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Using at-sea experiments to study the effects of airguns on the foraging behavior of sperm whales in the Gulf of Mexico

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ABSTRACT

Acoustic exposure and behavior of 8 sperm whales were recorded with acoustic and movement-recording tags before, during and after 5 separate 1–2 h controlled sound exposures of industry-provided airgun arrays. None of the 8 whales changed behavioral state (7 foraging, 1 resting) following the start of ramp-up at distances of 7–13 km, or full array exposures at 1–13 km. The most closely approached whale rested throughout exposure but started a foraging dive shortly after the airguns ceased, possibly indicating a delay in foraging during exposure. Using visual tracking and dead-reckoning of tagged animals, we found that their direction-of-movement was random with respect to the airguns, but correlated with their direction-of-movement just prior to the start of exposure, indicating that the tested whales did not show horizontal avoidance of the airguns. Oscillations in pitch generated by swimming movements during foraging dives were on average 6% lower during exposure than during the immediately following post-exposure period, with all 7 foraging whales exhibiting less pitching ($p = 0.014$). Buzz rates, a proxy for attempts to capture prey, were 19% lower during exposure but given natural variation in buzz rates and the small numbers of whales, this effect was not statistically significant ($P = 0.141$). Though additional studies are strongly recommended, these initial results indicate that sperm whales in the highly exposed Gulf of Mexico habitat do not exhibit avoidance reactions to airguns, but suggest they are affected at ranges well beyond those currently regulated due to more subtle effects on their foraging behavior.

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1. Introduction

The northern Gulf of Mexico contains a population of sperm whales that is increasingly exposed to airgun sounds used to search for hydrocarbon deposits in the seabed (MMS, 2004). Airguns produce a powerful sound,

with back-calculated on-axis array source levels >240 dB peak re $1 \mu\text{Pa}$ at 1 m (Richardson et al., 1995). Over 370,400 km (200,000 nmi) of seismic surveys are shot every year in the Gulf of Mexico, and deep-water exploration and production is predicted to increase markedly over the next few decades (MMS, 2004). Despite the increasing exposure and potential risk of disturbance, data regarding sperm whale reactions to airguns are sparse (Nowacek et al., 2007). Baleen whales have been reported to avoid or move away from airgun sources in several studies (Richardson et al., 1995). Analysis of marine mammal sightings from commercial seismic

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on the animal which varies from whale to whale. Nonetheless, measurement of pitching movements recorded by the tag provides an index of the relative **locomotion effort** of each individual whale, allowing assessment of the influence of airgun sounds on relative locomotion effort for each individual.

In 2002 and 2003, we attached Dtags to 8 sperm whales in order to record their foraging behavior during 5 controlled experimental exposures of airgun sounds in the northern Gulf of Mexico. In addition, data on the natural variability of sperm whale behavior was available from 13 non-exposed whales with Dtag data records sufficiently long to use as control data. Specifically, we tested the hypotheses that sperm whales would: (I) avoid an oncoming seismic survey vessel when airguns were operating, (II) interrupt their overall diving and foraging behavior with a gross change in behavioral state, (III) increase their locomotor activity to avoid the sound source or capture prey in increased noise, or (IV) have lower prey capture attempt rates when exposed to airgun pulses. Here we describe the methods by which we conducted the experiments and analyzed the resulting data. We detail some of the methodological challenges encountered in collecting and analyzing these data and explore the sample sizes required to uncover more subtle, but likely important effects. We conclude with implications of our results for management and suggestions for improving future studies using this type of methodology.

2. Methods

2.1. Field methods

The behavioral response experiments were performed in August–September of 2002 and June of 2003 in the northern Gulf of Mexico. The experimental procedure involved the following steps: (1) tagging one or more whales with Dtags, (2) following tagged whales at a distance to fix their surfacing locations, (3) after a pre-exposure period, exposing the tagged whales to sound from an airgun array on a dedicated seismic source vessel at a controlled distance, (4) continuing to follow tagged whales after the airguns were turned off to record post-exposure behavior, and (5) recovering the tag once it detached from the whale. At any one time, three vessels were involved in the study: a dedicated seismic vessel towing an industry-standard airgun array; a research vessel for visual observation and acoustic monitoring, and a rigid-hulled inflatable boat (RHIB) launched from the observation vessel for tagging.

Whales were initially detected and tracked using the observation vessel (R/V Gyre in 2002; R/V Maurice Ewing in 2003). Whales were located visually using big-eye binoculars or acoustically with a towed hydrophone array and real-time localization. Whales were approached for tagging from the RHIB and tags were attached to whales with suction cups, following published methods (Miller et al., 2004b). Where possible, up to 3 whales were tagged in the same group to increase the number of animals sampled and to improve the chances that at least one tag

would remain attached throughout the post-exposure period. A VHF beacon in the tag facilitated identification and visual tracking of each tagged whale using a directional VHF receiver on the observation vessel. Surfacing locations were fixed using bearing and range estimates from big-eye binoculars (Kinzey and Gerrodette, 2001), and were plotted real-time to assist in tracking.

During the pre-exposure period, a dedicated seismic source vessel was moved to an appropriate position with respect to the tagged whales and the airgun array was deployed. In 2002, M/V Rylan T. with the M/V Speculator on deck towed a 20 gun array with 13.8 MPa (2000 psi) firing pressure and a total volume of 27.5 liters (1680 in³). The far-field, vertical signature of the array had a back-calculated source level of 258 dB re 1 μ Pa at 1 m (peak-peak) in the 3–800 Hz frequency band (DeRuiter et al., 2006). The array was fired every 15 sec with a 30 min ramp-up from 1 to 20 guns. In 2003, seismic vessel R/V Kondor towed a 31 gun array (with three being spares) with 13.8 MPa (2000 psi) firing pressure and a total volume of 50.6 liters (3090 in³). The far-field, vertical signature of the Kondor array had a back-calculated source level of 261 dB re 1 μ Pa at 1 m (peak-peak) in the 3–218 Hz frequency band (DeRuiter et al., 2006). This array was also fired every 15 sec and began with a 30 min ramp up from 1 to 28 guns.

