Quantifying the Behavior of Humpback Whales (*Megaptera novaeangliae*) and Potential Responses to Sonar

E. Elizabeth Henderson,[1] Jessica Aschettino,[2] Mark Deakos,[3] Gabriela Alongi,[4] and Tara Leota[5]

[1]*NIWC Pacific, 53560 Hull Street, San Diego, CA 92152, USA*
E-mail: ehenders@spawar.navy.mil
[2]*HDR, 4144 Hermitage Point, Virginia Beach, VA 23455, USA*
[3]*HDR, 305 S. High Street, Suite 101, Wailuku, HI 96793, USA*
[4]*National Marine Mammal Foundation, 2240 Shelter Island Drive, Suite 200, San Diego, CA 92106, USA*
[5]*Kaua'i Sea Rider Adventures, PO Box 643, Kalaheo, Kaua'i, HI 96741, USA*

Abstract

Thirteen humpback whales (*Megaptera novaeangliae*) were tagged with LIMPET-configured SPLASH tags off Kaua'i, Hawai'i, near the Pacific Missile Range Facility (PMRF) in 2017 and 2018. The movement and dive behavior of the seven animals tagged in 2017 provided a baseline against which to compare the data from five of the six tagged whales in 2018 that remained in proximity of an active Navy training event occurring on PMRF. Although some extreme travel speeds (up to 18 km/h) were estimated for the whales in 2018, they did not co-occur with periods of mid-frequency active sonar (MFAS) and, in fact, travel speeds were reduced in two animals during periods of MFAS. The tagging effort took place at different points in the breeding season across years and in slightly different locations (offshore vs nearshore) and, therefore, some of the behavioral differences could have been due to targeting different sectors of the breeding population. One animal did have significant changes to their dive behavior during one period of sonar, with steep, deep dives occurring while the animal moved away from the location of the sonar activity and received levels up to 158 dB re 1 µPa. Thus, some behavioral response may have occurred in the presence of MFAS, but this appears to have been relatively limited, with the whales likely focused on breeding behavior. Further monitoring is necessary to address these confounding factors and to ensure that any temporary behavioral responses do not have long-term consequences to the population.

Key Words: humpback whales, *Megaptera novaeangliae*, satellite tagging, sonar, behavioral response

Introduction

Over the last decade, controlled exposure experiments (CEEs) have been conducted on several marine mammal species to determine the types and extent of behavioral responses to disturbances such as seismic airguns or navy sonars (Southall et al., 2012, 2016; Lam et al., 2016; Dunlop et al., 2017). The focal species for these studies have generally been animals that might be highly sensitive to a disturbance such as beaked whales (DeRuiter et al., 2013; Stimpert et al., 2014; Miller et al., 2015) but have also included potentially less sensitive species such as baleen whales and delphinids (Miller, 2012; Southall et al., 2016). The likelihood or degree of a response to a disturbance may be dependent on several factors, including the distance to the source, the characteristics of the signal itself (e.g., frequency, amplitude, and harmonics), and the directionality of the sound (Gailey et al., 2016), as well as the behavioral state of the individual animal and any previous experience with that source (or lack thereof) (Ellison et al., 2011; Harris et al., 2018b). As an example of behavioral context, blue whales (*Balaenoptera musculus*) exposed to the same simulated mid-frequency sonar signal while deep feeding or non-feeding were more likely to respond than blue whales that were shallow feeding (Goldbogen et al., 2013; Friedlaender et al., 2016). For an example of the context of behavioral and source characteristics on humpback whales (*Megaptera novaeangliae*), individuals exposed to seismic airguns while migrating to their breeding grounds demonstrated minimal or no response (Dunlop et al., 2015, 2016, 2017). In contrast, humpback whales exposed to low- and mid-frequency sonar while foraging demonstrated mixed responses (Sivle et al., 2016; Wensveen et al., 2017), and humpback whales exposed to killer whale (*Orcinus orca*) call playbacks demonstrated strong

responses (Curé et al., 2015). Although many of these studies have demonstrated that baleen whales may generally be less sensitive to sonar sources than other marine mammals, such as beaked whales, mid-frequency active sonar (MFAS) signals are still considered to be in the region of best hearing for baleen whales (U.S. Department of the Navy, 2017). Sonar is therefore still a concern when considering the long-term health of individuals and populations (Costa et al., 2016), particularly those that may be exposed regularly when their habitat overlaps with an area of frequent sonar use (Scales et al., 2017).

Another way to assess behavioral responses to a noise disturbance is to conduct an opportunistic observation study through the use of passive acoustics, satellite or other telemetry tags, or by conducting shore- or aerial-based observations (Robertson, 2014; Martin et al., 2015; Gailey et al., 2016; Manzano-Roth et al., 2016; Baird et al., 2017; Falcone et al., 2017). Observational behavioral response studies lose the ability to control certain variables in an exposure such as the distance to the source, the direction the source is traveling relative to the animal, or the received level at the animal. The benefits of this type of study are that they provide an opportunity to capture responses to real-world disturbances, where multiple sources may be present and the exposure could last for several days, and they lack any confounding variables that might be introduced in experimental set-ups (e.g., the presence of a research vessel during the exposure). However, in the case of passive acoustics or satellite tagging, the focal animals are not observed visually during the exposure, and their behavior and potential response must be inferred from the acoustic or tag data. In addition, the temporal resolution of position and dive data that can be derived from satellite tags is coarser than what can be derived from acoustic tags, although the overall duration of tag attachment is generally much longer for satellite tags. This makes understanding the baseline behavior with its inherent natural variation all the more critical in the assessment of any behavioral response to a disturbance when using these methods. Martin et al. (2015) detected decreased minke whale (*Balaenoptera acutorostrata*) boing calls during multi-day U.S. Navy training events on the U.S. Navy's Pacific Missile Range Facility (PMRF) but also found decreased calling during a period of high noise due to strong winds (Martin et al., 2018). Bowhead whale (*Balaena mysticetus*) call detections were reduced during periods of seismic airgun activity in the Alaskan Beaufort Sea (Blackwell et al., 2013, 2015), and Robertson et al. (2013) found a concurrent behavioral response in their dive behavior that would impact

abundance estimates from aerial surveys if not accounted for (Robertson, 2014).

