

Naval sonar disrupts foraging in humpback whales

Lise Doksaeter Sivle^{1,*}, Paul J. Wensveen², Petter H. Kvadsheim³,
Frans-Peter A. Lam⁴, Fleur Visser^{5,6}, Charlotte Curé⁷, Catriona M. Harris⁸,
Peter L. Tyack², Patrick J. O. Miller²

¹Institute of Marine Research, PO Box 1870 Nordnes, Bergen 5817, Norway

²Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews KY16 8LB, UK

³Norwegian Defence Research Establishment (FFI), Horten 3191, Norway

⁴Netherlands Organisation for Applied Scientific Research (TNO), PO Box 96864, 2509 JG, The Hague, The Netherlands

⁵Kelp Marine Research (KMR), 1624 CJ, Hoorn, The Netherlands

⁶Behavioural Biology, Institute of Biology, Leiden University, PO Box 9505, 2300 RA, Leiden, The Netherlands

⁷Cerema, Dter Est, Acoustics group, 67035, Strasbourg Cedex 2, France

⁸Centre for Research into Ecological and Environmental Modelling, Buchanan Gardens, University of St Andrews, St Andrews KY16 9LZ, UK

ABSTRACT: Modern long-range naval sonars are a potential disturbance for marine mammals and can cause disruption of feeding in cetaceans. We examined the lunge-feeding behaviour of humpback whales *Megaptera novaeangliae* 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, which can be identified by an 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 2 successive seasons, 13 humpback whales were tagged. All were subject to a no-sonar control exposure, and 12 whales were exposed to 2 consecutive sonar exposure sessions, with 1 h between sessions. 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 the pre-exposure level, but was not significant compared to the no-sonar control, likely due to a larger inter-individual variability because some individuals appeared to have habituated whereas others had not. Our results indicate that naval sonars operating near humpback whale feeding grounds may lead to reduced foraging and negative impacts on energy balance.

KEY WORDS: Humpback whale · *Megaptera novaeangliae* · Naval sonar · Behavioural response · Lunge feeding

Resale or republication not permitted without written consent of the publisher

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

sonars, as they 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

for supporting reproductive activities such as breeding and nursing 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. 2016) as well as in 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: Mysticeti) in the North Atlantic Ocean (Øien 2007), with the Norwegian and Barents Sea being important feeding grounds for the species in summer (Nøttestad & 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 2011, Simon et al. 2009, 2012, Ware et al. 2011, 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 to individuals at their feeding grounds, and collected behavioural parameters before, during and after being approached by a large ship transmitting sonar pulses.

MATERIALS AND 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 were described by Kvadsheim et al. (2015) and are 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 to 60 min 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 5 Hz sampling rate. Visual observations of the tracked whales were conducted to record group size (number of individuals in the group with 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 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 to 8 h of baseline data collection. The tagged humpback whale was then subject to three 10 min duration exposure sessions: 1 no-sonar control and 2 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 2 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 Fig. 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 sonar signal was a 1.3 to 2.0 kHz upswEEP transmitted every 20 s with a 0.5 s and 1.0 s 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 5 min 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 $\mu\text{Pa m}$ at the expected closest point of approach (designed to be 0 m from the animal based on its pre-exposure movement pattern). The source ship then 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 2 sonar exposures was planned to be minimum 1 h, or longer if animals were

apparently still responding. Each sonar exposure had a 10 min duration including 5 min of ramp-up followed by 5 min of full-power transmission. In 2 cases, the second sonar exposure lasted only 5 min, without the preceding ramp-up. The order of the 3 exposures was always the same; first the no-sonar control followed by the 2 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). Potential lunge events were then automatically detected using a ‘lunge detector’ programmed in MATLAB (MathWorks, version 2012b). This detector followed 2 steps: first, the detector extracted all potential lunges identified as noise peaks that (1) exceeded the 90th percentile of the 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 by 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

