



## The effect of close approaches for tagging activities by small research vessels on the behavior of humpback whales (*Megaptera novaeangliae*)

MICHAEL J. WILLIAMSON,<sup>1</sup> AILBHE S. KAVANAGH, and MICHAEL J. NOAD, Cetacean Ecology and Acoustics Laboratory, School of Veterinary Science, The University of Queensland, Gatton, Queensland 4343, Australia; ERIC KNIEST, School of Engineering, University of Newcastle, Callaghan, New South Wales 2038, Australia; REBECCA A. DUNLOP, Cetacean Ecology and Acoustics Laboratory, School of Veterinary Science, The University of Queensland, Gatton, Queensland 4343, Australia.

### ABSTRACT

Small research vessels are often used as platforms for tagging activities to collect behavioral data on cetaceans and they have the potential to disturb that group or individual. If this disturbance is ignored, results and conclusions produced by that study could be inaccurate. Here land-based behavioral data of migrating humpback whales (*Megaptera novaeangliae*) ( $n = 29$ ) were used to determine the effect of close approaches for tagging by research vessels on their diving, movement and surface behaviors. Groups of whales were tagged, using digital recording tags, by small research vessels, as part of a behavioral response study. In groups that were approached for tagging, temporary changes in movement behaviors during close approaches were found, with subsequent recovery to “pre-approach” levels. In female-calf groups more long-term changes in travel speed were found. Results suggest that, although close approaches for tagging by small vessels may cause behavioral changes in humpback whales, this change may be small and temporary. However, in female-calf groups, the behavioral change may be greater and longer lasting. This study shows that when using small vessels for behavioral research, disturbance, and recovery should be measured to ensure integrity of data used for other analyses.

Key words: BRAHSS, anthropogenic disturbance, behavior, cetacean, humpback whale, *Megaptera novaeangliae*, vessel.

In cetacean research, data are often collected from small vessels, either as standalone platforms, or in conjunction with land-based or aerial-based platforms. Research vessels are used for obtaining behavioral and acoustic data, conducting biopsy sampling, and deploying tags for various purposes. Compared to land or aerial platforms, data collected from small vessels can be more detailed, as data are collected at much smaller distances resulting in greater accuracy and fewer behaviors missed (Findlay and Best 1996). In addition, information can also be more easily collected at an individual level rather than group or population level (Tyack 1981) because individuals within a

<sup>1</sup>Corresponding author (e-mail: mikejwilliamson@outlook.com).

group can be more easily and accurately identified. However, there are a number of issues associated with using vessels as data collection platforms for research. Vessel-based data can be less cost-effective and may generate smaller sample sizes compared to land-based studies (Denardo *et al.* 2001, Elwen *et al.* 2009).

In order to obtain fine-scale behavioral data on cetaceans from small research vessels, close approaches between 5 m and 100 m are required. These have the potential to disturb the group or individual during data collection (Richardson *et al.* 1985, Clapham and Mattila 1993, Nowacek *et al.* 2001) due to the close proximity of the vessel required for data collection, and/or change in the noise levels from the research vessel (Au and Green 2000, Erbe 2002). In many studies, potential disturbance to whales by small vessels is mitigated by minimizing the movement of the vessel, engine noise, and changes in throttle setting, as well as maximizing the vessel distance from the study animal or group during behavioral observations (Miller *et al.* 2009). Despite these measures, animals may still be disturbed. One way to account for any potential disturbance is to delay any behavioral data collection following close approaches from research vessels until the animal or group has returned to "pre-approach" behavior. Some studies exclude the first two dive cycles after the initial approach by a research vessel to prevent the use of perturbed behavior (Croll *et al.* 2001, Baumgartner and Mate 2003, Nowacek *et al.* 2004), but present little objective evidence that animals return to pre-approach behavior after this time. As such, to fully assess any potential disturbance of close approaches on cetaceans, a comparison of the behavior of the target animal or group before, during, and after approaches from small vessels for behavioral sampling is necessary (Van Parijs and Corkeron 2001, Ribeiro *et al.* 2005). For example, Morete *et al.* (2007) continuously sampled humpback whale (*Megaptera novaeangliae*) group behaviors from land and monitored their reactions before, during, and after tourist and research vessels approached the group. However, this may not be feasible in studies that only use one small vessel to collect observational data (*e.g.*, Corkeron 1995, Miller *et al.* 2000), as data collection from land or an additional vessel is required. In the absence of land-based observations, to enable true controls, the effect of the research vessel can be assessed using a regressive technique, where the dependence of response variables (such as diving behaviors) to the research vessel at varying observation distances are examined (Lusseau 2003). However, this kind of method is not regularly undertaken. Overall, there is little investigation of the effect of research vessels on behavior, and when it is investigated, this is often subjective rather than objective.

When visually observing cetaceans from land-based or vessel-based platforms, only behaviors that occur at the water's surface can be observed. As a result, the majority of whale behavior will not be recorded due to the long periods of time these animals spend underwater. In order to supplement behavioral data, there is an increased reliance on tags that can provide an understanding of the three-dimensional movements of cetaceans (Johnson and Tyack 2003). However, close approaches to within several meters are required to attach tags because they are deployed using a long hand-held pole (Mate 1989), or shot at close range using a low velocity system (Heide-Jørgensen *et al.* 2001). Various reactions to close vessel approaches for pole attachment of suction cup tags have been observed in cetaceans. Strong, long-lasting reactions have been seen in bottlenose dolphins (*Tursiops truncatus*) (Schneider *et al.* 1998). However, in other species, such as humpback whales (Stimpert *et al.* 2012) and fin whales (*Balaenoptera physalus*) (Giard and Michaud 1997), either mild reactions, or no reaction, have been observed. Varying reactions have also been seen within species,

depending on the speed and movement of the research vessel when conducting tagging approaches. For example Stimpert *et al.* (2012) found that slow approaches caused minimal apparent impact on group behavior when tagging Antarctic humpback whales compared to faster methods.

Potential disturbance of cetaceans from research vessels may be dependent on several factors, such as speed of approach, duration of approach, and angle of approach (Watkins 1981, Alves *et al.* 2010, Stimpert *et al.* 2012). Group composition has also been found to be an important factor when looking at behavioral responses. There is evidence that the age and sex composition of a group affect the likelihood of a reaction to disturbance (Cantor *et al.* 2010, Reisinger *et al.* 2014). Female fin whales, southern right whales (*Eubalaena australis*), and humpback whales have been found to be sensitive to biopsy sampling (Clapham and Mattila 1993, Brown *et al.* 1994, Gauthier and Sears 1999, Best *et al.* 2005). However, competitive groups of male humpbacks show very little response (Clapham and Mattila 1993, McCauley *et al.* 2000). Additionally, studies have found that humpback whale females with young calves, in particular, seem to have an increased sensitivity to disturbance in regards to biopsy sampling, anthropogenic noise, and vessel traffic (Bauer *et al.* 1993, Clapham and Mattila 1993, McCauley *et al.* 2000, Stamation *et al.* 2010, Stimpert *et al.* 2012). Therefore, when analyzing behavioral responses in cetaceans, to prevent masking of significant effects, it may be useful to examine any potential variability between cohorts.

Many behavioral studies on humpback whales have involved tagging and/or vessel-based data collection at close proximity, and it has not always been feasible to take into account the effect of noise from the approaching vessel, or to include any measure of behavioral response of the group or individual to the vessel. As part of a larger project investigating the behavioral response of Australian humpback whales to seismic surveys (BRAHSS) (Cato *et al.* 2013, Dunlop *et al.* 2015), we were able to track individuals by both land and small vessel observation platforms, giving us the opportunity to evaluate the impact of close approach by our research vessels. Although the primary objective of the BRAHSS project was to assess how these animals react to seismic sound exposures while migrating, no seismic airgun operations were conducted during the observations reported for this study.