Humpback whales have been the focal species for multiple CEEs with different source types (Sivle et al., 2016; Dunlop et al., 2017; Wensveen et al., 2017); that, coupled with the fact that they are abundant in Hawai'i and co-located with an active Navy range, makes them a good candidate for an opportunistic behavioral response study. The PMRF underwater hydrophone array is located in the offshore waters northwest of Kaua'i (Figure 1) and has been used to conduct testing and training events in the area since the late 1960s (U.S. Department of the Navy, 2011). This area is part of the breeding habitat of humpback whales that migrate to Hawaiian waters during the winter and spring from Alaskan feeding grounds (Calambokidis et al., 2001). It has been demonstrated that whales utilize the offshore waters of the range based on acoustically tracking singers throughout the breeding season (Henderson et al., 2018a). The baseline behavior of any cetacean species on a Navy instrumented range can be used to evaluate potential behavioral responses to Navy activity, and quantifying the temporal and spatial use of the area allows researchers to assess the likelihood that an animal will be exposed to training activities. Since they are abundant in nearshore
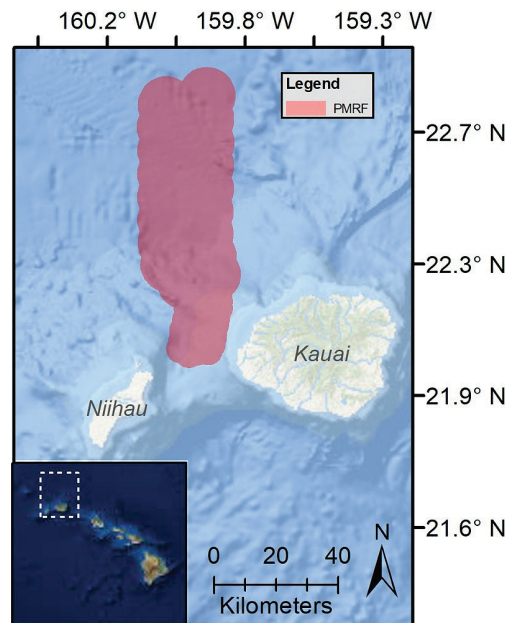

Figure 1. Inset map of the main Hawaiian Islands and a larger map of Kaua'i and Ni'ihau islands, with two areas of the Pacific Missile Range Facility (PMRF) highlighted in red. Figure used with permission by Cameron Martin.

waters, and because acoustically active humpback whales can be detected and tracked on the range, this species is an ideal candidate for tagging and tracking both on and off the range. Therefore, the goals of this study were to photo-identify, satellite tag, and track humpback whales in the offshore waters of Kaua'i, in particular near PMRF, with the objectives of documenting their behavior and habitat use in these waters, determining if animals found in the area spend extended periods of time on or near the range, and quantifying the impact of MFAS on their behavior and distribution. This last objective was achieved by comparing movement and dive behavior of tagged whales during MFAS training and non-training periods to determine if a change in behavior was associated with MFAS.

Methods

Observations and Tagging
Vessel-based satellite tagging and photo-identification were conducted 17-24 March 2017 and 4-12 February 2018 in the waters around Kaua'i and between Kaua'i and Ni'ihau, the northwestern-most islands of the main Hawaiian Islands (Figure 1). Surveys were conducted using a 6.7-m rigid hulled inflatable boat (RHIB). When a humpback whale or group was sighted, the boat followed the whale(s) as a focal follow while maintaining a distance of at least 100 m from the individual or group. Sighting data were entered into an electronic application, COMPASS (Richlen et al., 2017), as well as on handwritten datasheets. Data collected on focal follow groups included sighting location and time, whale behavior, individual behavioral roles, group size, and identification photos of the left and right sides of the dorsal fin and fluke when possible. Photos were taken using one of three digital SLR cameras (Canon 50D, 7D, or 7D Mark II) with a 100-400 mm zoom lens. Following the field effort, individual identification photos were compiled and compared across individuals to identify whales encountered more than once.

Based on the whale's behavior, such as their dive times, the number of respirations per surfacing, and their response to the presence of the boat, a decision was made on whether to attempt to approach a whale for satellite tagging. If a lone animal or individual in a group was determined to be a good candidate for tagging, they were approached within 100 m in a steady and safe manner. No individual was approached within 15 m for a tagging attempt more than three times; in two cases, multiple animals in the same group were approached, but tagging approaches were made for different individuals. Location-dive tags (Wildlife Computers SPLASH10-292 and SPLASH10-F-333) in the

Low-Impact Minimally Percutaneous External-electronics Transmitter (LIMPET) configuration (Andrews et al., 2008) were used for tagging and were attached with two titanium darts with backward-facing petals to the dorsal fin or area just below the dorsal fin. The 2017 tags were Argos satellite only tags (SPLASH10-292), while the tags used in 2018 were enhanced with Fastloc-GPS (SPLASH10-F-333) to improve location accuracy and frequency, particularly when the whales were within line-of-sight of one of three Wildlife Computers Mote receivers (e.g., Jeanniard-du-Dot et al., 2017) installed on Kaua'i, Ni'ihau, and O'ahu. Tags were remotely deployed from the RHIB with a DanInject JM Special 33 pneumatic projector (DanInject ApS, Børkop, Denmark). Tags were programmed to transmit 21 h/d (based on availability of satellites in the area) with up to 750 transmissions per day and to record dive start and end times, maximum depth, and dive durations for dives greater than 5 m in depth and 30 s in length at 75 s intervals. The tagged whale was visually monitored for any response to the tagging event immediately after it was tagged. The group was followed until photographs had been obtained of all individual dorsal fins and flukes whenever possible, with particular attention to the tagged whale.

Satellite Track Data Analysis
Track positions were estimated using the Argos Data Collection and Location System with a Kalman filtering algorithm, and further screened using the Douglas-Argos Filter, Version 8.50 (Douglas et al., 2012) available in Movebank (https://www.movebank.org). Additional manual filtering was conducted to remove erroneous locations appearing on land or resulting in initial unrealistic humpback whale travel speeds of greater than 15 km/h (Noad & Cato, 2007). All locations were utilized for analysis regardless of location class (based on estimated error and number of messages received), unless they were removed during the filtering process. When both Argos and Fastloc-GPS data were available, both data types were used in track analyses. GPS location errors were less than 100 m (Dujon et al., 2014), while Argos location errors could be greater than 4 km, with the errors from Argos A and B class location errors having unbounded accuracy (although they have been estimated to have errors up to 6.2 and 10.3 km, respectively [Costa et al., 2010]).