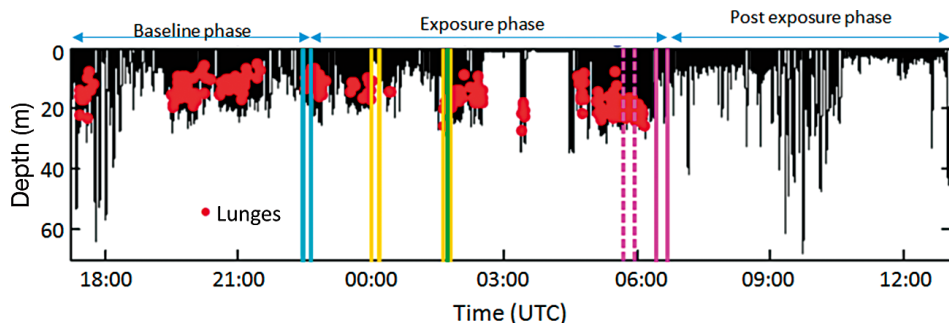


Fig. 1. Example of the entire 18 h tag record of a humpback whale *Megaptera novaeangliae* (ID mn12_164a) with the different periods of the tag record indicated. ‘Baseline phase’ is the period preceding any exposure. ‘Exposure’ includes the 3 sessions analyzed in this study (no-sonar control in blue, sonar 1 and sonar 2 in yellow), plus the killer whale playback (in pink) analysed by Curé et al. (2015). The green line in sonar 2 indicates that this particular exposure was conducted as a no ramp-up, thus only lasting 5 min. 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

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 by 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 3 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 3 sessions, the number of lunges was divided into 3 different phases: during the exposure period (Dur), before (Pre) the exposure and after (Post) the exposure session, the last 2 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 min).

The data were analysed using a Poisson generalized estimation equation (GEE) model in R software version 3.0.2 (R Core Team 2013) using the *geepack* package (Højsgaard et al. 2006). GEEs allow us to estimate population average parameters from correlated and clustered data by appropriately inflating the standard errors (Hardin & 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, 2 of the tagged animals were part of the same group and therefore could not be assumed to be independent of each other. 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 & Hilbe 2003). The response variable was the number of lunges in a given phase (Pre, Dur or Post phases). Because 2 animals were subjected to 5 min exposures instead of 10 min 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 2-way interaction between phase and *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 0, 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 0.

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_158a) was subject only to the no-sonar control due to a premature tag release. The remaining 12 whales were all subject to 3 exposure sessions: first a no-sonar control followed by 2 sonar sessions.

The sonar sessions resulted in escalating dose from a sound pressure level of 80–100 dB re 1 μ Pa to maximum of 160–180 dB re 1 μ Pa (Kvadsheim et al. 2015).

In total, we identified 3875 lunge events throughout the entire tag records for all animals, with lunging depth averaging (\pm 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

Table 1. Overview of experiments. For each tagged humpback whale *Megaptera novaeangliae*, 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 3 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 the 3 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

Whale ID	Date	Total no. lunges	No-sonar control			Sonar 1			Sonar 2						
			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	09:23:00	0	0	0	10:46:00	0	0	0	Solitary
mn11_158a	07.06.2011	158	18:37:00	3	1	2	-	-	-	-	-	-	-	-	-
mn11_160a	09.06.2011	103	07:16:00	0	0	0	09:14:00	0	0	0	10:36:00	0	0	0	Mother-calf pair
mn11_165e	14.06.2011	304	17:40:00	2	0	5	19:56:00	9	2	1	21:03:00	0	0	0	Mother-calf pair
mn11_165d	14.06.2011	522	17:40:00	6	3	7	19:56:00	10	1	1	21:03:00	0	0	0	Mother-calf pair
mn12_161a	09.06.2012	193	22:44:00	5	2	1	00:59:00	0	0	0	02:23:00	0	0	0	Solitary pair
mn12_164a	12.06.2012	325	22:28:00	0	7	7	00:00:30	7	0	0	01:38:00	7	0	6	Solitary pair, no calf
mn12_170a	18.06.2012	255	08:49:00	0	0	0	10:41:00	7	4	0	12:32:00	16	9	10	Pair, no calf
mn12_170b	18.06.2012	92	08:49:00	0	0	0	10:41:00	0	0	0	12:32:00	6	0	1	Pair, no calf
mn12_171a	19.06.2012	909	16:48:00	12	11	16	18:37:00	15	8	11	19:52:00	9	1	1	Pair, no calf
mn12_178a	26.06.2012	360	05:15:00	8	7	10	07:25:30	0	4	7	08:46:00	5	7	2	Group of 2-3, no calf
mn12_179a	27.06.2012	0	13:51:00	0	0	0	15:07:00	0	0	0	16:19:00	0	0	0	Solitary
mn12_180a	28.06.2012	355	21:01:00	10	4	5	22:55:00	15	1	0	00:55:00	0	0	0	Mother-calf pair

well as a clear increase in flow noise in the spectrogram (Fig. 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 (Table 1). 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 3 session 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 (Fig. 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 ses-

