Figure 2). There were also significant differences in the number of overlapped and highly overlapped calls per minute across the exposure phases (overlapped call rate: $\chi^2 = 17.26$, $p = 0.0002$; highly overlapped call rate: $\chi^2 = 18.84$, $p < 0.001$; Table 2). The number of overlapped calls per minute was significantly lower during post-exposure compared to pre-exposure (Z = -3.21; adjusted-p = 0.004) and during exposure

Table 2. Average call rates recorded within killer whale groups in the periods pre (Pre), during (Dur), and post (Post) exposure to navy sonar signals. Note that two exposure sessions did not have post-exposure data due to the tag detaching early from the whale. The tags with exposure sessions without post-exposure are marked with a †. Call rates are given as number of calls per minute for all call types, for calls overlapped by more than 0% of their duration, and for "highly overlapped" calls that were overlapped by 50% or more of their duration. Statistics presented are the mean, standard deviation (in parentheses), and range (in brackets). Periods with no high-quality calls detected are indicated by "Zero," and those experiments for which a post-exposure period was not available are marked as "NA." *Sonar signal was a 2 to 1 kHz downsweep.

Tag ID	Sonar signal type (kHz)	Number of calls/ minute			Number of calls with > 0% overlap/minute			Number of calls with ≥ 50% overlap/minute		
		Pre	Dur	Post	Pre	Dur	Post	Pre	Dur	Post
oo06_317s†	1-2	0.30 (0.77) [0-3]	Zero	NA	Zero	Zero	NA	Zero	Zero	NA
oo06_327s	6-7	2.06 (3.13) [0-12]	2.74 (5.22) [0-18]	Zero	0.38 (1.60) [0-9]	0.79 (1.70) [0-6]	Zero	0.18 (0.76) [0-4]	0.38 (1.16) [0-6]	Zero
oo08_149a	6-7	0.02 (0.14) [0-1]	0.25 (1.08) [0-7]	Zero	Zero	Zero	Zero	Zero	Zero	Zero
	1-2	Zero	Zero	Zero	Zero	Zero	Zero	Zero	Zero	Zero
	6-7	0.30 (0.70) [0-3]	0.40 (1.00) [0-4]	0.63 (1.69) [0-7]	Zero	Zero	Zero	Zero	Zero	Zero
oo09_144a†	1-2	2.79 (4.58) [0-18]	10.82 (14.90) [0-46]	Zero	1.65 (2.66) [0-11]	6.91 (11.34) [0-33]	Zero	0.41 (1.48) [0-7]	4.65 (7.90) [0-22]	Zero
	6-7	Zero	Zero	Zero	Zero	Zero	Zero	Zero	Zero	Zero
	2-1*	Zero	Zero	NA	Zero	Zero	NA	Zero	Zero	NA

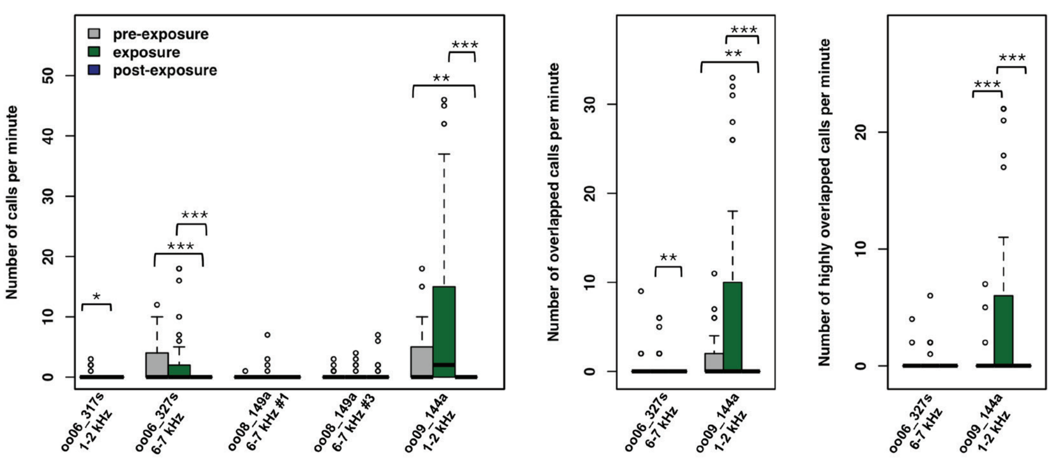
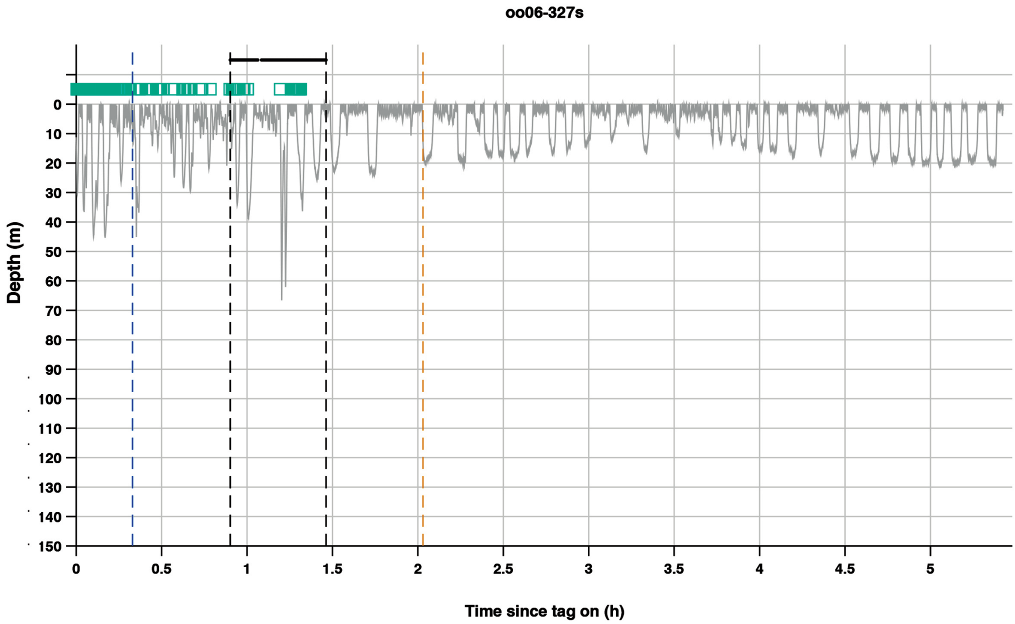


Figure 2. Boxplots of all exposure sessions with call production and overlap. For each tag deployment ID on the x-axis, there is a boxplot for each of the pre-, during, and post-exposure phases. For oo06_317s, which did not have a post-exposure phase, only two boxplots are shown—for the pre- and during exposure phases. Please note, however, that for some of the deployments, the median and interquartile values are zero. Exposure sessions not shown here were those that did not have calls in any phase as detailed in Table 2. For example, for deployment o08_149a, only exposure sessions number 1 and 3 are pictured, both to 6 to 7 kHz sonar, because the killer whales (*Orcinus orca*) were silent across all phases of exposure session number 2. Horizontal lines represent medians, boxes represent interquartiles, and whiskers represent values within 1.5 times the interquartile range from the boxes. Outliers are plotted as single points. Asterisks denote significant differences at a significance level of $p < 0.05$ (*), $p < 0.01$ (**), or $p < 0.001$ (***).