Track data were time-interpolated in 20-min intervals using either a simple random walk or a correlated random walk in the *R* package 'foieGras' (Jonsen & Patterson, 2019) and then analyzed using the *R* package 'adehabitatLT' (Calenge, 2006, 2015), both designed for the analysis of animal trajectories based on telemetry

data. This analysis was conducted to identify different behavioral states (e.g., milling or traveling) along each humpback whale track. To do this, the interpolated track locations were estimated via a continuous time random walk from Kalman filter-based Argos locations, including the error ellipse information, plus the GPS data when available for the 2018 tracks (using the location error value for Class 3 Argos locations for the GPS data). The simple random walk method can over-fit data with many available locations but interpolates straight lines over longer gaps, whereas the correlated random walk method better fits data with small gaps but can over-smooth larger gaps to create non-existent loops (Jonsen & Patterson, 2019; I. Jonsen, pers. comm., 2 May 2019); both methods were tested with these track data.

Four different Markovian behavioral states (i.e., track segments with homogenous properties) were established *a priori* and parsed into these state-specific periods using a Bayesian partitioning method developed by Guéguen (2001, 2009). Three of these four states were determined by combining the 20-min-distance data from all interpolated tracks and finding the top three modes, with a standard deviation of 0.8 km for all states. The model for State 1 represented milling or Area Restricted Search (ARS) behavior and was defined as having a mean 20-min travel distance of 0.2 km (0.7 km/h). The model for State 2 was an intermediary or transition behavior and had a mean 20-min travel distance of 1.1 km (3.2 km/h). The model for State 3 represented directed travel behavior and had a mean 20-min travel distance of 2.1 km (6.5 km/h). The value used for State 1 was similar to but slightly lower than those found in the literature for non-traveling or milling behavior (Lagerquist et al., 2008; Kennedy et al., 2014), while the value for State 3 was similar to but higher than those published for directed travel or migration (Lagerquist et al., 2008; Horton et al., 2011; Kennedy et al., 2014).

The distribution of 20-min-distance data contained a lengthy tail of very large 20-min-distances. Because this skew could not be represented by a 20-min-distance mode but still represented a state that did not comfortably fit in any of the other three categories, a fourth state was added corresponding to a mean relative angle of 0° with a standard deviation of 45°. The relative turning angle was defined as the successive angle between track segments and was calculated as the change in angle between the heading of the previous segment and the heading of the current segment. Qualitatively, this State 4 represents an extreme state of directed, fast travel.

With these state models defined, the behavioral model was applied to each track, generating the probability density that a change may have occurred in the behavioral state at each track segment. Next, the optimal number of transitions for each behavioral state was applied using the log-likelihood for the total number of behavioral segments. Note that the same model parameters for each behavioral state were used as starting values for the model selection process for all tracks, but that the final summary statistics for each state in each year were driven by the data and, therefore, could differ from the initial parameters.

Dive data were analyzed using the *R* package 'diveMove' (Luque, 2007) to obtain the total number of dives, dive depths, dive durations, and descent and ascent rates. Dives calculated to be longer than 45 min were discarded as these typically indicated periods of data dropout.

Behavioral Response and Received Level Estimation

Received levels were estimated using the parabolic propagation model Peregrine (Heaney & Campbell, 2016). Locations for all ships during active periods of MFAS were selected for every Argos or GPS whale position. The propagation of the sonar signal from the ship to the whale (assuming the animal was near the surface [15 m depth]) was estimated at each location using the nominal source levels and mean frequencies for each sonar type as multiple ships were present with different sonar types. A depth of 15 m was used for the whale since the animal was assumed to be at the surface at the time of a position transmission. Transmission loss values were estimated in magnitude within a radius of 1,000 m of the whale position, taking into account all but the worst Argos position error distances (e.g., location errors A, B, or 0; no Z error locations were retained after filtering), and then the mean, median, maximum, and standard deviation of the transmission loss magnitude within this ellipse were derived, and received levels in dB re 1 µPa and cumulative sound exposure levels (cSELs) in dB re 1 µPa^{2}s were calculated. For the single series of dives that co-occurred with MFAS and were statistically different than baseline dives, the received level was estimated at the surface and bottom of each dive during the exposure period, with the location at each time taken from the satellite track interpolated over 1-min intervals. Generalized Estimating Equation (GEE) models were utilized to determine the significance of the presence of MFAS on dive behavior and behavioral state using 'geepack' in *R* (Højsgaard et al., 2006, 2016). GEE models were used because they can accommodate categorical response and explanatory variables, and data can be clustered by individual to account for correlation within each

individual (Bailey et al., 2013). In these models, the data were grouped by year and individual, and the dive or behavior metrics were included as predictor variables along with the presence of MFAS. The family was assumed to be poisson since the data occur at constant sampling rates of 75 s (dive data) and 20 min (track behavior data), and an AR1 correlation structure was used to account for the autocorrelation among variables within each individual. Standard errors were estimated using a jackknife method. Generalized Linear Models (GLMs) were also utilized to assess the impact of the presence of MFAS on dive metrics within each individual using the *R* package 'glm2' (Marschner & Donoghoe, 2018). In this case, a quasipoisson family was used due to overdispersion of the data.

Results

Tagging Effort
In 2017, a total of 8 d of survey effort were conducted in the channel between Kaua'i and Ni'ihau (Figure 2), resulting in 60 groups of humpback whales that ranged in size from one to six animals (mean = 2.3). From those groups, at least 85 unique individuals were encountered based on dorsal fin identification, and seven unique individuals were successfully tagged (Table 1). Fluke photographs were collected from 58 humpback whales (50 of which had dorsal fin identifications as well), with two individuals resighted on different days. The majority of groups encountered were traveling from east to west across the channel. Mean sea state was 2.9, mean cloud cover was 24%, mean swell height was 0.9 m, and mean wind speed was 10 kts.

