Naval sonar disrupts foraging in humpback whales

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Abstract

Modern long-range naval sonars are a potential disturbance for marine mammals and can lead to disruption of feeding in cetaceans. This study examined the lunge-feeding behaviour of humpback *(Megaptera novaeangliae*) whales before, during and after controlled exposure experiments with naval sonar by use of acoustic and motion sensor archival tags attached to each animal. Lunge-feeding by humpback whales entails a strong acceleration to increase speed before engulfing a large volume of prey-laden water, that can be identified by their acoustic signature characterized by a few seconds of high-level flow-noise followed by a rapid reduction, coinciding with a peak in animal acceleration. Over two successive seasons, 13 humpback whales were tagged. All were subject to a no-sonar control exposure, and 12 to two consecutive sonar exposure sessions, with 1 h of period between. The first sonar session resulted in an average 68% reduction in lunge rate during exposure compared to pre-exposure, and this reduction was significantly greater than any changes observed during the no-sonar control. During the second sonar session, reduction in lunge rate was 66% during sonar exposure compared to pre-exposure level, but was not significant compared to the no-sonar control, likely due to a larger inter-individual variability because some individuals seem to have habituated and others not. Our results indicate that naval sonars operating near humpback whale feeding grounds may lead to reduced foraging and negative impact on energy balance.

INTRODUCTION

The past decade has led to increasing focus on behavioural responses of marine mammals to anthropogenic sound and their biological significance for individuals and populations (Wartzok et al. 2005). One of the main causes for concern is powerful naval sonar, as it can lead to strong, potentially lethal effects such as strandings (Cox et al. 2006, D'Amico et al. 2009), as well as a range of behavioural responses scaling from low to high severity (Miller et al. 2012, Sivle et al. 2015). A behavioural response of major concern is disruption of feeding. Disrupted feeding activity may lead to lower energy reserves to support reproductive activities such as breeding and females' ability to nurse calves (e.g. New et al. 2014, for an example in elephant seals; Meyer-Gutbrod et al., 2015 for right whales). Cessation or reduction of feeding in response to naval sonar has been observed in several species of toothed whales (Miller et al. 2012, Isojunno et al. 2015) as well as for blue whales (Goldbogen et al. 2013).

However, very little is known about behavioural responses of other baleen whale species to naval sonar. This is of particular importance, as their annual cycle is generally typified by a distinct, seasonal foraging period in high latitude feeding grounds, alternated by periods of low-feeding rates during long-range migration and breeding/nursing periods in low latitude breeding grounds (Clapham et al. 1999).

Humpback whales (*Megaptera novaeangliae*) are among the most numerous of the baleen whales (sub-order: *Mysticete*) in the North Atlantic Ocean (Øien 2007), with the Norwegian and Barents Sea being important feeding grounds for the species in summer (Nøttestand & Olsen 2004,Nøttestad et al. 2014). There, they feed on zooplankton and small schooling fish such as herring and capelin (Christensen et al. 1992, Øien 2007).

Humpback whales feed by lunging, a technique that involves engulfing a large volume of prey-rich water using a flexible buccal cavity and filtering out seawater leaving prey inside the baleen plates (Goldbogen et al. 2007). These lunging events can clearly be seen by a visual observer when they occur close to the surface. Using multi-sensor recording tags, sampling the whales' movements at sufficiently high frequencies, lunge events can also be identified when they occur at depth. When a humpback whale lunges, it accelerates forward in a burst of fluke strokes before engulfing a targeted patch of prey-rich water. As the whale opens its jaws, it rapidly decelerates due to the transfer of momentum to the engulfed water (Simon et al. 2012) and increased drag (Goldbogen et al. 2006, 2007). A lunge can therefore be detected by an increase in speed followed by a subsequent abrupt drop in speed, resulting in an acoustic signature comprising a few seconds of high-level flow noise followed by a rapid reduction in noise level (see Goldbogen et al. 2006, Ware et al. 2011, Simon et al. 2009, 2012 for studies on lunging in fin, blue, bowhead and humpback whales, respectively).

Here, we used controlled experiments at sea to investigate whether exposure to 1.3-2.0 kHz naval sonar affected the feeding rates of humpback whales. We attached high resolution acoustic and motion sensor tags on individuals on their feeding ground, and collected behavioural parameters before, during and after being approached by a large ship transmitting sonar pulses.

METHODS

Data collection

Fieldwork was conducted in the Barents Sea between Bear Island and Spitsbergen in June 2011 and 2012 aboard the research vessel "H.U. Sverdrup II" (Kvadsheim et al. 2011, 2012). Details of the experiments are described in Kvadsheim et al. (2015) and summarized here: Humpback whales were detected visually from the flying bridge of the research vessel. After a whale was sighted, surface behaviour was recorded for 30-60 minutes before a tag boat was launched to deploy a tag, and surface behaviour sampling continued until the end of the experiment.