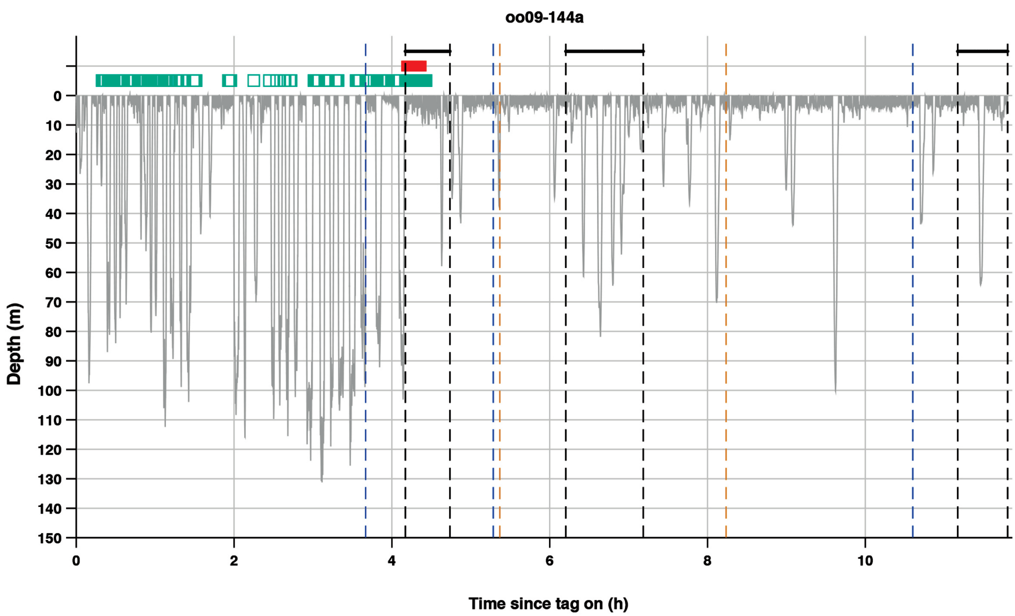


Figure 3. Time-depth profiles of deployments oo06_327s (top) and oo09_144a (bottom) illustrating call production (blue squares above dive profile) across the entire deployment. Highly frequency-modulated calls produced in deployment oo09_144a are shown separately as red squares. For each exposure session, a blue vertical dashed line marks the start of the pre-exposure period, black dashed vertical lines mark the start and end of the sonar exposure period(s), and an orange dashed vertical line marks the end of the post-exposure periods used in the analyses. Deployment oo09_144a included three exposure sessions: (1) 1 to 2 kHz upsweeps, (2) 6 to 7 kHz upsweeps, and (3) 2 to 1 kHz downsweeps. The last exposure session did not have post-exposure data because the tag detached from the whale before the programmed release time.

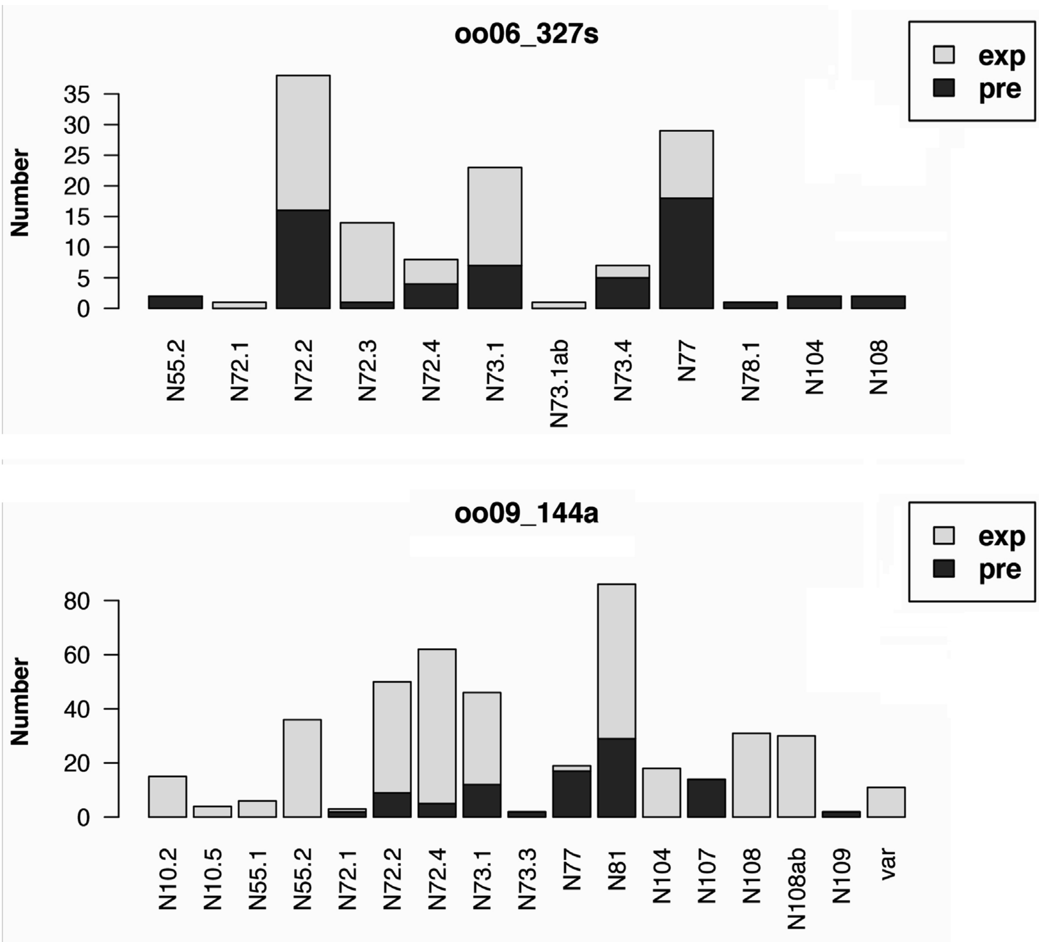


Figure 4. Barplots of all call types and subtypes produced during the pre-exposure and exposure periods for oo06_327s/6 to 7 kHz session (top) and oo09_144a /1 to 2 kHz session (bottom). Calls were not produced during either of the post-exposure periods. Call categories (types and subtypes) are presented on the x-axis, and number of calls produced are presented on the y-axis. Note the axes differ between plots. "exp" stands for exposure, and "pre" stands for pre-exposure periods. Call categories are given as an alphanumeric code starting with N for Norway and followed either by a whole number for call types (e.g., N104) or by a decimal indicating subtypes (N72.1). N108ab and N73.1ab represent aberrant versions of call type N108 and call subtype N73.1, respectively. Call category "var" represents calls that resembled but could not be confirmed as call type N108ab.

(Z = 3.89; adjusted-p = 0.0003), but not significantly different between pre-exposure and during exposure (Z = 0.68; adjusted-p = 1) (Table 2; Figure 2). In contrast, the number of highly overlapped calls per minute was significantly higher during exposure compared to pre-exposure (Z = 3.20; adjusted-p = 0.004) and post-exposure (Z = 4.15; adjusted-p = 0.0001), but not significantly different between post-exposure and pre-exposure (Z = -0.95; adjusted-p = 1) (Table 2; Figure 2).