The aims of this study were to use land-based observations to (1) determine if the behavior of a group of humpback whales changed during and after a close approach for tagging, (2) determine if focal groups that were approached for tagging attempts behaved differently to focal groups that were not approached for tagging attempts, (3) determine if different tagging strategies caused different behavioral reactions amongst groups approached for tagging attempts, (4) determine if groups subjected to tagging attempts returned to pre-approach behavior before vessel-based focal follows commenced, and (5) specifically determine the reaction of female-calf groups to close approaches for tagging.

## METHODS

### *Study Site*

The study site was located at Peregian Beach (26°30'S, 153°05'E), Queensland, on the east coast of Australia, approximately 150 km north of Brisbane (Fig. 1).

Humpback whales migrate along the eastern Australian coast from low latitude breeding grounds inside the Great Barrier Reef to high latitude feeding grounds in the Antarctic during the austral spring months, often within 10 km of shore (Chittleborough 1965). This field site has the advantage of elevated land-based locations close to the shore from which observations of humpback whales can be undertaken. Experiments took place during September and October of 2010 and 2011.

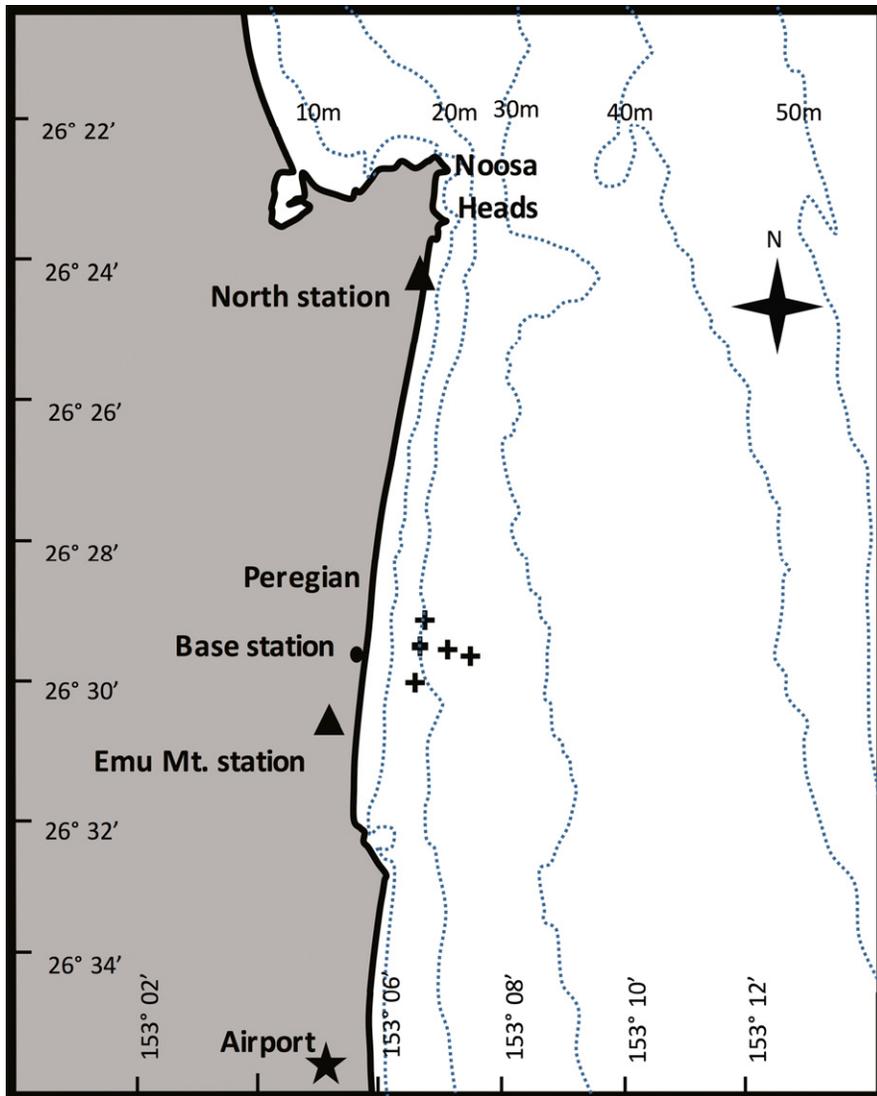


Figure 1. The study site at Peregian Beach on the Sunshine Coast of eastern Australia. Land-based survey stations (Emu Mt. and North Station), the location of the hydrophone array, and the base station, where signals from the array were transmitted, are indicated.

### *Land Data Collection*

Data were collected from two survey sites; “North Station,” the balcony of an apartment located 8.6 km north of Peregian Beach (30 m above sea level, 30 m from the shore), and “Emu Mt. Station,” the peak of Emu Mountain, 3 km south of Peregian beach (73 m above sea level, 700 m from the shore). Both had unobstructed views to the ocean. The behavioral data for this study came from land-based focal follows of humpback whale groups, where all visible behaviors of the group were recorded (Mann 1999). A group was defined as whales surfacing synchronously within 100 m of each other (Whitehead 1983, Corkeron 1995). Three individuals made up each focal follow team; a spotter, a theodolite operator and a computer operator, with two focal follow teams located at each of the two stations. The theodolite operator used a surveyor’s theodolite (Leica models TCRM1103+, TC407, or TC1105) to take a “fix” of the group at each surfacing in order to track the movements of the group. Information from the fix was transmitted to a notebook computer running VADAR whale tracking software (Visual and Acoustic Detection and Ranging; <http://cyclops-tracker.com/>; E. Kniest, University of Newcastle) that automatically calculated the positions of whales using the vertical and horizontal angles to the group measured by the theodolite’s elevation and azimuth. Other behavioral observations, not captured by the theodolite operator, were called out by the spotter (*e.g.*, blow, breach, pectoral slap, fluke slap, no blow rise or surfacing, peduncle slap, inverted fluke slap, *etc.*). The spotter or theodolite operator also called out social interactions such as splitting apart into two groups and joining together of two groups. All data were entered into VADAR.

### *Tagging*

Humpback whales were closely approached by research vessels in order to deploy suction cup attached DTAGS (Johnson and Tyack 2003). Whale groups were behaviorally assessed (using travel speed, surfacing frequency and travel direction) as candidates for tag attempts. If a group was deemed suitable, one adult group member was targeted for tagging. Target animals were approached from behind and to the side, and a 6 m carbon fiber pole was used to attach a DTAG between the blow hole and dorsal fin of the whale. If tagging was successful the vessel would then reduce speed, cease close approaches, retreat to between 100 and 200 m from the whales, and conduct a focal follow on the group in order to collect data as part of the BRAHSS (Cato *et al.* 2013) investigation. If tagging attempts ceased without deploying tags, the vessel backed off and then conducted a behavioral focal follow on the group. These groups were categorized as “tagging attempt” (TA) groups ( $n = 23$ ).

Close approaches for tagging were defined as an assertive vessel approach within 6 m of the target individual with the intention to tag (*i.e.*, the TA groups). They were either classed as “Cat1” or “Cat2” (Table 1). Cat1 attempts ( $n = 16$  groups) were defined as one or more close approaches at minimal speed (vessel engines usually idling) to a logging or resting whale, or a close approach to a whale with a regular speed and little course variation. During the Cat1 close approaches, the vessel’s speed and course matched the regular speed and course of the whale. Cat2 ( $n = 7$  groups) were defined as one or more close approaches to a whale that had a relatively high speed and/or directional changes. Cat2 close approaches often required a vessel speed greater than that of the whale. These were often brief bursts of speed to catch up to a whale as it was surfacing and deploy the tag. The close approach type recorded was

Table 1. Description of conditions and parameters for each boat phase.