If weather conditions allowed for effective mitigation (see below), the seismic vessel was directed to approach the tagged whales at an oblique angle during both the ramp-up and the planned 90 min full-array exposure period. Each whale was tracked as well as possible from the observation vessel until the tag detached from the whale and was recovered. After completing each experiment, all vessels moved 37 km (20 nm) before renewing the search for whales to reduce the risk of re-testing the same group of animals.

The US Federal research permit under which the whale tagging and exposure experiments were conducted required that no marine mammal or sea turtle be exposed to sound levels above 180 dB re 1 μ Pa (rms). To comply with this requirement, the experiment on whales sw254a-c (Table 1) was halted for 19 min when dolphins were sighted near the seismic vessel, and then restarted once the dolphins were resighted outside of the mitigation zone. Because the 19 min silent period followed a period of exposure, it was classified as part of the post-exposure condition. Two experiments were stopped early, after 30 and 66 min, because darkness hindered mitigation procedures. The presence of an ongoing commercial seismic survey operation in the area forced us to break off one planned experiment before transmissions were started because exposure to the commercial survey made it impossible to collect pre-exposure control data.

2.2. Data analysis

Sensor data collected by the tag, comprising depth (resolution of 0.5 m), acceleration in 3-axes, and magnetic field strength in 3-axes, were filtered and down-sampled from a raw sampling rate of 23.5 Hz (2000–July 2003) or

Table 1

Experiment details including whale IDs, three measures of the sound level of pulses received at the whale (Madsen et al., 2006) and source-whale distance during the full array condition.

Experiment#/yr	1/2002	2/2002	2/2002	2/2002	3/2003	4/2003	4/2003	5/2003
Whale	sw253a	sw254a	sw254b	sw254c	sw164a	sw165a	sw165b	sw173b
Tag on time	16:38	10:13	10:28	10:34	9:48	13:35	13:38	14:46
Tag off	20:58	21:45	22:52	22:56	23:20	06:19	06:05	20:38
Exposure start	17:59	12:16	12:16	12:16	18:26	17:01	17:01	17:23
Exposure end	19:15	14:20	14:20	14:20	19:26	19:01	19:01	19:23
SPL pk-pk	142–162	136–155	136–152	139–155	140–157	137–160	135–160	131–162*
SPL rms	120–144	121–140	121–135	125–139	125–146	123–146	119–147	111–147*
SEL	106–127	105–123	108–118	106–123	112–129	106–130	105–130	94–131*
Start dist (km)	11.5	11.7	12.1	11.5	12.1	No info	12.5	7.4
Full-array dist (km)	8.4–12.8	6.5–9.9	5.7–9.9	5.0–9.2	11.0–11.7	No info	3.1–10.2	1.4–5.7

SPL refers to sound pressure level in dB re $1 \mu\text{Pa}$, and SEL to sound exposure level in dB re $1 \mu\text{Pa}^2\text{s}$.

* Maximum value underestimates the actual received level, as some signals were clipped. Times given are local time.

50 Hz (2003) to a decimated rate of 5.88 or 5 Hz, respectively (Johnson and Tyack, 2003). The pressure data from the depth sensor were converted to meters using calibrated values. The data from the magnetometers and accelerometers were converted to heading, pitch, and roll using the techniques described in Johnson and Tyack (2003) and Miller et al. (2004b). Scoring of buzzes (Miller et al., 2004a) and division of dives into descent, bottom and ascent phases followed published techniques (Miller et al., 2004b; Watwood et al., 2006).

Our statistical design treated each whale recording as an individual sample selected at random for tagging, but we broke off attempts to tag whales that reacted to our tagging approaches, so there may be some bias in the sample of animals actually tagged towards those that are less responsive to small vessel approach. For each tag recording, we classified up to 90 min of data before the start of ramp-up as the “pre-exposure” condition, the 30 min ramp-up period as “ramp-up” condition, the period when all guns were firing as “full-array” condition, and up to 90 min of data following the termination of airgun firing as “post-exposure” condition. Movement and foraging behavior were quantified during each condition, and we compared the observed differences statistically.

Two of the experiments were conducted on more than one tagged animal within the same group. Here, we treat each individual as an independent subject because we consider it unlikely that the reaction of one sperm whale could influence the reaction of other whales for such individual-specific behaviors as pitching movements and buzzes during prey capture. Although sperm whales separate by hundreds to thousands of meters during foraging dives, their clicks are audible over these ranges allowing coordination of foraging and movements. Therefore, we cannot rule out that sperm whales within a group may react to the same airgun exposure in some correlated manner. Because we feel this concern is greatest for horizontal movement as animals may track each other's movements, we also analyzed the horizontal-movement response data with the group as the unit of analysis.

2.3. Research effects on behavior

Our research protocol was designed to minimize the influence of our observation and tagging activities on the behavior of the study whales, particularly effects that might not be consistent throughout the different phases of each experiment. The use of a towed hydrophone array and big eye binoculars enabled the observation vessel to track whales while standing off at several kilometers distance. Tracking began as soon as a whale was tagged, and the mode in which the observation vessel moved with respect to the whales was independent of the different phases of the experiment. Using this procedure, we feel that any influence of the observation vessel itself should be minor and constant throughout the experiment. We attempted to minimize the impact of tagging by approaching whales slowly in a small boat from behind, and avoiding any sudden movements. Short-term behavioral reactions to the tag attachment were generally minor (as defined by Weinrich et al., 1992) such as a brief dive or change in swimming speed or direction. Tagging did not appear to provoke a concerted change in the general movement direction of the group.

