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Recommended Citation

Dunlop RA, Noad MJ, McCauley RD, Kniest E, Slade R, Paton D, Cato DH. 2017 The behavioural response of migrating humpback whales to a full seismic airgun array. *Proc. R. Soc. B* 284: 20171901.
<http://dx.doi.org/10.1098/rspb.2017.1901>

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Research



Cite this article: Dunlop RA, Noad MJ, McCauley RD, Kniest E, Slade R, Paton D, Cato DH. 2017 The behavioural response of migrating humpback whales to a full seismic airgun array. *Proc. R. Soc. B* **284**: 20171901. <http://dx.doi.org/10.1098/rspb.2017.1901>

Received: 24 August 2017

Accepted: 14 November 2017

Subject Category:

Behaviour

Subject Areas:

behaviour, environmental science

Keywords:

anthropogenic noise, behavioural response study, biological significance, humpback whale, seismic airgun

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Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.3940267>.

The behavioural response of migrating humpback whales to a full seismic airgun array

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Despite concerns on the effects of noise from seismic survey airguns on marine organisms, there remains uncertainty as to the biological significance of any response. This study quantifies and interprets the response of migrating humpback whales (*Megaptera novaeangliae*) to a 3130 in³ (51.31) commercial airgun array. We compare the behavioural responses to *active* trials (array operational; $n = 34$ whale groups), with responses to *control* trials (source vessel towing the array while silent; $n = 33$) and *baseline* studies of normal behaviour in the absence of the vessel ($n = 85$). No abnormal behaviours were recorded during the trials. However, in response to the *active* seismic array and the *controls*, the whales displayed changes in behaviour. Changes in respiration rate were of a similar magnitude to changes in *baseline* groups being joined by other animals suggesting any change group energetics was within their behavioural repertoire. However, the reduced progression southwards in response to the *active* treatments, for some cohorts, was below typical migratory speeds. This response was more likely to occur within 4 km from the array at received levels over 135 dB re 1 $\mu\text{Pa}^2\cdot\text{s}$.

1. Introduction

The increased use of the marine environment by humans has resulted in increased ocean sound over the last several decades [1]. Anthropogenic sound sources are highly variable in character and include impulsive sounds from geophysical exploration for oil and gas, port developments and wind-farm construction, sonar sounds from military and civilian operations and continuous broadband noise from commercial shipping. The impact of these sources on marine animal physiology and behaviour, though studied for more than 30 years, is still poorly understood [2–4]. Without first understanding impacts of these sources, mitigation and management strategies are difficult to develop and implement. Extensive reviews of the effects of sound on marine organisms have led to the development of precautionary criteria for hearing and physiological responses in various taxa (e.g. fishes and sea turtles [5] and marine mammals [6]). These tend to focus on animals close to sources with high source levels. However, behavioural reactions may occur at much greater distances, be more variable, context dependent and less predictable than effects of noise exposure on hearing and physiology [6]. In addition, it is not yet known how significant, in terms of adverse effects (if any) on the population, these responses actually are [5,7].

In assessing the impact of sound on marine mammals, the National Research Council [8] defined an effect as ‘biologically significant’ if it keeps

enough animals from growing, surviving and reproducing, thereby potentially affecting the survival of the population. If the impact is biologically significant, there are obvious repercussions for the conservation of that population. Various links from response to life functions, vital rates and population effects has been put into a model framework known as Population Consequences of Disturbance [9–11]. The first step of this model is to determine if, and how, the changes in individual hearing, behaviour and/or physiology are related to the sound source in terms of the type, level and proximity of the sound source and the animal's response. Later steps relate this response to a change in one or more life functions (e.g. mating, migration), a change in vital rates (e.g. reproduction; [12]), and finally, to population-level effects (e.g. [13,14]). While these pathways are conceptually simple, measuring the impact of a behavioural change, from the initial disturbance, to just a change in a life function, let alone through to population effects, is difficult, as is determining whether any of the responses could be considered to be biologically significant. Progress can, however, be made by comparing behavioural responses to noise with normal (baseline) behaviour, and this is the approach used in this paper.

Seismic airgun arrays generate intense sound pulses intended to penetrate the sea floor to image the subsea strata in exploration for oil and gas or research. Arrays can consist of 20+ airguns fired every 8–15 s for periods lasting longer than 24 h (depending on the length of the survey line). An entire survey can last for months and may be conducted over several thousand square kilometres, though the sound field generated varies spatially and temporally. There have been a number of studies focusing on the effects of noise from seismic airguns on the behaviour of large whales. Reactions ranged from no detectable response (e.g. [14–16]), to small changes in travel course, speed and dive/respiration parameters [17–24] and vocal responses (e.g. [25–28]), to displacement of animals from an area [29–30]. It is therefore apparent that the behavioural response of large whales to seismic airguns is not a simple one but varies widely, likely due to differences in social context [17,18,31], environmental context [17,18,30], behavioural state and individual variability. None of these studies, however, attempted to assess the response in terms of its biological significance, making it difficult to assess the implications, if any, of these responses.

The BRAHSS (Behavioural Response of Humpback whales to Seismic Survey) project is a large-scale study with the overall aim of quantifying the behavioural response of humpback whales (*Megaptera novaeangliae*) to various seismic airgun array operational modes, including ramp-up (a mitigation measure used to prevent whales being exposed to levels that might cause a physiological effect). This study builds on three previous experiments [17,18,32] that used small experimental arrays. Using a full commercial seismic array as the source, we aim to quantify the response of migrating humpback whales (after accounting for social and environmental effects) and look for evidence of 'recovery' after the airguns ceased firing. Secondly, we compare these responses with normal (baseline) behaviour as a first step in assessing any biological significance. Thirdly, we relate the response magnitude to received level (RL) and proximity to the source in order to assess the 'zone' at which any significant responses are most likely to occur.