Humpback whales were tagged with a multi-sensor tag (Dtag, Johnson & Tyack 2003) attached to the whale with suction cups using a hand-held carbon fibre pole, or a pneumatic remote deployment system. The Dtag recorded sound and depth, 3-dimensional acceleration, and 3-dimensional magnetometer data, allowing a fine reconstruction of whale behaviour. Audio data were sampled at 96 kHz, other non-acoustic sensors at 50 Hz later decimated to 5Hz sampling rate. Visual observations of the tracked whale were conducted to record group size (number of individuals in the group of the tagged individual) and group composition (i.e. calf presence/absence) (see protocol details in Visser et al. 2014). Pairs of whales were considered potential mother-calf pairs if they were composed of an adult and a smaller-sized individual that remained closely associated throughout the tracking record (Lockyer 1984, Panigada et al. 2005, Curé et al. 2015).

A VHF beacon on the tagged whale was tracked by a VHF digital radio direction-finder (DFHorten). Controlled sonar exposure sessions started after 2-8 hours of baseline data collection. The tagged humpback whale was then subject to three 10min duration exposures sessions: one no-sonar control and two sonar exposures. The no-sonar control was always conducted first to test how whales responded to the ship alone, before they heard sonar transmitted from the ship, so that if the sonar might sensitize them, it should not be associated with the ship sound. The two consecutive sonar sessions (sonar 1 and sonar 2) were conducted to investigate potential habituation or sensitization to the sonar. An example of a full experiment data record is shown in figure 1, and other examples can be found in Kvadsheim et al. 2015. The no-sonar control session consisted of the source vessel approaching the tagged whale in the same way as during a sonar exposure, but without any sonar transmission. This control was done to be able to clearly separate any potential reaction to the approaching vessel from responses to the sonar transmission. The sonar source was a multi-purpose towed acoustic source, SOCRATES II (TNO, The Hague, The Netherlands). The sonar signal was a 1.3-2.0 kHz upsweep transmitted every 20s with a 0.5s and 1.0s duration for ramp-up and full-power periods, respectively. During each sonar exposure session, transmission was initiated at a planned distance of 1250 m from the tagged whale, as this was the distance covered during 5 min at 8 knots sailing speed. The source ship approached the whale for 5min at 8 knots on a constant course while gradually increasing the transmitted source level (ramp-up procedure) from 152 dB to a maximum source level of 214 dB re 1 μPa·m at the expected closest point of approach (CPA, designed to be 0m from the animal based on its pre-exposure movement pattern). Then, the source ship continued to transmit at full power for another 5 min while moving away from the animal. This procedure was done to achieve a gradual increase of the received sound level as the ship moved towards the animal, as well as to simulate a "worst case scenario" with the source ship moving directly towards it. The time interval between the two sonar exposures was planned to be minimum one hour, or longer if animals was apparently still responding. Each sonar exposure had a10-minute duration including 5 min of ramp up followed by 5 min of full power transmission. In two cases, the second sonar exposure lasted only 5 minutes, without the preceding ramp-up. The order of the three exposures was always the same; first the no-sonar control followed by the two sonar exposures.

Lunge detection

Lunges were detected following the method of Simon et al. (2012), using the relative drop in flow-noise within a short time window when a lunge event occurs. Sound recordings of the Dtag were first low-pass filtered (6-order Butterworth filter at 500 Hz) and the sound pressure level (root mean square) of 40 ms blocks was calculated and resampled to the same sampling rate as the non-acoustic data (i.e. 5 Hz). Then, potential lunge events were automatically detected using a “lunge detector” programmed in MATLAB (The MathWorks, version 2012b). This detector followed two steps: first, the detector extracted all potential lunges identified as noise peaks that 1) exceeded the 90% excedance level the 90th percentile ofthe flow-noise samples recorded from the same tag record in periods when the animal was deeper than 5 m, and 2) were followed by at least a 12 dB drop in flow noise within 5 s. This 5 s period was truncated if the whale reached the surface (defined as a depth of 0.5 m) to discard drops in the noise when the tag is in the air as the whale surfaced to breathe. The reason for only using noise data when the descending animal was deeper than 5 m was to avoid loud surfacing splashes being detected as lunges (see fig. 2c). In the second step, each detected lunge was evaluated visually to confirm that it was not a false positive. Since a lunge is accompanied with a peak in the jerk signal (i.e. rate of change of acceleration; Simon et al. 2012), a peak in the jerk signal needed to be identified for a detection to be assigned as a lunge. In uncertain cases, the data were further evaluated by inspecting the spectrogram and listening to the sound file to determine whether a detected lunge was real or not. In rare cases when the lunge assignment was still uncertain, the suggested lunge was discarded.