In 2018, 9 d of survey effort were conducted, which was constrained to the nearshore waters off Kaua'i due to poor weather conditions (Figure 2). Although in general the mean cloud cover (25%) and wind speeds (11.6 kts) were similar in 2018 compared to 2017, mean sea state was slightly higher at 3.3, and mean swell height was considerably higher at 1.4 m. However, being earlier in the breeding season, more whales were encountered in 2018 than in 2017, with 92 groups that ranged in size from one to nine (mean = 1.8). There were 105 unique humpback whales photographed based on dorsal fins, and 78 individuals identified with fluke photographs (65 of the flukes came from the same individuals as the dorsal fin identifications). There were once again two within-year resights on different days, but there were no resights of animals cataloged in 2017. Six whales were tagged, making the total number of whales tagged for both years 13 (Table 1). Tags transmitted between 1.6 and 12.5 d, with a mean of 5.6 d.

Most of the tagged whales were believed to be probable males judging by their behavior, although it was not clear if some of the dyads were male–male or male–female. Competitive groups usually consist of a single female being pursued by two or more males (Clapham et al., 1992). The primary defending male is usually easily identified by behaviors such as head lunging, linear bubble trails, and chasing challenging secondary escorts (Tyack & Whitehead, 1982; Baker & Herman, 1984). He is positioned directly next to the female, allowing her to be identified as well as the remaining secondary male escorts. Most pairs of whales (dyads) consist of a male and female (Brown & Corkeron, 1995; Herman et al., 2011). Based on in-water observations, the female generally surfaces first and initiates the sounding dive for the next long dive. In cases with no clear whale leading and often moving more than 30 m apart from one another, these partners have generally been sexed as males (M. Deakos, pers. comm., 11 June 2019). The gender of humpback whales can be determined by identifying the presence or absence of a hemispheric lobe during underwater observations (Lockyer, 1984); however, no genders were confirmed visually in this study. All animals looked healthy (e.g., none of the whales appeared to be thin or malnourished). The only reactions observed from the surface to the tagging were a peduncle swish by one individual and an accelerated dive by two others. All individuals returned to their original behavior immediately following a response. No reaction was observed among the 10 other humpback whales tagged.

Track and Movement Behavior
In 2017, all the humpback whales traveled west after being tagged and spent appreciable time (1.0 to 7.9 d; mean = 2.45 d) in proximity to Ni'ihau. In addition, five of the animals spent the remainder of their time tagged near other islands or seamounts (Figure 3). This led to the cumulative distance traveled exceeding the straight-line distance traveled by as much as eight times (Table 2). However, the two animals that had the longest tag attachments, 158671 and 164791, had fairly long straight-line distances and appeared to have begun their migration toward Alaska.

In contrast, in 2018, five of the six tagged humpback whales also spent time around Ni'ihau, although one of those whales began moving east past Kaua'i before turning back and traveling to Ni'ihau. The sixth whale traveled east to O'ahu instead. Only one whale continued on to other seamounts beyond Ni'ihau, and none of these six whales appeared to begin their migration (Figure 4). These whales had even longer cumulative distances compared to their straight-line distances (Table 2).
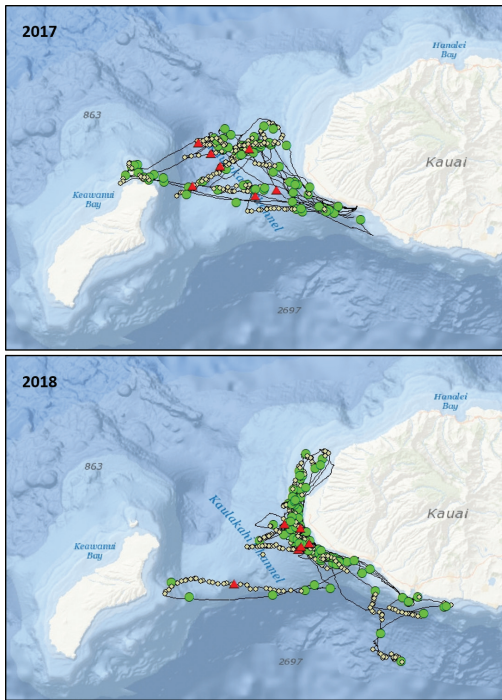
Figure 2. Effort tracklines and sighting locations for 2017 (top) and 2018 (bottom). Initial sighting locations are shown in large green circles, the smaller white diamonds show repeated sightings of focal follows, and the red triangles are tagging locations.

During the track fitting and interpolation modeling, the correlated random walk method was used in all 2017 tracks to interpolate the tracks as the simple random walk method did not fit the data well due to the larger gaps in the track data resulting from using Argos positions only. However, because of the inclusion of GPS data in 2018, the correlated random walk method oversmoothed the tracks and created non-existent loops; therefore, the simple random walk method was used on six out of seven tracks (the one track with Argos-only data was fit with the correlated random walk method). During the *a priori* model assignment of behavioral states, three distance values and one turning angle value were selected using a histogram of all 20-min travel distances for all 13 interpolated whale tracks. The resulting patterns in speed and directivity are reflected in the different behavioral state models fit to each track (e.g., Figures 5 & 6). It should be noted that the use of correlated random walks vs simple random walks created smoother tracks in 2017 than in 2018, with resulting lower overall turning angles (Table 3); however, the relative magnitude of turning angles were similar between behavioral

states across years (e.g., turning angles were highest in State 1 and lowest in State 3).

The first three behavior states were based on the distance parameter and corresponded to milling or Area Restricted Search (ARS; State 1), an intermediary behavior (State 2), and directed travel (State 3). State 1 (milling) was indicated by low travel speeds and higher turning angles, and it occurred in all tracks when the animals were in shallow water close to islands or over seamounts (Figures 5 & 6). There was an intermediate speed and turning angle behavior (State 2) that typically occurred before and after the presumed milling, which may have corresponded to animals slowing down or speeding up as they approached or left shallower water or changed behaviors. More directed travel (State 3) seemed to occur at faster speeds with lower turning angles as the animals moved across open water in a directed manner. These three states had very similar values in distance traveled and travel speed between 2017 and 2018 (Table 3). The depths at which these behaviors occurred were also similar, with milling (State 1) occurring in shallow, nearshore waters; directed travel (State 3) occurring in deep offshore waters; and the transition behavior (State 2) occurring in depths between these. However, the water depths were on the order of two times deeper in 2017 than in 2018; this is likely due to the fact that all the animals moved away from the islands and started traveling between seamounts in 2017, leading to more time in deeper waters compared to the tagged whales in 2018 that largely remained near the islands. State 4, based on relative turn angle, was only selected in the model for two animals in 2018. While the turning angles were very similar to those found in State 3 in 2018 (though with a much lower standard deviation), the distance traveled and speed were double those values for State 3.