2. Methods

(a) Study design

Detailed data collection methodology has been presented elsewhere [17,18] and is summarized here as well as in the electronic supplementary material, methods section. Data were collected during the southward migration of the eastern Australian humpback whales in September and October 2014 and 2015. Experimental trials were carried out using a dedicated seismic source vessel with a 51.31 (3130 in³) airgun array (2014). Data were collected on groups of whales when no trials were occurring (*baseline* behavioural data; 2014 and 2015). Experiments were designed to obtain adequate sample sizes (based on power analysis; see [33]).

As in previous work at this site, focal groups of humpback whales (including male and female adults as well as calves) were 'followed' as they moved southwards through the study area. Inshore focal follows were conducted by four teams of observers on two land stations (11.5 km apart) and offshore follows by four teams on separate <7 m length, boats. A previous study found the data from the two platforms to be complementary [34]. 'Scan' teams at both stations gathered spatial and behavioural data ad libitum on all groups in the area.

The study area was monitored acoustically using a fixed array and moored recorders. The fixed array of five hydrophone buoys were moored 1.5–2.5 km off the coast and radioed data to a shore station to acoustically track singing whales [35]. Six calibrated underwater acoustic recorders [36] were used to cover the full study area with different receiver to array azimuths and variable bathymetry paths (36 deployments of 1–5 days each). The received sound exposure levels (SEL in dB re 1 $\mu\text{Pa}^2\cdot\text{s}$) of airgun signals at whale groups as a function of time along their tracks [37] were estimated using an empirical propagation model developed for the site at ranges greater than 1 km and modelled and verified source propagation at ranges <1 km. Predictions of SEL incorporated the effect of array directionality and different seafloor types (see electronic supplementary material for further details).

The source vessel used in this study was the *RV Duke*, a 65 m, 2031 ton seismic exploration vessel. Once activated, the power of the airgun array 'ramped-up', during the first 20 min. As in previous work, the ramp-up was designed to progress in approximately 6 dB steps so that the increase in level is likely to be clear to the whales. The array was towed at 4.5 knots (8.3 km h⁻¹), 80–100 m astern the *RV Duke* with an 11 s shot interval at 6 m depth.

Each trial followed a 'before/during/after' design. In the *before* period (60 min), the *RV Duke* approached the start of the transect at reduced speed (less than 4 kt) from the southeast to maintain maximum separation with the whale groups. The *during* transect (see table 1 for duration of stages) was northwards into their migratory path. In the *after* period, the ship slowly left the study site and the whale groups were well south of the ship. Trials were balanced between being *active*, with the airguns firing, or *control*, where the airguns were towed along the same transect but were not operated. Observers were blind to the 'treatment' as well as phase. Data were also collected from *baseline* groups (no source vessel in the study area) for at least 90 min when trials were not underway.

(b) Behavioural analysis

The behavioural record for each trial group was compared with the general behaviour of *baseline* groups to look for evidence of abnormal, or a cessation of 'normal', behaviours. Response variables were group dive time and respiration (blow) rate (per individual per 10 min), rates of various surface behaviours (per group per 10 min; 'breach behaviours', 'tail slapping behaviours'

Table 1. Detailing the structure of treatments in the ‘during’ phase, including the array volumes used in ramp-up. Volumes are total volumes and may be a single airgun or a number of airguns operated simultaneously. Mean (and range) of received airgun SELs at the focal whale groups used in the analysis and distance (proximity) from the source.

treatment	duration of stage (min)	gun volumes (in ³)	received SEL dB re 1 $\mu\text{Pa}^2\cdot\text{s}$ (mean and range)	source distance (proximity) m (mean and range)
ramp-up (first during phase)	30 (4 \times 5 min stages and 1 \times 10 min full array stage)	ramp-up 40, 250, 500, 1440, full array 3130	131 (76–166)	6878 (636–14 240)
full array (second during phase)	30	3130	130 (75–157)	8281 (3488–15 810)
control first 30 min	30	not applicable	not applicable	6244 (922–15 640)
control second 30 min	30	not applicable	not applicable	7521 (1093–13 950)

and ‘pectoral slapping behaviours’) and measures of group movement per 10 min including (i) group speed of southward movement (speed south), (ii) the change in group swim speed (speed variation) and (iii) group course deviation from south (‘course 180’, a measure of their deviance from their general southwards migratory direction). See electronic supplementary material for further details on calculating these.

Each dive and each 10 min time bin were annotated with various contextual social and environmental variables. Groups were categorized as *female-calf*, *female-calf-escort*, *multiple adults*, *adult pair* or *lone animals* according to their group composition. Group social behaviour was categorized as *pre-split* (up to 10 min before the split), *post-split* (up to 10 min after the split), *pre-join*, *post-join* (as with splitting) or no change in group membership (*stable*). Additional measured social variables included the distance of the nearest other group to the focal group (within 1 km, 1–2 km, 2–5 km and beyond 5 km), distance of the nearest singing whale (using the same distance categories), number of other groups in the study area (a proxy for density) and number of singing whales in the study area. Environmental variables included wind speed, distance of the group from shore, water depth and broadband background noise level (5 Hz–1.8 kHz), all averaged over the 10 min time bins.