Statistical analysis

We were interested in examining whether the lunge-feeding rate of the whales changed across the three types of exposure sessions: the no-sonar control and both sonar sessions. The no-sonar control was used as a negative control to separate a potential effect of the source ship itself to an effect of the sonar. Both sonar sessions, i.e. sonar 1 and sonar 2, were compared to the no-sonar control. For each of the three sessions, the number of lunges was divided into three different phases: during the exposure period (*Dur*), before (*Pre*) the exposure and after (*Post*) the exposure session, the last two phases corresponding respectively to the periods immediately preceding (*Pre*) or following (*Post*) the exposure and being of equal duration as the exposure session (10 or 5 minutes).

The data were analysed using a Poisson Generalized Estimation Equation (GEE) model in R software version 3.0.2 (R Development Core Team 2013) using the geepack (Højsgaard et al., 2006). GEEs allow us to estimate population average parameters from correlated and clustered data by appropriately inflating the standard errors (Hardin and Hilbe, 2003). This allows us to account for differences between individual whales as well as correlation within individual whales, as most tagged whales were tested with multiple types of exposures. In this analysis, two of the tagged animals were part of the same group and therefore could not be assumed to be independent of each another. Therefore, we set the tagged whale group ID as the blocking unit in the model instead of the tagged whale ID. We assumed an independent correlation structure within the blocks and used a standard robust sandwich variance estimate for all reported results (Hardin and Hilbe, 2003). The response variable was the number of lunges in a given phase (*Pre, Dur* or *Post* phases) Due to two animals being subjected to 5-minute exposures instead of 10-minute exposures, a weighting term for exposure duration was included to account for the unequal time over which lunges were counted. Explanatory covariates included phase (*Pre, Dur, Post*), session_order (no-sonar control, sonar 1, sonar 2) and the two-way interaction term phase: session_order.

Hypothesis-based model selection was performed using p-values and backwards selection. The Wald test statistics and p-value for each parameter estimate in a GEE model indicate the significance of the difference between factor levels, not the contribution of the factor covariate to model fit. Therefore for model selection, we used the p-values given by an ANOVA (sequential Wald test) on the fitted model object with a significance threshold of 0.05. For inference purposes we used prediction plots generated from the selected model. The 95% confidence intervals for the predictions presented were calculated using a parametric bootstrap on the GEE-based covariance matrix from the selected model. Upper and lower quantiles (2.5 and 97.5) were calculated from 5000 bootstrap iterations.

In addition, we used the output from the 5000 bootstraps to make comparisons between specific factor level combinations of interest. We calculated the differences between predictions for different factor levels across all bootstraps as well as a 95% confidence interval for these differences. We concluded that there was a significant increase or decrease in the number of lunges in cases where the upper and lower confidence limits for the differences were exclusively positive or negative. Where the confidence interval included zero we concluded that there was no significant difference between factor levels as there was a 95% chance that the true difference between factor levels was zero.

In the statistical analysis, all animals (n=13) were used, independent of foraging status prior to exposure (feeding or not feeding). This is assumed to resemble the real world situation where animals encountering a sonar vessel will either be in a feeding or non-feeding state at the start of exposure.

RESULTS

We successfully tagged 13 humpback whales, 5 in 2011 and 8 in 2012 (Table 1). One whale (mn11_157a) was subject only to the no-sonar control due to a premature tag release. The remaining 12 whales were all subject to three exposure sessions: first a no-sonar control followed by two sonar sessions.

The sonar sessions resulted in escalating dose from SPL of 80-100 dB re 1µPa to maximum of 160-180 dB re 1µPa (Kvadsheim et al. 2015).

A total number of 3875 lunge events were identified throughout the entire tag records for all animals, with lunging depth averaging (±SD) 25 ±39 m and ranging from 0.79 to 169 m. Feeding activity could be observed at any time of day. Lunges were typically detected at the start of the ascent of a dive, corresponding to an increase in the jerk signal and the fluke stroke rate as well as a clear increase in flow noise in the spectrogram (Figure 2).