In addition, call type production during the first sonar exposure to oo09_144a differed from that during the pre-exposure phase. During exposure, the killer whales produced 12 call types and subtypes of which only half were the same as those produced during pre-exposure. The whales in that group also produced variable and aberrant calls which were not produced during the pre-exposure period (Figure 4, bottom). Some of the variable calls resembled the aberrant version of call type N108 but could not be confirmed due to overlap with other calls. Combining all call types and subtypes measured, there were significant differences in all call time and frequency parameters between the pre-exposure (n = 49 calls) and exposure (n = 135 calls) (duration: W = 2,340, adjusted-p = 0.01;

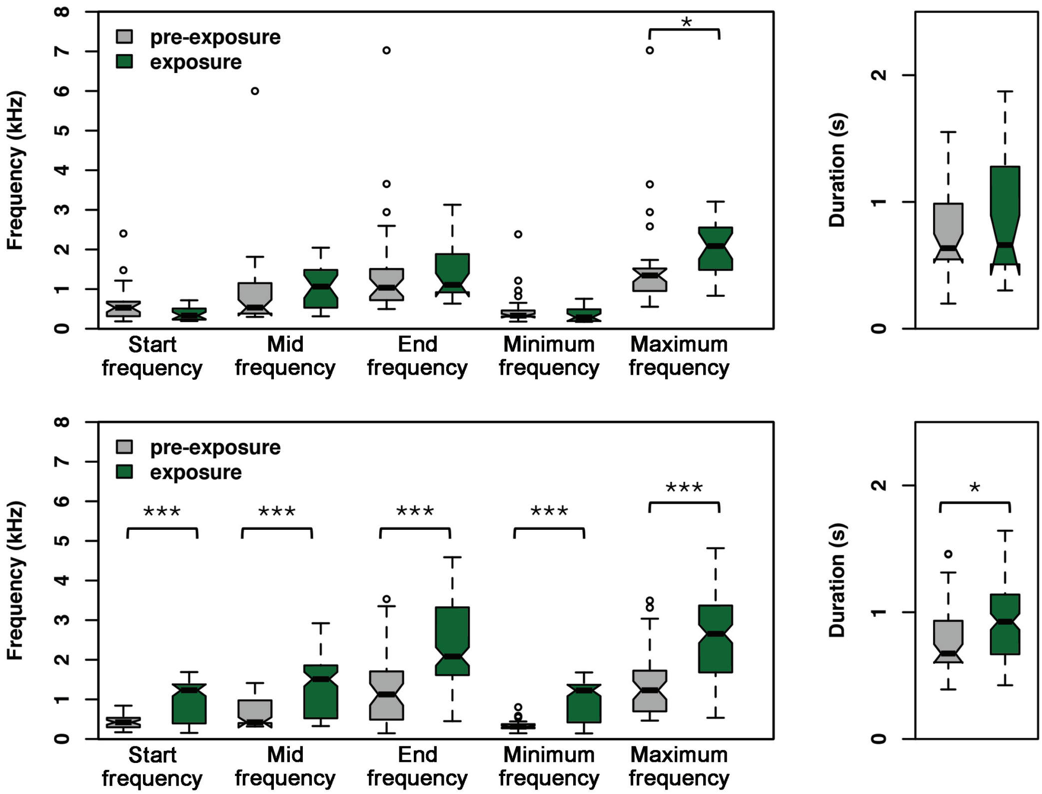


Figure 5. Boxplots of all frequency and time parameters measured for calls produced during pre-exposure and exposure periods for oo06_327s/6 to 7 kHz session (top) and oo09_144a/1 to 2 kHz session (bottom). Calls were not produced during either of the post-exposure periods. Horizontal lines represent medians, boxes represent interquartiles, and whiskers represent values within 1.5 times the interquartile range from the boxes. Outliers are plotted as single points. Asterisks denote significant differences at a significance level of $p < 0.05$ (*), $p < 0.01$ (**), or $p < 0.001$ (***).

start frequency: W = 907, adjusted-$p < 0.0001$; end frequency: W = 1,597, adjusted-$p < 0.0001$; mid frequency: W = 956, adjusted-$p < 0.0001$; minimum frequency: W = 655, adjusted-$p < 0.0001$; maximum frequency: W = 1,377, adjusted-$p < 0.0001$; Figure 5, bottom).

Call Production Timing in Relation to Sonar Transmissions in oo09_144a

The production of highly overlapped calls and highly frequency-modulated calls in response to sonar was only observed during the 1 to 2 kHz upsweep session in deployment oo09_144a (see results above). This vocal response started immediately following the first sonar transmission, with an increase in call rate and overlap of calling, indicating an early onset of vocal response (Figure 6). The background noise level measured on the tag was 93 (±5) dB re 1 µPa in the one-third octave band (base 10) centered around 2 kHz just prior to the first sonar transmission when the animal was performing shallow dives (von Benda-Beckmann et al., 2016), and the estimated sonar received sound pressure level was 91 dB re 1 µPa (Miller et al., 2012). Therefore, the sonar transmission may have been just barely audible to the tagged killer whale (assuming that the one-third octave bandwidth is a reasonable proxy of the auditory filter bandwidth of the upsweep). Figure 6 shows a detail of the killer whales' vocal response, illustrating the early onset of the response and the tight temporal link of call production to sonar transmissions. On average, the time interval between the start of the 1-s sonar transmission and the start of the succeeding highly frequency-modulated call was 2.29 ± 2.47 s (min. = 0.49; max. = 8.78), with 75% of calls ($n = 40$) occurring within 2 s of the start of a sonar transmission.

High-Frequency Whistle Production

There were no statistically significant differences in high-frequency whistle production rate between any of the exposure sessions and pre- and post-exposure periods (Table 3). In most cases, high-frequency whistles were produced in the early minutes of the pre-exposure period and at low sample sizes, which likely restricted the power of the analyses conducted. The only case of high-frequency whistle production during exposure occurred in deployment oo08_149a during which a bout of 11 high-frequency whistles was recorded just before the end of the second 6 to 7 kHz exposure, coinciding with a calf separation event (see Miller et al., 2012, Figure 9 therein). Approximately 3 min later, in the beginning of the post-exposure period, another bout of seven high-frequency whistles was recorded, but no other high-frequency whistles were detected in the remainder of the deployment.