To evaluate whether the foraging behavior of sperm whales is influenced by tagging, the behavior of an individual should ideally be recorded before and after tagging. This approach is impractical in this case because of the uncertainty as to which individual animal in a group would be tagged, and because diving parameters of individual sperm whales in a group are difficult to observe without tags. Instead, Miller et al. (2005) examined the dive durations, buzz rates, and pitching movements during the bottom foraging phase of each dive for non-exposed sperm whales, tagged in the same area, for which the tag remained attached for at least two ($N = 24$) or four dives ($N = 13$). Relative to the second dive post tagging, the first dive had a lower bottom-phase buzz rate (-14.4% paired $t_{23} = -2.17$, $P = 0.041$), a non-significant decrease in pitching movements (-4.9% $t_{23} = -1.49$, $P = 0.15$), and shorter duration (-7.3% , $t_{23} = -2.45$, $P = 0.024$). Using repeated measures ANOVA, dives 2–4 did not differ for buzz rates or pitching energy (buzz-rate: $F_{2,11} = 0.240$,

$P = 0.79$; pitching-energy: $F_{2,11} = 0.148$, $P = 0.86$), though dive 4 was 5.8% shorter than the mean of dives 2 and 3 ($F_{2,11} = 3.81$, $P = 0.055$). These results indicate that foraging behavior during the first post-tagging dive is affected by tagging, but that subsequent dives show little sign of a more prolonged effect.

2.4. Direction of movement (avoidance)

We fixed the location of each tagged whale at the surface as often as possible using big-eye binoculars. However, surfacing events were often missed because the whales traveled large distances between surfacings, and the observation vessel was not always able to track the tagged whale acoustically while it was diving. In a few cases, a low tag position on the whale resulted in infrequent radio signals further complicating visual tracking.

We estimated whale tracks throughout each tag deployment first by geo-referencing the track using the tag-deployment position, and then dead-reckoning subsequent positions based on the whale depth and orientation recorded by the tag, an average swimming speed, and an average current direction and speed (Johnson and Tyack, 2003; Wilson and Wilson, 1988; Mitani et al., 2003; Zimmer et al., 2005). The last three parameters are not measured by the tag, so we estimated them iteratively to fit the predicted surfacing locations with those obtained visually over an entire whale's track (Fig. 3). To check the effectiveness of this estimation, we measured the discrepancy between a sample of 16 visually-fixed locations and the final derived track, with mean error of $370\text{ m} \pm 223\text{ m}$ (95% CI). Thus, we consider location and whale-to-source distances reported here to be accurate to roughly $\pm 0.5\text{ km}$, except for whale sw165b (Madsen et al., 2006). Whale sw165b was only sighted once after tagging and its track is considered no more accurate than $\pm 1\text{ km}$. Whale sw165a was excluded from movement and range analyses as we had no confirmed sightings after tagging.

For avoidance analyses, we calculated each whale's direction of movement over successive 30 min intervals, dictated by the 30 min duration of the ramp-up period. Movement during each interval was measured as the vector joining the whale's location at the start and end of the interval. The angle between the mean movement vector (r) and the mean bearing to the source over the same interval was calculated. The Rayleigh "R" statistic is equal to nr , where n represents the number of samples (Zar, 1984). The "z-statistic" (R^2/n or nr^2) was used to test hypotheses of whale movement for each comparison. This test was done once using each whale as an independent unit, and again combining the whales of experiment 2 (sw254a-c) into a single data unit.

2.5. Foraging behavior during deep dives

As discussed above, some foraging parameters recorded by the tag during the first dive following tag deployment appear to be affected by the act of tagging, indicating that a post-tagging recovery period should be

included in the design of studies using such detailed metrics of foraging behavior. Although airgun exposures started at least 80 min after tagging, some tag recordings made in 2002 did not contain sufficient dives prior to exposure to be able to exclude the first dive after tagging. Therefore, to reduce the risk of making comparisons to 'baseline' behavior that had been influenced by tagging, we did not use the pre-exposure condition as a baseline for studying effects on foraging behavior in the 2002 experiments. We had solved this problem by 2003, indicated by long intervals between tagging and the start of exposure (Table 1). However, rather than split an already small data set, we used the post-exposure condition as the non-exposure condition for comparison. We also excluded the "ramp-up" period, which contained a mix of very low exposure levels at the start and higher levels near the end. Therefore, the primary contrast used for testing for effects of airguns in our study compared pitching energy and buzz-rates during the full-array exposure condition to those during the post-exposure condition.

Buzzes were identified in the acoustic record by their distinctive acoustic characteristics (Miller et al., 2004a). Pitching movements were quantified for each tag record. Both orientation changes (e.g., pitching) and specific acceleration (e.g., thrust and heave) during swimming contribute to the accelerometer signal, and the relative magnitude of these depend on the position of the tag on the whale. To eliminate bias due to animal orientation, pitching movements were quantified in terms of changes in the whale's orientation, with reference to its local mean orientation. The orientation of the whale at each sample was represented by two direction cosine matrices, one constructed from the instantaneous accelerometer and magnetometer measurements, and another constructed from the same measurements filtered with a low-pass-filter (0.1 Hz) to remove the signal at the fluking rate. The whale-relative elevation angle between the smoothed and instantaneous orientations was taken as representing pitching movements during fluking, and the RMS level of this time series was then calculated over the appropriate time interval. The resulting metric, for which we coin the term 'pitching effort', combines information about the rate and relative strength of fluking motions.

In our sperm whale sample, pitching effort increased by an average of 41.1% within 15 s of a buzz relative to movements between buzzes ($N = 42$ whales, $t_{41} = 10.49$, $P < 0.001$). Therefore, to avoid a potential confound where pitching effort results are correlated with buzz-rate results, we excluded pitching movements within $\pm 15\text{ s}$ of the end of the buzz. This means that we only examined pitching movements during the search phase of echolocation-mediated foraging, and not during prey capture attempts.

We then calculated buzz rates and pitching effort during the bottom phase of deep dives (Fig. 1). The timing of the airgun exposure was not synchronized to the dive intervals and so the bottom phase of some dives spanned both exposure and post-exposure conditions. To account for this, we divided each dive into blocks (see Fig. 1), counting the buzzes and pitching movements separately

whales during the full-array exposure condition (Table 1). In some cases, the approach distance was restricted by the presence of other whales in the vicinity of the tagged whale and, in one case, uncertainty as to the location of the tagged whale. The maximum m-weighted (Southall et al., 2008) sound pressure levels of airgun sounds recorded by the tags (Madsen et al., 2006) were at least 152–162 dB peak-peak re 1 μ Pa (135–147 dB rms re 1 μ Pa, sound exposure level of 118–131 dB re 1 μ Pa²s). Pulse received levels were not correlated with source distance beyond 6 km, likely due to complex acoustic propagation through a stratified water column and the seafloor (DeRuiter et al., 2006; Madsen et al., 2006).

