Aquatic Mammals 2008, *34*(1), 71-83, DOI 10.1578/AM.34.1.2008.71

Overt Responses of Humpback Whales (*Megaptera novaeangliae*), Sperm Whales (*Physeter macrocephalus*), and Atlantic Spotted Dolphins (*Stenella frontalis*) to Seismic Exploration off Angola

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Abstract

A total of 2,769 h of marine mammal observation was conducted from a seismic survey vessel off Angola between August 2004 and May 2005. A dual-source airgun array firing a total volume of either 5,085 in^3 (Survey 1) or 3,147 in^3 (Survey 2) in an alternate source activation sequence was active during 51% of the analysed effort. A total of 207 sightings of humpback whales ($n = 66$), sperm whales ($n = 124$), and Atlantic spotted dolphins ($n = 17$) was recorded. The encounter rate (sightings/h) of humpback and sperm whales did not differ significantly according to airgun operational status. The mean distance to humpback and sperm whale sightings was greater during full-array operations than during guns off, but this difference was not significant. Atlantic spotted dolphin encounters occurred at a significantly greater distance from the airgun array ($p < 0.001$) during full-array operations than during guns off. Positive-approach behaviour by Atlantic spotted dolphins ($n = 9$) occurred only during guns-off periods. There was no evidence for prolonged or large-scale displacement of each species from the region during the 10-mo survey duration. Sperm whale sightings showed a significant increase ($p < 0.001$) during the survey, while Atlantic spotted dolphin encounters occurred at similar rates. A decreased occurrence of humpback whale sightings ($p < 0.001$) corresponded with established seasonal migration out of the survey area. Contrary to expectation based on perceived sensitivity, Atlantic spotted dolphins exhibited the most marked overt response to airgun sound of the three cetacean species examined.

Key Words: humpback whale, *Megaptera novaeangliae*, sperm whale, *Physeter macrocephalus*, Atlantic spotted dolphin, *Stenella frontalis*, seismic survey, airguns, Angola

Introduction

Airgun arrays used during modern geophysical seismic surveys typically have source levels in the region of 220 to 248 dB re: 1 μPa at 1 m, with highest energy produced in the 10.0 to 200.0 Hz frequency bandwidth (Greene & Richardson, 1988; Richardson & Würsig, 1997; Gulland & Walker, 2001). The dominant low-frequency output overlaps with baleen whale signals, including those of blue whales (*Balaenoptera musculus*) (16.0 to 25.0 Hz; Stafford et al., 1994); fin whales (*B. physalus*) (20.0 Hz; Watkins, 1981); humpback whales (*Megaptera novaeangliae*) (25.0 to 360.0 Hz; Thompson et al., 1986); gray whales (*Eschrichtius robustus*) (20.0 to 200.0 Hz; Cummings et al., 1968); right whales (*Eubalaena* spp.) (50.0 to 500.0 Hz; Clark, 1982); bowhead whales (*Balaena mysticetus*) (100.0 to 400.0 Hz; Ljungblad et al., 1982); and minke whales (*B. acutorostrata*) (60.0 to 200.0 Hz; Winn & Perkins, 1976). In the absence of audiograms, the auditory sensitivity of baleen whales is assumed to be highest at low frequencies.

Odontocete signals are produced at higher frequencies than those of baleen whales. Sperm whales (*Physeter macrocephalus*) produce broadband clicks with peak energy and auditory sensitivity in the 5.0 to 25.0 kHz range (Ridgway & Carder, 2001; Møhl et al., 2003). Small odontocetes produce a variety of tonal sounds at frequencies of 0.5 to 20.0 kHz and pulsed sounds at 0.5 to 150.0 kHz (Popper, 1980), with peak auditory sensitivity at 10.0 to 150.0 kHz (Richardson et al., 1995). The low-frequency energy produced by airgun arrays therefore overlaps to a lesser extent with odontocete signals, with a correspondingly lower perceived impact. However, airgun sound can dominate the 0.2 to 22.0 kHz frequency range within a 2-km radius of a source (Goold & Fish, 1998), and energy in the 0.3 to 3.0 kHz frequency range may dominate airgun sound received in surface waters (Madsen et al., 2006). Consequently, odontocetes may be able to detect airgun pulses at ranges of tens of kilometres (Richardson & Würsig, 1997).

Most previous studies on the responses of cetaceans to open-water seismic exploration fall into three categories: (1) controlled playback experiments (e.g., Malme et al., 1984; Richardson et al., 1986; Ljungblad et al., 1988; McCauley et al., 1998; Tyack et al., 2003), (2) observations from independent platforms during seismic surveys (e.g., Reeves et al., 1984; Richardson et al., 1986; McCauley et al., 1998; Yazvenko et al., 2007), and (3) observations from the source (or guard) vessel during seismic surveys (e.g., Swift, 1994; Goold, 1996; McCauley et al., 1998; Miller et al., 2005; Moulton & Miller, 2005; Stone & Tasker, 2006).

Playback experiments have been conducted on captive odontocetes to determine the exposure levels at which temporary threshold shift (a likely prelude of permanent hearing loss) occurs (Schlundt et al., 2000; Finneran et al., 2002), and on free-ranging baleen and sperm whales to determine whether airguns elicit a behavioural reaction (e.g., Malme et al., 1984; Dalheim, 1987, as summarised in Richardson et al., 1995; Tyack et al., 2003). However, the airgun volumes used in field playback experiments (typically ranging from 20 to 100 in^3; e.g., Malme et al., 1984; McCauley et al., 2000) are only a fraction of those used during actual 3-D and 4-D geophysical seismic surveys, which are typically in the region of 3,000 to 5,000 in^3 and may occasionally reach 12,000 in^3 volume.