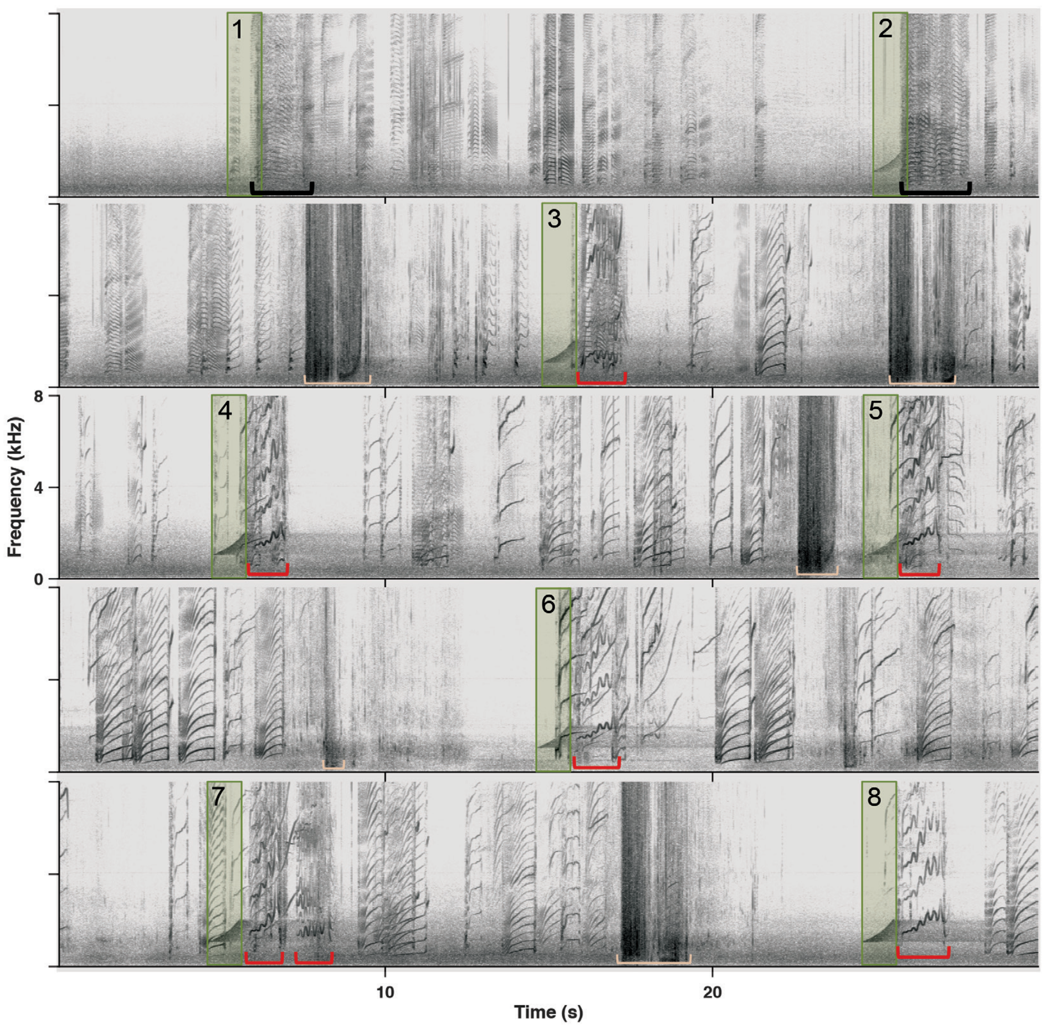


Figure 6. Spectrogram showing the first 145 s of the 1 to 2 kHz exposure, including eight sonar pings and vocal responses of killer whales, as recorded on a DTAG in deployment oo09_144a (see corresponding sound file; the supplemental sound file for this article is available on the *Aquatic Mammals* website). Green bars highlight the location of the 1 to 2 kHz sonar pings in the spectrogram (numbered in sequence), while light pink lines highlight periods with surfacing sounds. The first ping is not visible in the spectrogram. The first two sonar pings (top panel) are followed by periods of increased calling and overlapped calls (black lines). From the third sonar ping (second panel) onwards, the whales started producing highly frequency-modulated calls (highlighted with a red line) after each sonar transmission shown. Note that all panels have the same x- and y-axis scales.

Table 3. Average rates of high-frequency whistle production by killer whales in the periods pre (Pre), during (Dur), and post (Post) exposure to navy sonar signals. Note that two exposure sessions did not have post-exposure data due to the tag detaching early from the whale. The tags with exposure sessions without post-exposure are marked with a †. High-frequency whistle rates are given as number of whistles per minute. Statistics presented are the mean, standard deviation (in parentheses), and range (in brackets). Periods with no high-quality, high-frequency whistles detected are indicated by "Zero," and those experiments without a post-exposure period are marked as "NA." *Sonar signal was a 2 to 1 kHz downsweep.

Tag ID	Sonar type (kHz)	Number of high-frequency whistles/minute		
		Pre	Dur	Post
oo06_317s†	1-2	0.64 (2.89) [0-16]	Zero	NA
oo06_327s	6-7	Zero	Zero	Zero
oo08_149a	6-7	0.08 (0.55) [0-4]	Zero	Zero
	1-2	Zero	Zero	Zero
	6-7	Zero	0.37 (2.01) [0-11]	0.23 (1.28) [0-7]
oo09_144a†	1-2	0.85 (3.19) [0-17]	Zero	Zero
	6-7	Zero	Zero	Zero
	2-1*	Zero	Zero	NA

Discussion

In this study we identified clear but varied vocal responses of killer whales to a case study set of experimental exposures to navy sonar. Significant changes in vocal behaviour were identified in three out of five exposure sessions during which whales were calling (Figure 2). Two of those involved whale groups (oo06_327s and oo09_144) that were in a feeding state and, thus, very vocally active, immediately before exposure, and one group (oo06_317s) that had switched from feeding to travel behaviour shortly before the start of exposure and was vocalising little in the pre-exposure period. Feeding whales (oo06_327s and oo09_144) switched to travel behaviour when exposed to sonar, accompanied by cessation of sound production and avoidance of the sound source (Miller et al., 2014). In contrast, whales that were in a non-feeding state and less vocally active prior to exposure (oo06_317s and oo08_149a) did not always change their vocal behaviour in response to sonar exposure. In these deployments, there was also no change in diving mode (Miller et al., 2012; Sivle et al., 2012), but there was horizontal avoidance of the approaching sound source in some of the exposure sessions (Miller et al., 2014). Thus, the changes in call rates identified herein may be one component of a broader change in behavioural states that may occur independent of sonar exposure. Lower calling rates could be a simple byproduct of the cessation of foraging, although it is possible that less calling is also a response to a potential threat as has been noted for the silencing responses of beaked whales to sonar (Wensveen et al., 2019).

Most tag deployments were on herring-eating killer whales, which vocalise most during feeding and socialising, and least during travelling (Simon et al., 2007a; Samarra & Miller, 2015). However, deployment oo08_149a was on a group that potentially predated on marine mammals. To the best of our knowledge, the vocal behaviour of whales with different dietary preferences has not been studied in Norway. Nevertheless, it is possible that the variation in vocal responses to sonar we observed may also be related to natural variations in vocal behaviour of different ecotypes of killer whales—that is, more vocally active fish-eating whales compared to less vocally active mammal-eating whales (Deecke et al., 2005). High-frequency whistles were produced at much lower rates, and the only time they were observed during a sonar exposure session (oo08_149a) coincided with a temporary calf separation (Miller et al., 2012).

For all three exposure sessions where significant changes in call rates were identified (oo06_317s, oo06_327s, and oo09_144a), call rates decreased to zero during exposure, but in deployments oo06_327s and oo09_144a, the killer whales called for a period of the exposure before becoming silent (Figure 3). In the case of deployment oo06_327s, the number of overlapped calls was higher during exposure (and pre-exposure), compared to post-exposure (Figure 2), until the whales became silent. In the case of deployment oo09_144a, call rates initially increased during exposure, albeit not significantly; the increased call rate was timed closely to the sonar pings; and the rate of overlapped and highly overlapped calls was higher during exposure compared to post-exposure until the whales became silent halfway through the exposure. Increasing sound production rates may be a behavioural change to compensate for masking effects and to ensure that information is still transmitted to conspecifics. A short-term vocal adjustment to mitigate the effects of noise on communication has been reported in several marine mammal species, in various behavioural contexts, and as a response to different noise sources, including increases in sound production rate (e.g., Rendell & Gordon, 1999; Di lorio & Clark, 2010).

However, in this study (Figure 3), a two-stage response appeared to have occurred, composed of an initial increase followed by a decrease in call rate. This observation matches Lesage et al. (1999) who described increases in beluga (*Delphinapterus leucas*) call rates during the first minutes of exposure to vessel noise followed by decreases as vessels approached more closely. Similarly, Buckstaff (2004) found that bottlenose dolphin (*Tursiops truncatus*) whistle rates initially increased as vessels approached but then declined significantly as the vessels passed and for a period thereafter. Blackwell et al. (2015) showed that bowhead whales (*Balaena mysticetus*) initially increased call rates when exposed to airgun pulses during seismic surveys until a plateau was reached, after which call rates decreased while noise levels continued to increase.

Given the social nature of killer whales and the fact that the observed vocal responses coincided with changes in behaviour to travelling away from the sonar source, it is possible that the initial increase in vocal rate was a result of changes in group cohesion or a way to coordinate the group's behaviour prior to switching to travelling when the whales became silent. Increased signal production rates may be a strategy to reduce signal degradation or may reflect heightened arousal and promote social cohesion (Buckstaff, 2004). Because the whales in our study changed vocal behaviour as well as behavioural state to a behaviour where they are typically silent (i.e., travelling; Simon et al., 2007a), it is difficult to determine if the whales' vocal response was also a response to increasing noise levels or presence of a perceived threat. In addition, vocalisation rates were calculated only as number per unit of time and not adjusted for group size. There were no apparent changes in group size during one exposure session (oo09_144a/1 to 2 kHz upsweep), but no data on group size were collected for the other exposure sessions during which changes in calling behaviour were observed (oo06_317s/1 to 2 kHz upsweep; oo06_327s/6 to 7 kHz). Changes in group size or group spacing are likely to affect the rate of high-quality calls received on the animal-attached tag. Understanding the influence of these different factors on killer whale vocal responses to noise would require more comprehensive sampling with larger sample sizes in the future.