3.1. Behavioral state of the tagged whales

We first examined whether whales changed their behavioral state during exposure to airgun sounds. Six of the eight exposed whales conducted uninterrupted foraging dives throughout the exposure (e.g. Fig. 1). Another whale, sw253a, made deep dives for 49.4 min after the start of full-array exposure. It then performed a 17.8 min shallow dive during which the exposure period ended. It resumed deep diving 13.1 min after the final airgun pulse. While this behavior may indicate an aversion to deep-diving near the end of the full-array condition, short shallow dives between long dives are not atypical, so without replicates, we cannot conclude that this change of dive-pattern was in response to the airgun sounds.

A link between airgun exposure and behavioral state was more strongly indicated in the resting whale sw173b. Sperm whales worldwide conduct stereotyped resting

drift dives during which they maintain a vertical posture near the sea surface (Miller et al., 2008).

The tag data for whale sw173b recorded the whale to be in a resting bout that lasted 265 min. The resting bout started 14 min after the tag was deployed, continued throughout pre-exposure, rampup and full-array conditions, and ceased 4 min after the final airgun pulse (Fig. 2; Supplementary Video). It is unknown if the whale had been resting prior to tag attachment. The foraging dive performed by this whale in the post-exposure condition appeared to be typical. The resting bout of sw173b was the longest of all 44 resting bouts recorded from 59 sperm whales worldwide (Miller et al., 2008). The 16 other resting bouts observed in the Gulf of Mexico were significantly shorter, with an upper quartile value of 36.6 min. While this single observation remains anecdotal, it seems unlikely that the whale would rest for such an unusually long time and cease resting behavior so closely following the final airgun pulse by chance alone.

3.2. Direction of movement (avoidance)

The direction of movement of the 7 whales measured from the derived tracks over 30-min intervals was randomly distributed with respect to the bearing to the seismic vessel both during ramp-up and full-array conditions (ramp-up $r = 0.57$, $z_7 = 2.3$, $0.1 < p < 0.2$; full-array $r = 0.52$; $z_7 = 1.9$; $0.1 < p < 0.2$; Fig. 3, panel 8). Inspection of the tracks themselves (Fig. 3) shows that the whales did not make strong turns away from the source vessel throughout the transmission periods.

Instead, direction of movement during exposure matched movement in previous conditions (movement

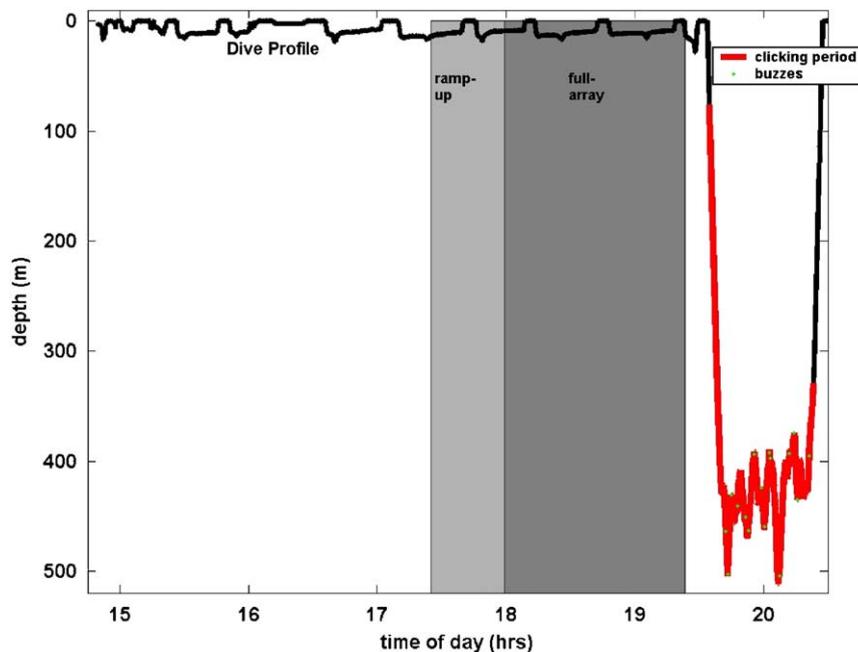


Fig. 2. Whale sw173b rested motionless and silently within a body length of the water surface throughout pre-exposure, ramp-up and full-array conditions. Within 4 min of the final airgun pulse, the whale ceased resting and produced a set of click sounds for 49 s (Supplementary Video). The whale re-surfaced for 4.4 min, and then made a deep foraging dive in the post-exposure condition with a bottom-phase buzz rate of 22.5/h.