Dive Behavior
Dive data are summarized in Table 4. The number of dives recorded for each whale ranged from 17 to 669, with mean dive durations ranging from 6.3 to 13.0 min (min = 1.3, max = 45, SD = 6.3). A GLM of dive duration included "year" as a significant predictor (coef. = -0.09, SE = 0.024, t = -3.83, p = 0.001), indicating that dives were generally longer for whales tagged in 2017 than in 2018. "Year" was also a significant predictor for mean dive depth (coef. = -0.16, SE = 0.04, t = -3.57, p < 0.001), with mean dive depths deeper in 2017 than in 2018.

Behavioral Response and Received Levels
In 2018, five of the six tagged whales were exposed to MFAS while the tags were attached (Table 5).

Table 1. Sighting and tag transmission information for the 13 SPLASH LIMPET-configured satellite tags deployed on humpback whales (*Megaptera novaeangliae*) off Kaua'i, Hawai'i. The tags in 2018 were also Fastloc-GPS configured. The total number of locations indicates positions used for analysis and includes both Argos and GPS locations.

Tag ID	Time deployed (d/mo/y)	Last transmission (d/mo/y)	Min # days attached (# total locations/ GPS locations)	Age class	Group information
158569	19/3/2017 1045 h	21/3/2017 1600 h	2.3 (27/0)	Adult	Dyad
158570	20/3/2017 0929 h	26/3/2017 1032 h	6.0 (87/0)	Subadult	Pair subadult males
158571	22/3/2017 0902 h	30/3/2017 1136 h	8.1 (106/0)	Subadult	Single animal
164790	22/3/2017 1547 h	25/3/2017 1435 h	3.0 (58/0)	Adult	Competitive pod of five animals (2° escort)
164791	21/3/2017 1126 h	2/4/2017 2141 h	12.5 (129/0)	Subadult	Pair subadult males
164792	22/3/2017 1641 h	24/3/2017 2311 h	2.3 (34/0)	Adult	Competitive pod of five animals (2° escort)
164793	24/3/2017 0827 h	25/3/2017 2250 h	1.6 (23/0)	Adult	Pair adult males, joined with competitive pod of five animals (2° escort)
173784	7/2/2018 0828 h	15/2/2018 2323 h	8.6 (133/27)	Subadult	Pair subadult males
173785	6/2/2018 1403 h	8/2/2018 0930 h	1.8 (26/0)	Adult	Dyad
173786	10/2/2018 1215 h	18/2/2018 1107 h	8.0 (125/102)	Adult	Dyad
173787	11/2/2018 1149 h	14/2/2018 0814 h	2.9 (67/57)	Adult	Dyad
173788	12/2/2018 1137 h	18/2/2018 0625 h	5.8 (234/229)	Adult	Competitive pod of 5 animals (1° escort)
173789	12/2/2018 1212 h	18/2/2018 1109 h	6.0 (138/120)	Adult	Competitive pod of 9 animals (2° escort)

The best GEE of track behavior for all animal tracks combined did not include speed or turning angle but did include distance traveled between interpolated positions (coef. < 0.001, SE < 0.001, Wald $= 32.34, p < 0.001$) and the presence of MFAS as significant predictors (coef. < 0.001, SE < 0.001, Wald $= 5.23, p = 0.22$). In fact, an ANOVA comparing GEEs with and without MFAS as a predictor variable indicate that MFAS is a significant predictor of track behavioral state ($\chi^2 = 49.5, p < 0.001$), with two of the whales spending more time in State 1 during periods of MFAS. The occurrence of State 4 in two whales in 2018 did not co-occur with periods of sonar and actually occurred between periods of sonar. The percentage of behavioral transitions that occurred at the onset or cessation of sonar ranged from 5 to 40% of the total number of transitions between states across all five whales. The whales experienced between three and 28 individual bouts of sonar (defined as periods of sonar separated by at least a half hour), and they changed their behavior at the onset between 6 to 67% of sonar bouts. One whale, 173787, changed behavior only five times along its track; two changes occurred at the onset of sonar, and this individual only experienced three bouts of sonar total. This made it the only whale that changed its behavior relative to the onset of sonar more often than chance given the number of

behavioral transitions and sonar bouts experienced by each whale.