For two of the three exposure sessions in which vocal responses were detected (oo06_327s and oo09_144a), there was an increase in maximum frequency of the fundamental frequency of calls produced during exposure compared to the pre-exposure period (Figure 5). An increase in signal frequency outside of the dominant frequency band of noise (short-term, e.g., in bottlenose dolphins: Heiler et al., 2016; van Gikel et al., 2017; and long-term, e.g., in right whales [*Eubalaena glacialis* and *Eubalaena australis*]: Parks et al., 2007) has been reported in other species and considered to be a potential way to prevent in-band masking. Out-of-band masking release also contributes to the masking of killer whale calls in the presence of pulsed sonar signals (Branstetter et al., 2024). The shifts in the fundamental frequency contour parameters observed during the 1 to 2 kHz sonar exposure session of deployment oo09_144a were typically not to frequencies outside the sonar band, suggesting that the whales in the tagged whale's group were not changing spectral parameters to avoid spectral masking. However, the dataset analysed herein was not appropriate for a comprehensive masking study, so we cannot exclude that changes in other masking indicators (e.g., animals increasing source levels or shifting energy between harmonics during sound production) in response to the sonar may have occurred. Killer whales are known to increase call frequency during high arousal and excited contexts, which often involve apparent altercations and rough play (Ford, 1989). These structural changes in discrete calls are thought to reflect variations in the emotional state of the sound-producing whale (Ford, 1989). Indeed, Morton's (1977) motivational structure rules suggest that friendly or fearful animals emit calls of higher frequency. Thus, it is also possible that increases in frequency observed in our study might have been an expression of the signallers' motivational state rather than a strategy to avoid masking.

In deployment oo06_327s, call type production changed little in response to sonar exposure (6 to 7 kHz). In contrast, in deployment oo09_144a, call type production differed between pre-exposure and 1 to 2 kHz sonar exposure, and, specifically, there was production of highly frequency-modulated calls that were not produced during pre-exposure (Figure 4). Altering signal frequency modulation when exposed to noise has been reported in bottlenose dolphins but with a shift towards less modulated, simplified signals (e.g., Morisaka et al., 2005; Fouda et al., 2018). Less-modulated signals should be less susceptible to masking by noise and, therefore, may be beneficial in noisier conditions (Morisaka et al., 2005). In killer whales, calls with increased frequency modulation are often associated with high arousal behaviours, particularly in social contexts, and are believed to function in motivational expression (Ford, 1989; Rehn et al., 2007). Graham & Noonan (2010) showed increases in vocalisation rate and call frequency modulation specifically associated with aggressive contexts between an adult male and an adult female in captivity. Some of these calls were possibly produced by the non-aggressor potentially signalling subordination or distress.

In addition to the increased production of highly frequency-modulated calls, the production of calls in general, and, in particular, of the highly frequency-modulated calls with high degrees of overlap, was timed very closely to the sonar ping emissions (Figure 6). A response at such narrow time windows relative to sonar pings indicates a response specifically to the sonar signal. Similar responses were also recently described in common dolphins (*Delphinus delphis*; Casey et al., 2024). This was suggested to be potential amplification of the behaviour of group members—that is, one dolphin signalling as a response to the sonar and others following the same behaviour or, alternatively, as a means for multiple animals to exchange communication signals for contact with conspecifics in the presence of an unknown acoustic stimulus. Given that calls with increased frequency modulations are associated with high arousal contexts and believed to express the motivational state of the signalling killer whale (Ford, 1989; Rehn et al., 2007), it is possible that the vocal response observed herein served similar functions to those suggested for common dolphins by Casey and colleagues (2024). Specifically, the production of highly frequency-modulated calls may have reflected the motivational state of some members of the group in response to an unknown stimulus, which triggered other members to also produce calls which often overlapped. We suggest that future studies investigate call frequency modulation rate as well as timing relative to sonar pings to better describe killer whale vocal responses.

All killer whales that responded to sonar exposure eventually became silent at some point during the exposure period. In addition, there were similarities in the vocal responses of those whales that continued calling during exposure (oo06_327s and oo09_144a), such as consistent increases in call maximum frequency and increased rates of overlapped calls. However, the response to 1 to 2 kHz upsweeps in deployment oo09_144a was more intricate, involving calling with high rates of overlap timed very closely to the arrivals of sonar transmissions and changes to the types of calls used. In all cases, the groups were feeding prior to sonar exposure; thus, the behavioural context appeared to be similar. From this small set of case studies, we cannot reach firm conclusions, but we hypothesise that certain contextual differences could have modulated how these groups responded acoustically to sonar.

In addition to the differences in the sonar upsweep signals to which they were exposed (6 to 7 kHz in oo06_327s and 1 to 2 kHz in oo06_317s and oo09_144a), there were also differences in group composition and potentially dietary preferences between the deployments. In deployment oo06_317s, the tagged killer whale was feeding on herring with a large group of 50 to 80 animals but switched from feeding to travel behaviour before the start of the sonar exposure. In deployment oo06_327s, an estimated 70 to 80 animals of all sex and age classes were present in a herring feeding aggregation, and the tagged whale was an adult female often associated with a small animal. In deployment oo09_144a, an adult male was tagged, and the group was composed of about 15 animals, including calves, that were presumably feeding on herring. Finally, deployment oo08_149a was on a group of seven possibly mammal-eating whales, including a newborn calf. The effect of these differences, if any, on the vocal responses observed remains unknown due to the small sample size of our study but suggests that contextual variables should be considered in future studies investigating the factors driving vocal responses.

While there were clear changes in calling behaviour for some of the exposure sessions, the possible function of changes in the production of high-frequency whistles were less obvious, except in the case of a calf separation event. Given the lack of knowledge on the function or behavioural context of high-frequency whistle production, further studies will be necessary to understand what role these signals may play in killer whale acoustic communication.

In conclusion, our study describes vocal responses in feeding killer whales that were concurrent with changes in behavioural state from feeding to travelling. Changes in vocal behaviour included increased call rate associated with increased call maximum frequency, increased production of overlapped calls, and, in one deployment, production of highly frequency-modulated calls. These responses may primarily reflect changes in the motivational state of signalling individuals rather than strategies to avoid masking. However, our sample sizes are low, and further data are needed to further our understanding of the drivers behind vocal adjustments in different noise and behavioural contexts. This includes studies of modern continuous sonar signals where the masking potential is greater than with the conventional pulsed sonar signals studied herein.

Note: The supplemental sound file for this article is available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/supplemental-material.

Acknowledgments

We greatly appreciated all the professional and skilled support of captain and crew of RV *H.U. Sverdrup II*, as well as the support of fieldwork participants. This work was funded by the Norwegian Ministry of Defence, the Netherlands Ministry of Defence, the Office of Naval Research, and WWF Norway. Experiments were carried out under permits from the Norwegian Authority for Animal Experimentation (Permit Numbers 2004/20607, 2007/61201, and 2009/35289), in compliance with ethical use of animals in experimentation. The research protocols were approved by the University of St Andrews' Animal Welfare and Ethics Committee and the Woods Hole Oceanographic Institution's Institutional Animal Care and Use Committee.