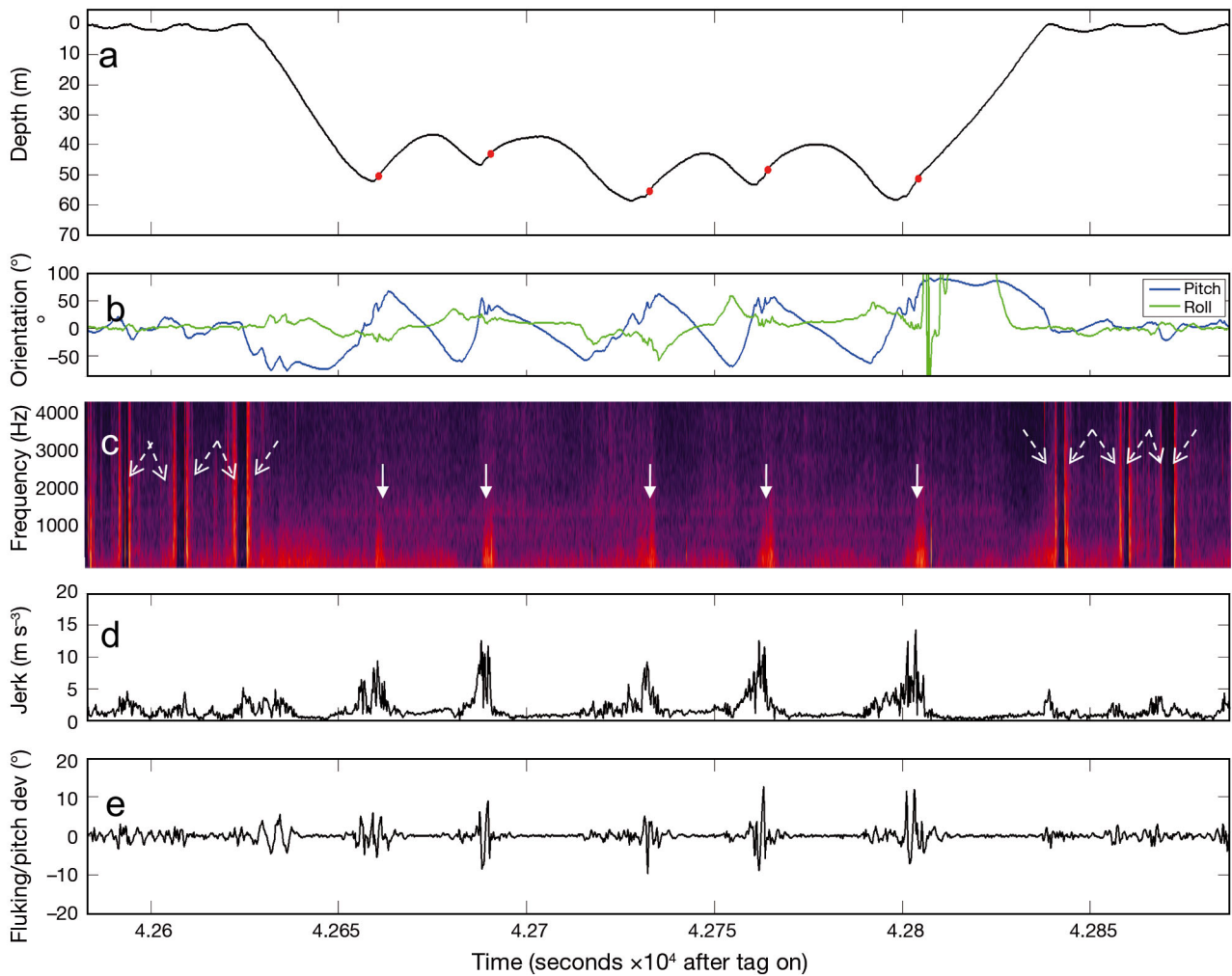


Fig. 2. Typical example of a 5 min sample of Dtag data (mn12_170a) illustrating a foraging dive by a humpback whale *Megaptera novaeangliae* with 5 lunge-feeding events. (a) Depth profile with lunges indicated as red dots. (b) Body orientation of the whale in degrees shown as up-down pitch angle (blue) 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 (solid arrows). The loud paired broadband impulses are splashes when the animal surfaces (dashed arrows). (d) Jerk signal (acceleration rate of change) showing acceleration peaks at times of lunges. (e) Fluke stroke activity in degrees, derived as the pitch deviation, showing that the whale is actively fluke-stroking 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