There was a large variation between individuals in response to the exposures. In 16 of the 31 exposure sessions (20 sonar sessions and 11 no-sonar control sessions), whales were feeding prior to exposure onset. All 6 whales feeding prior to the first sonar exposure (sonar 1) reduced their lunge rate. One animal (mn12_178a), however, initiated lunge feeding during sonar 1 (Table 1). Of the 5 whales feeding prior to the second sonar exposure (sonar 2), 4 reduced their lunge rate, while 1 whale (mn12_178a) increased its lunge rate (Table 1). For the no-sonar control, 7 whales were feeding prior to exposure. All 7 reduced their lunge rate during exposure, whereas 1 whale (mn12_164a) initiated lunging during exposure (Table1). The largest decrease in number of lunges was recorded for humpback whale mn12_180a during the first sonar exposure, with a drop from 15 lunges in the *Pre* phase to 1 lunge in the *Dur* phase.

For all three sessions types (no-sonar control, sonar 1, sonar 2) there was an overall reduction in the observed lunge rate in the *Dur* phase compared to the *Pre* phase (Figure 3). The mean reduction in *Dur* relative to *Pre* was 24% for no-sonar control, 68% for sonar 1 and 66% for sonar 2. The selected model following the backwards selection procedure was the full model with both main effect terms and the interaction term. The interaction term phase:session_order significantly contributed to model fit according to the ANOVA ($p<0.001$) and so both main effect terms were also retained. Hence, there was a significant effect of phase (*Pre, Dur, Post*) on lunge rate but this effect differed across the exposure types (no-sonar control, sonar 1, sonar 2). We used the bootstrap predictions of the number of lunges from this selected model to quantify the differences between phases of particular sessions.This analysis indicated that the reduction in lunges for sonar 1 and sonar 2 from the *Pre* to the *Dur* phase were significant as the upper and lower confidence bounds for the difference were exclusively positive (95% confidence, Table 2, Figure 3). However, this was not the case for the no-sonar control (95% chance that the true difference between *Pre* and *Dur* was zero) (Table 2). Moreover, the reduction from *Pre* to *Dur* for sonar 1 was significantly different from the reduction from *Pre* to *Dur* for no-sonar control (95% confidence), but this was not the case for sonar 2 (Table 2).

The number of lunges over a 10 minute period was still reduced in the *Post* period compared with the Pre period, with an average reduction from *Pre* to *Post* of 68% and 48% for sonar 1 and sonar 2, respectively (see Table 2 and Fig. 3 for uncertainty around these mean reductions). These differences represent significant reductions between the *Pre* and *Post* phases for the two sonar exposures (95% confidence; Table 2). Again, for the no-sonar control, there was no significant reduction in the lunge rate between the *Pre* and *Post* phases as the 95% confidence interval of the differences included zero.

DISCUSSION

Effect of sonar on feeding

Humpback whales reduced their lunge rate during exposure to an approaching vessel transmitting naval low-frequency sonar signals (1.3-2.0 kHz). Animals were exposed to the same sonar signals during two consecutive sessions, and in both cases the reduction represented a significant change in lunge rates (95% confidence; Table 2). When the whales were exposed to the same vessel approaching in the same way but without the sonar transmitting, the reduction in lunge rate was not significantly different from lunge rate in the baseline period (*Pre* phase*)* before any exposures, indicating that the response can be attributed to the sonar exposure and not to the vessel approaching. Furthermore, the reduction during sonar 1 differed from no-sonar control, but sonar 2 did not (Table 2), despite the relatively similar average reduction (68 and 66%, respectively). The individual variation during sonar 2 was much greater than for sonar 1, which probably explains the lack of significant effects of sonar 2. The large individual variability may indicate that some animals habituated, while others did not. An alternative explanation is that there was a cumulative effect of two exposures and that animals had not fully recovered from the first exposure at the start of the second (the feeding rate in the *Pre* period of sonar 2 was somewhat lower than in the *Pre* period of sonar 1) but not significantly different (Table 2), indicating this not to be an overall explanation. Our data does not give any indication of sensitisation to the sonar, as weaker, not stronger responses were seen to the second exposure. The whales did not resume their pre-exposure feeding rate immediately after the end of sonar exposure (mean lunge rate for sonar1/sonar 2 of *Pre* = 0.53/0.42 and *Post* = 0.17/0.14 lunges/minute), showing reduced lunge rates post-exposure (Table 2), indicating whales did not immediately resume feeding activity following sonar exposure.

Beside the hypothesis that naval sonar signals might directly affect the feeding behaviour of humpbacks, another possibility to explain the decrease in feeding activity is that the prey reacted to the sonar, e.g. by diving, thus becoming less accessible for the whale predator. We do not know what the tagged humpback whales were feeding on, but green and brown feces were seen regularly in vicinity of the tagged whales, indicating both fish and krill. This is supported by reports of humpback whales in the Barents Sea feeding on zooplankton such as krill and amphipods as well as capelin and to some degree herring (Skern-Mauritsen et al. 2011; Nøttestad et al. 2014).Only for herring are the sonar signals within audible range (Enger 1967), but several studies have shown that herring do not show any behavioural response to such sonar signals even at very high received levels (Doksæter et al. 2009, 2012, Sivle et al. 2012). A change in prey distribution is therefore not likely to be the cause of the decreased feeding activity.