Field studies conducted concurrently with seismic surveys usually aim to measure the short-term behavioural reactions of cetaceans to airgun arrays. To date, such studies have predominantly centred on baleen whales, particularly bowhead, gray, and humpback whales, and reactions have varied from few observable effects to noticeable changes in swimming speed and direction, changes in sighting rate, abrupt behavioural changes (e.g., cessation of feeding), localised displacement, and changes in vocalisation rate/type (Malme et al., 1984; Richardson et al., 1986, 1995, 1999; Richardson & Würsig, 1997; McCauley et al., 1998, 2000; Moore & Clarke, 2002; Moulton & Miller, 2005; Yazvenko et al., 2007).

Comparatively few studies have examined the reaction of odontocetes to seismic surveys. Stone & Tasker (2006) report no obvious responses of sperm whales to airgun sound based on surface behaviour, while Swift (1994), Madsen et al. (2002), and Tyack et al. (2003) observed that sperm whales continued producing normal vocal patterns in the presence of airgun sound. Apparent cessation of vocalisations was reported in the Southern Ocean (Bowles et al., 1994), however, and there are indications of altered foraging behaviour (P. J. O. Miller, pers. comm.) in response to airgun pulses. A decrease in small odontocete sighting rate has been observed during airgun activity (Stone & Tasker, 2006), and avoidance of airguns by common dolphins (*Delphinus delphis*) was reported during seismic surveys in the Irish Sea (Goold, 1996). Miller et al. (2005) reported apparent avoidance of seismic survey operations by beluga whales (*Delphinapterus leucas*) of 10 to 20 km, suggesting that odontocete responses may potentially occur at relatively large ranges from the airgun source.

This paper describes the occurrence of humpback whales, sperm whales, and Atlantic spotted dolphins (*Stenella frontalis*) during a 3-D seismic survey off Angola on the west coast of Africa. The dataset presented here provides an important contribution to available literature due to its relatively long duration (10 mo) and high level of consistency (same geographic area, survey vessel, seismic equipment, and observers). Due to both the difficulties with detecting behavioural changes in marine mammals and the use of the source vessel as the research platform, no attempt was made to identify subtle individual behavioural responses (e.g., changes in surfacing rate) to the airguns. Instead, this paper considers the overt responses analysed by Harris et al. (2001), Moulton & Miller (2005), and Stone & Tasker (2006) to address the following questions: (1) whether (a) sighting rate and (b) sighting distances were similar whether airguns were active or inactive; and (2) whether sighting rate changed over the 10-mo duration of the seismic survey as an indication of displacement from the survey area.

Materials and Methods

Study Area and Seismic Survey

Marine mammal monitoring occurred over a 288-d period between 1 August 2004 and 15 May 2005, during two consecutive geophysical 3-D seismic surveys off northern Angola (Figure 1). The centre of the prospect was situated 120 km off the Congo River mouth. The majority of survey effort (97%) occurred in water depths of 1,000 to 3,000 m (Figure 1). The two seismic surveys encompassed an acquisition area of 5,492 km^2, with additional intermittent coverage conducted outside the prospect region.

During both surveys, a dual source airgun array (Bolt airguns, long-life type 1500/1900) was towed astern of a seismic survey vessel (M/V Geco Triton at 83 m in length), travelling at a constant speed of 4 to 5 kts. Each airgun array consisted of three sub-arrays comprising 24 guns of individual volumes of 30 to 290 in^3, producing a total airgun volume of 5,085 in^3 (Survey 1) or 3,147 in^3 (Survey 2) (Table 1). The total volume was fired at shot intervals of approximately 10 s (25-m shot interval) via alternate activation of the

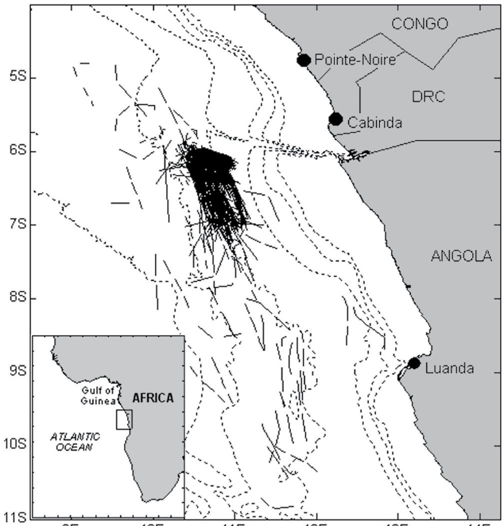

Figure 1. Location of the study area and marine mammal survey effort (solid lines); bathymetry (dotted lines): 200 m, 500 m, 1,000 m, 2,000 m, 3,000 m, and 4,000 m.

two arrays. Throughout the surveys, a *soft start* (or *ramp-up*) procedure (Joint Nature Conservation Committee, 2004) was implemented, which involved gradually increasing airgun volume over a 20-min period to encourage marine mammals to move away from the airgun source prior to reaching full volume. Other marine mammal mitigation measures implemented during the survey included a delay to airgun activation if marine mammals were observed within a 500-m exclusion zone around the airgun array and a shut-down of the airguns should a whale calf be observed within the exclusion zone during seismic production.

Observation Methods

Marine mammal watches were conducted by a single observer located at an eye height of 18 m on the vessel's helideck, which permitted 360º views around the vessel. The observer had a dual role of implementing marine mammal mitigation measures and collecting marine mammal data within the study area. The same two experienced cetacean observers worked alternate rotations as the single onboard observer throughout the survey, following standardised protocols and data collection methods. Data were collected throughout daylight hours and in all weather conditions. During marine mammal "search mode," the observer scanned 360º around the vessel with the naked eye and with 10 × 42 Leica binoculars. Scans focussed on the area within 1 km of the airgun array (situated 180 or 340 m astern of the vessel) and on the 180º-sector ahead of the ship in order to detect animals before they entered the 500-m exclusion zone around the airgun array. Airgun status (full-array operational, partial-array operational [tests or soft start], or guns off) and effort logs (comprising GPS position, water depth, and environmental data, including Beaufort sea state) were completed for every marine mammal watch. A sighting was defined as each observation of a group (or solitary animal) of marine mammals. The position, species, number of animals, group age/sex composition, water depth, and airgun status were recorded for each sighting. When group size was given as a range, the "best estimate" of numbers was used for analysis.