There were periods of dive data that co-occurred with MFAS for all five whales in 2018, although for one whale (173784), that was only for a single dive. For all of the 2018 whales combined, MFAS was not a significant predictor of dive duration (coef $= 0.04$, SE $= 0.04$, Wald $= 1.2, p = 0.29$). In three of the four whales that co-occurred with sonar for more than one dive, MFAS was also not a statistically significant predictor for changes in dive metrics in individual GLMs. However, one whale did include MFAS as a significant predictor of changes in dive duration, descent rate, maximum depth, standard deviation of dive depth, and bottom distance (amount of up-and-down movement while at the bottom of the dive) (Table 6). This whale also had the closest point of approach (CPA) to the ships at 17.3 km (Figure 7). During the 3-h period of MFAS, the whale performed a series of dives with steep descents and ascents, with little time at the bottom, and with each succeeding dive deeper than the dive before (max dive depths 23 to 147 m; Figure 8). The maximum received levels for these dives were also modeled both at the surface and bottom of each dive (based on the 1-min interpolated locations), and estimated levels ranged between 95.9 and 158.4 dB re 1 μPa
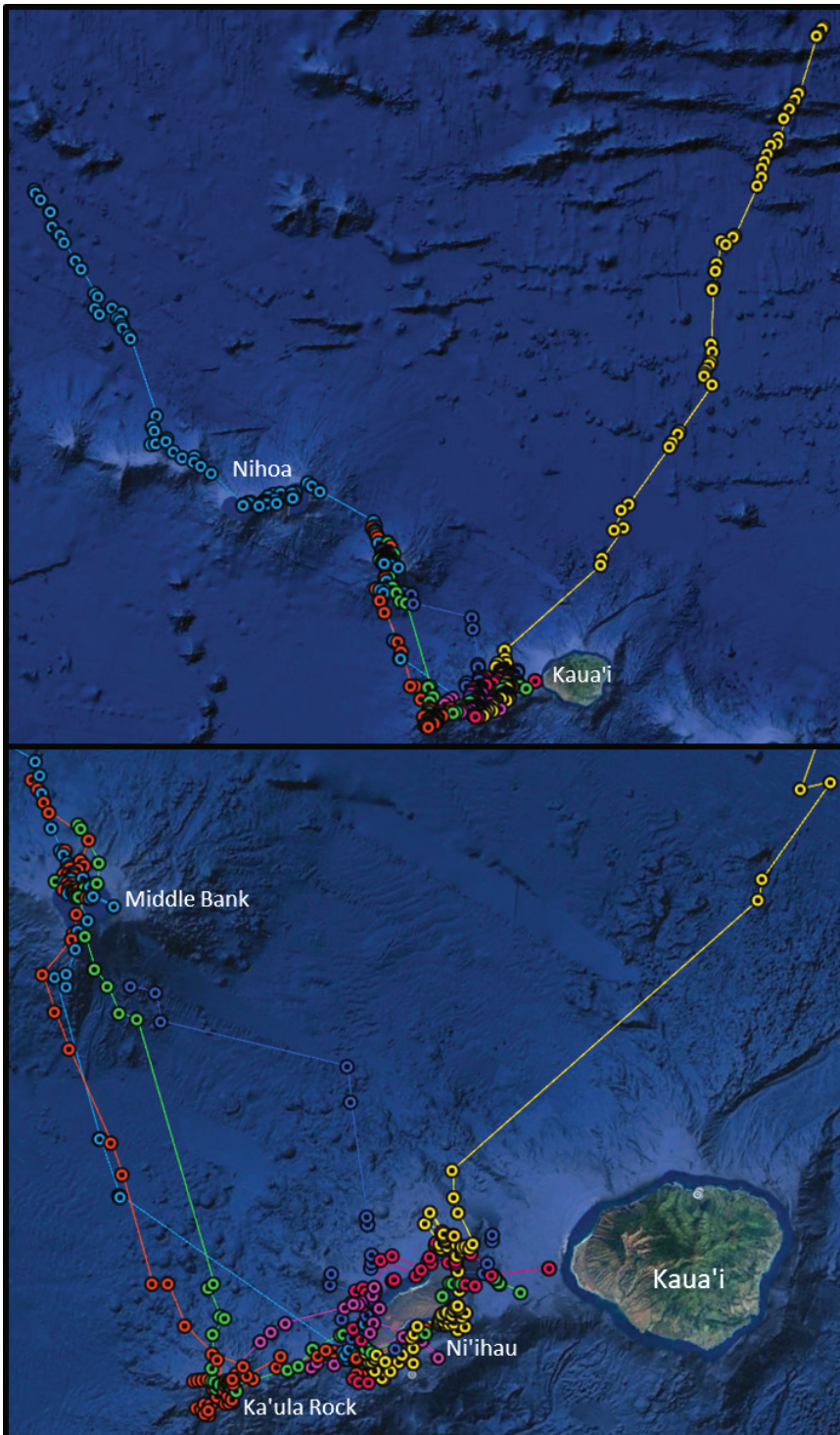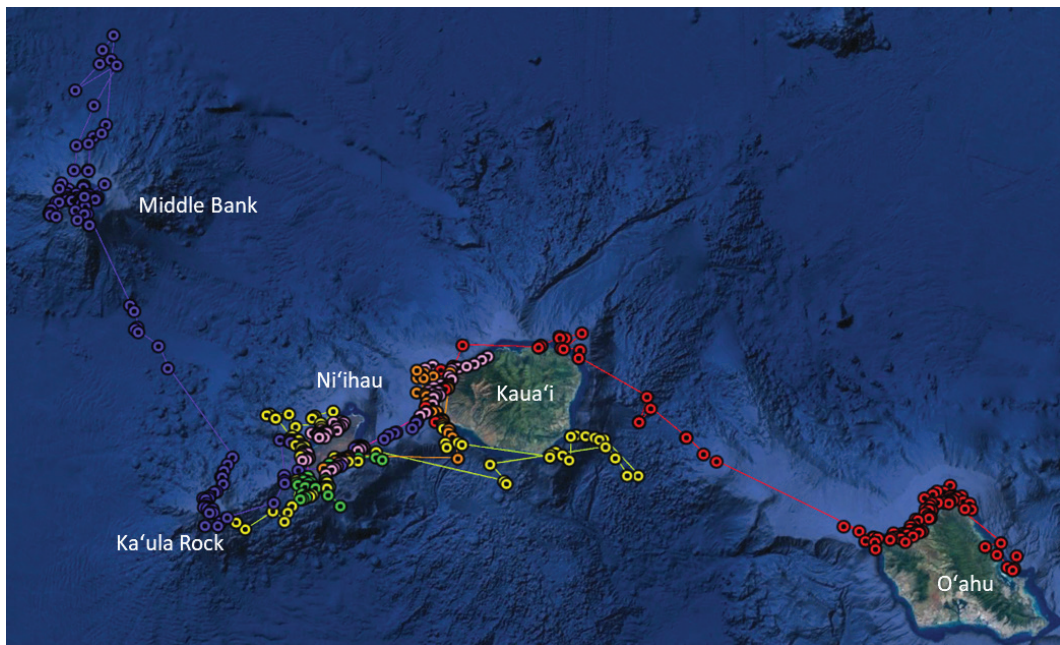
Figure 3. Satellite tracks of humpback whales (*Megaptera novaeangliae*) tagged in 2017. Each color represents a unique whale, and each dot is an Argos position. The top map gives the full extent of all tracks, while the bottom map is zoomed in to the islands of Kauaʻi and Niʻihau and the Middle Bank seamount to show the track movements in that area.