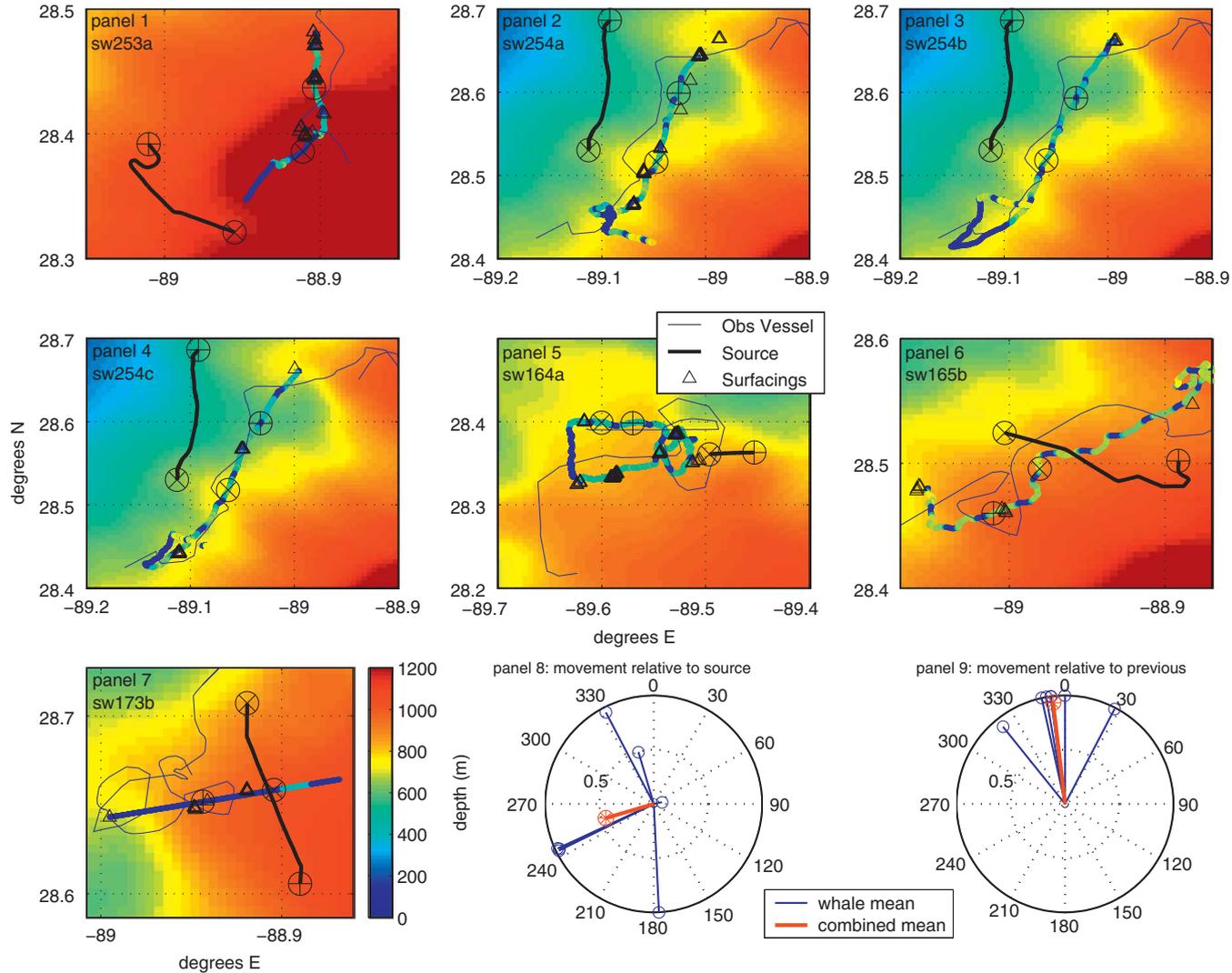


Fig. 3. Panels 1–7: Geometries of each of the behavioral response experiments. Surface observations of the tagged whale are shown in black triangles, and each whale's derived track is shown as a colored line where the color represents the depth of the whale. The movements of the observation vessel are shown as a light line, and the position of the source vessel during transmissions is shown as a thicker line. The position of each whale and the source vessel at the start, and end, of the transmission period is indicated with a circled "+", and "X", respectively. Note that whale sw165a is not included as no visual position was obtained after the tag was deployed. Panels 8 & 9: Rayleigh diagram of the travel direction of the sperm whales. Each line indicates the mean direction for a single whale (blue) and the combined mean (red) with the length of the line equal to the value of Rayleigh's "r" statistic. Panel 8: travel direction during the full-array condition relative to the airgun source. Panel 9: travel direction during the full-array condition relative to travel direction in the previous conditions (pre-exposure and rampup).

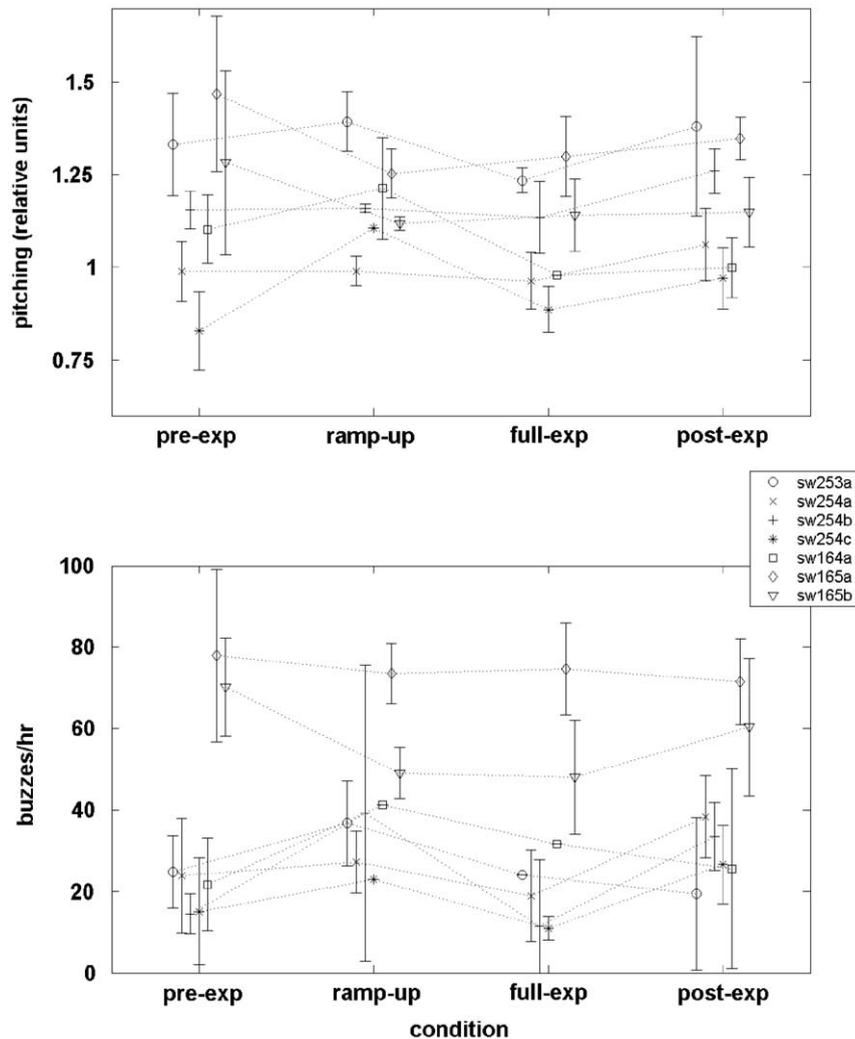


Fig. 4. Pitching effort (top) and buzz-rate (bottom) by condition for each of the tested whales. Data shown are the mean and SD (error bars) of the bottom-phase intervals. Note that statistical analyses compared only the differences between the full-array and post-exposure conditions.