The initial sighting distance and the closest observed point of approach (CPA) of each sighting (or nearest individual) to the airgun array was determined using a combination of naked-eye estimation, a simple measuring stick based upon the Heinemann equation (Heinemann, 1981) and/or the ship's radar (the latter during calm seas). An overall behavioural category (e.g., travelling, feeding, logging) was allocated to each sighting, with distinct individual behaviours (e.g., tail-lobbing and breaching) also noted. For dolphin schools (where direction of movement in relation to the vessel was usually well-defined and straightforward to determine), three categories were developed to describe approach behaviour:

Table 1. Source parameters utilised during each survey

Parameter	Survey 1	Survey 2
Survey duration	Aug 2004–Jan 2005	Jan–May 2005
Seismic line duration (h)	8.0-12.0	1.5-4.0
Total airgun volume (in^3) per array	5,085	3,147
Source amplitude (Bar-m, peak to peak)	109	81
Airgun pressure (psi)	2,000	2,000
Source depth (m)	8	4
Recorded frequency bandwidth (Hz)	5-70	8-120
Minimum spectrum level within frequency bandwidth (dB re: 1 μPa per Hz @ 1 m)	208	203
Firing interval (m)	25.00	18.75

(1) *neutral* when no obvious observable change in direction or behaviour in relation to the ship/airguns occurred; (2) *negative* exemplified by a change in heading away from the ship or sudden adverse change in behaviour (e.g., fast swim away from ship); or (3) *positive* defined as actively approaching and swimming alongside the vessel (including bow- and wake-riding, and swimming alongside/in front of the towed seismic equipment, particularly the paravanes).

Data Analysis

Analysis was restricted to the three species for which there were at least 15 sightings: humpback whales, sperm whales, and Atlantic spotted dolphins (Table 2). Conveniently, these three species also represent a range of contrasting cetacean types, including a mysticete and both large and small odontocetes.

The raw data were examined to determine the effects of distance and environmental conditions on the detection rate of each species in order to ensure a reasonable likelihood of detection for comparisons relative to airgun status. Since over 80% of sightings occurred at distances ≤ 6 km from the airguns, all sightings recorded at closest approach distances > 6 km were eliminated from the analyses. Since the detection of cetacean species decreases with increasing sea state (Clarke, 1982), survey analyses are typically restricted to data collected in sea state ≤ 4 (e.g., Hammond et al., 2002; Fulling & Mullin, 2003), although occasionally up to sea state 6 (e.g., Barlow, 2006). The raw data analysis indicated that the detection rate for each of the three species was broadly comparable up to sea state 4. All data collected in sea state ≥ 5, in low visibility (< 6 km), or high swell height (> 2.5 m) were therefore eliminated from the analyses.

Species occurrence was assessed using two related terms: (1) the number of sightings/h of observation time (encounter rate), and (2) the number of animals/h of observation time (relative abundance). The occurrence of each species was analysed in relation to airgun activity at the time of the first detection. For humpback and sperm whales (the sample size of Atlantic spotted dolphins was insufficient), a chi-squared goodness-of-fit test was used to test whether the observed encounter rate differed from expected values according to airgun status. Differences in the closest approach distance of each species to the airguns according to airgun activity were tested using Mann-Whitney tests. An additional 27 sightings were removed from the distance analyses because their duration overlapped with more than one airgun status category.

To examine the potential displacement of cetacean species from the study area over the 10-mo study period, data were pooled into three consecutive survey periods: Period 1 (Aug-Oct; 93 d); Period 2 (Nov-Jan; 92 d); and Period 3 (Feb-May; 104 d). For humpback and sperm whales, a chi-squared goodness-of-fit test was used to test whether the species encounter rate differed from expected in each survey period.

Results

A total of 2,601.4 h of marine mammal observation effort conducted between August 2004 and May 2005 met conditions suitable for analysis. Effort was similar between survey periods, with 898.4 h of effort in Aug-Oct, 777.3 h in Nov-Jan, and 925.7 h in Feb-May. Airguns were active for 1,313.9 h (51%) of the total observation time. Most (1,201.4 h or 91%) airgun activity comprised full-array seismic; the remaining 112.4 h (9%) comprised partial-array seismic, involving 96.5 h of soft start and 15.9 h of airgun testing. Airgun activity varied between survey periods, with Periods 1 and 3 having a higher proportion of observation time with active airguns (62 and 57%, respectively) than Period 2 (29%).

A total of 207 sightings of humpback whales, sperm whales, and Atlantic spotted dolphins were recorded during the survey (Table 2). Of these, a total of 164 sightings of humpback whales (n = 52), sperm whales (n = 96), and Atlantic spotted dolphins (n = 16) met the criteria for inclusion in the analyses. Forty-six percent of these sightings had a duration of less than 20 min, including 63% of the humpback whale, 36% of the sperm whale, and 44% of the Atlantic spotted dolphin sightings

Table 2. Number of encounters (all data) of three cetacean species during the seismic survey

	Total encounters		Group size		
Species	No. of sightings	No. of individuals	Mean	SE	Range
M. novaeangliae	66	130	1.97	0.11	1-4
P. macrocephalus	124	1,199	9.67	0.82	1-65
S. frontalis	17	2,198	129.29	33.28	1-425

(Figure 2). Thirty-four percent of sightings had duration exceeding 40 min; sperm whale comprised 76% of these due predominantly to their behaviour of repeatedly diving within a relatively small spatial area.