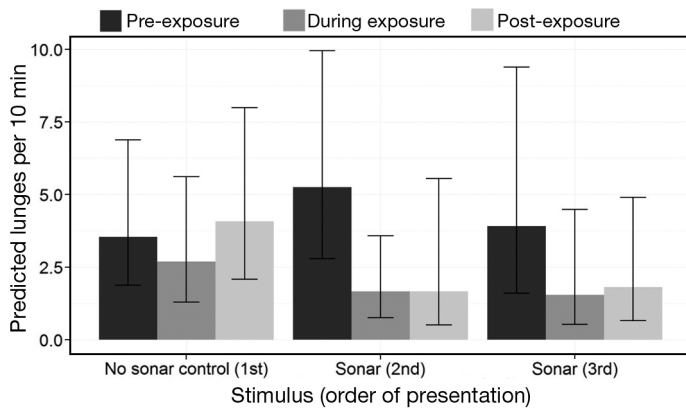


Fig. 3. Generalized estimation equation (GEE) model results. Predicted number of lunges made by a humpback whale *Megaptera novaeangliae* for 10 min time periods obtained from the selected GEE model. The bars show predictions from the selected model for each combination of the factor covariates, while error bars indicate 95% confidence intervals from a parametric bootstrap. See Table 2 for tests of significance of specific contrasts

Table 2. Comparisons between different factor level combinations (each a combination of 1 factor level of session_order and 1 factor level of period). Period could be 1 of the 3 phases (Pre, Dur, Post; see Table 1) or 1 of the 2 magnitudes of change between phases Pre and Dur (Pre_Dur) and between phases Pre and Post (Pre_Post). The comparisons were 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. *Comparisons where the quantiles do not span 0, suggesting that there is some difference between factor levels at the 95 % confidence level

Combination 1	Combination 2	Mean difference	Lower 2.5 percentile	Upper 2.5 percentile	
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 1 Pre_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	*

sions. 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, Fig. 3). However, this was not the case for the no-sonar control (95 % chance that the true difference between Pre and Dur was 0; 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 min 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 2 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 0.

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 dur-

ing 2 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 2 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 do not give any indication of sensitization 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 min⁻¹), showing reduced lunge rates post-exposure (Table 2), indicating that whales did not immediately resume feeding activity following sonar exposure.

Besides 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 faeces were seen regularly in the 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-Mauritzen 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 1 whale actually initiated feeding (mn12_178a, sonar 1). In a sonar exposure with 2 tagged individuals (mn12_170ab), 1 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 or 3 animals, some were 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). In a parallel study (see next section), 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 grounds 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 a 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 exercise 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 by 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 h (Sivle et al. 2015). Killer whales do regularly target humpback whales (Jefferson et al. 1991, McCordic et al. 2014), and prey are expected to

make fitness-reducing behavioural decisions if they are balanced by a reduction in predation pressure on fitness. Sonar exposure seems to induce an alteration of the foraging activity similar to the response seen when there is an immediate risk of predation attacks. This indicates that 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 whales are exposed frequently, as it entails reduction of feeding in a seasonal prime feeding habitat.

Acknowledgements. We appreciate the effort of the entire 3S field research team during data collection as well as the staff on 'H.U. Sverdrup'. The project was funded by the Norwegian Ministry of Defence, the US Office of Naval Research, the Netherlands Ministry of Defence and DGA French Ministry of Defence. P.L.T. received funding from the MASTS pooling initiative (The Marine Alliance for Science and Technology for Scotland), and their support is gratefully acknowledged. MASTS is funded by the Scottish Funding Council (grant reference HR09011) and contributing institutions. Statistical analyses were supported by the Multi-study Ocean acoustics Human effects Analysis (MOCHA) project funded by the United States Office of Naval Research grant N00014-12-1-0204.