Table 2

ANOVA table showing the sum-of-squares and degrees of freedom calculated using the split-plot design.

Source of variation:	Degrees of freedom (d.f.)	Sum-of-squares (SS)	
		Pitching effort	Buzz rate
Experimental condition (COND)	1	0.027	317.7
Experiment versus control whales (EorC)	1	0.924	55.2
Interaction of COND and EorC*	1	0.033	277.4
Individual whale nested within EorC (IND)	18	9.849	25459.2
Interaction of COND and IND**	18	0.079	2106.1
Error	59	1.285	9829.7

* The mean-square (SS/d.f.) of this term is the numerator in the ANOVA hypothesis test.

** This mean-square of this term is the denominator in the hypothesis test.

direction during ramp-up relative to pre-exposure CI: -36.2° to $+12.0^\circ$, $r = 0.92$, $z_7 = 5.9$, $p < 0.001$; full-array vs combined pre-exposure and ramp-up CI: -34.1° to $+18.5^\circ$, $r = 0.93$, $z_7 = 6.1$, $p < 0.001$; Fig. 3, panel 9). This result is

important because it demonstrates that our small sample size in this case was adequate to obtain statistical significance for the strongly consistent behavior of the tested whales.

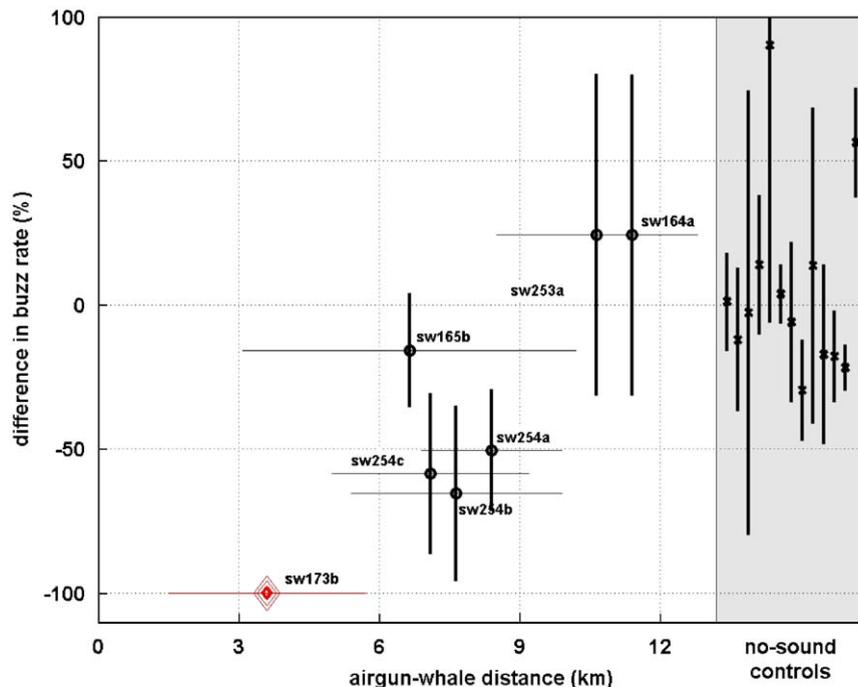


Fig. 5. The percentage difference in buzz rate during exposure compared to post-exposure conditions, relative to the post-exposure rate, is plotted against the distance from the seismic vessel to the whale (left section of figure) for 7 of the 8 experimental whales (sw165a is not indicated because no tracking information was available for this whale after tagging). The vertical bars indicate one standard error of the percent difference in buzz rate. The horizontal lines indicate the range of distances between source and whale during full-array exposure, and the symbol is plotted at the mean of the closest and furthest distances. Black symbols are used to indicate the mean difference in buzz rate observed during the bottom phases of deep dives. The red diamond corresponds to the 100% difference in buzz rate observed for whale sw173b and is coloured to reflect the different behavior of this whale: sw173b made no foraging dives during exposure, but started foraging shortly after the final seismic pulse. The right section of the figure shows percent difference in buzz rate between mock exposure and post-exposure conditions for the 13 no-sound control whales with vertical bars indicating the standard error.

the prey ingested. However, the interpretation that lower buzz-rates predict lower foraging rates could only be incorrect if whales had a higher success rate, or caught more valuable prey, when airgun sounds were present than under normal conditions.

Playback experiments of seismic pulses to captive squid (*Sepioteuthis australis*) have revealed responses including increase in swimming speed, depth changes, and increased startle responses (McCauley et al., 2000) at levels of 156–161 dB rms re $1 \mu\text{Pa}$. Seismic survey operations have also been noted to impact fish distribution and catch rates of commercial fisheries (Engås et al., 1996; Slotte et al., 2004, but see Wardle et al., 2001). Though the squid and fish species tested to date are different from the primary prey of sperm whales in the Gulf of Mexico, all squid and fish for which hearing has been measured have acute hearing in the frequency range of air gun pulses (Packard et al., 1990, Popper et al., 2003). It is therefore possible that some of the behavioral changes observed in the sperm whales may result from behavioral changes in their prey. Such ecosystem-level implications of disturbance clearly constitute an important area for further research.

The sample size from this study was insufficient to generate conclusive results on the effect of seismic

airguns on the foraging of sperm whales in the Gulf of Mexico. We found consistent, but small, changes in pitching effort which is a behavior completely under each animal's control. However, our sample size was too small for conclusive results on buzz-rates, which, as an interaction between whale and prey, have additional sources of variability. Nonetheless, our results provide preliminary evidence that airgun operations might affect the foraging behavior of sperm whales negatively, possibly reducing their foraging rate even at the moderate received levels and large ranges between whale and sound source used here. Behavioral changes may include, at one extreme, delay of diving to avoid high-intensity exposure when horizontally close to an airgun array, and, at lower levels, disruption of the whales' foraging, perhaps linked with behavioral reactions of prey, as mentioned above.