Each measured response variable was modelled against various predictor variables in a mixed model with group ID as the random effect (using the lme4 package in ‘R’ [38]). ‘Dive time’, ‘course 180’ and ‘course variation’ were log transformed to result in a normal distribution. ‘Speed south’ and ‘speed variation’ were normally distributed. ‘Blow rate’ data were analysed using a Poisson model. Surface behaviour data were analysed in 30 min time bins (due to zero inflation). The number of breaches within a 30 min time bin was counted, as these were usually singular events, analysed using the glmmADMB package (<http://glmmadmb.r-forge.r-project.org>). Models assumed a negative binomial distribution with zero inflation to account for the skew towards zero. Tail slapping and pectoral slapping occurred in bouts which were highly variable in duration (with between 3 and over 40 behaviours per bout) and therefore scored from 0 to 3 depending on how many of the 10 min time bins (within each 30 min time bin) contained bouts. These ordinal data were analysed using a cumulative link effects mixed model fitted with Laplace approximation using the ‘ordinal’ package in ‘R’ [39] with a ‘probit’ function.

First a ‘base’ model was generated for each response variable which incorporated significant ($p < 0.05$) social and

environmental predictor variables [40,41]. This ‘base’ model included all data from *baseline* ($n = 85$), *control* ($n = 33$) and *active* ($n = 34$) groups. To test for additional changes in behaviour (aim 1) in response to the presence of the ship (*control*), the ‘ramp-up’ procedure (first 30 min of *active*) and the full seismic array (the second 30 min of *active*), the interaction term (phase \times treatment) was added and tested for significant improvement using a maximum likelihood ratio test (with the degrees of freedom being d.f.1 [base model] – d.f.2 [experimental model]). Effect sizes from response models were calculated (back-transformed, if necessary) and reported with standard errors in tables (in the electronic supplementary material) and plotted with 95% confidence intervals. The tables include the effect sizes of significant variables and the results of the likelihood ratio comparison between base and experimental models. Residual plots were visually inspected and did not reveal any obvious deviations from homoscedasticity or normality. Residuals for any ‘Poisson’ models were checked for over-dispersion.

Significant responses were selected for further analysis to address the second aim, to determine if the response to the treatments lay outside the range of normal behaviours after accounting for changes due to social or environmental variables. The interaction effect of treatment (*baseline* or *active*) and the strongest social or environmental predictor were modelled for each response variable using procedures outlined above.

To develop the dose–response model (aim 3), using only *control* and *active* groups, a measure of group deviance (change in movement behaviour from their predicted pathway, DD_{gp} , as developed in [42]) was used. An increase in DD_{gp} equates to a bigger change in movement behaviour (e.g. slowing of speed south and/or increase in course deviance). Following the model framework developed in [32] using a 20 in³ airgun and a four-stage array, a two-dimensional smooth surface was used as the interaction between RL and SVP (received level and source vessel proximity, both continuous covariates). A complex region spatial smoother (CReSS) [43] with a spatially adaptive local smoothing algorithm [44] was used to fit this two-dimensional smooth, which was then used as one of the covariates. ‘Water depth’ and ‘wind speed’ were also included. Model selection of covariates was undertaken using fivefold cross-validation. The optimal model was then rerun in a generalized estimating equation (GEE) framework to deal with the lack of independence of model residuals with focal ID as the panel structure. Predictions were made from the best model and a