Boat phase	Proximity/activity of vessel
before	>200 m from group (minimum of 15 min).
approachNTA	First 30 min after vessel comes within 200 m of group, no tagging attempts.
approachC1	Last tagging attempt approach was Cat1 in the approach phase.
approachC2	Last tagging attempt approach was Cat2 in the approach phase.
after0–20NTA	The first 20 min following the approachNTA phase.
after0–20C1	The first 20 min after successful tagging or tagging attempts cease, in groups where the final tagging attempt was Cat1.
after0–20C2	The first 20 min after successful tagging or tagging attempts cease, in groups where the final tagging attempt was Cat2.
after20–40NTA	The second 20 min following the approachNTA phase.
after20–40C1	The second 20 min after successful tagging or tagging attempts cease, in groups where the final tagging attempt was Cat1.
after20–40C2	The second 20 min after successful tagging or tagging attempts cease, in groups where the final tagging attempt was Cat2.

the final close approach type conducted in the approach. In other words, if the group was first approached using a Cat1 attempt then subsequently approached using a Cat2 attempt, the close approach category for that group was recorded as Cat2 (Table 1). Close approaches for tagging ceased when either a tag was deployed, or tagging attempts were aborted. Tag approaches were kept to a minimum whenever possible, with 21 out of 23 groups approached three times or less.

If a group was not deemed to be suitable for tagging, no close approaches were undertaken, and the vessel broke from the whales and searched for a new group for tagging. However, occasionally, rather than break from the animals, a focal follow was conducted (Mann 1999) for data collection as part of the BRAHSS study. These were categorized as “no tagging attempt” (NTA) ( $n = 6$  groups). The methodology for both NTA and TA groups was the same, except that there were no close approaches to the NTA groups. The closest point of approach to whales from these groups ranged from 100 to 200 m and the vessel remained at this distance for the duration of the interaction. As a result, these NTA groups were used as a baseline with which to compare the behavior of the TA groups. This allowed us to determine if behavioral change was seen, whether it was a result of close approaches or just the presence of the vessel itself.

### Study Design

The study followed a “before, during, and after” design where land-based observations of behaviors of whale groups were recorded before, during, and after close approaches from research vessels. Data collected in the “before” phase during this study were considered to be unaffected by close approaches by vessels and representative of unaffected “normal” migratory behavior. All other boat phases were compared against the before phase in the analyses. In this study the “during” phase was referred to as the “approach” phase. Groups were divided into tagging attempt groups (TA; attempts to deploy a DTAG, including both Cat1 and Cat2 categories;  $n = 23$ ) or no tagging attempt groups (NTA; where no attempt was made to attach a tag;  $n = 6$ ) (Table 1). For all groups, the before phase was defined as the period prior to one of

the research vessels approaching to within 200 m of the group. A minimum duration of 15 min (with a maximum of 40 min) was given for the before phase in order to ensure data from at least two complete dive cycles (a long dive followed by its subsequent surfacing interval) were obtained. If it was determined that the group was a suitable candidate for tagging (whales moved in a consistent direction, at a consistent speed, and without excessively long dive times), the approach phase was initiated and close approaches for tagging undertaken. These groups were classed as TA. In TA groups the approach phase was defined as one or more close approaches to a target individual with the intention to tag. The approach phase lasted for an average of 31 min, however, this varied between 2 min (if a tag was immediately deployed) and 1 h. In this phase, the research vessel was always within 200 m of the whales. The “after” phase began once there was a successful placement of a tag, or if close approaches were aborted. In the after phase the vessel would reduce speed and cease close approaches, retreat to between 100 and 200 m, and follow the group at slow speeds before starting behavioral observations as part of the BRAHSS investigation. In this study, the after phase was curtailed to 40 min to match the maximum time of data collection for the before phase.

For the purpose of this analysis, the approach phase in NTA groups was defined as the first 30 min after first approach of the group that occurred within 200 m (to make it comparable in terms of mean period of the approach phase in TA groups), and was followed by 40 min of after phase.

Phase (before, approach, and after) was used as the predictor variable for analysis. The approach and after phases were divided into groups that had tagging attempts (TA, Cat1 and Cat2) and groups that had no tagging attempts (NTA). The after phase was divided into the first 20 min after the attempt phase (after 0–20) and the second 20 min after the attempt phase (after 20–40) (Table 1).

### *Response Variables*

A number of response variables were used to measure dive, movement, and surface behaviors. These were chosen based on the response variables used for the BRAHSS investigation (Kavanagh 2014, Dunlop *et al.* 2015). They are similar to those used in previous studies evaluating behavioral responses of humpback whales to close vessel approaches, biopsy (Brown *et al.* 1994) and vessel presence (Scheidat *et al.* 2004, Morete *et al.* 2007, Stamation *et al.* 2010). Humpback whale dives are usually divided into “deep dives,” where the group is submerged for long periods, and “surfacing dives,” which are a bout of short, shallow dives where the animals in the group emerge repeatedly to breathe and conduct other surface behaviors (Dolphin 1987, Winn *et al.* 1995). In this study, the length of the deep dive (called group dive duration) and the length of the surfacing dives (which encompasses a bout of short shallow dives, called group surface interval duration) were used as the two diving behavior response variables. Firstly, all dives were separated into deep dives and surfacing dives. To do this a histogram was created, as described by Dunlop *et al.* (2013), using the log of the sighting lag time (time between successive sightings of animals in the focal group). The lag time was used as the measure of the group dive time. A best fit density function for the histogram was estimated by choosing the most appropriate bandwidth. Given that there are two dive categories, deep and surfacing, which are differentiated by the length of the dive (long and short), it was expected that the distribution of the data would be bimodal with the trough of the two distributions separating deep dives (long) from surfacing dives

(short) (Godwin *et al.* 2016). For this data set, the trough was positioned at a lag sighting time of 75 s (Fig. S1). The longest dive in the data set was 478 s and, as such, dives between 75 and 478 s were categorized as a deep dive. Those less than 75 s classed as surfacing dives. The group surface interval duration (the length of time of a bout of short surfacing dives) was calculated as the time between the end of one deep dive and the start of the next. These group surface interval durations ranged from 5 s to 995 s.

In order to assess potential changes in the pattern of movement, four measures of group movement behavior were used; group travel speed, group course variation, group speed of net southwards movement, and group course deviation from 180° magnetic. Group travel speed and group course variation (speed and changes in course) were measured to indicate any potential change in fine-scale movement through the study area. Group travel speed was defined as the time taken to travel the distance between successive surfacings. Group course variation was defined as the change in course between successive surfacings. As all groups in the investigation were migrating southwards, group speed of net southwards movement was also measured, as a change in this may not be picked up by measuring changes in speed or course alone. Additionally, group course deviation from 180° magnetic was measured as an indication of a general change in migratory direction (*e.g.*, in a more easterly or westerly direction).

When analyzing movement and surface active behaviors, small errors may be produced when measuring whale positions over the intrinsically highly variable dive periods of the whales (ranging in the orders of 10 s to 10 min). To reduce this high variance, measures of movement and surface active behaviors were analyzed in time bins, which provided some averaging of course and speed over a reasonable time period. In this data set the mean group dive duration was 284 s and mean group surface interval duration was 105 s. Consequently, time bins of 10 min were used to ensure that data from at least one complete dive cycle (a deep dive followed by its subsequent surfacing time interval) were captured in each time bin. The start of the approach phase was designated time zero, and bins were calculated every 10 min before and after that point; T-1 was the 10 min preceding the approach phase (*i.e.*, the last 10 min of the before period), T1 was the first 10 min of the approach phase and so on. Time bins that contained transitions from an approach to an after phase (*i.e.*, where the approach phase ended within a time bin) were treated as approach bins to ensure that no after bin periods contained observations where the vessel was in close approach.