Species Occurrence

Humpback whales were mostly recorded as single and pairs of adult animals, with 18% of the total sightings including calves (Weir, in press). Although the encounter rate of humpback whales was slightly higher during full array (0.022 sightings/h) than guns off (0.016/h) (no encounters were recorded during partial-array operations) (Table 3), the frequency of encounters did not differ significantly from expected ($\chi^2 = 3.78$, df = 2, $p = 0.15$). Relative abundance was slightly higher during full-array (0.046 animals/h) than guns-off (0.029 h) seismic (Table 3).

Over half of Angolan sperm whale encounters consisted of nursery groups of calves, juveniles, and adult females (the latter indicated by observed calluses on the dorsal fins of some closer individuals; see Kasuya & Ohsumi, 1966). The encounter rate of sperm whales was similar during full array (0.033 sightings/h) and guns off (0.027/h), with no encounters during partial-array operations (Table 3). There was no significant difference in the frequency of sperm whale encounters according to airgun status ($\chi^2 = 4.19$, df = 2, $p = 0.12$). Sperm whales had similar relative abundance during full-array (0.31 animals/h) and guns-off (0.23 h) seismic (Table 3).

The Atlantic spotted dolphin encounter rate (Table 3) was lowest during full-array (0.004 sightings/h) operations and higher during guns-off (0.007/h) and partial-array (0.009/h) seismic. The relative abundance of Atlantic spotted dolphins

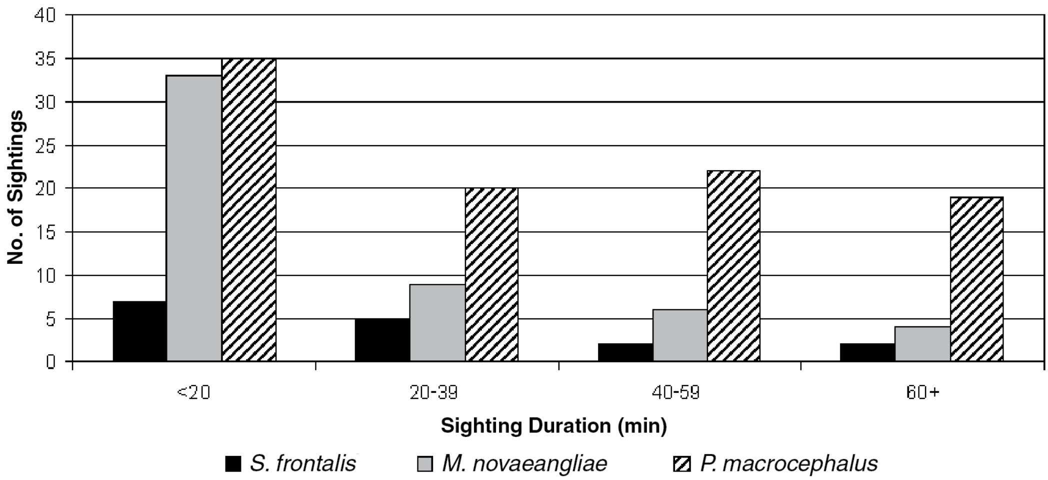

Figure 2. Total duration of Atlantic spotted dolphin ($n = 16$), humpback whale ($n = 52$), and sperm whale ($n = 96$) encounters

Table 3. Observation effort, encounter rate (with number of sightings), and relative abundance (with number of individuals) according to seismic airgun status; data collected in Beaufort sea state < 5, visibility ≥ 6 km, and swell ≤ 2.5 m, and limited to sightings ≤ 6 km from the ship and occurring within a single airgun category.

	Airgun status			
	Full array	Partial array	Guns off	Total
Total effort (h)	1,201.4	112.4	1,287.5	2,601.4
M. novaeangliae				
Sightings/h	0.022 (27)	0.000	0.016(20)	0.018 (47)
Animals/h	0.046 (55)	0.000	0.029 (37)	0.035 (92)
P. macrocephalus				
Sightings/h	0.033 (40)	0.000	0.027 (35)	0.029 (75)
Animals/h	0.310 (372)	0.000	0.230 (296)	0.257 (668)
S. frontalis				
Sightings/h	0.004 (5)	0.009 (1)	0.007 (9)	0.006 (15)
Animals/h	0.472 (567)	0.311 (35)	0.967 (1245)	0.710 (1847)

was double during guns-off (0.967 sightings/h) than during full-array (0.472/h) seismic (Table 3).

Sighting Distances

The distance analysis of humpback whale encounters provided varying results (Figure 3a). Although the closest approach distance of humpback whale encounters was further from the airguns during full-array seismic compared with guns off, this difference was not significant ($\overline{\chi}$ = 3,050 m, SD = 1,856, *n* = 27 vs $\overline{\chi}$ = 2,700 m, SD = 1,905, *n* = 20, respectively) (Mann-Whitney *U* = 244, *n* = 47, *p* = 0.57). However, the encounter rate was higher during full array than guns off in all three of the