Literature Cited

Alves, A., Antunes, R., Bird, A., Tyack, P. L., Miller, P. J. O., Lam, F-P. A., & Kvadsheim, P. H. (2014). Vocal matching of naval sonar signals by long-finned pilot whales (*Globicephala melas*). *Marine Mammal Science*, *30*(3), 1248-1257. https://doi.org/10.1111/mms.12099

Andriolo, A., Reis, S. S., Amorim, T. O. S., Sucunza, F., de Castro, F. R., Maia, Y. G., Zerbini, A. N., Bortolotto, G. A., & Rosa, L. D. (2015). Killer whale (*Orcinus orca*) whistles from the western South Atlantic Ocean include high frequency signals. *The Journal of the Acoustical Society of America*, *138*(3), 1696-1701. https://doi.org/10.1121/1.4928308

Antunes, R., Kvadsheim, P. H., Lam, F-P. A., Tyack, P. L., Thomas, L., Wensveen, P. J., & Miller, P. J. O. (2014). High thresholds for avoidance of sonar by free-ranging long-finned pilot whales (*Globicephala melas*). *Marine Pollution Bulletin*, *83*(1), 165-180. https://doi.org/10.1016/j.marpolbul.2014.03.056

Au, W. W. L., Ford, J. K. B., Horne, J. K., & Allman, K. A. N. (2004). Echolocation signals of free-ranging killer whales (*Orcinus orca*) and modeling of foraging for Chinook salmon (*Oncorhynchus tshawytscha*). *The Journal of the Acoustical Society of America*, *115*(2), 901-909. https://doi.org/10.1121/1.1642628

Balcomb III, K. C., & Claridge, D. E. (2001). A mass stranding of cetaceans caused by naval sonar in the Bahamas. *Bahamas Journal of Science*, *2*, 2-12.

Barrett-Lennard, L. G., Ford, J. K. B., & Heise, K. A. (1996). The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour*, *51*(3), 553-565. https://doi.org/10.1006/anbe.1996.0059

Blackwell, S. B., Nations, C. S., McDonald, T. L., Thode, A. M., Mathias, D., Kim, K. H., Greene, C. R., Jr., & Macrander, A. M. (2015). Effects of airgun sounds on bowhead whale calling rates: Evidence for two behavioral thresholds. *PLOS One*, *10*, e0125720. https://doi.org/10.1371/journal.pone.0125720

Branstetter, B. K., Felice, M., Robeck, T., Holt, M. M., & Henderson, E. E. (2024). Auditory masking of tonal and conspecific signals by continuous active sonar, amplitude modulated noise, and Gaussian noise in killer whales (*Orcinus orca*). *The Journal of the Acoustical Society of America*, *156*(4), 2527-2537. https://doi.org/10.1121/10.0028626

Buckstaff, K. C. (2004). Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science*, *20*(4), 709-725. https://doi.org/10.1111/j.1748-7692.2004.tb01189.x

Casey, C., Fregosi, S., Oswald, J. N., Janik, V. M., Visser, F., & Southall, B. (2024). Common dolphin whistle responses to experimental mid-frequency sonar. *PLOS One*, *19*(4), e0302035. https://doi.org/10.1371/journal.pone.0302035

D'Amico, A., Gisiner, R. C., Ketten, D. R., Hammock, J. A., Johnson, C., Tyack, P. L., & Mead, J. (2009). Beaked whale strandings and naval exercises. *Aquatic Mammals*, *35*(4), 452-472. https://doi.org/10.1578/AM.35.4.2009.452

Deecke, V. B., Ford, J. K. B., & Slater, P. J. B. (2005). The vocal behaviour of mammal-eating killer whales: Communicating with costly calls. *Animal Behaviour*, *69*(2), 395-405. https://doi.org/10.1016/j.anbehav.2004.04.014

DeRuiter, S. L., Boyd, I. L., Claridge, D. E., Clark, C. W., Gagnon, C., Southall, B. L., & Tyack, P. L. (2013a). Delphinid whistle production and call matching during playback of simulated military sonar. *Marine Mammal Science*, *29*(2), E46-E59. https://doi.org/10.1111/j.1748-7692.2012.00587.x

DeRuiter, S. L., Southall, B. L., Calambokidis, J., Zimmer, W. M. X., Sadykova, D., Falcone, E. A., Friedlaender, A. S., Joseph, J. E., Moretti, D., Schorr, G. S., Thomas, L., & Tyack, P. L. (2013b). First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. *Biology Letters*, *9*(4), 20130223. https://doi.org/10.1098/rsbl.2013.0223

Di lorio, L., & Clark, S. W. (2010). Exposure to seismic survey alters blue whale acoustic communication. *Biology Letters*, *6*(1), 51-54. https://doi.org/10.1098/rsbl.2009.0651

Ellison, W. T., Southall, B. L., Clark, C. W., & Frankel, A. S. (2012). A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. *Conservation Biology*, *26*(1), 21-28. https://doi.org/10.1111/j.1523-1739.2011.01803.x

Filatova, O. A., Fedutin, I. D., Burdin, A. M., & Hoyt, E. (2007). The structure of the discrete call repertoire of killer whales *Orcinus orca* from southeast Kamchatka. *Bioacoustics*, *16*(3), 261-280. https://doi.org/10.1080/09524622.2007.9753581

Filatova, O. A., Guzeev, M. A., Fedutin, I. D., Burdin, A. M., & Hoyt, E. (2013). Dependence of killer whale (*Orcinus orca*) acoustic signals on the type of activity and social context. *Biology Bulletin*, *40*(9), 790-796. https://doi.org/10.1134/S1062359013090045

Filatova, O. A., Ford, J. K. B., Matkin, C. O., Barrett-Lennard, L. G., Burdin, A. M., & Hoyt, E. (2012). Ultrasonic whistles of killer whales (*Orcinus orca*) recorded in the North Pacific (L). *The Journal of the Acoustical Society of America*, *132*(6), 3618-3621. https://doi.org/10.1121/1.4764874

Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orc*a) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, *67*(3), 727-745. https://doi.org/10.1139/z89-105

Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, *69*(6), 1454-1483. https://doi.org/10.1139/z91-206

Fouda, L., Wingfield, J. E., Fandel, A. D., Garrod, A., Hodge, K. B., Rice, A. N., & Bailey, H. (2018). Dolphins simplify their vocal calls in response to increased ambient noise. *Biology Letters*, *14*(10), 20180484. https://doi.org/10.1098/rsbl.2018.0484

Frantzis, A. (1998). Does acoustic testing strand whales? *Nature*, *392*(6671), 29. https://doi.org/10.1038/32068

Goldbogen, J. A., Southall, B. L., DeRuiter, S. L., Calambokidis, J., Friedlaender, A. S., Hazen, E. L., Falcone, E. A., Schorr, G. S., Douglas, A., Moretti, D. J., Kyburg, C., McKenna, M. F., & Tyack, P. L. (2013). Blue whales respond to simulated mid-frequency military sonar. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1765), 20130657. https://doi.org/10.1098/rspb.2013.0657

Graham, M. A., & Noonan, M. (2010). Call types and acoustic features associated with aggressive chase in the killer whale (*Orcinus orca*). *Aquatic Mammals*, *36*(1), 9-18. https://doi.org/10.1578/AM.36.1.2010.9

Harris, C. M., Thomas, L., Falcone, E. A., Hildebrand, J., Houser, D., Kvadsheim, P. H., Lam, F-P. A., Miller, P. J. O., Moretti, D. J., Read, A. J., Slabbekoorn, H., Southall, B. L., Tyack, P. L., Wartzok, D., & Janik, V. M. (2017). Marine mammals and sonar: Dose-response studies, the risk-disturbance hypothesis and the role of exposure context. *Journal of Applied Ecology*, *55*(1), 396-404. https://doi.org/10.1111/1365-2664.12955

Heiler, J., Elwen, S. H., Kriesell, H. J., & Gridley, T. (2016). Changes in bottlenose dolphin whistle parameters related to vessel presence, surface behaviour and group composition. *Animal Behaviour*, *117*(1), 167-177. https://doi.org/10.1016/j.anbehav.2016.04.014