Table 2. Track travel speed and daily, cumulative, and straight-line distances for all satellite tracks of humpback whales

Tag ID	Median speed (km/h)	Cumulative distance (km)	Straight-line distance (km)	Mean daily distance (km/d)
158569	2.8	143.5	46.4	63.5
158570	2.4	379.2	166.9	62.8
158571	3.6	826.4	548.8	102.5
164790	4.0	295.9	156.0	100.3
164791	2.0	816.2	582.5	66.6
164792	3.3	166.0	19.8	73.1
164793	3.7	226.6	113.0	142.5
2017 mean values	3.1	407.7	233.3	87.3
173784	2.8	627.5	148.2	69.7
173785	1.7	81.4	22.9	27.1
173786	2.0	475.8	82.2	52.9
173787	1.3	133.5	45.7	45.2
173788	4.0	504.2	217.5	72.0
173789	1.4	291.3	31.9	41.6
2018 mean values	2.2	352.3	91.4	51.4

Figure 4. Satellite tracks of humpback whales tagged in 2018. Each color represents a unique whale, and each dot is an Argos position (no Fastloc GPS position data are included in this figure).

(SD 0.58 dB re 1 µPa). The received levels were reduced as the animal dove to deeper depths, and they were greatest at the surface (Figure 8). The modeled cSEL of the dives over the whole exposure period from multiple ships was 167.5 dB re 1 µPa²s. This was similar to but slightly higher than the estimated SEL for the same period when the whale was modeled just at the surface due to the increased resolution of the interpolated track for this analysis (Table 5). Along with these significant changes to the dive behavior, the whale's movement behavior also transitioned at the onset

Figure 5. The track for tagged whale 158570 from 2017 with milling (State 1) in yellow, directed travel (State 3) in red, and the intermediary transition behavior (State 2) in green

of sonar, but only from State 1 to State 2, and it did not rise to a higher state until it transited to Niʻihau in State 4 between periods of sonar. Another bout of sonar began when the whale reached Niʻihau, at which time its behavior transitioned again back to State 2.

Discussion

Thirteen humpback whales were tracked with satellite tags off the island of Kauaʻi in 2017 and 2018, although at different points in the breeding season. In both years, most or all of the tagged whales traveled from Kauaʻi to Niʻihau. In 2017, this movement occurred not only in all the tagged whales but was observed in most of the whales encountered (Henderson et al., 2018b). Three tagged whales continued traveling southwest to Kaʻula Rock; and then, for the six tags that remained active, four turned northwest to travel along the Hawaiian archipelago, with only one animal heading directly north from Niʻihau. In contrast, in 2018, two animals headed east toward the island of Oʻahu, with one animal remaining there for the duration of the tag deployment, while the other turned

around partway and traveled west to Niʻihau. Unfortunately, the tag attachment durations were relatively short such that only one tag remained attached long enough in 2018 to observe the travel from Niʻihau to Middle Bank, the first seamount in the archipelago northwest of Kaʻula Rock. In addition, four of the whales spent considerable time in the nearshore waters of Kauaʻi before traveling to Niʻihau or Oʻahu in 2018, while all whales tagged in 2017 traveled directly to Niʻihau.

These differences in habitat use may be due to the timing and location of the tagging effort between both years such that the more offshore effort in 2017 captured animals already transiting to Niʻihau. In contrast, weather conditions during the tagging effort were worse in 2018 than in 2017, with higher Beaufort Sea States and swell heights, which led to more effort spent closer to shore rather than in the channel between Kauaʻi and Niʻihau. Female humpback whales with calves have been shown to preferentially occur in nearshore shallow waters (Johnston et al., 2007; Craig et al., 2014; Pack et al., 2018), with males following suit, so whales are typically observed close to shore. The movement to Niʻihau observed in this study
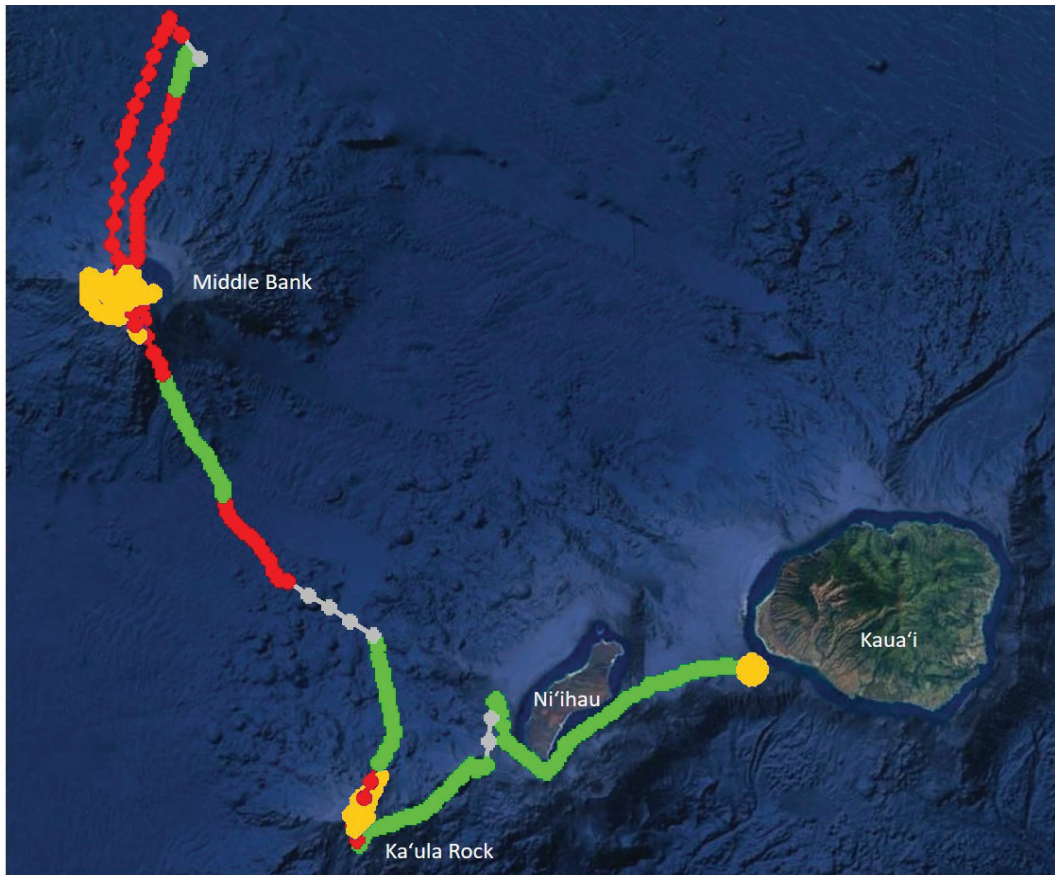
Figure 6. Track 173784 from 2018. The colors represent the same behavioral states as in Figure 5, with milling in yellow, transition in green, and directed travel in red, while the gray indicates that the turning angle model was a better fit than the distance models (see the purple track in Figure 4 as well).