Data were filtered to retain only behaviors associated with theodolite measured positions. As the group was likely to be underwater, the position of the group was usually not known at the end of each 10 min bin (and start of subsequent bin). The end-bin position was therefore estimated by assuming straight line and constant speed travel between the last measured position in the bin and the first measured position in the next bin. End-bin positions were interpolated for all bins in the focal follow. Course and speed made good were then calculated for each 10 min bin using these end-bin positions, giving each bin course and speed equal weighting because they are calculated over the same period. If no theodolite position was available for one or two sequential time bins, either because the whales did not surface or because the whales surfaced but a theodolite measurement was missed, the bin edge positions were still interpolated using the positions in the adjacent bins. If a position was not available for more than two bins in a row, positions were not estimated and these bins were excluded from the analysis. Missed positions across more than one bin were

infrequent and, as such, any reduction to variance of course and speed from this calculation was minimal.

Group course variation was calculated by subtracting the estimated course for each time bin from that of the previous bin. Group travel speed was estimated by measuring the distance between the interpolated positions of a group of whales at the start and end of a time bin, then using the time taken to travel that distance to calculate the swimming speed in km/h. In addition to travel speed and course variation, speed of net southward movement was also estimated by using only change in latitude and ignoring longitude. A negative speed south indicated net northward movement over the 10 min bin. Finally, course deviation from 180° magnetic was used as a measure of the extent to which the direction of travel of a group of whales differed from a direct southerly course (180°). This was estimated by taking the absolute value of the difference between the course over the time bin and 180° magnetic. An increase in course deviation would indicate deviation away from the general migratory movement pattern.

Surface active behaviors (hence forth known as SABs) were defined as any behavior that involved all or part of the body, a pectoral flipper or a fluke exiting then forcibly reentering the water. These behaviors included breaching behaviors, pectoral behaviors and fluke behaviors (Pacheco *et al.* 2013). The presence or absence of SABs within each 10 min bin was noted with 1 indicating presence and 0 indicating absence. Although these behaviors have been categorized in other studies (Noren *et al.* 2009), in this study all SABs were grouped for analysis due to the relatively short time periods used for the vessel phases and therefore small sample size of each surface behavior.

### *Data Analysis*

A total of 29 focal follows were analyzed. Groups were included only if the distance from the land survey platform was less than 15 km, because it was assumed that behaviors would be missed from land if groups were beyond this distance. As sea conditions also affect group sightability, in that higher sea states can result in more behaviors being missed from land (Bryden *et al.* 1990, Findlay and Best 1996), only groups where the wind speed was 28 km/h (Beaufort sea state 4) or less were used.

### *Statistical Analyses*

All statistical analyses were carried out in R version 3.0.2 (R Core Team 2013). Group dive duration, group surface interval duration, group course variation and group course deviation from 180° magnetic were log transformed to normalize the data. Resulting data were modeled using linear mixed models (LMMs) in the lme4 package (Bates *et al.* 2013). For binomially distributed data (presence/absence of surface-active behavior) the glmer function was used within the same package. In all models, Group ID was included as a random factor due to the nonindependence of the data. *P*-values were calculated using the lmerTest function (Kuznetsova *et al.* 2013) within the lme4 package. *P*-values of <0.05 were considered to be significant. Within-model estimates and effect sizes (back transformed if necessary) are reported as well as *t* and associated *P*-values. Effect sizes with the 95% confidence intervals were calculated using model estimates. Residuals of each model were checked for homoscedasticity and errors were checked for normality.

Analyses were carried out both using the term “boat phase” (see Table 1) as a predictor variable with the before phase considered unaffected normal migratory behavior and used as the intercept for the models. Sample size did not allow us to introduce cohort as an additional effect. As such, two analyses were carried out to allow us to reduce the variability associated with multiple social cohorts in our sample. The two analyses were therefore not intended as a comparison but composed of two parts. (1) Analysis 1 used data from all humpback whale groups sampled to assess if there was change in humpback whale behavior regardless of cohort. (2) Analysis 2 used data from female-calf (FC) groups alone (Table 2). This was undertaken in order to assess the effects of close approaches on the most common, and potentially most sensitive, group composition, which may be masked in analysis 1 due to the variability in behavior of the multiple group compositions. The first analysis tested aims 1–4: (1) if humpback whales significantly changed their behavior during and after close approaches from research vessels, (2) determine if NTA groups behaved significantly differently to TA groups, (3) determine if different tagging strategies (Cat1 and Cat2) caused different behavioral reactions and, (4) determine if TA groups returned to pre-approach behavior following close approaches. In this analysis all tag approaches (NTA, Cat1 and Cat2) were included. The second analysis tested aim 5: the reaction of female-calf (FC) groups tag approaches. All FC groups that were closely approached for tagging attempts were included in the analysis. However, due to sample size, FC groups that were not approached for tagging attempts (NTA) were not analyzed and all tag approaches (Cat1 and Cat2) were pooled.

## RESULTS

Focal follows used for analysis lasted between 78 min and 171 min, totaling 50 h of data. The number of focal groups for each model parameter is shown in Table 2. The before phase was used as the intercept for all model outputs.

### *Analysis 1: The Group Response to Close Vessel Approaches, Approach Type, and Recovery*

Mean group dive duration was 243 s (95% CIs 215, 277) and mean group surface interval duration was 59 s (95% CIs 48, 72) for groups in the before phase. All groups, regardless of whether they were closely approached for tagging attempts, did not significantly change their dive duration, or group surface interval duration, during the approach and after phases.

In terms of changes in movement behavior, groups significantly increased (from a mean of 3.7 km/h [95% CIs 3.0, 4.3]) their travel speed by 0.8 km/h ( $t = 2.45$ ,  $P = 0.02$ , 95% CIs 0.2, 1.5) during the approach phase of Cat1 tagging attempts

*Table 2.* Number of focal follows (no tagging attempt (NTA), tagging attempt Cat1 approach and tagging attempt Cat2 approach) for each boat phase for all group compositions combined and for female-calf (FC) groups only.

	Before	Approach			After 0–20 min			After 20–40 min		
		NTA	Cat1	Cat2	NTA	Cat1	Cat2	NTA	Cat1	Cat2
Total	29	6	16	7	6	16	7	6	16	7
FC	19	4	10	5	4	10	5	4	10	5

(Table S1, Fig. 2). This change in movement behavior was, however, short-term in that the travel speed of Cat1 groups in the after phases (0–20 min and 20–40 min) was not significantly different to the before phase (Table S1, Fig. 2). In contrast, Cat2 groups did not significantly change their travel speed in the approach phase. However, these groups increased their travel speed by 1.9 km/h ( $t = 3.56$ ,  $P < 0.001$ , 95% CIs 0.8, 2.9) during the first 20 min period of the after phase (0–20 min) (Table S1, Fig. 2). Again, this change in behavior was short-term in that the travel speed of Cat2 groups in the second 20 min of the after phase (20–40 min) was not significantly different to the before phase (Table S1, Fig. 2). This suggests that after 20 min, the Cat2 groups had returned to pre-approach behavior. Despite these changes in group travel speed, their variation in course did not significantly change (from a mean of  $14^\circ$  [95% CIs 9, 21] in the before phase).