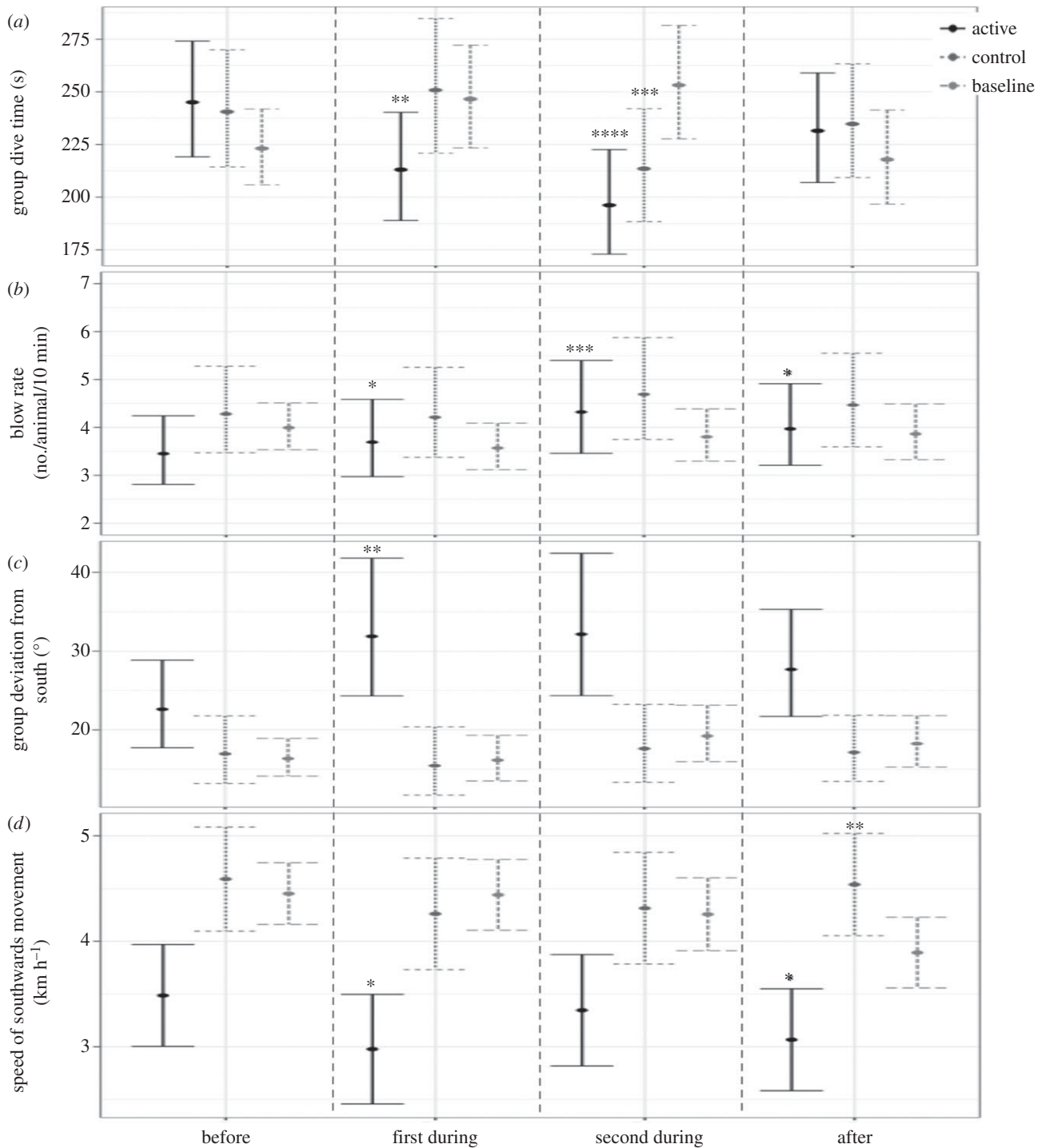


Figure 1. Group dive, respiration and movement responses, including 95% confidence intervals, *before*, *first and second phase of during*, and *after* the *active* ($n = 34$ groups) and *control* treatments ($n = 33$ groups) and *baseline* groups ($n = 85$ groups). Within-model p values (setting the *before* phase and *baseline* groups as the intercept) are represented as $*(p < 0.05)$, $** (p < 0.01)$, $*** (p < 0.001)$ and $**** (p < 0.0001)$.

parametric bootstrap from the GEE model was used to calculate 95% confidence intervals.

3. Results

(a) General behavioural response (aim 1)

None of the groups exhibited any behaviours that were outside their normal repertoire of behaviours (e.g. continuous surface activity, female–calf separation) and none of the groups ceased to migrate or turned and continued to head northwards after the trial was over. Groups continued to generally move southwards and socially interact during *active* and *control* treatments.

Group median dive time was 220 s with a median ‘blow rate’ (per individual) of 4 blows per 10 min (though up to 26 blows per 10 min in socially interacting groups). Both depended on the group composition and social behaviour (whether it was splitting or joining) with dive time also depending on the distance to shore (electronic supplementary material, tables A1 and A2; [40]). In response to the ‘ramp-up’ and ‘full array’ phase, groups significantly reduced their ‘dive time’ (by 45 s and almost 1 min respectively; figure 1a) and individuals had an elevated ‘blow rate’ (by 1 blow/individual/10 min equating to a 20% increase; figure 1b). ‘Blow rate’ remained significantly elevated in the *after* phase suggesting a prolonged effect of the airgun stimulus. Minimum

(usually start) received SEL during follows in the ‘ramp-up’ phase ranged from 90 to 149 dB re $1 \mu\text{Pa}^2\text{s}$ and generally escalated in the *during* phase. The maximum SEL reached during any follow was over 100 dB re $1 \mu\text{Pa}^2\text{s}$ in all groups suggesting the source was audible (louder than background noise), the highest received level being 166 dB re $1 \mu\text{Pa}^2\text{s}$. Since this was a commercial seismic array operating in a realistic scenario relative to the whale movements, the range of received levels could be considered typical of exposure during seismic surveys.

Control groups displayed significantly shorter (by 45 s) dive times in the second 30 min (figure 1a) suggesting the dive response was also a response to the ship. All *control* groups came within 5.5 km of the vessel apart from one with a minimum approach distance of 8.4 km and had a similar range of proximities to the vessel compared to *active* groups (table 1). Group ‘dive time’ recovered to pre-exposure dive times once the airguns had ceased firing and the ship had left the area (figure 1a).

All groups, taken together, generally migrated along a median deviance from ‘course 180’ of 18° (i.e. south-south-east) and varied their course by a median of 19° between successive 10 min time bins, though less so in deeper water (see electronic supplementary material, table A3; [40]). The average ‘speed south’ of all groups was 4.1 km h^{-1} with a mean ‘speed variation’ between successive time bins of 0.002 km h^{-1} . In terms of social effects, female–calf groups made slower progress south compared to most other group compositions (electronic supplementary material, table A3; [40]). In response to ‘ramp-up’, groups significantly increased their ‘course 180’ by a further 10° (generally, though not always, heading further east; figure 1c) and moved southwards more slowly (by 0.5 km h^{-1} ; figure 1d). This reduction in speed south within the *active* trials persisted into the after phase. They did not significantly change their ‘speed variation’ (i.e. neither sped up nor slowed down) suggesting this reduction in ‘speed south’ was a consequence of course deviation, rather than a change in travel speed. Note, in the *before* phase, *active* group ‘speed south’ was lower (though not significantly) compared to the *control* and *baseline* groups (reasons for this will be discussed later). ‘Course 180’ and ‘course variation’ remained elevated in the ‘full array’ phase, though not significantly (figure 1c), and had almost returned to *baseline* by the *after* phase. Groups also significantly increased their ‘speed south’ after *controls* suggesting some movement response to the ship (figure 1d).

(b) Surface behaviour

The mean breaching rate (per group per 30 min) in all measured groups was 1.8, though groups could breach up to 80 times in 30 min. Group breaching rates increased in higher wind speeds and differed according to the distance of the nearest neighbour (see electronic supplementary material, table A4; [41]). In response to the experimental treatments, groups were significantly more likely to breach in the first 30 min of both *active* ($p < 0.05$) and *control* ($p < 0.0001$) treatments (by an additional 0.5 breach per 30 min with an upper 95% CI of 3 in *active* trials and 0.6 per 30 min in *control* trials with an upper 95% CI of 4). This suggests some effect of the presence of the ship on surface behaviour rates.