Overall, the difference in buzz-rates between exposure and post-exposure appeared to depend on the distance between the whale and the sound source (Fig. 5). The relationship between buzz rate and received sound pressure levels of the airgun sounds was not as clear as the relationship with distance, perhaps because received levels did not decline monotonically with distance. The received levels of airgun signals show a complex pattern of variation with range and depth, and may increase with range at some ranges and depths (Madsen et al., 2006). Sperm whales may have been influenced more by the

seismic surveys using airguns. The sperm whales in our study did not respond to startup and approach of an airgun array with any major changes in behavioral state or direction of movement. Thus, surface observations alone would likely conclude that airguns do not result in noticeable changes in sperm whale behaviour. However, even from a small sample of animals with likely extensive prior exposure to seismic surveys, our tag data indicate that exposure to airgun sounds may affect the foraging behavior of sperm whales at exposure levels well below the current 160 dB re 1 μ Pa (rms) threshold used by NMFS to predict disruption of behavior (Allen, 2004). The sperm whales in this study had consistently lower pitching effort when exposed to airguns and we observed a substantially (19%) lower buzz rate during full-array exposure relative to the post-exposure condition, though that difference was not statistically significant. That result combined with a putative delay of foraging for one whale raises a concern that feeding rates may be impacted by seismic surveys, but more data are required to test if those differences were not due to natural variations in buzz-rates and behavioral state transitions. Unlike baleen whales in previous studies (Richardson et al., 1995), the sperm whales in our study did not avoid airguns either during ramp-up or full array conditions. Sperm whales in the Gulf of Mexico may not automatically swim away from airguns starting nearby in order to avoid closer-range danger zones, raising questions about the efficacy of ramp-up as a mitigation protocol. Delay or avoidance of deep diving, which we observed in one whale, may provide some protection from high sound levels under a nearby airgun array, but may increase the risk that the seismic vessel approach animals closely at the surface. Future studies should focus on testing hypotheses pertaining to behavioral parameters that reflect the overall fitness of the animals using experiments on naive animals.

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Appendix A. Supporting Information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2009.02.008.

References

- Allen, L.K., 2004. Federal Register 69, 67535–67539.
- Bowles, A.E., Smultea, M., Wursig, B., De Master, D.P., Palka, D., 1994. Relative abundance and behavior of marine mammals exposed to transmissions from the Heard Island Feasibility Test. *Journal of the Acoustical Society of America* 96 (4), 2469–2484.
- Burgess, W.C., Tyack, P.L., LeBoeuf, B.J., Costa, D.P., 1998. A programmable acoustic recording tag and first results from free-ranging northern elephant seals. *Deep-Sea Research II* 45, 1327–1351.
- DeRuiter, S.L., Lin, Y.-T., Newhall, A.E., Miller, P.J.O., Tyack, P.L., Lynch, J.F., 2006. Acoustic modeling of airgun pulses in the Gulf of Mexico and comparison with recordings from Dtags deployed on sperm whales (*Physeter macrocephalus*). *Journal of the Acoustical Society of America* 120, 4100–4114.
- Engås, A., Løkkeborg, S., Ona, E., Soldal, A.V., 1996. Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). *Canadian Journal of Fisheries and Aquatic Sciences* 53, 2238–2249.
- Johnson, M., Aguilar de Soto, N., Madsen, P.T., in press. Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags. *Marine Ecology Progress Series*.
- Johnson, M.P., Hickmott, L.S., Aguilar de Soto, N., Madsen, P.T., 2008. Echolocation behaviour adapted to prey in foraging Blainville's beaked whale (*Mesoplodon densirostris*). *Proceedings of the Royal Society of London B* 275, 133–139.
- Johnson, M.P., Madsen, P.T., Zimmer, W.M.X., Aguilar de Soto, N., Tyack, P., 2004. Beaked whales echolocate on prey. *Proceedings of the Royal Society of London B (Biology Letters Supplement)* 271, S383–S386.
- Johnson, M.P., Madsen, P.T., Zimmer, W.M.X., Aguilar de Soto, N., Tyack, P.L., 2006. Foraging Blainville's beaked whales (*Mesoplodon densirostris*) produce distinct click types matched to different phases of echolocation. *Journal of Experimental Biology* 209, 5038–5050.
- 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 Oceanic Engineering* 28 (1), 3–12.
- Kinzey, D., Gerrodette, T., 2001. Conversion factors for binocular reticules. *Marine Mammal Science* 17, 353–361.
- Madsen, P.T., Johnson, M., Miller, P.J.O., Aguilar de Soto, N., Tyack, P.L., 2006. Quantitative measures of air gun pulses recorded on sperm whales (*Physeter macrocephalus*) using acoustic tags during controlled exposure experiments. *Journal of the Acoustical Society of America* 120, 2366–2379.
- Madsen, P.T., Johnson, M., Aguilar de Soto, N., Zimmer, W.M.X., Tyack, P.L., 2005. Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *Journal of Experimental Biology* 208, 181–194.
- Madsen, P.T., Mohl, B., Nielsen, B.K., Wahlberg, M., 2002a. Male sperm whale behaviour during exposures to distant seismic survey pulses. *Aquatic Mammals* 28, 231–240.
- Madsen, P.T., Payne, R., Kristiansen, N.U., Wahlberg, M., Kerr, I., Möhl, B., 2002b. Sperm whale sound production studied with ultrasound-time-depth recording tags. *Journal of Experimental Biology* 213, 1899–1906.
- Madsen, P.T., Wahlberg, M., Möhl, B., 2002c. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behavioral Ecology and Sociobiology* 53, 31–41.
- Mate, B.R., Stafford, K.M., Ljungblad, D.K., 1994. A change in sperm whale (*Physeter macrocephalus*) distribution correlated to seismic surveys in the Gulf of Mexico. *Journal of the Acoustical Society of America* 96 (2), 3268–3269.