As whales were migrating south, we used two further measures of movement behavior; group net southward movement and group course deviation from  $180^\circ$ . Group speed of net southward movement had a mean of 3.1 km/h (95% CIs 2.2, 3.9) in the before phase, but there was no evidence of any significant change in their net movement south, despite short-term changes in group speed in both Cat1 and Cat2 groups. Group course deviation from  $180^\circ$  had a mean of  $23^\circ$  (95% CIs 17, 32) in the before phase. During the approach phase Cat2 groups significantly increased group course deviation from  $180^\circ$  by  $19^\circ$  ( $t = 2.06$ ,  $P = 0.04$ , 95% CIs 1, 38) (Table S2, Fig. 3) and therefore deviated further from a southerly course (Table S2, Fig. 3). As there was no significant difference in the after phases (0–20 min and 20–40 min), it seemed they resumed their original course once the approach phases had ended. There was no evidence of any increase in course deviation from  $180^\circ$  in Cat1 groups.

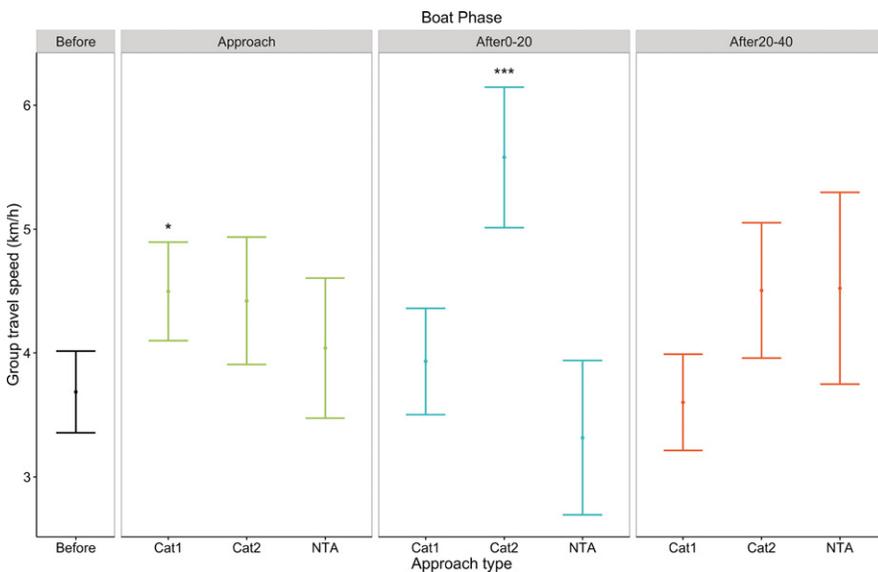


Figure 2. Plot showing group travel speed by boat phase and approach category. All values were compared to the before phase. An asterisk indicates any significant results where \*\*\*  $< 0.001$ , \*\*  $< 0.01$ , and \*  $< 0.05$ .

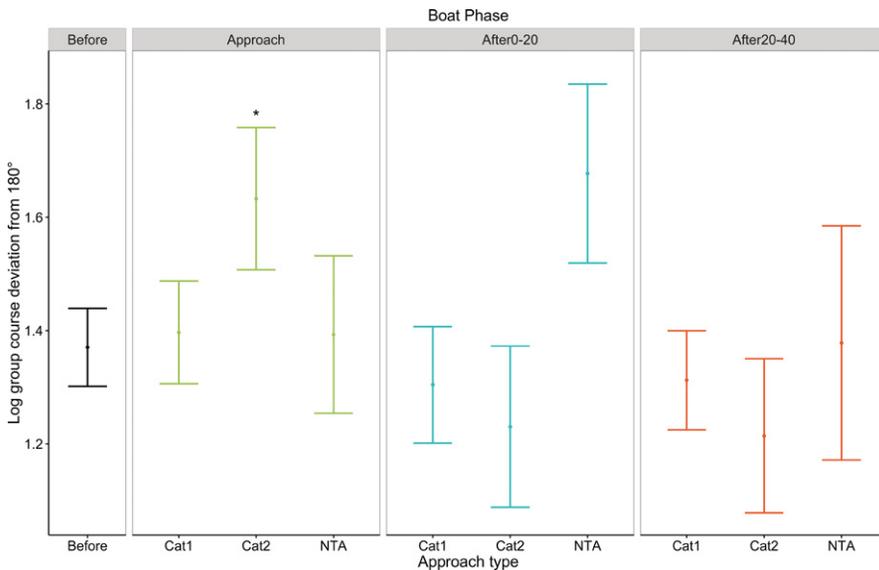
NTA (no tagging attempt) groups displayed no significant change in any of the tested movement response variables (group travel speed, group speed of net southwards movement, group course variation and group course deviation from 180°).

Surface active behaviors occurred in 26.9% ( $n = 25$ ) of the 93 time bins in the before phase. There was no evidence of any increase or decrease in the presence of surface active behaviors, during either the approach or after phases, in response to close approaches.

#### *Analysis 2: Testing the Response of Female-Calf Groups Only*

In total, 15 female-calf (FC) groups were used in the analysis (Table 2) and focal follows lasted between 80 and 166 min for each group, totaling 28 h of focal follow data. Due to low sample size, NTA groups were excluded and Cat1 and Cat2 approach types were pooled. FC groups did not significantly change their dive behavior (dive duration or surface interval duration) in response to tagging attempts (from a mean dive duration of 218 s [95% CIs 182, 263] and surface interval duration of 77 s [95% CIs 58, 101]).

In terms of movement behavior, the average travel speed of female-calf groups (with a mean of 2.9 km/h [95% CIs 2.1, 3.8]) was slower than the average speed of the population in this study. When closely approached for tagging attempts, female-calf groups significantly increased their travel speed by 1.3 km/h ( $t = 3.54$ ,  $P = 0.001$ , 95% 0.5, 1.8) in the approach phase and continued to display an increase in speed in the after 0–20 phase (by 1.3 km/h [ $t = 3.11$ ,  $P = 0.002$ , 95% CIs 0.6, 2] and after 20–40 phase (by 0.8 km/h [ $t = 2.56$ ,  $P = 0.01$ , 95% CIs 0.2, 1.6]; Table S3, Fig. 4). Despite this change in travel speed, there was no evidence



*Figure 3.* Plot showing log group course deviation from 180° by boat phase and approach category. All values were compared to the before phase. An asterisk indicates any significant results where \*\*\* < 0.001, \*\* < 0.01, and \* < 0.05.

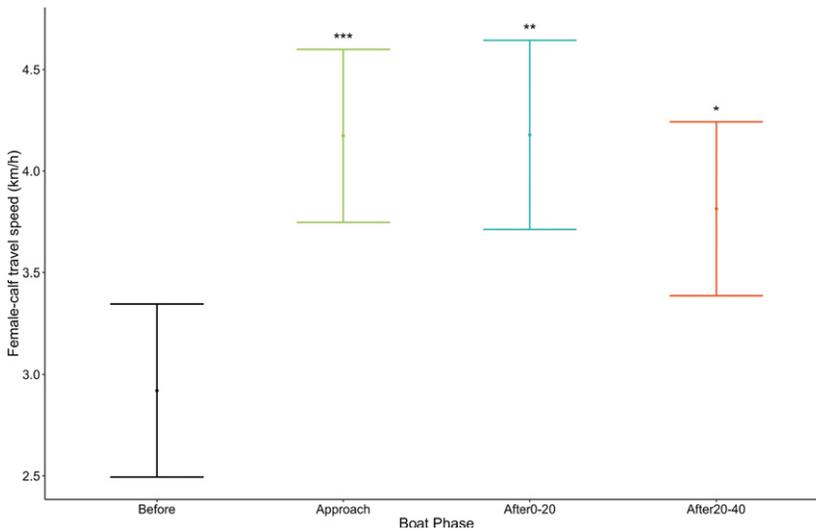


Figure 4. Plot showing female-calf travel speed by boat phase. All values were compared to the before phase. An asterisk indicates any significant results where \*\*\* <0.001, \*\* <0.01, and \* <0.05.

of any change in speed of net southward movement (from a mean of 2.4 km/h [95% CIs 1.3, 3.5]) suggesting that although there were changes in travel speed in these groups up to 40 min after tagging attempts had ceased, this did not result in a change in their general progression south. Mean female-calf course variation was  $15^\circ$  (95% CIs 8, 26) and mean FC course deviation from  $180^\circ$  was  $33^\circ$  (95% CIs 23, 49). Neither of these parameters significantly changed in response to tagging attempts.