Reasons for individual variability

Behavioural responses of marine mammals to sound depend on contextual variables, including external factors such as sound source level, signal characteristics, background noise levels, rise time of the signal and time of day, as well as internal factors such as current activity, motivation, past experience with the sound, age, sex and presence of offspring (Wartzok et al. 2003). Although the present dataset overall showed that humpback whales reduced their foraging activity during experimental sonar exposures, there was substantial variability between the different individuals tested. Some whales responded by a total cessation of feeding immediately after exposure started (e.g. mn12_164a, sonar 1), some showed a moderate reduction of feeding (e.g. mn12_170a sonar 1), and one whale actually initiated feeding (mn12_178a sonar 1). In a sonar exposure with two tagged individuals (mn12_170ab), one of the whales stopped feeding (tag b), while the other continued (tag a) (see Kvadsheim et al. 2015 for plots of all experiments).

Responses of humpback whales to various stimuli may depend on group composition (Tyack 1983, Dunlop et al. 2013, Curé et al. 2015). In our dataset, some animals were in groups of 2-3 animals, some solitary (Table 1). For the no-sonar control, animals in groups (e.g. mother-calf pairs) had a higher reduction in lunge rate than the solitary animals, indicating that animals in groups may be more reactive to disturbance. McCauley et al. (1998) suggested that different classes (e.g. age, sex, group composition) of humpback whales may have different sensitivity to seismic signals, e.g. adult males may be less likely to alter their behaviour. This may also apply to the humpback whales in the present study, with the strongest reduction in foraging activity seen in animals associated with a calf (mn11_160a and mn12_180a). The same humpbacks with calves in the present study also responded more strongly to predator (killer whale) sound playbacks than other group composition classes (Curé et al. 2015). Thus, it could be that groups with calves in general react more strongly to any potential disturbance stimuli, such as naval sonar, immediate predator presence, or vessel approach.

Biological significance of reduced feeding activity

Humpback whales migrate to high-latitude waters in summer to feed in order to accumulate energy reserves to be invested in low-latitude breeding in winter. Time and behaviour on the feeding ground must therefore be optimized to acquire energy, with whales maximizing their daily intake by feeding on high prey densities and using as little time as possible to find and capture prey (Friedlaender et al. 2013). During one lunge, a humpback whale can engulf a volume of water and prey equal to two-thirds of its body mass (Pivorunas 1979, Goldbogen et al. 2007). Thus, every lunge missed may decrease food intake. The biological significance of feeding disruption will depend on the duration of the response as well as how often the whales are exposed. A full scale naval sonar exercises may last for hours and even days, thus with potential consequences for whale energy acquisition within this period. Such a full scale sonar operation may involve additional components such as multiple ships, submarines and underwater communication equipment that may add to this disturbance.

In addition to sonar, these humpback whales were also exposed to playbacks of mammal-eating killer whale (*Orcinus orca*) feeding sounds simulating an increased predation risk (reported in Curé et al. 2015). The humpback whales abruptly stopped lunging activity when exposed to killer whale feeding sounds (Curé et al. 2015), and often did not resume feeding within 1 hour (Sivle et al. 2015). Killer whales do regularly target humpback whales (Jefferson et al. 1991; McCordic et al. 2013), and prey are expected to undertake fitness-reducing behavioural decisions if they are balanced by a reduction in predation pressure on fitness. Sonar exposure seem to induce an alteration of the foraging activity similar to the response seen when there is an immediate risk of predation attacks. This indicatethat the humpback whales use similar strategies of response to different disturbance stimuli, but also that they may be willing to compromise with fitness enhancing activities also when exposed to sonar.

Conclusions

The current study documents that naval sonar can disrupt feeding behaviour in humpback whales when the sonar operates in close vicinity to the whales, and that feeding behaviour can remain disrupted after the end of exposure. The observed response to sonar may be of high biological relevance if they are exposed frequently as it entails reduction of feeding in a seasonal prime feeding habitat.

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Table and figure legends

Table 1. Overview of experiments. For each tagged animal, the date of tag deployment and total number of lunges exhibited by the tagged whale and detected during the tag record are given. Each of the three exposure sessions, i.e. no-sonar control, sonar 1 and sonar 2, are described in more detail with their start time and number of lunges in their three phases *Pre* (pre-exposure), *Dur* (during exposure) and *Post* (post-exposure). The group composition of the tagged whales is also given for each of the experimental sessions.