Tail slapping and pectoral slapping scores (0–3) were similar between the different group compositions despite

the differences in group number and membership and related to group social behaviour and wind speed (see electronic supplementary material, tables). There was no change in either behaviour in response to *active* or *control* trials. Groups continued to use these signals socially while the airguns were operating and in the vicinity of the ship.

(c) The comparison of the observed reaction with baseline behaviour (aim 2)

The strongest effects in the *baseline* dataset predicting group ‘dive times’ and individual ‘blow rates’ were group composition and the social behaviour of the group (electronic supplementary material, tables A1 and A2). Groups containing a calf as well as *multiple adult* groups (which sometimes contained a calf), tended to have shorter dive times compared to other adult-only cohorts (figure 2a) as did socially interacting groups (figure 2b). Individual ‘blow rates’ were between 4 and 6 blows/individual/10 min for all group compositions (figure 3c) but elevated during social interactions (figure 3d).

The greatest dive/respiratory response in the experiment was within groups during the full array phase of the *active* treatments (figure 1a,b). If accounting for the effect of group composition, only *multiple adult* groups and *adult pairs* responded in this way. These cohorts significantly decreased their dive time (by over 1 min; figure 2a) with a concurrent elevation in respiratory rate (by 3 blows/individual/10 min; figure 2c). Dive times, especially in *multiple adult* groups, fell below *baseline* group dive times, even *baseline* groups containing a calf or *baseline* groups changing in membership, suggesting dive behaviour in these groups was outside normal *baseline* behaviour. Although ‘blow rates’ in groups exposed to the airguns were elevated, they were not significantly different to ‘blow rates’ within joining groups (figure 2d). ‘Dive times’ and ‘blow rates’ within interacting groups (splitting and joining), however, were similar between *baseline* and *active* groups (figure 2b,d).

Movement behaviour was most dependent on group composition (electronic supplementary material, table A3). *Baseline multiple adult* groups tended to deviate more from south (at 24°) and progress faster south (at 5 km h^{-1}) compared to other group compositions. These larger groups comprise multiple adult males competing for the primary escort position to the female and as such, can move somewhat erratically in terms of course and speed [40]. In response to the ramp-up phase of the *active* treatments, groups generally increased their ‘course 180’ (figure 1c) and decreased their ‘speed south’ (figure 1d). When accounting for group composition, the most significant change in ‘course 180’ was within *female–calf* groups, which increased their course deviation by 20° compared to *baseline* groups (figure 3a), resulting a 1 km h^{-1} decrease in speed south (figure 3b). *Female–calf–escort* groups also increased their ‘course 180’ (though not significantly), resulting in a similar decrease in ‘speed south’ (of 1 km h^{-1}) to *female–calf* groups. The most significant change in ‘speed south’ occurred in *adult pairs*, which reduced their speed south by half of their original speed, travelling at only 2.5 km h^{-1} (figure 3b).

(d) The effect of source received level and proximity (aim 3)

Changes in movement behaviour, re-measured as the deviance of the group from their prior course and speed

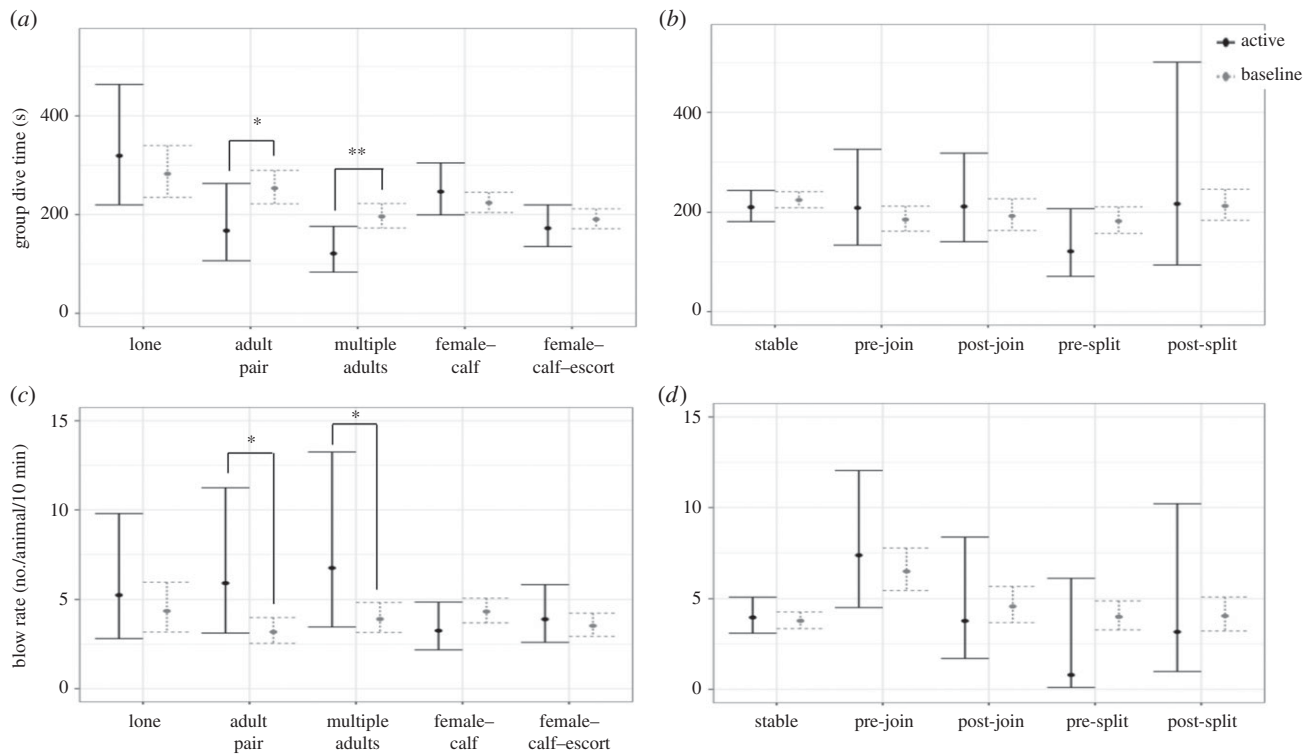


Figure 2. Group dive and respiration responses including 95% confidence intervals modelled within different social compositions (*a,b*) and social interactions (*c,d*) for *baseline* data compared to groups within the during phase of *active* treatments. Within-model *p* values are represented as *($p < 0.05$), **($p < 0.01$) and ***($p < 0.001$). Group sample sizes were 85 baseline and 34 active groups equating to 15 385 dive data-points and 1367 10 min data-points (blow rate).