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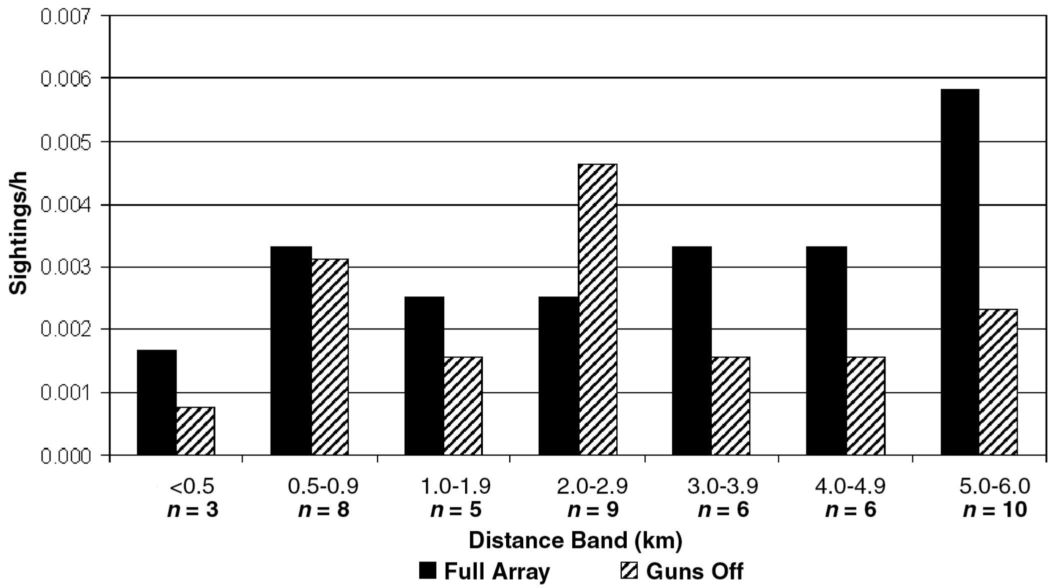

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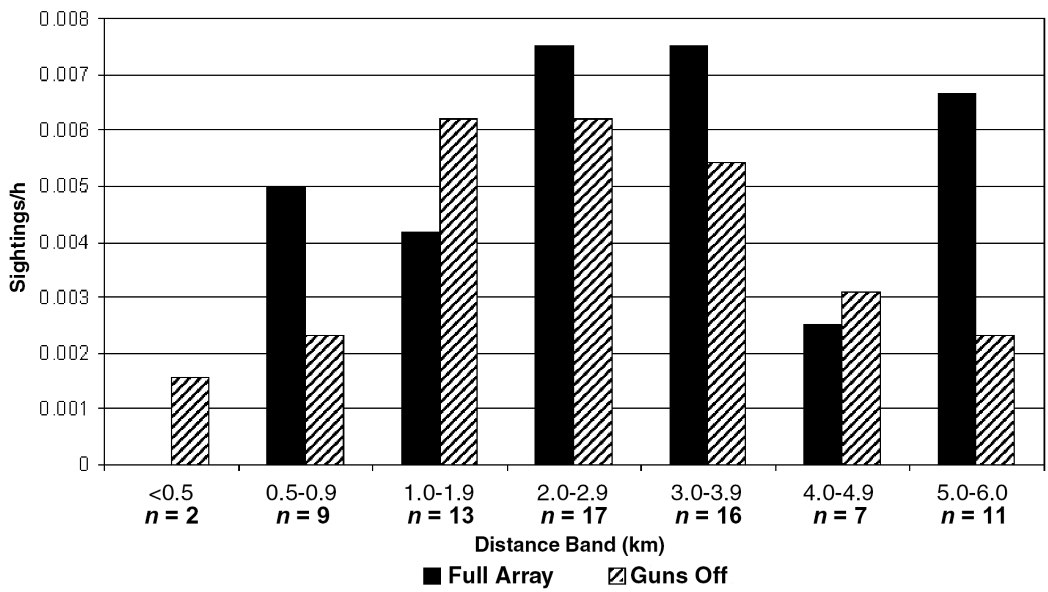

Figure 3. Distance-related encounter rate of (A) humpback whale (*n* = 47) and (B) sperm whale (*n* = 75) according to airgun status

seven distance bands situated < 2 km from the source. In distance bands beyond 3 km from the source, the full-array encounter rates were over twice those of guns off.

Sperm whales were only sighted within 0.5 km of the airgun array during guns off (Figure 3b). Encounter rate was either similar to or higher during full array than guns off in most other distance bands, however, and was markedly higher at 0.5 to 0.9 km and at 5 to 6 km (Figure 3b). Although the closest distance of sperm whale sightings was further from the airguns during full-array seismic compared to guns off, this difference was not significant ($\bar{\chi}$ = 3,039 m, SD = 1,702, n = 40 vs $\bar{\chi}$ = 2,594 m, SD = 1,478, n = 35, respectively) (Mann-Whitney U = 587, n = 75, p = 0.23). The behaviour of sperm whales rarely changed during encounters, with animals frequently engaged in socialising bouts and feeding dives without obvious reaction as the active source passed.

Since Atlantic spotted dolphins were difficult to conclusively distinguish from other *Stenella* dolphin species at greater range, positive identification, and consequently, analysis, was restricted to within a 2-km zone around the airguns. There were no encounters with Atlantic spotted dolphins within the 500-m exclusion zone during full-array seismic (Figure 4a). In contrast, all encounters during guns off involved dolphins approaching within 500 m of the airguns (Figure 4a). Consistent with this finding, Atlantic spotted dolphin encounters occurred at significantly greater distances from the airguns during full array ($\bar{\chi}$ = 1,080 m, SD = 409, n = 5) than guns off ($\bar{\chi}$ = 209 m, SD = 111, n = 9) (Mann-Whitney U = 0, n = 14, $p < 0.001$). Atlantic spotted dolphins approached the vessel to bow-/wake-ride only during guns off (Figure 4b). In contrast, Atlantic spotted dolphin encounters during full-array seismic involved either *neutral* behaviour or, more commonly, a *negative* response during which animals visibly detoured around the ship's track and moved away (usually at high speed with apparent flight reaction).

Two Atlantic spotted dolphin encounters are noteworthy due to fine-scale correlation of behaviour with changes in airgun activity. On 16 April 2005 at 10:00 GMT, a soft start commenced, and at 10:02 GMT, a pod of 35 Atlantic spotted dolphins was observed 1.2 km away and approaching with apparent intent to bow-ride. At 10:04 GMT, the dolphins veered rapidly away from the vessel while 490 m from the source; airgun volume at this time had reached approximately 198 in^3. On 19 April 2005, 2 min after full-array activity had ceased following over 3 h of continuous firing, a pod of 25 dolphins was observed at 200 m porpoising towards the starboard bow. The dolphins subsequently crossed the vessel stern beneath the towed cables to within 10 m of the inactive airgun array and then travelled away from the vessel.