Surface active behaviors occurred in 26% ( $n = 13$ ) of the 10 min time bins. There was no evidence of any significant change in the occurrence of these behaviors during, or after, close approaches in FC groups.

## DISCUSSION

The results of this study show that close approaches for tagging do result in a short-term behavioral response in humpback whale groups. In contrast, no behavioral change was found in groups where a focal follow was conducted, but close approaches for tagging attempts were not undertaken (NTA) suggesting that it was the tagging attempts, rather than vessel presence, that caused the behavioral change. Where a behavioral change did occur in our study, this change was dependent on the type of approach. Humpback whale groups changed their travel speed briefly in response to Cat1 approaches. However, Cat2 approaches led to a more sustained behavioral change with groups deviating more from a southerly direction in the approach phase and then increasing their travel speed in the after 0–20 phase. This behavioral change was however temporary in that they recovered to before approach behavior by 20–40 min after the final approach. It seems that at slower, more passive approach speeds (*e.g.*, Cat1), humpback whales simply increased their

swimming speeds to avoid the vessel. When a faster, more active approach type (*e.g.*, Cat2) was used, humpback groups may not have been able to out-swim the vessel and altered their course instead. When these approaches ended, humpback whales then used speed to move away from the vessel for a short period of time before returning to pre-approach behavior. Interestingly, for female-calf groups, changes in travel speed were more sustained, with no “recovery” within the 40 min period used in this study.

The behavioral changes in speed and course variables seen in this study are indicative of flight avoidance techniques (Lima and Dill 1990, Whittaker and Knight 1998, Lemon *et al.* 2006). Two types of flight avoidance techniques are evident in cetaceans; vertical and horizontal. Whereas vertical avoidance is associated with changes in diving behavior, such as increased dive times and decreased surfacing times, horizontal avoidance is associated with increased speeds and changes in direction (Bauer and Herman 1986, Lemon *et al.* 2006). The horizontal avoidance responses found in this study are most likely induced by an increase, or change, in vessel proximity, speed and movement, or received engine noise (Au and Green 2000, Erbe 2002). In this study, we were able to account for variability in approach speed and maneuverability (by dividing the approach type into Cat1 and Cat2), but the sample size was not large enough to take the length of time of approach into account, nor any difference in behavior between those that were successfully tagged and those that were not. Increased speeds and directional changes in response to approaching vessels have been reported previously in humpback whales (Au and Green 2000, Scheidat *et al.* 2004, Morete *et al.* 2007, Alves *et al.* 2010) and other cetacean species such as bowhead whales (*Balaena mysticetus*) (Richardson *et al.* 1985), killer whales (*Orcinus orca*) (Williams and Ashe 2007), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Steckenreuter *et al.* 2011), and fin whales (Jahoda *et al.* 2003), indicating that our findings are relatively common responses to close approaches by small vessels amongst cetaceans. The use of maneuverability and changes in course by humpback whales to Cat2 approaches are similar to avoidance tactics used by humpback whales against predators, such as killer whales, which they are unable to out-swim (Ford and Reeves 2008).

Our results also indicate that close approaches for tagging cause a more sustained response, for at least 40 min following tagging attempts, in female-calf groups. The most likely explanation for this result is that female-calf groups changed from one behavioral state to another. Many (9 out of 15) female-calf groups were resting (defined by Kavanagh [2014] as having slow swimming speeds, low surface-active behavior rates, a speed of southerly movement close to zero, and relatively high course variation). When first approached for tagging, these resting female-calf groups moved off, changing their behavior to traveling (defined by Kavanagh [2014] as having medium or average migratory swimming speeds and low levels of surface-active behavior). Therefore, this change in behavior is likely to be a reflection of the change in state rather than an abnormal increase in speed *per se*. However, when analyzing the behavioral response of female-calf groups, we were not able to separate the approach types, and therefore, whether a specific approach type (*e.g.*, Cat2) caused the stronger responses seen in female-calf groups could not be differentiated. Additionally, whether following female-calf groups without close approaches to tag an animal caused behavioral change could not be established.

A study of swimming speeds of southbound migrating female-calf groups at the same study site found a mean swimming speed of 3.1 km/h but with a bimodal

distribution correlating to two different behavioral states; resting and traveling (Noad and Cato 2007). Female-calf groups in this study, even when displaying an increase in speed, were well within the normal range of speeds found by Noad and Cato (2007) and were similar to speeds of other group compositions in the investigation. Therefore, although it is important to note that there is significant behavioral change in female-calf groups in response to tagging attempts, this change did not cause them to do something outside the repertoire of normal migration behavior. Many studies have found that females with young calves are more likely to exhibit avoidance behavior in response to novel anthropogenic stimulus compared to other cohorts (Gauthier and Sears 1999, McCauley *et al.* 2000, Wartzok *et al.* 2003, Best *et al.* 2005). In humpback whales, female-calf groups in particular have shown increased sensitivity to vessel traffic and close approaches from research vessels (Bauer *et al.* 1993, Clapham and Mattila 1993, Brown *et al.* 1994, Stamation *et al.* 2010, Stimpert *et al.* 2012). Therefore, behavioral observation studies that use close vessel approaches may need to take group composition into account when collecting data on potentially sensitive cohorts, such as humpback whale female-calf groups.

Calculating movement and behavior parameters can be subject to high variance due to the wide variation in the number of sightings for any given time period. This study therefore took a broad-scale approach to the analyses where measurements were reduced to only two per 10 min time bin (or presence/absence in the case of surface behaviors). Reducing measurements in this way may miss fine-scale, or more subtle, changes in behavior. Despite the changes in movement behavior found in this study, there was no evidence of any change in rates of surface active behaviors nor any change in behavior of groups in response to vessel presence without tagging attempts (NTA). However, the sample size of NTA groups ( $n = 6$ ) was small. As such, it is likely that statistical power was low, and, therefore, the likelihood that the nonsignificant results found in NTA groups reflect a true effect is reduced (Wisiz *et al.* 2008, Button *et al.* 2013). Although further investigations on vessel presence on humpback whale behavior should be carried out to confirm this result, it should not be completely discounted due to sample size. The variance in the NTA samples was similar, or less than, the variance in TA samples (Table S4, S5). Additionally, analyses undertaken on this population by Dunlop *et al.* (2015) revealed no significant difference in diving and movement behaviors between focal groups of humpback whales followed from land only (no research vessel present) and followed from small research vessel platforms. As such, the lack of significant response in NTA groups found in this study, combined with the evidence in Dunlop *et al.* (2015), suggests the significant changes in behavior found in this study were due to close approaches by research vessels, rather than just the presence of the vessel.

At the population level, this study found a behavioral change in groups to close approaches by research vessels, with quick recovery to pretag attempt behaviors once the close approaches had ceased. A more sustained reaction was evident in female-calf groups, indicating that this cohort may be sensitive to close vessel approaches for tagging. The use of digital tags is now a common part of behavioral studies on cetaceans, and close approaches are required for their application. However, there are few dedicated studies on the behavioral effects of close approaches for tagging. This study indicates the importance of assessing the effect of research techniques on cetacean behavior and investigations such as these should be undertaken, where appropriate, to ensure the validity of relevant data collected.