LITERATURE CITED

- Christensen I, Haug T, Øien N (1992) Seasonal distribution, exploitation and present abundance of stocks of large baleen whales (Mysticeti) and sperm whales (*Physeter macrocephalus*) in Norwegian and adjacent waters. *ICES J Mar Sci* 49:341–355
- Clapham PJ, Young SB, Brownell RL Jr (1999) Baleen whales: conservation issues and the status of the most endangered populations. *Mammal Rev* 29:37–62
- Cox TM, Ragen TJ, Read AJ, Vos E and others (2006) Understanding the impacts of anthropogenic sound on beaked whales. *J Cetacean Res Manag* 7:177–187
- Curé C, Sivle LD, Visser F, Wensveen PJ and others (2015) Predator sound playbacks reveal strong avoidance responses in a fight strategist baleen whale. *Mar Ecol Prog Ser* 526:267–282
- D'Amico A, Gisiner RC, Ketten DR, Hammock JA, Johnson C, Tyack PL, Mead J (2009) Beaked whale strandings and naval exercises. *Aquat Mamm* 35:452–472
- Doksæter L, Godø OR, Handegard NO, Kvadsheim PH, Lam FP, Donovan C, Miller PJ (2009) Behavioral responses of herring (*Clupea harengus*) to 1–2 and 6–7 kHz sonar signals and killer whale feeding sounds. *J Acoust Soc Am* 125:554–564
- Doksæter L, Handegard NO, Godø OR, Kvadsheim PH, Nordlund N (2012) Behavior of captive herring exposed to naval sonar transmissions (1.0–1.6 kHz) throughout a yearly cycle. *J Acoust Soc Am* 131:1632–1642
- Dunlop RA, Noad MJ, Cato DH, Kniest E, Miller PJ, Smith JN, Stokes MD (2013) Multivariate analysis of behavioural response experiments in humpback whales (*Megaptera novaeangliae*). *J Exp Biol* 216:759–770
- Enger PS (1967) Hearing in herring. *Comp Biochem Physiol* 22:527–538
- Friedlaender AS, Tyson RB, Stimpert AK, Read AJ, Nowacek DP (2013) Extreme diel variation in the feeding behavior of humpback whales along the western Antarctic Peninsula during autumn. *Mar Ecol Prog Ser* 494: 281–289
- Goldbogen JA, Calambokidis J, Shadwick RE, Oleson EM, McDonald MA, Hildebrand JA (2006) Kinematics of foraging dives and lunge-feeding in fin whales. *J Exp Biol* 209:1231–1244
- Goldbogen JA, Pyenson ND, Shadwick RE (2007) Big gulps require high drag for fin whale lunge feeding. *Mar Ecol Prog Ser* 349:289–301
- Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Pyenson J, Schorr G, Shadwick RE (2011) Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *J Exp Biol* 214: 131–146
- Goldbogen JA, Southall BL, DeRuiter SL, Calambokidis J and others (2013) Blue whales respond to simulated mid-frequency military sonar. *Proc R Soc Lond B Biol Sci* 280: 20130657
- Hardin JW, Hilbe JM (2003) Generalized estimating equations. Chapman & Hall/CRC, Boca Raton, FL
- Højsgaard S, Halekoh U, Yan J (2006) The R package gee-pack for generalized estimating equations. *J Stat Softw* 15:i02
- Isojunno S, Curé C, Kvadsheim PH, Lam FPA, Tyack PL, Wensveen PJ, Miller PJO (2016) Sperm whales reduce foraging effort during exposure to 1–2 kHz sonar and killer whale sounds. *Ecol Appl* 26:77–93
- Jefferson TA, Stacey PJ, Baird RW (1991) A review of killer whale interaction with other marine mammals: predation to co-existence. *Mammal Rev* 21:151–180
- Johnson MP, Tyack PL (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J Oceanic Eng* 28:3–12
- Kvadsheim P, Lam FP, Miller PJO, Doksæter L and others (2011) Behavioural response studies of cetaceans to naval sonar signals in Norwegian waters—3S-2011 CruiseReport. FFI-rapport 2011/01289. Forsvarets forsknings-institutt/Norwegian Defence Research Establishment (FFI), Kjeller. <http://rapporter.ffi.no/rapporter/2011/01289.pdf>
- Kvadsheim P, Lam FP, Miller P, Wensveen P and others (2012) Behavioural responses of cetaceans to naval sonar signals in Norwegian waters—the 3S-2012 cruise report. FFI-rapport 2012/02058. Norwegian Defence Research Establishment (FFI), Kjeller. <http://rapporter.ffi.no/rapporter/2012/02058.pdf>