Table 2. Comparisons between different factor level combinations (each a combination of one factor level of session_order and one factor level of period). Period could be one of the three phases (*Pre*, *Dur*, *Post*) or one of the two magnitudes of change between phases *Pre* and *Dur* (Pre_Dur) and between phases *Pre* and *Post*) (Pre_Post). The comparisons are made by calculating the difference between factor level combinations over 5000 bootstrap iterations. Here we report the mean difference and the lower and upper 2.5 percentiles. A “*” indicates comparisons where the quantiles do not span zero, suggesting that there is some difference between factor levels at the 95% confidence level.

Figure 1: An example of the entire 18 h tag record of mn12_164awith the different periods of the tag recorded indicated. Baseline period is the period preceding any exposure. Exposure includes the three sessions analyzed in this study (no-sonar control in blue, sonar 1 and sonar 2 in yellow), plus the killer whale playback (in pink) analyzed in Curé et al. 2015. Exposures were always conducted in this same order. The last post-exposure recovery period after all exposure sessions was particularly long to evaluate potential recovery time in cases of severe responses.

Fig.2. Typical example of a 5minute sample of Dtag data (mn12_170a) illustrating a foraging dive with five lunge feeding events. a) Depth profile with lunges indicated as red filled circles, b) Body orientation of the whale in degrees shown as up-down pitch angle (blue) and roll angle about the body axis (green), c) Spectrogram of the sound recording with a 4 kHz upper cut-off showing increase in the flow-noise corresponding to the occurrence of the lunges(arrows). The loud paired broadband impulses are splashes when the animal surfaces (arrows). d) Jerk signal (acceleration rate of change) showing accelerationpeaks at times of lunges e) Fluke stroke activity in degrees, derived as the pitch deviation, showing the whale is actively fluke stroke during lunges. The jerk signal was used in the second step of the lunge detection to verify whether a detected lunge was not a false positive.

Fig. 3. GEE model results. Predicted number of lunges for 10-minute time periods obtained from the selected GEE model. The bars show predictions from the selected model for each combination of the factor covariates, while error bars indicate 95 percentile confidence intervals from a parametric bootstrap. See Table 2 for tests of significance of specific contrasts.

Table 1

			No-sonar control					Sonar 1					Sonar 2				
Whale id	**Date**	**Total # lunges**	**Start time (UTC)**	**Pre**	**Dur**	**Post**	**Group composition**	**Start time (UTC)**	**Pre**	**Dur**	**Post**	**Group composition**	**Start time (UTC)**	**Pre**	**Dur**	**Post**	**Group composition**
mn11_157a	06.06.2011	85	07:08:50	0	0	0	solitary	09:23:00	0	0	0	solitary	10:46:00	0	0	0	solitary
mn11_158a	07.06.2011	158	18:37:00	3	1	2	group of 4 animals, no calf	-	-	-	-	-	-	-	-	-	-
mn11_160a	09.06.2011	103	07:16:00	0	0	0	mother/ calf pair	09:14:00	0	0	0	mother/ calf pair	10:36:00	0	0	0	mother/ calf pair
mn11_165e	14.06.2011	304	17:40:00	2	0	5	mother/ calf pair	19:56:00	9	2	1	mother/ calf pair	21:03:00	0	0	0	mother/ calf pair
mn11_165d	14.06.2011	522	17:40:00	6	3	7	mother/ calf pair	19:56:00	10	1	1	mother/ calf pair	21:03:00	0	0	0	mother/ calf pair
mn12_161a	09.06.2012	193	22:44:00	5	2	1	solitary	00:59:00	0	0	0	solitary	02:23:00	0	0	0	solitary
mn12_164a	12.06.2012	325	22:28:00	0	7	7	solitary	00:00:30	7	0	0	group went from 1 to 2 animals during exposure	01:38:00	7	0	6	group of 2 animals, no calf
mn12_170a	18.06.2012	255	08:49:00	0	0	0	group of 2 animals, no calf	10:41:00	7	4	0	group of 2 animals, no calf	12:32:00	16	9	10	group of 2 animals, no calf
mn12_170b	18.06.2012	92	08:49:00	0	0	0	pair, no calf	10:41:00	0	0	0	pair, no calf	12:32:00	6	0	1	pair, no calf
mn12_171a	19.06.2012	909	16:48:00	12	11	16	solitary	18:37:00	15	8	11	pair, no calf	19:52:00	9	1	1	pair, no calf
mn12_178a	26.06.2012	360	05:15:00	8	7	10	group of 3 animals, no calf	07:25:30	0	4	7	group of 2 animals, no calf	08:46:00	5	7	2	group of 2-3 animals, no calf
mn12_179a	27.06.2012	0	13:51:00	0	0	0	solitary	15:07:00	0	0	0	solitary	16:19:00	0	0	0	solitary
mn12_180a	28.06.2012	355	21:01:00	10	4	5	mother/ calf pair	22:55:00	15	1	0	mother/ calf pair	00:55:00	0	0	0	mother/ calf pair