## ACKNOWLEDGMENTS

Funding was provided as part of 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, Conoco-Phillips, 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. We would like to thank all the BRAHSS team members particularly Douglas Cato, Louise Bennett, Verity Steptoe, David Paton, Rob Slade, David Donnelly, and the BRAHSS volunteers for their assistance with data collection.

## LITERATURE CITED

- Alves, L. C. P. d. S., S. Moreira, P. C. Simões-Lopes and A. Andriolo. 2010. Behavioral responses of humpback whales, *Megaptera novaeangliae* (Cetacea: Balaenopteridae), to satellite transmitter deployment procedures. *Zoologia (Curitiba)* 27:1–6.
- Au, W. W. L., and M. Green. 2000. Acoustic interaction of humpback whales and whale-watching boats. *Marine Environmental Research* 49:469–481.
- Bates, D., M. Maechler, B. Bolker and S. Walker. 2013. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-2. Available at <https://github.com/lme4/lme4/>.
- Bauer, G. B., and L. M. Herman. 1986. Effects of vessel traffic on the behavior of humpback whales in Hawaii. Report from Kewalo Basin Marine Mammal Laboratory, University of Hawaii, Honolulu, for U.S. National Marine Fisheries Service, Honolulu, HI.
- Bauer, G. B., J. R. Mobley and L. M. Herman. 1993. Responses of wintering humpback whales to vessel traffic. *The Journal of the Acoustical Society of America* 94:1848–1848.
- Baumgartner, M. F., and B. R. Mate. 2003. Summertime foraging ecology of North Atlantic right whales. *Marine Ecology Progress Series* 264:123–135.
- Best, P. B., D. Reeb, M. B. Rew, P. J. Palsbøll, C. Schaeff and A. Brandão. 2005. Biopsying southern right whales: Their reactions and effects on reproduction. *The Journal of Wildlife Management* 69:1171–1180.
- Brown, M. R., P. J. Corkeron, P. T. Hale, K. W. Schultz and M. M. Bryden. 1994. Behavioral responses of east Australian humpback whales *Megaptera novaeangliae* to biopsy sampling. *Marine Mammal Science* 10:391–400.
- Bryden, M. M., G. P. Kirkwood and R. W. Slade. 1990. Humpback whales, area V. An increase in numbers off Australia's east coast. Pages 271–277 in K. R. Kerry and G. Hempel, eds. Antarctic ecosystems. Springer-Verlag, Berlin, Germany.
- Button, K. S., J. P. A. Ioannidis, C. Mokrysz, B. A. Nosek, J. Flint, E. S. J. Robinson and M. R. Munafò. 2013. Power failure: Why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience* 14:365–376.
- Cantor, M., T. Cachuba, L. Fernandes and M. H. Engel. 2010. Behavioural reactions of wintering humpback whales (*Megaptera novaeangliae*) to biopsy sampling in the western South Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 90:1701–1711.
- Cato, D. H., M. J. Noad, R. A. Dunlop, et al. 2013. A study of the behavioural response of whales to the noise of seismic air guns: Design, methods and progress. *Acoustics Australia* 41:91–100.
- Chittleborough, R. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Marine and Freshwater Research* 16:33–128.
- Clapham, P. J., and D. K. Mattila. 1993. Reactions of humpback whales to skin biopsy sampling on a West Indies breeding ground. *Marine Mammal Science* 9:382–391.

- Corkeron, P. J. 1995. Humpback whales (*Megaptera novaeangliae*) in Hervey Bay, Queensland: Behaviour and responses to whale-watching vessels. *Canadian Journal of Zoology* 73:1290–1299.
- Croll, D. A., C. W. Clark, J. Calambokidis, W. T. Ellison and B. R. Tershy. 2001. Effect of anthropogenic low-frequency noise on the foraging ecology of Balaenoptera whales. *Animal Conservation* 4:13–27.
- Denardo, C., M. Dougherty, G. Hastie, R. Leaper, B. Wilson and P. M. Thompson. 2001. A new technique to measure spatial relationships within groups of free-ranging coastal cetaceans. *Journal of Applied Ecology* 38:888–895.
- Dolphin, W. F. 1987. Dive behavior and estimated energy expenditure of foraging humpback whales in southeast Alaska. *Canadian Journal of Zoology* 65:354–362.
- Dunlop, R. A., M. J. Noad, D. H. Cato, E. Kniest, P. J. O. Miller, J. N. Smith and M. D. Stokes. 2013. Multivariate analysis of behavioural response experiments in humpback whales (*Megaptera novaeangliae*). *The Journal of Experimental Biology* 216:759–770.
- Dunlop, R. A., M. J. Noad, R. D. McCauley, E. Kniest, D. Paton and D. H. Cato. 2015. The behavioural response of humpback whales (*Megaptera novaeangliae*) to a 20 cubic inch air gun. *Aquatic Mammals* 41:412–433.
- Elwen, S. H., P. B. Best, D. Reeb and M. Thornton. 2009. Diurnal movements and behaviour of Heaviside's dolphins, *Cephalorhynchus heavisidii*, with some comparative data for dusky dolphins, *Lagenorhynchus obscurus*. *South African Journal of Wildlife Research* 39:143–154.
- Erbe, C. 2002. Underwater noise of whale-watching boats and potential effects on killer whales (*Orcinus orca*), based on an acoustic impact model. *Marine Mammal Science* 18:394–418.
- Findlay, K. P., and P. B. Best. 1996. Assessment of heterogeneity in sighting probabilities of humpback whales within viewing range of Cape Vidal, South Africa. *Marine Mammal Science* 12:335–353.
- Ford, J. K. B., and R. R. Reeves. 2008. Fight or flight: Antipredator strategies of baleen whales. *Mammal Review* 38:50–86.
- Gauthier, J., and R. Sears. 1999. Behavioral response of four species of balaenopterid whales to biopsy sampling. *Marine Mammal Science* 15:85–101.
- Giard, J., and R. Michaud. 1997. L'observation des rorquals sous surveillance par la telemetrie VHF [Observation of whales under surveillance by VHF telemetry]. *Le Naturaliste Canadien* 121:25–29.
- Godwin, E. M., M. J. Noad, E. Kniest and R. A. Dunlop. 2016. Comparing multiple sampling platforms for measuring the behavior of humpback whales (*Megaptera novaeangliae*). *Marine Mammal Science* 32:268–286.
- Heide-Jørgensen, M. P., L. Kleivane, N. Øien, K. L. Laidre and M. V. Jensen. 2001. A new technique for deploying satellite transmitters on baleen whales: Tracking a blue whale (*Balaenoptera musculus*) in the North Atlantic. *Marine Mammal Science* 17:949–954.
- Jahoda, M., C. L. Lafortuna, N. Biassoni, *et al.* 2003. Mediterranean fin whale's (*Balaenoptera physalus*) response to small vessels and biopsy sampling assessed through passive tracking and timing of respiration. *Marine Mammal Science* 19:96–110.
- Johnson, M. P., and P. L. Tyack. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering* 28:3–12.
- Kavanagh, A. S. 2014. The behaviour of humpback whales: An analysis of the social and environmental context variables affecting their behaviour on migration. Ph.D. thesis, School of Veterinary Science, The University of Queensland, Gatton, Australia. 179 pp.
- Kuznetsova, A., P. B. Brockhoff and R. H. B. Christensen. 2013. lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-3. Available at <http://CRAN.R-project.org/package=lmerTest>.