Temporal Occurrence

The frequency of humpback whale encounters differed significantly among the three consecutive survey periods (χ^2 = 63.13, df = 2, $p < 0.001$). More encounters occurred during Period 1 (χ^2 = 40.72, df = 1, $p < 0.001$), and fewer encounters occurred during Periods 2 (χ^2 = 5.85, df = 1, $p < 0.05$) and 3 (χ^2 = 16.56, df = 1, $p < 0.001$) than expected (Table 4).

The frequency of sperm whale sightings differed significantly among the three survey periods (Table 4) (χ^2 = 80.23, df = 2, $p < 0.001$). Fewer encounters than expected occurred during Period 1 (χ^2 = 27.43, df = 1, $p < 0.001$) and Period 2 (χ^2 = 3.98, df = 1, $p < 0.05$), while the final survey period produced more encounters than expected (χ^2 = 48.83, df = 1, $p < 0.001$).

Sightings of Atlantic spotted dolphins occurred in five of the ten survey months (Table 4). Encounter rate was similar between Periods 1 and 2, but doubled in Period 3 due to a relatively high number of sightings during April.

Discussion

The limitations of using a source vessel as a platform from which to assess the behavioural responses of free-ranging cetaceans include potential influences from the observation platform (even during periods without airgun use), the inability to detect avoidance responses occurring at distances beyond visible range, and difficulties in monitoring subsurface animals. Nevertheless, an assessment of overt marine mammal responses to airguns can be conducted from a source platform using criteria such as encounter rate and distance (e.g., McCauley et al., 2000; Harris et al., 2001; Stone & Tasker, 2006). The relatively high level of standardisation in survey vessel, observers, and study area in the 10-mo dataset presented here also reduces the other limitations occurring in many seismic datasets such as short temporal and spatial scales, multiple observers (causing bias in detection rate), and low sample size in many geographical areas. Although none of the data were collected under conditions of zero acoustic disturbance (due to the presence of the vessel and equipment), airgun sound was the only variable acoustic source during the survey. The observation duration of the cetacean encounters may also impact upon the conclusions drawn on responses of each species to airgun sound. Approximately one-third of sightings had observation duration exceeding 40 min, increasing observer accuracy in assessing parameters such as

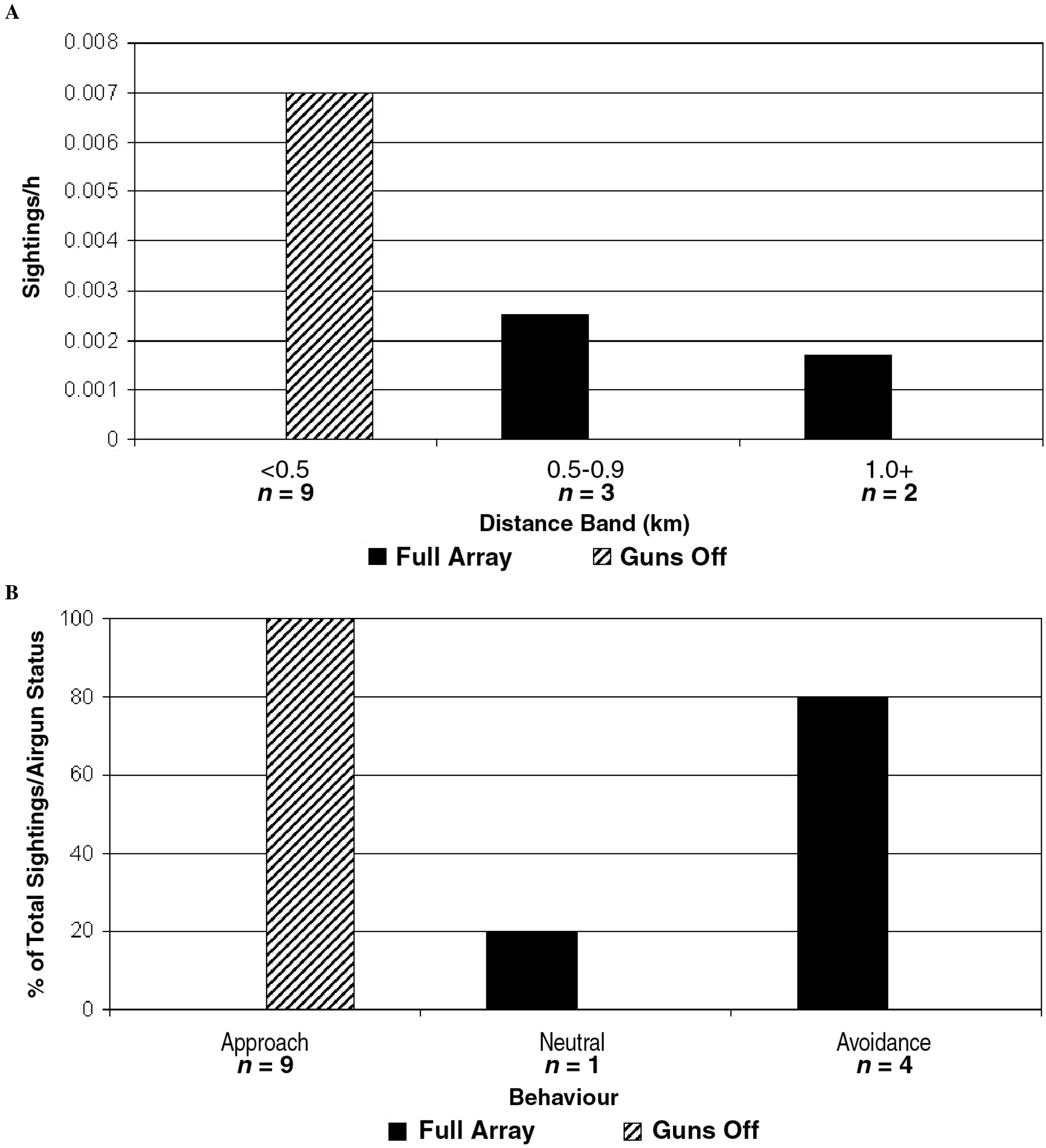

Figure 4. Response of Atlantic spotted dolphins (*n* = 14 sightings) to airgun sound shown by (A) distance-related encounter rate and (B) frequencies of behaviour according to airgun status

behavioural and directional responses, group size, and closest distance of approach.