(group deviance), was significantly dependent on the combination of RL and SVP along with environment variables of wind speed and water depth. Spatially, within the CRESS term (the interaction between proximity and the received level of the airgun array), animals were more likely to avoid this source (deviate from their path) at received levels over $135 \text{ dB re } 1 \mu\text{Pa}^2\text{s}$ and when the source was less than 4 km away (figure 4). In other words, significant changes in group movement behaviour were more likely to occur within a specific received level/proximity 'zone'.

4. Discussion

For a change in behaviour to be considered biologically significant, it should have an effect on one or more life functions (e.g. migration, survival, mating), affecting individual vital rates (e.g. maturation, reproduction) and ultimately leading to population effects [8–13]. For example, an animal that is under stress can exhibit behaviours outside their normal behavioural repertoire and/or cease to exhibit typical behaviours [45]. If this stressor is chronic, then the animal is likely to have a reduced likelihood of surviving and reproducing. In this study, no abnormal behaviours, such as instances of a female separating from her calf or sustained bouts of high energy surface behaviours (which are considered abnormal behaviour indicative of a stress response in humpback whales), were observed. We also continued to observe typical behaviours including singing, socializing with conspecifics, using social signals such as surface slapping, and general migratory travel southwards. Given the lack of abnormal behaviours, and the continued prevalence of typical behaviours, we found no evidence that they were under significant additional stress (as defined

above) during the experimental trials. Put another way, the behaviour of the whales appeared to be driven primarily by other whales and the need to socialize and migrate, and the addition of a seismic vessel and airguns had little impact on that. Other studies, specifically looking at the effects of seismic airgun noise on large whale behaviour (e.g. [14–25]), also did not report any gross changes in behaviour.

Groups of migrating humpback whales, however, responded to a full seismic array by changing the magnitude and rates of typical behaviours, such as their movement patterns, dive/respiratory parameters and rates of breaching behaviours. These changes were dependent on the group composition and were, for the most part, small, variable, temporary (did not last into the after phase) and were likely a response to the presence of the ship as well as the airguns. Changes in 'blow rate' interestingly did not occur in the *control* trials and did last into the *after* phase, indicating a potential response to just the airgun array. These changes were, however, within the normal behavioural repertoire of migrating groups, and of a lesser magnitude compared to the group's respiratory response to changes in social context. Individual respiration rates were clearly elevated in joining groups, and remained elevated after joining, probably due to the change in group social dynamics. It cannot be assumed, however, that because an animal shows little or no response, that it is not vulnerable [46]. Female-calf groups, originally thought to be the most 'sensitive' (due to the presence of a young calf), did not change their dive/respiratory behaviour. However, the reactions of these groups may be constrained by the energetic demands of the calf in that the calf was already respiring at a high rate and therefore had little scope to increase further. In addition, female-calf groups in this study were migrating and an earlier study suggested resting humpback whale female-calf