Isojunno, S., Curé, C., Kvadsheim, P. H., Lam, F-P. A., Tyack, P. L., Wensveen, P. J., & Miller, P. J. O. (2016). Sperm whales reduce foraging effort during exposure to 1-2 kHz sonar and killer whale sounds. *Ecological Applications*, *26*(1), 77-93. https://doi.org/10.1890/15-0040

Johnson, M. P., & Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Ocean Engineering*, *28*(1), 3-12. https://doi.org/10.1109/JOE.2002.808212

Kuningas, S., Kvadsheim, P. H., Lam, F-P. A., & Miller, P. J. O. (2013). Killer whale presence in relation to naval sonar activity and prey abundance in northern Norway. *ICES Journal of Marine Science*, *70*(7), 1287-1293. https://doi.org/10.1093/icesjms/fst127

Lesage, V., Barrette, C., Kingsley, M. C. S., & Sjare, B. (1999). The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River estuary, Canada. *Marine Mammal Science*, *15*(1), 65-84. https://doi.org/10.1111/j.1748-7692.1999.tb00782.x

Melcón, M. L., Cummins, A. J., Kerosky, S. M., Roche, L. K., Wiggins, S. M., & Hildebrand, J. A. (2012). Blue whales respond to anthropogenic noise. *PLOS One*, *7*(2), e32681. https://doi.org/10.1371/journal.pone.0032681

Miller, P. J. O. (2002). Mixed-directionality of killer whale stereotyped calls: A direction of movement cue? *Behavioral Ecology and Sociobiology*, *52*(3), 262-270. https://doi.org/10.1007/s00265-002-0508-9

Miller, P. J. O., Biassoni, N., Samuels, A., & Tyack, P. L. (2000). Whale songs lengthen in response to sonar. *Nature*, *405*, 903.

Miller, P. J. O., Antunes, R. N., Wensveen, P. J., Samarra, F. I. P., Alves, A. C., & Tyack, P. L. (2014). Dose-response relationships for the onset of avoidance of sonar by free-ranging killer whales. *The Journal of the Acoustical Society of America*, *135*(2), 975-993. https://doi.org/10.1121/1.4861346

Miller, P. J. O., Kvadsheim, P. H., Lam, F-P. A., Wensveen, P. J., Antunes, R., Alves, A. C., Visser, F., Kleivane, L., Tyack, P. L., & Sivle, L. D. (2012). The severity of behavioural changes observed during experimental exposures of killer (*Orcinus orca*), long-finned pilot (*Globicephala melas*), and sperm (*Physeter macrocephalus*) whales to naval sonar. *Aquatic Mammals*, *38*(4), 362-401. https://doi.org/10.1578/AM.38.4.2012.362

Miller, P. J. O., Antunes, R., Alves, A. C., Wensveen, P., Kvadsheim, P., Kleivane, L., Nordlund, N., Lam, F-P., van IJsselmuide, S., Visser, F., & Tyack, P. (2011).

*The 3S experiments: Studying the behavioural effects of naval sonar on killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), and long-finned pilot whales (*Globicephala melas*) in Norwegian waters* (Scottish Oceans Institute Technical Report SOI-2011-001). Scottish Oceans Institute. http://soi.st-andrews.ac.uk/pageset.aspx?psr=443

Miller, P. J. O., Kvadsheim, P. H., Lam, F-P. A., Tyack, P. L., Curé, C., DeRuiter, S. L., Kleivane, L., Sivle, L. D., van IJsselmuide, S. P., Visser, F., Wensveen, P. J., von Benda-Beckmann, A. M., Martín López, L. M., Narazaki, T., & Hooker, S. K. (2015). First indications that northern bottlenose whales are sensitive to behavioural disturbance from anthropogenic noise. *Royal Society Open Science*, *2*(6), 140484. https://doi.org/10.1098/rsos.140484

Morisaka, T., Shinohara, M., Nakahara, F., & Akamatsu, T. (2005). Effects of ambient noise on the whistles of Indo-Pacific bottlenose dolphin populations. *Journal of Mammalogy*, *86*(3), 541-546. https://doi.org/10.1644/1545-1542(2005)86[541:EOANOT]2.0.CO;2

Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, *111*, 855-869. https://doi.org/10.1086/283219

National Marine Fisheries Service (NMFS). (2005). *Assessment of acoustic exposures on marine mammals in conjunction with* USS Shoup *active sonar transmission in the eastern Strait of Juan de Fuca and Haro Strait, 5 May 2003*. NOAA Office of Protected Resources.

Parks, S. E., Clark, C. W., & Tyack, P. L. (2007). Short- and long-term changes in right whale calling behavior: The potential effects of noise on acoustic communication. *The Journal of the Acoustical Society of America*, *122*(6), 3725-3731. https://doi.org/10.1121/1.2799904

Rehn, N., Teichert, S., & Thomsen, F. (2007). Structural and temporal emission patterns of variable pulsed calls in free-ranging killer whales (*Orcinus orca*). *Behaviour*, *144*(3), 307-329. https://doi.org/10.1163/156853907780425703

Rendell, L. E., & Gordon, J. C. D. (1999). Vocal response of long-finned pilot whales (*Globicephala melas*) to military sonar in the Ligurian Sea. *Marine Mammal Science*, *15*(1), 198-204. https://doi.org/10.1111/j.1748-7692.1999.tb00790.x

Riesch, R., & Deecke, V. B. (2011). Whistle communication in mammal-eating killer whales (*Orcinus orca*): Further evidence for acoustic divergence between ecotypes. *Behavioural Ecology and Sociobiology*, *65*(7), 1377-1387. https://doi.org/10.1007/s00265-011-1148-8

Riesch, R., Ford, J. K. B., & Thomsen, F. (2006). Stability and group specificity of stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia. *Animal Behaviour*, *71*(1), 79-91. https://doi.org/10.1016/j.anbehav.2005.03.026

Samarra, F. I. P., & Miller, P. J. O. (2015). Prey-induced behavioural plasticity of herring-eating killer whales. *Marine Biology*, *162*(4), 809-821. https://doi.org/10.1007/s00227-015-2626-8

Samarra, F. I. P., Deecke, V. B., Vinding, K., Rasmussen, M. H., Swift, R., & Miller, P. J. O. (2010). Killer whales (*Orcinus orca*) produce ultrasonic whistles. *The Journal of the Acoustical Society of America*, *128*(5), EL205-EL210. https://doi.org/10.1121/1.3462235

Saulitis, E. L., Matkin, C. O., & Fay, F. H. (2005). Vocal repertoire and acoustic behavior of the isolated AT1 killer whale subpopulation in southern Alaska. *Canadian Journal of Zoology*, *83*(8), 1015-1029. https://doi.org/10.1139/z05-089

Selbmann, A., Deecke, V. B., Fedutin, I. D., Filatova, O. A., Miller, P. J. O., Svavarsson, J., & Samarra, F. I. P. (2021). A comparison of Northeast Atlantic killer whale (*Orcinus orca*) stereotyped call repertoires. *Marine Mammal Science*, *37*(1), 268-289. https://doi.org/10.1111/mms.12750

Shapiro, A. D. (2008). *Orchestration: The movement and vocal behavior of free-ranging Norwegian killer whales (*Orcinus orca*)* (Unpub. doctoral dissertation). Massachusetts Institute of Technology, Cambridge, and the Woods Hole Oceanographic Institution, Woods Hole, MA.