- Kvadsheim P, Lam FP, Miller P, Sivle LD and others (2015) The 3S2 experiments—studying the behavioral effects of naval sonar on northern bottlenose whales, humpback whales and minke whales. FFI-rapport 2015/01001. Norwegian Defence Research Establishment (FFI). <http://rapporter.ffi.no/rapporter/2015/01001.pdf>
- Lockyer C (1984) Review of baleen whale (Mysticeti) reproduction and implications for management. Rep Int Whaling Comm 6:27–50
- McCaughey RD, Jenner MN, Jenner C, McCabe KA, Murdoch J (1998) The response of humpback whales (*Megaptera novaeangliae*) to offshore seismic survey noise: preliminary results of observations about a working seismic vessel and experimental exposures. APPEA J 38:692–707
- ✦ McCordic JA, Todd SK, Stevick PT (2014) Differential rates of killer whale attacks on humpback whales in the North Atlantic as determined by scarification. J Mar Biol Assoc UK 94:1311–1315
- ✦ Meyer-Gutbrod EL, Greene CH, Sullivan PJ, Pershing AJ (2015) Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population Mar Ecol Prog Ser 535:243–258
- ✦ Miller PJO, Kvadsheim PH, Lam FPA, Wensveen PJ and others (2012) The severity of behavioral changes observed during experimental exposures of killer (*Orcinus orca*), long-finned pilot (*Globicephala melas*), and sperm (*Physeter macrocephalus*) whales to Naval sonar. Aquat Mamm 38:362–401
- ✦ New LF, Clark JS, Costa DP, Fleishman E and others (2014) Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. Mar Ecol Prog Ser 496:99–108
- Nøttestad L, Olsen E (2004) Whales and seals: top predators in the ecosystem. In: Skjoldal HR (ed) The Norwegian Sea ecosystem. Tapir Academic Press, Trondheim, p 395–434
- ✦ Nøttestad L, Sivle LD, Krafft BA, Langaard L and others (2014) Ecological aspects of fin whale and humpback whale distribution during summer in the Norwegian Sea. Mar Ecol 35:221–232
- Øien N (2007) Hval i Norskehavet (Whales in Norwegian waters). In: Skogen M, Gjørseter H, Robbenstad Y (eds) Havets ressurser og miljø. Fisken og Havet, særnummer 1. Institute of Marine Research, Bergen, p 89–90
- Panigada S, Notobartolo Di Sciara G, Zanardelli-Panigada M, Airoidi S, Borsani JF, Jahoda M (2005) Fin whales (*Balaenoptera physalus*) summering in the Ligurian Sea: distribution, encounter rate, mean group size and relation to physiographic variables. J Cetacean Res Manag 7: 137–145
- Pivorunas A (1979) Feeding mechanisms of baleen whales. Am Sci 67:432–440
- R Core Team (2013). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Simon M, Johnson M, Tyack P, Madsen PT (2009) Behaviour and kinematics of continuous ram filtration in bowhead whales (*Balaena mysticetus*). Proc R Soc Lond B Biol Sci 276:3819–3828
- ✦ Simon M, Johnson M, Madsen PT (2012) Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. J Exp Biol 215: 3786–3798
- ✦ Sivle LD, Kvadsheim PH, Ainslie MA, Solow A, Handegard NO, Nordlund N, Lam FPA (2012) Impact of naval sonar signals on Atlantic herring (*Clupea harengus*) during summer feeding. ICES J Mar Sci 69:1078–1085
- ✦ Sivle LD, Kvadsheim PH, Curé C, Isojunno S and others (2015) Severity of expert-identified behavioural responses of humpback whale, minke whale and northern bottlenose whale to naval sonar. Aquat Mamm 41: 469–502
- ✦ Skern-Mauritzen M, Johannesen E, Bjørge A, Øien N (2011) Baleen whale distributions and prey associations in the Barents Sea. Mar Ecol Prog Ser 426:289–301
- ✦ Tyack P (1983) Differential response of humpback whales, *Megaptera novaeangliae* to playback of song or social sounds. Behav Ecol Sociobiol 13:49–55
- ✦ Visser F, Miller PJO, Antunes R (2014) The social context of individual foraging behaviour in long-finned pilot whales (*Globicephala melas*). Behaviour 151:1453–1477
- ✦ Ware C, Friedlaender AS, Nowacek DP (2011) Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. Mar Mamm Sci 27:587–605
- ✦ Wartzok D, Popper AN, Gordon J, Merrill J (2003) Factors affecting the responses of marine mammals to acoustic disturbance. Mar Technol Soc J 37:6–15
- Wartzok D, Altmann W, Au W and others (2005) Marine mammal populations and ocean noise: determining when noise causes biologically significant effects. NRC report. National Academies Press, Washington, DC

Editorial responsibility: Per Palsbøll,
Groningen, The Netherlands

Submitted: February 11, 2016; Accepted: November 2, 2016
Proofs received from author(s): December 9, 2016