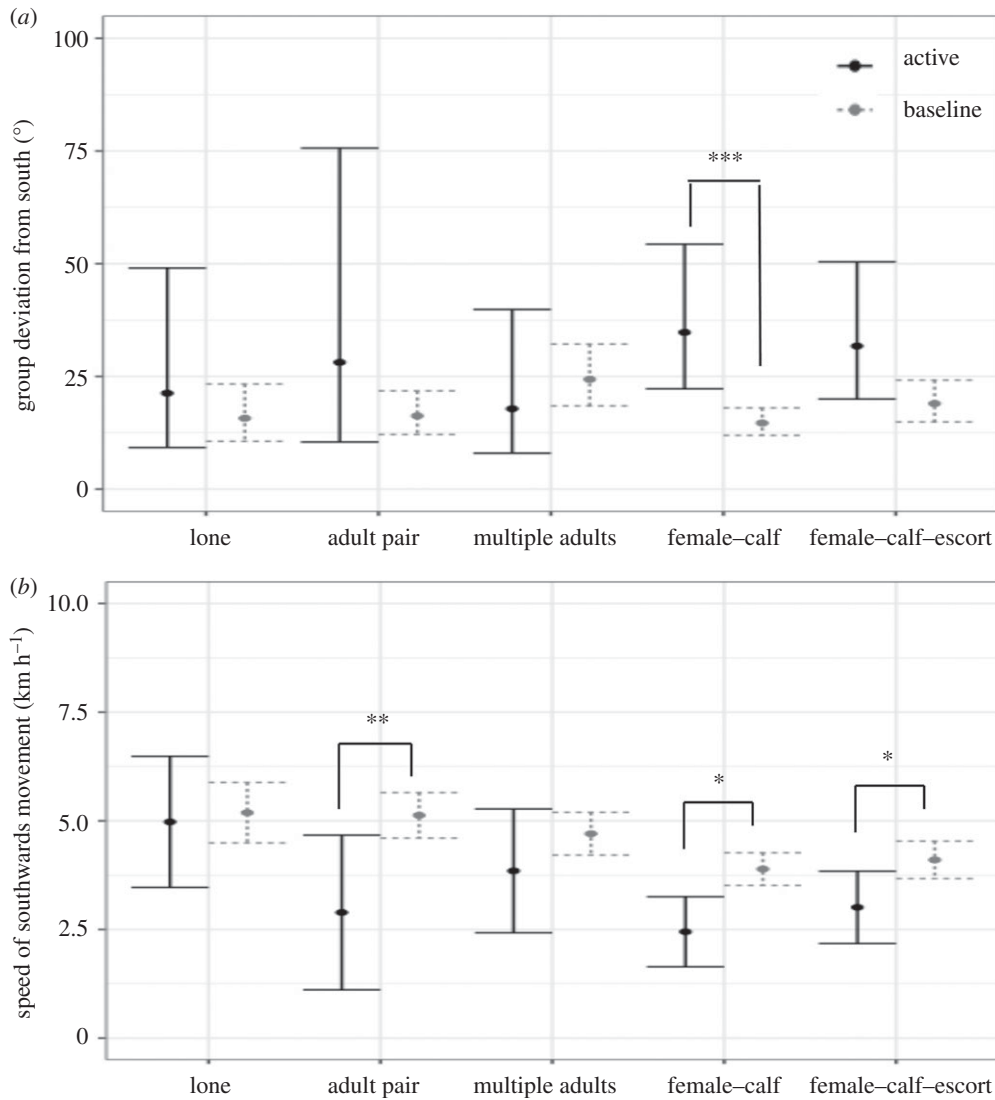


Figure 3. Group movement responses including 95% confidence intervals modelled within different social compositions (*a,b*) for *baseline* data compared to groups within the during phase of *active* treatments. Within-model *p* values are represented as * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$). Group sample sizes were 85 *baseline* and 34 *active* groups equating to 1367 10 min data-points.

groups may be more sensitive to the effects of seismic airgun sound and therefore more likely to respond [21]. The cohort studied here, however, was more likely to change movement behaviour (as discussed below) rather than dive/respiratory behaviour, illustrating a suite of measured response variables should be measured when dealing with different groups.

Groups exposed to the *active* seismic array made about a 1 km per hour slower progression south compared to most *baseline* groups (due mostly to a deviance off their normal course rather than a slowing down of travel speed). The majority of whale groups were NE to NW of the source at the start of the *during* phase and moving generally south, thus approaching the source. It should be noted that the speed south of groups in the *active* trials were already lower in the *before* phase compared to *baseline* or *control* groups. The procedure in setting up of the *active* trials is likely to have contributed to this. In *active* trials, due to strict mitigation protocols, start times had to be delayed if whales were sufficiently close to cause a shut-down in the *during* phase meaning the ship was sometimes in the start position for longer compared to *control* trials (and groups, we know, also responded to the presence of the ship). Otherwise, conditions were similar between

active, *baseline* and *control* trials, such as the distribution of social groups and the range of distances from the vessel start position. The reduction in speed south from the *before* to the ramp-up phase of the *active* exposure was, however, statistically significant.

Group composition was a factor in that adult pairs reduced their speed south 2.5 km h⁻¹ in response to the seismic airgun array, travelling about half of their original speed south. Female-calf groups were the most 'responsive' in terms of changes in course deviation from south, resulting in a 1 km h⁻¹ reduction in speed south, again moving slower than *baseline* groups. These changes, to some extent, persisted into the *after* phase of the *active* trials. Resting female-calf pairs have been found to show avoidance responses at relatively low received levels (129 dB re 1 $\mu\text{Pa}^2\cdot\text{s}$) compared to migrating humpback whales, which showed clear course changes at received levels of 144–151 dB re 1 $\mu\text{Pa}^2\cdot\text{s}$ [21]. The dose-response model presented here showed that a change in movement behaviour was more likely to occur within 4 km from the ship at received levels over 135 dB re 1 $\mu\text{Pa}^2\cdot\text{s}$. These values are similar to those obtained for a smaller experimental array [32] suggesting some consistency in these results despite differences in array size and towpath