The study revealed variation in the overt responses of three cetacean species to airgun sound. No conspicuous localised avoidance of active airguns by humpback or sperm whales was indicated. However, Atlantic spotted dolphins showed a marked short-term and localised displacement from the region of active airguns.

Although not significant, the encounter rate of humpback whales was higher during full-array seismic than guns off, particularly 3 to 6 km from the source. This increased encounter rate could be interpreted as a lack of avoidance of the airgun source. However, increased encounter rates during active seismic surveying might also potentially arise from animals spending more time near the surface (thereby increasing their detection) in a *vertical avoidance* response to lower levels

Table 4. Monthly encounter rate and relative abundance of three cetacean species over the duration of the seismic surveys

	M. novaeangliae		*P. macrocephalus*		*S. frontalis*	
	Sightings/h (N = 52)	Animals/h (N = 106)	Sightings/h (N = 96)	Animals/h (N = 931)	Sightings/h (N = 16)	Animals/h (N = 2,197)
Period 1	0.050	0.106	0.003	0.031	0.004	0.718
August	0.049	0.118	0.010	0.097	0.007	0.381
September	0.054	0.097	0.000	0.000	0.000	0.000
October	0.048	0.103	0.000	0.000	0.006	1.719
Period 2	0.008	0.013	0.023	0.220	0.004	0.926
November	0.007	0.010	0.003	0.037	0.000	0.000
December	0.005	0.010	0.015	0.146	0.000	0.000
January	0.011	0.018	0.051	0.471	0.011	2.608
Period 3	0.001	0.001	0.081	0.791	0.010	0.899
February	0.000	0.000	0.017	0.146	0.007	1.009
March	0.000	0.000	0.102	0.737	0.000	0.000
April	0.000	0.000	0.138	1.616	0.023	1.121
May	0.008	0.008	0.068	0.666	0.008	1.892
Total	0.020	0.041	0.037	0.358	0.006	0.845

of received sound in the upper water column (the "Lloyd mirror" phenomenon; Urick, 1983) (Richardson et al., 1995; McCauley et al., 1998; Harris et al., 2001).

The findings for humpback whales broadly agree with those reported by McCauley et al. (2000), although the latter study occurred in a shallow water area and with a smaller airgun array (2,678 in^3). McCauley et al. (2000) found no gross disruption of humpback whale movements in the region of a seismic source vessel based on encounter rates off Australia. However, localised responses were observed among some humpback whales during both studies. For example, we observed three humpback whale sightings approaching to or within 500 m of the airgun array during full-array status, comprising groups of two and three animals and a single adult female (which breached to reveal its genital slit). McCauley et al. (1998, 2000) also reported close approaches to the seismic source by some humpbacks, suggesting that male humpback whales might actively approach airguns when mistaking the pulses for the sounds produced by the breaches, flipper slaps, and lob-tails of competitors during the breeding season. Angola appears to form part of a humpback whale breeding ground (Best et al., 1999; Weir, in press), and similar approach and follow behaviour has certainly been observed on at least three occasions in response to small-volume (70 in^3) seismic surveys in Angolan waters (pers. obs.), although the sex of the animals could not be determined. Whales observed within 500 m of the large-volume airgun source were not all males and did not exhibit follow behaviour, although tail-lobbing was noted during two of the encounters.

Focal-follow studies in Australia indicated that some humpback whale pods containing calves showed avoidance at ranges of 7 to 12 km from a 2,678 in^3 seismic source (McCauley et al., 2000), and responsive movements of particular individuals or age/sex classes at a longer range than examined here cannot be dismissed.

Several studies have focussed on the responses of sperm whales to airgun sound, due to increasing expansion of seismic exploration into deep-water habitat. Published reactions of sperm whales to anthropogenic sound are inconclusive, however. Sperm whales temporarily ceased click production in response to sonar and pinger pulses (e.g., Watkins & Schevill, 1975; Watkins et al., 1993), and cessation of vocalisations in response to distant (> 200 km) airgun sound was reported by Bowles et al. (1994). However, sperm whales were not found to exhibit changes in distribution or in their acoustic or surface behaviour in response to detonations (Madsen & Møhl, 2000) or to airgun sound in most studies (Swift, 1994; Madsen et al., 2002; Tyack et al., 2003; Stone & Tasker, 2006).

During this study, sperm whales off Angola showed few overtly observable responses to airgun sound. The encounter rate and mean distance were similar during full-array seismic and guns off, although it is possible that individuals/groups may have spent longer periods at the surface during full-array seismic, perhaps increasing their detection. The absence of overt responses to airgun sound reported for solitary males in Norway (Madsen et al., 2002), bachelor groups and solitary males in the UK (Swift, 1994; Stone & Tasker, 2006), and nursery groups in Angola described here suggest a consistent lack of strong responses by sperm whales regardless of social structure, age and sex class, or geographic location. However, recent evidence of a change in foraging behaviour of sperm whales exposed to airgun pulses (P. J. O. Miller, pers. comm.) indicates that some responses may be more subtle than tested for here.