Table 2

Combination 1	**Combination 2**	**Mean Difference**	**Lower 2.5 percentile**	**Upper 2.5 percentile**	*** indicates a difference at the 95% confidence level**
No sonar control pre	No sonar control dur	0.86	-0.797	2.82	
No sonar control pre	No sonar control post	-0.56	-2.63	1.23	
Sonar 1 pre	Sonar 1 dur	3.72	1.24	7.71	*
Sonar 1 pre	Sonar 1 post	3.59	0.171	7.77	*
Sonar 2 pre	Sonar 2 dur	2.55	0.48	6.28	*
Sonar 2 pre	Sonar 2 post	2.22	0.74	5.125	*
Sonar 1 pre-dur	No sonar control pre-dur	2.84	0.2	6.6	*
Sonar 2 pre-dur	No sonar control pre-dur	1.65	-1.86	6.44	
Sonar 1pre-post	No sonar control pre-post	4.03	0.49	8.51	*
Sonar 2 pre-post	No sonar control pre-post	2.81	0.33	6.6	*
Sonar 1 Pre	Sonar 2 Pre	1.27	4.81	6.85	

Figure 1

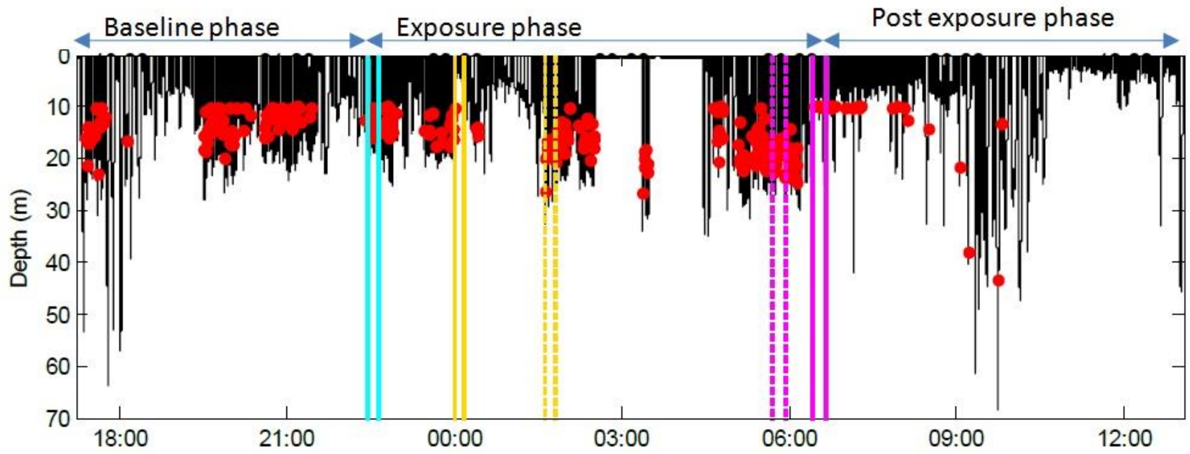


Figure 2

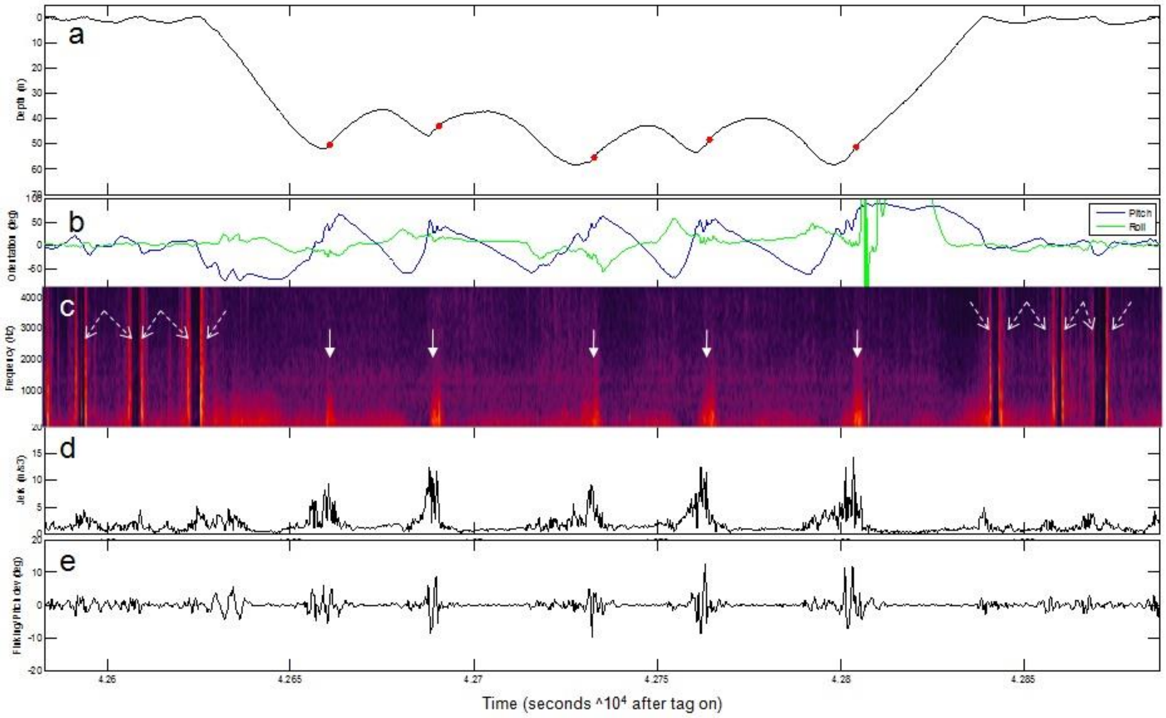
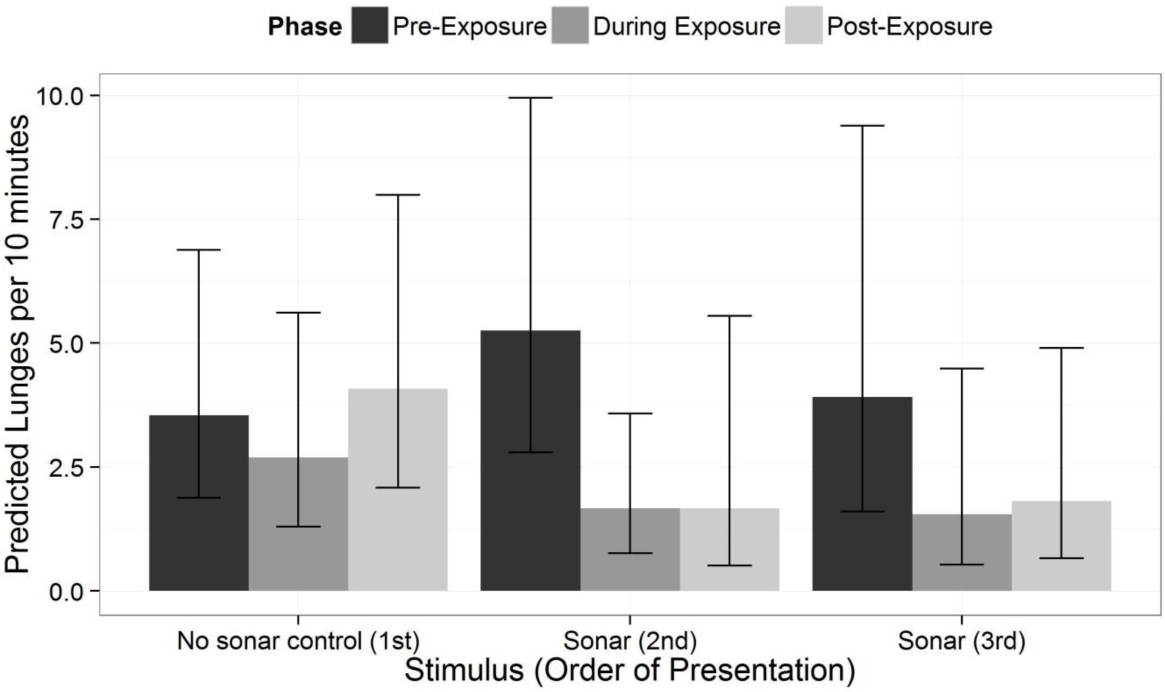


Figure 3


Phase
Pre-Exposure
During Exposure
Post-Exposure
Predicted Lunges per 10 minutes
10.0
7.5
5.0
2.5
0.0
No sonar control (1st)
Sonar (2nd)
Sonar (3rd)
Stimulus (Order of Presentation)