- McCauley, R.D., Fewtrell, J., Duncan, A.J., Jenner, C., Jenner, M.-N., Penrose, J.D., Prince, R.I.T., Adhitya, A., Murdoch, J., McCabe, K., 2000. Marine seismic surveys—a study of environmental implications. *APPEA Journal* 40, 692–708.
- Miller, P.J.O., Aoki, K., Rendell, L.E., Amano, M., 2008. Stereotypical resting behavior of the sperm whale. *Current Biology* 18, R21–R23.
- Miller, P.J.O., Johnson, M.P., Tyack, P.L., 2004a. Sperm whale behaviour indicates the use of rapid echolocation click buzzes 'creaks' in prey capture. *Proceedings of the Royal Society of London B* 271, 2239–2247.
- Miller, P.J.O., Johnson, M.P., Tyack, P.L., Terray, E.A., 2004b. Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *Journal of Experimental Biology* 207, 1953–1967.
- Miller, P.J.O., Tyack, P.L., Biassoni, N., Johnson, M.P., 2005. Short-term effects of suction cup tagging on the deep-diving behaviour of sperm whales. In: *Abstracts of the Second International Symposium of Biologging Science*, St. Andrews, Scotland.
- Mitani, Y., Sato, K., Ito, S., Cameron, M., Sini, D.B., Naito, Y., 2003. A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intensity data: results from two lactating Weddell seals. *Polar Biology* 26, 311–317.
- MMS, 2004. Geological and Geophysical Exploration for Mineral Resources on the Gulf of Mexico Outer Continental Shelf: Final Programmatic Environmental Assessment. OCS EIS/EA MMS 2004-054. New Orleans, US Minerals Management Service, 487pp.
- Nowacek, D.P., Thorne, L.H., Johnston, D.W., Tyack, P.L., 2007. Responses of cetaceans to anthropogenic noise. *Mammal Review* 37, 81–115.
- NRC/National Research Council, 2005. Marine Mammal Populations and Ocean Noise. Determining When Noise Causes Biologically Significant Effects. The National Academies Press, Washington, DC.
- Packard, A., Karlsen, H.E., Sand, O., 1990. Low frequency hearing in cephalopods. *Journal of Comparative Physiology A* 166, 501–505.
- Popper, A.N., Fay, R.R., Platt, C., Sand, O., 2003. Sound detection mechanisms and capabilities of teleost fishes. In: Collin, S.P., Marshall, N.J. (Eds.), *Sensory Processing in Aquatic Environments*. Springer, New York, pp. 3–38.
- Richardson, W.J., Greene Jr., C.R., Malme, C.I., Thomson, D.H., 1995. *Marine Mammals and Noise*. Academic Press, San Diego, CA.
- Slotte, A., Hansen, K., Dalen, J., Ona, E., 2004. Acoustic mapping of pelagic fish distribution and abundance in relation to a seismic shooting area off the Norwegian west coast. *Fisheries Research* 67, 143–150.
- Southall, B., Bowles, A.E., Ellison, W.T., Finneran, J.J., Gentry, R.L., Greene Jr., C.R., Kastak, D., Ketten, D.R., Miller, J.H., Nachtigall, P.E., Richardson, W.J., Thomas, J.A., Tyack, P.L., 2008. Structure of the noise exposure criteria. *Aquatic Mammals* 33 (4), 427–436.
- SPSS, 1996. *Systat 6.0 for Windows*. SPSS, Inc., Chigago, IL.
- Stone, C.J., Tasker, M.L., 2006. The effects of seismic airguns on cetaceans in UK waters. *Journal of Cetacean Research and Management* 8, 255–263.
- Teloni, V., Johnson, M.P., Miller, P.J.O., Madsen, P.T., 2008. Shallow food for deep divers: dynamic foraging behavior of male sperm whales in a high latitude habitat. *Journal of Experimental Biology and Marine Ecology* 354, 119–131.
- Tyack, P., Gordon, J., Thompson, D., 2004. Controlled exposure experiments to determine the effects of noise on large marine mammals. *Marine Technology Society Journal* 37 (4), 41–53.
- Wardle, C.S., Carter, T.J., Urquhart, G.G., Johnstone, A.D.F., Ziolkowski, A.M., Hampson, G., Mackie, D., 2001. Effects of seismic air guns on marine fish. *Continental Shelf Research* 21, 1005–1027.
- Watwood, S.L., Miller, P.J.O., Johnson, M.P., Madsen, P.T., Tyack, P.L., 2006. Deep-diving foraging behavior of sperm whales (*Physeter macrocephalus*). *Journal of Animal Ecology* 75, 814–825.
- Weinrich, M.T., Lambertson, R.H., Belt, C.R., Schilling, M.R., Iken, H.J., Syrjala, S.E., 1992. Behavioural reactions of humpback whales *Megaptera novaeangliae* to biopsy procedures. *Fishery Bulletin* 90, 588–598.
- Whitehead, H., Weilgart, L., 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour* 118, 275–296.
- Williams, T.M., 1999. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philosophical Transactions of the Royal Society of London B* 354, 193–201.
- Williams, T.M., Fuiman, L.A., Horning, M., Davis, R.W., 2004. The cost of foraging by a marine predator, the Weddell Seal *Leptonychotes weddellii*: pricing by the stroke. *Journal of Experimental Biology* 207, 973–982.
- Wilson, R.P., Wilson, M.-P.T., 1988. Foraging behaviour in four sympatric cormorants. *Meeresforschung* 32, 155–158.
- Wilson, R.P., Liebsch, N., Davies, I.M., Quintana, F., Weimerskirch, H., Storch, S., Lucke, K., Siebert, U., Zankl, S., Müller, G., Zimmer, I., Sclaro, A., Campagna, C., Plötz, J., Bornemann, H., Teilmann, J., McMahon, C.R., 2007. All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep-Sea Research II* 54, 193–210.
- Zar, J.H., 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ.
- Zimmer, W.M.X., Tyack, P.L., Johnson, M.P., Madsen, P.T., 2005. Three-dimensional beam pattern of regular sperm whale clicks confirms bent-horn hypothesis. *Journal of the Acoustical Society of America* 117, 1473–1485.