- Lemon, M., T. P. Lynch, D. H. Cato and R. G. Harcourt. 2006. Response of travelling bottlenose dolphins (*Tursiops aduncus*) to experimental approaches by a powerboat in Jarvis Bay, New South Wales, Australia. *Biological Conservation* 127:363–372.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Lusseau, D. 2003. Male and female bottlenose dolphins *Tursiops* spp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine Ecology Progress Series* 257:267–274.
- Mann, J. 1999. Behavioral sampling methods for cetaceans: A review and critique. *Marine Mammal Science* 15:102–122.
- Mate, B. 1989. Satellite-monitored radio tracking as a method for studying cetacean movements and behaviour. Report of the International Whaling Commission 39:389–391.
- McCauley, R. D., J. Fewtrell, A. J. Duncan, *et al.* 2000. Marine seismic surveys—a study of environmental implications. *APPEA Journal* 40:692–708.
- Miller, P. J. O., N. Biassoni, A. Samuels and P. L. Tyack. 2000. Whale songs lengthen in response to sonar. *Nature* 405:903.
- Miller, P. J. O., M. P. Johnson, P. T. Madsen, N. Biassoni, M. Quero and P. L. Tyack. 2009. Using at-sea experiments to study the effects of airguns on the foraging behavior of sperm whales in the Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers* 56:1168–1181.
- Morete, M. E., T. L. Bisi and S. Rosso. 2007. Mother and calf humpback whale responses to vessels around the Abrolhos Archipelago, Bahia, Brazil. *Journal of Cetacean Research and Management* 9:241–248.
- Noad, M. J., and D. H. Cato. 2007. Swimming speeds of singing and non-singing humpback whales during migration. *Marine Mammal Science* 23:481–495.
- Noren, D. P., A. H. Johnson, D. Rehder and A. Larson. 2009. Close approaches by vessels elicit surface active behaviors by southern resident killer whales. *Endangered Species Research* 8:179–192.
- Nowacek, S. M., R. S. Wells and A. R. Solow. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science* 17:673–688.
- Nowacek, D. P., M. P. Johnson and P. L. Tyack. 2004. North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 271:227–231.
- Pacheco, A. S., S. Silva, B. Alcorta, N. Balducci, C. Guidino, M. A. Llapapasca and F. Sanchez-Salazar. 2013. Aerial behavior of humpback whales *Megaptera novaeangliae* at the southern limit of the southeast Pacific breeding area. *Revista de Biología Marina y Oceanografía* 48:185–191.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reisinger, R. R., W. C. Oosthuizen, G. Péron, D. Cory Toussaint, R. D. Andrews and P. J. N. de Bruyn. 2014. Satellite tagging and biopsy sampling of killer whales at subantarctic Marion Island: Effectiveness, immediate reactions and long-term responses. *PLOS ONE* 9:e111835.
- Ribeiro, S., F. A. Viddi and T. R. Freitas. 2005. Behavioural responses of Chilean dolphins (*Cephalorhynchus eutropia*) to boats in Yaldad Bay, southern Chile. *Aquatic Mammals* 31:234–242.
- Richardson, J. W., M. A. Fraker, B. Würsig and R. S. Wells. 1985. Behaviour of bowhead whales *Balaena mysticetus* summering in the Beaufort Sea: Reactions to industrial activities. *Biological Conservation* 32:195–230.
- Scheidat, M., C. Castro, J. Gonzalez and R. Williams. 2004. Behavioural responses of humpback whales (*Megaptera novaeangliae*) to whale watching boats near Isla de la Plata,

- Machalilla National Park, Ecuador. *Journal of Cetacean Research and Management* 6:63–68.
- Schneider, K., R. W. Baird, S. Dawson, I. Visser and S. Childerhouse. 1998. Reactions of bottlenose dolphins to tagging attempts using a remotely-deployed suction-cup tag. *Marine Mammal Science* 14:316–324.
- Stamation, K. A., D. B. Croft, P. D. Shaughnessy, K. A. Waples and S. V. Briggs. 2010. Behavioral responses of humpback whales (*Megaptera novaeangliae*) to whale-watching vessels on the southeastern coast of Australia. *Marine Mammal Science* 26:98–122.
- Steckenreuter, A., R. Harcourt and L. Möller. 2011. Distance does matter: Close approaches by boats impede feeding and resting behaviour of Indo-Pacific bottlenose dolphins. *Wildlife Research* 38:455–463.
- Stimpert, A. K., D. Mattila, E. M. Nosal and W. W. L. Au. 2012. Tagging young humpback whale calves: Methodology and diving behavior. *Endangered Species Research* 19:11–17.
- Tyack, P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology* 8:105–116.
- Van Parijs, S. M., and P. J. Corkeron. 2001. Boat traffic affects the acoustic behaviour of Pacific humpback dolphins, *Sousa chinensis*. *Journal of the Marine Biological Association of the United Kingdom* 81:533–538.
- Wartzok, D., A. N. Popper, J. Gordon and J. Merrill. 2003. Factors affecting the responses of marine mammals to acoustic disturbance. *Marine Technology Society Journal* 37:6–15.
- Watkins, W. A. 1981. Reaction of three species of whales *Balaenoptera physalus*, *Megaptera novaeangliae*, and *Balaenoptera edeni* to implanted radio tags. *Deep Sea Research Part A. Oceanographic Research Papers* 28:589–599.
- Whitehead, H. 1983. Structure and stability of humpback whale groups off Newfoundland. *Canadian Journal of Zoology* 61:1391–1397.
- Whittaker, D., and R. L. Knight. 1998. Understanding wildlife responses to humans. *Wildlife Society Bulletin* 26:312–317.
- Williams, R., and E. Ashe. 2007. Killer whale evasive tactics vary with boat number. *Journal of Zoology* 272:390–397.
- Winn, H. E., J. D. Goodyear, R. D. Kenney and R. O. Petricig. 1995. Dive patterns of tagged right whales in the Great South Channel. *Continental Shelf Research* 15:593–611.
- Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham and A. Guisan and NCEAS Predicting Species Distributions Working Group. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14:763–773.

Received: 30 July 2015  
Accepted: 21 March 2016

#### SUPPORTING INFORMATION

The following supporting information is available for this article online at <http://onlinelibrary.wiley.com/doi/10.1111/mms.12324/supinfo>.

*Figure S1.* Graph of the analysis to calculate the bout criterion interval (BCI) used to distinguish between long dives and surface intervals. Graph of the frequency distribution of interval lengths is shown. As width classes were not equal, probability densities (frequency/density of interval lengths in each time bin) were used. The BCI is highlighted with an arrow.

*Table S1.* Model estimates effect *t*-values and *P*-values for group travel speed data. Effect sizes have been back transformed where necessary. Estimates indicate increase (positive value) or decrease (negative value) in response variable when the predictor variable changed by one unit.

*Table S2.* Model estimates, effect, *t*-values, and *P*-values for logged group course deviation from 180° data are presented. Effect sizes have been back transformed where necessary. Estimates indicate increase (positive value) or decrease (negative value) in response variable when the predictor variable changed by one unit.

*Table S3.* Model estimates, effect, *t*-values, and *P*-values for travel speed data in FC groups approached for tagging are presented. Effect sizes have been back transformed where necessary. Estimates indicate increase (positive value) or decrease (negative value) in response variable when the predictor variable changed by one unit.

*Table S4.* Summary statistics for group travel speed data are presented. *n* is the frequency of data points for the explanatory variable in the data set. Mean, standard deviation (SD), and standard error (SE) are also presented.

*Table S5.* Summary statistics for logged group course deviation from 180° are presented. *n* is the frequency of data points for the explanatory variable in the data set. Mean, standard deviation (SD), and standard error (SE) are also presented.