Simon, M., McGregor, P. K., & Ugarte, F. (2007a). The relationship between the acoustic behaviour and surface activity of killer whales (*Orcinus orca*) that feed on herring (*Clupea harengus*). *Acta Ethologica*, *10*(2), 47-53. https://doi.org/10.1007/s10211-007-0029-7

Simon, M., Wahlberg, M., & Miller, L. A. (2007b). Echolocation clicks from killer whales (*Orcinus orca*) feeding on herring (*Clupea harengus*) (L). *The Journal of the Acoustical Society of America*, *121*(2), 749-752. https://doi.org/10.1121/1.2404922

Simon, M., Ugarte, F., Wahlberg, M., & Miller, L. A. (2006). Icelandic killer whales *Orcinus orca* use a pulsed call suitable for manipulating the schooling behaviour of herring *Clupea harengus*. *Bioacoustics*, *16*(1), 57-74. https://doi.org/10.1080/09524622.2006.9753564

Simonis, A. E., Baumann-Pickering, S., Oleson, E., Melcón, M. L., Gassmann, M., Wiggins, S. M., & Hildebrand, J. A. (2012). High-frequency modulated signals of killer whales (*Orcinus orca*) in the North Pacific. *The Journal of the Acoustical Society of America*, *131*(4), EL295-EL301. https://doi.org/10.1121/1.3690963

Sivle, L. D., Kvadsheim, P. H., Fahlman, A., Lam, F-P., A., Tyack, P. L., & Miller, P. J. O. (2012). Changes in dive behaviour during naval sonar exposure in killer whales, long-finned pilot whales, and sperm whales. *Frontiers in Physiology*, *3*, 1-11. https://doi.org/10.3389/fphys.2012.00400

Sivle, L. D., Wensveen, P. J., Kvadsheim, P. H., Lam, F-P. A., Visser, F., Curé, C., Harris, C. M., Tyack, P. L., & Miller, P. J. O. (2016). Naval sonar disrupts foraging in humpback whales. *Marine Ecology Progress Series*, *562*, 211-220. https://doi.org/10.3354/meps11969

Southall, B. L., Nowacek, D. P., Miller, P. J. O., & Tyack, P. L. (2016). Experimental field studies to measure behavioral responses of cetaceans to sonar.

Endangered Species Research, *31*(1), 293-315. https://doi.org/ 10.3354/esr00764

Southall, B. L., Durban, J. W., Calambokidis, J., Casey, C., Fahlbusch, J. A., Fearnbach, H., Flynn, K. R., Fregosi, S., Friedlaender, A. S., Leander, S. G. M., & Visser, F. (2024). Behavioural responses of common dolphins to naval sonar. *Royal Society Open Science*, *11*(10), 240650. https://doi.org/10.1098/rsos.240650

Stimpert, A. K., DeRuiter, S. L., Southall, B. L., Moretti, D. J., Falcone, E. A., Goldbogen, J. A., Friedlaender, A., Schorr, G. S., & Calambokidis, J. (2014). Acoustic and foraging behavior of a Baird's beaked whale, *Berardius bairdii*, exposed to simulated sonar. *Scientific Reports*, *4*, 7031. https://doi.org/10.1038/srep07031

Strager, H. (1993). *Catalogue of underwater calls from killer whales (*Orcinus orca*) in northern Norway* (Master's dissertation). University of Aarhus, Aarhus, Denmark.

Strager, H. (1995). Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca* Linnaeus, 1758, in the waters of northern Norway. *Canadian Journal of Zoology*, *73*(6), 1037-1047. https://doi.org/10.1139/z95-124

Thomsen, F., Franck, D., & Ford, J. K. B. (2001). Characteristics of whistles from the acoustic repertoire of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *The Journal of the Acoustical Society of America*, *109*(3), 1240-1246. https://doi.org/10.1121/1.1349537

Thomsen, F., Franck, D., & Ford, J. K. B. (2002). On the communicative significance of whistles in wild killer whales (*Orcinus orca*). *Naturwissenschaften*, *89*(9), 404-407. https://doi.org/10.1007/s00114-002-0351-x

Trickey, J. S., Reyes, M. V. R., Baumann-Pickering, S., Melcón, M. L., Hildebrand, J. A., & Iñíguez, M. A. (2014). *Acoustic encounters of killer and beaked whales during the 2014 SORP cruise* (IWC Report SC/65b/SM12). International Whaling Commission.

Tyack, P. L., Zimmer, W. M. X., Moretti, D., Southall, B. L., Claridge, D. E., Durban, J. W., Clark, C. W., D'Amico, A., DiMarzio, N., Jarvis, S., McCarthy, E., Morissey, R., Ward, J., & Boyd, I. L. (2011). Beaked whales respond to simulated and actual navy sonar. *PLOS One*, *6*(3), e17009. https://doi.org/10.1371/journal.pone.0017009

van Gikel, C., Becker, D. M., Gowans, S., & Simard, P. (2017). Whistling in a noisy ocean: Bottlenose dolphins adjust whistle frequencies in response to real-time ambient noise levels. *Bioacoustics*, *27*(4), 391-405. https://doi.org/10.1080/09524622.2017.1359670

Van Opzeeland, I. C., Corkeron, P. J., Leyssen, T., Similä, T., & Van Parijs, S. M. (2005). Acoustic behavior of Norwegian killer whales, *Orcinus orca*, during carousel and seiner foraging on spring-spawning herring. *Aquatic Mammals*, *31*(1), 110-119. https://doi.org/10.1578/AM.31.1.2005.110

von Benda-Beckmann, A. M., Wensveen, P. J., Samarra, F. I. P., Beerens, S. P., & Miller, P. J. O. (2016). Separating underwater ambient noise from flow noise recorded on stereo acoustic tags attached to marine mammals. *Journal of Experimental Biology*, *219*(15), 2271-2275. https://doi.org/10.1242/jeb.133116

Watkins, W. A. (1967). Harmonic interval: Fact or artifact in spectral analysis of pulse trains. In W. N. Tavolga (Ed.), *Marine bioacoustics* (Vol. 2, pp. 15-42). Pergamon Press.

Weiß, B. M., Ladich, F., Spong, P., & Symonds, H. (2006). Vocal behaviour of resident killer whale matrilines with newborn calves: The role of family signatures. *The Journal of the Acoustical Society of America*, *119*(1), 627-635. https://doi.org/10.1121/1.2130934

Weiß, B. M., Symonds, H., Spong, P., & Ladich, F. (2007). Intra- and intergroup vocal behavior in resident killer whales, *Orcinus orca*. *The Journal of the Acoustical Society of America*, *122*(6), 3710-3716. https://doi.org/10.1121/1.2799907

Wensveen, P. J., von Benda-Beckmann, A. M., Ainslie, M. A., Lam, F-P. A., Kvadsheim, P. H., Tyack, P. L., & Miller, P. J. O. (2015). How effectively do horizontal and vertical response strategies of long-finned pilot whales reduce sound exposure from naval sonar? *Marine Environmental Research*, *106*, 68-81. https://doi.org/10.1016/j.marenvres.2015.02.005

Wensveen, P. J., Kvadsheim, P. H., Lam, F-P. A., von Benda-Beckmann, A. M., Sivle, L. D., Visser, F., Curé, C., Tyack, P. L., & Miller, P. J. O. (2017). Lack of behavioural responses of humpback whales (*Megaptera novaeangliae*) indicate limited effectiveness of sonar mitigation. *Journal of Experimental Biology*, *220*(22), 4150-4161. https://doi.org/10.1242/jeb.161232

Wensveen, P. J., Isojunno, S., Hansen, R. R., von Benda-Beckmann, A. M., Kleivane, L., van IJsselmuide, S., Lam, F-P. A., Kvadsheim, P. H., DeRuiter, S. L., Curé, C., Narazaki, T., Tyack, P. L., & Miller, P. J. O. (2019). Northern bottlenose whales in a pristine environment respond strongly to close and distant navy sonar signals. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1899), 20182592. https://doi.org/10.1098/rspb.2018.2592

WWF Norway. (2001). *Lack of environmental assessment resulted in negative impact on fish and tourism* (MOD Archive No. 01/01309-1). Letter from WWF Norway to Norwegian Minister of Defense. (In Norwegian)

Yurk, H., Barrett-Lennard, L., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, *63*(6), 1103-1119. https://doi.org/10.1006/anbe.2002.3012