Contrary to expectations based on perceived sensitivity, Atlantic spotted dolphins exhibited the most marked overt response to airgun sound, maintaining a greater distance from the airguns and an absence of positive-approach behaviour during full-array seismic vs guns off. This species clearly avoided approaching the vessel when the airgun array was firing, but readily approached to bow-ride when the airguns were inactive. Two examples of fine-scale correlations in Atlantic spotted dolphin occurrence and behaviour with airgun use indicate that these responses may be short-term and also occur over relatively short ranges from the source.

Airgun source levels are sufficiently high that despite having poor hearing sensitivity at low frequencies, small odontocete species at times are expected to detect seismic surveys at 50 to 100 km (Richardson & Würsig, 1997). Higher-frequency acoustic energy is also produced from airgun arrays and may dominate the 0.2 to 22.0 kHz frequencies up to 2 km away (Goold & Fish, 1998). Given that Atlantic spotted dolphins use sound in at least the 0.1 to 18.0 kHz range (Herzing, 1996), airgun sound should be clearly audible to them. However, the audiogram of another *Stenella* species (*S. coeruleoalba*) suggests that although Atlantic spotted dolphins may detect sound at frequencies as low as 0.5 kHz, their sensitivity peaks at far higher frequencies in the 29.0 to 123.0 kHz range (Kastelein et al., 2003). The response of Atlantic spotted dolphins to airgun sound might therefore be expected to be greatest at relatively close range to the source.

In general, the behavioural effects of airgun sound on small odontocetes have been little studied. Stone (2003) reported apparent displacement of dolphins by 0.5 km from active airguns in UK waters, while Moulton & Miller (2005) recorded similar dolphin sighting rates for guns on and guns off during a survey off Nova Scotia. These studies used combined-species analyses, however, which may potentially mask the responses of individual species. For example, Moulton & Miller reported several instances of pilot whales (*Globicephala melas*) approaching within 300 m of active airguns, which may have biased a combined-species analysis.

Goold (1996) identified an apparent avoidance zone of 1 km around airguns for common dolphins, which is similar to the results for Atlantic spotted dolphins reported here. Avoidance in the region of 10 to 20 km around a seismic survey has been reported for beluga whales (Miller et al., 2005), however, suggesting that odontocete displacement can potentially occur at a much greater distance than examined for in most studies.

The apparent avoidance of airgun sound by Atlantic spotted dolphins might not occur during all seismic surveys. High-resolution seismic surveys utilise much smaller airguns, and Atlantic spotted dolphins were observed to bow-ride on three occasions during a survey using a 70 in^3 airgun (pers. obs.). Several other sources of high-frequency sound operated during the seismic surveys reported here, notably three Simrad EA 500 echo-sounders (at frequencies of 18.0, 38.0, and 200.0 kHz, respectively) located on the vessel's hull, and clusters of acoustic ranging devices (Sonardyne sips2 transceivers, operating in the 65.0 to 110.0 kHz frequency band and at maximum source level of 193 dB re: 1 µPa at 1 m) fitted at intervals along each hydrophone streamer. However, both were active independently of airgun use, and dolphins therefore appeared to be reacting primarily to airgun sound.

Prolonged displacement from important habitat (e.g., feeding and/or breeding sites) with long-term implications for population fitness is considered one of the major potential impacts on cetaceans from airgun sound (Richardson et al., 1995; Gordon et al., 2004). Humpback whales were the only species with a significant decrease in occurrence over the survey duration. However, this was not considered attributable to airgun sound but to the seasonal migration of animals away from their West African breeding grounds. Similar seasonal movements during the course of a seismic survey have been shown for other areas and species—for example, humpback whales off Australia (McCauley et al., 2000), bowhead and beluga whales in the Beaufort Sea (Miller et al., 2005), and common dolphins in the Irish Sea (Goold, 1996)—and it is important to consider such seasonal migrations when evaluating the potential displacement of animals from the region of a seismic survey.

Atlantic spotted dolphins showed similar occurrence in the three consecutive study periods with no evidence of displacement from the study area. The occurrence of sperm whales increased over the survey duration to peak in April, indicating that whales were not deterred from moving into an area where airgun sound had occurred regularly during the previous 8 mo. This result agrees with Swift (1994) who recorded increased acoustic detections of sperm whales during a 3-mo seismic survey off Scotland. The increase in numbers observed in the Angola survey area was likely attributable to foraging patterns since a historical abundance of sperm whales in this region correlates with an area of high seasonal productivity (Jaquet, 1996).

To conclude, this study found few obvious visible responses of humpback and sperm whales to seismic airgun sound off Angola, while striking short-term and short-range responses for Atlantic spotted dolphins were observed. However, only overt responses were examined, and subtle or longer-range responses may not have been detected. For example, bowhead and gray whales exhibited subtle changes in dive pattern and orientation in response to airgun sound (Richardson et al., 1986; Gailey et al., 2007), humpback whales exposed to pressure waves from underwater explosives apparently suffered severe ear injury despite exhibiting no noticeable behavioural reaction to the sound (Todd et al., 1996), and sperm whales may alter foraging behaviour despite a lack of obvious directional avoidance of airgun arrays (P. J. O. Miller, pers. comm.).

Acknowledgments

This work was carried out under the sponsorship of BP Exploration (Angola) Ltd and their partners in Block 31. I am grateful to Nathan Gricks for collecting portions of the field data presented here. The captains and crews of the *Geco Triton* provided assistance and hospitality during these surveys—my particular thanks to Hans Jacob Krogsrud, Miguel Mabansag, Piotr Sacewicz, Óle Skogsholm, and all seismic observers and bridge officers. Jonathan Gordon, Bill Streever, Ian Threadgold, and Anne Walls made useful comments on the first draft of this manuscript. I am grateful to W. John Richardson and Mari A. Smultea for reviewing and making comments to improve this manuscript.

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