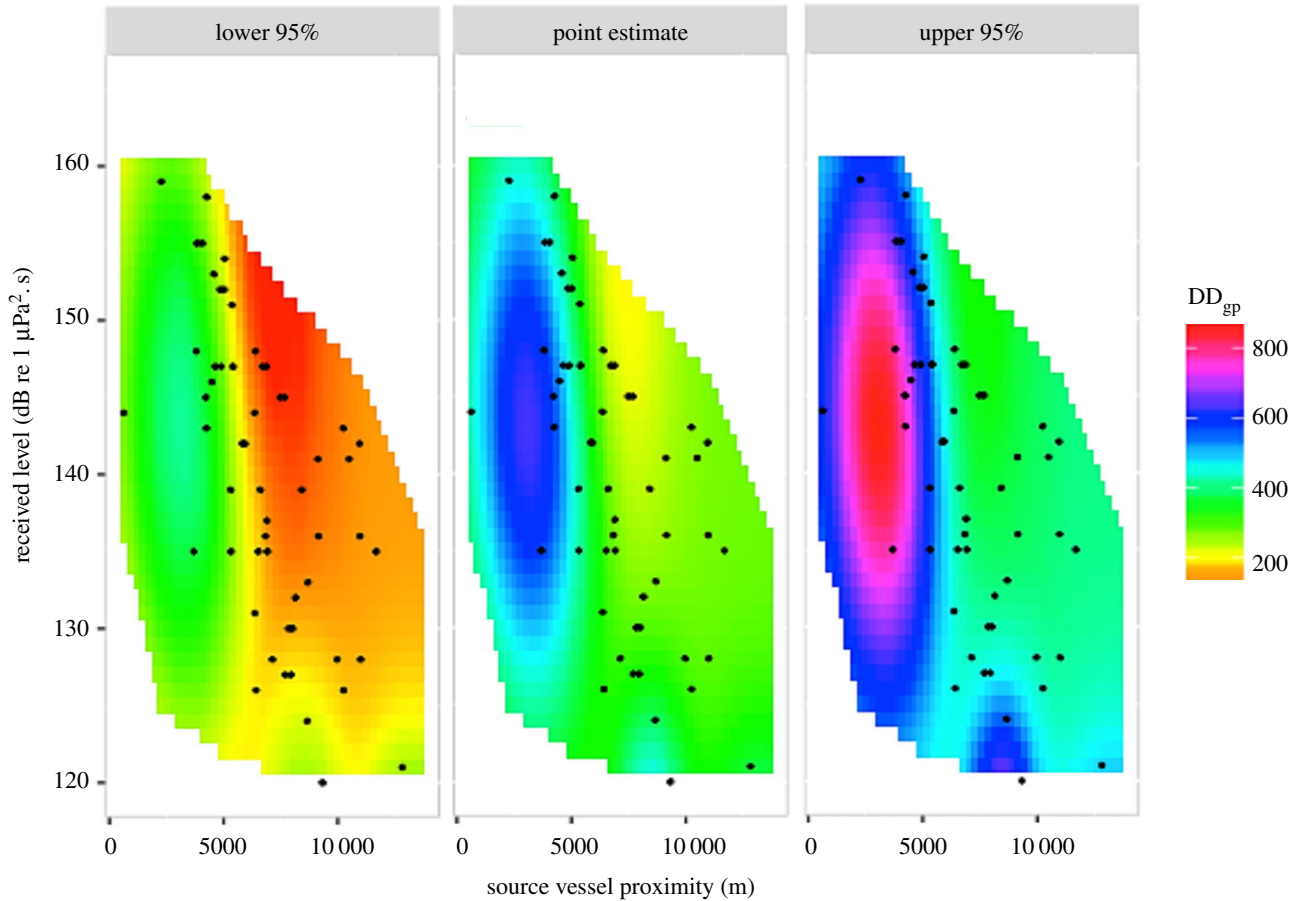


Figure 4. The estimated response (DD_{gp}) of groups to the received level of airgun noise at a range of proximities, where an increase in DD_{gp} equates to a greater movement deviation. The colour represents the estimated response, while the dots give the measured received level and proximity values. The cReSS smoother term accounts for the relationship between the received level and proximity through its local radial basis functions.

direction. Previous studies of the response of baleen whales to airguns have shown a wide range of received levels for which some measure of disturbance was observed. While the current results generally lie within this range, differences in methods of measuring responses and received levels, as well as differences in behavioural and social conditions, limit the extent that comparisons can be made. It should also be noted that the values reported here are specific to our context (migrating humpback whales returning to feeding grounds) and may need to be updated depending on species, sound source and context.

Whether or not the changes in travel behaviour found here translate to a longer-term effect on migratory behaviour and thus a lasting effect on life functions requires further study. Disturbances to the optimal migration strategy has been found to theoretically increase overall energy use in humpback whales by altering average velocity and increasing the total travelled distance due to displacement [47]. Extreme capital breeders, such as humpback whales, may be vulnerable to changes in the energetic costs of migration. These changes may have implications for the growth potential of calves [47] and may be a problem for lactating females in that it would delay these whales replenishing their energy reserves. In this experiment, the exposure phase only lasted for 1 h and the whales were migrating so that most were moving away from the source meaning they were only likely to be in the ‘zone of avoidance’ for a short period of time. Even with a seismic survey that continues for many hours in an area, migrating whales are only likely to be

exposed for a relatively short period of time before they move away as part of their migration. However, the situation might be different for animals which were resident (e.g. feeding grounds), or temporarily resident (e.g. resting areas during migration) in an area, for part of the survey where sustained exposure is possible.

This study found no evidence of gross changes in behaviour in migrating humpback whales in response to a full commercial seismic array. Progression southwards, however, was significantly lower compared to normal (baseline) behaviour in response to the airgun array. This response was more likely to occur if groups within a specific received level/proximity zone, meaning any assessment of biological significance should incorporate both spatial and temporal parameters. To do this, an estimate of the potential exposure time within the avoidance ‘zone’ could be modelled using likely survey tracks and the whale movements relative to the source [10].

Ethics. The project operated under animal ethics approval from the University of Queensland Animal Ethics Committee, a Queensland Government Environment, and Heritage Protection permit (WISP14781414) and an Australian Government Access to Biological Resources in a Commonwealth Area for Non-Commercial Purposes permit (AU-COMM2014-246).

Data accessibility. The article’s supporting data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.gd0qc> [48].

Authors’ contributions. R.D., M.N., R.M. and D.C. conceived the study, designed the study and helped draft the manuscript. R.D. carried out the data analysis. M.N. and R.D. coordinated the data collection. E.K. designed one of the main data collection tools. R.M. analysed all

acoustic data. R.S. and D.P. collected field data. All authors gave final approval for publication.

Competing interests. We have no competing interests in that funding agencies had no input into experimental design, data collection, data analysis or interpretation or the writing of the paper.

Funding. Funding was provided as part of the Joint Industry Programme on E&P Sound and Marine Life (JIP), managed by the International Association of Oil & Gas Producers (IOGP). The

principal contributing companies to the programme are BG Group, BHP Billiton, Chevron, ConocoPhillips, Eni, ExxonMobil, IAGC, Santos, Statoil and Woodside. The United States Bureau of Ocean Energy Management (BOEM), Origin Energy, Beach Energy and AWE provided support specifically for the BRAHSS study.

Acknowledgements. We would like to thank all the BRAHSS team members particularly Louise Bennett and Verity Steptoe and the BRAHSS volunteers for their assistance with data collection.

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