Table 3. Markovian state switching movement behavior model results for 2017 and 2018

	State counts	Distance (km)	Relative angle (degrees)	Water depth (m)	Speed (km/h)
			2017		
State 1	1,091	0.3 ± 0.2	0.7 ± 17.7	490.63 ± 459.8	0.9 ± 0.5
State 2	719	1.1 ± 0.4	-0.4 ± 11.3	1,114.63 ± 1,104.9	3.2 ± 1.2
State 3	563	2.2 ± 0.5	0.5 ± 3.2	2,405.16 ± 1,490.0	6.6 ± 1.7
State 4	0	NA	NA	NA	NA
			2018		
State 1	1062	0.4 ± 0.3	-0.9 ± 45.1	284.40 ± 240.0	1.1 ± 0.8
State 2	852	1.0 ± 0.5	-1.4 ± 43.9	365.98 ± 325.3	3.0 ± 1.5
State 3	306	2.3 ± 0.9	-0.6 ± 32.9	1,078.12 ± 1,127.0	6.8 ± 2.6
State 4	13	5.2 ± 0.8	0.2 ± 0.7	2,363.2 ± 1,538.2	15.6 ± 2.4

Table 4. Dive data from satellite tagged humpback whales. Note that 45 min was the maximum allowed dive duration before a data dropout was assumed to have occurred.

Tag ID	Number dives	Mean duration (min)	Max duration (min)	Mean ± SD depth (m)	Max depth (m)
158569	153	6.3	25.0	32.0 ± 8.9	358.5
158570	262	10.9	45.0	35.4 ± 10.6	297.5
158571	348	10.3	36.3	29.7 ± 7.36	238.5
164790	242	9.1	45.0	26.9 ± 7.4	171.0
164791	271	9.9	28.8	39.1 ± 8.9	395.5
164792	72	11.4	35.0	39.7 ± 8.7	287.5
164793	71	7.8	33.8	31.8 ± 7.8	238.5
2017 mean values	203	9.7	35.6	33.0	284.0
173784	247	9.5	32.5	28.5 ± 5.5	282.0
173785	17	10.5	21.3	27.3 ± 8.4	82.0
173786	313	13.0	40.0	33.1 ± 9.3	282.0
173787	153	9.6	25.0	31.3 ± 4.8	212.0
173788	669	6.3	27.5	37.5 ± 10.2	349.0
173789	630	8.6	33.8	15.6 ± 2.1	158.0
2018 mean values	338	8.9	30.0	28.3	227.5

may represent movement to another island, comparable to the one whale that transited to Oʻahu. Alternately, it may be the first stop as animals begin their migration away from the islands. Some inter-island movements have been recorded (Cerchio, 1998; Cerchio et al., 1998; Mate et al., 1998, 2019; Calambokidis et al., 2001) and appear to be more common than previously believed (Mate et al., 2019), although whales may be more likely to be observed off the same island within a season (Calambokidis et al., 2001). The few tagging or passive acoustic studies that have been conducted in Hawaiʻi (Mate et al., 1998, 2019) or north of Hawaiʻi (Abileah et al., 1996; Norris et al., 1999) found that whales traveled generally north once they left the main Hawaiian islands, with movement behavior becoming more directed once they leave the main islands (beyond 50 km; Mate et al., 2019). Studies on other breeding grounds have found similar directed movement once the whales leave the main breeding grounds, but with some time spent near seamounts first (Lagerquist et al., 2008; Garrigue et al., 2010; Horton et al., 2017).

Another marked difference between years was the Navy training exercise that occurred on the PMRF range during and after the tagging effort in 2018. While the epicenter of the training activity was 30 to 60 km north of the tagging effort, there were multiple ships present and actively maneuvering during the tagging period, and then

periodically using sonar over 5 d while the animals were still in the area. The whale that traveled to Oʻahu was at the northeastern corner of Kauaʻi when the sonar began (Figure 4: red track, whale 173788). While the travel to Oʻahu is likely a normal breeding season behavior, it could also have been a mechanism for the animal to reduce its received levels by avoiding the sonar. This animal did spend significantly more time in State 1 during sonar periods than during non-sonar periods; however, it was far enough from the range that it received few pings, and most received levels were close to 100 dB re 1 µPa. Similarly, the whale that did travel to Middle Bank (whale 173784; Figure 6) received multiple bouts of sonar while there and also spent more time in State 1 during periods of sonar, although it was at Middle Bank at that time where whales are generally found to be milling. After the cessation of one bout of sonar that occurred while the animal was over the seamount, the animal began traveling north, which could have indicated the beginning of migration. It then suddenly turned around, swimming up to speeds that in some cases exceeded known burst speeds for humpback whales (18 km/h [estimated using the interpolated track data] vs 15 km/h recorded by Noad & Cato, 2007), and it returned to Middle Bank, only to be exposed to more sonar after it had resumed State 2 behavior. However, there was no sonar occurring during its fast travel

Table 5. Propagation-modeled received levels of MFAS (estimated over 1 s and averaged in µPa) at the surface for each satellite tagged whale along with the distances to the closest ship

Tag ID	RL mean (dB re 1 µPa)	RL median (dB re 1 µPa)	RL max (dB re 1 µPa)	cSEL (dB re 1 µPa2s)	Mean distance (km)	Min/max distance (km)
173784	99.9	126.0	133.2	141.6	121.6	109/134
173786	129.1	136.9	151.4	162.8	59.8	27/107
173787	146.3	153.7	158.4	165.2	33.7	17/101
173788	109.2	104.3	137.4	138.8	202.0	62/253
173789	116.7	116.0	146.1	151.5	67.1	36/96

Table 6. Dive variables for which MFAS was a significant predictor and the associated coefficient estimate, standard error, *t* value, and *p* value from the GLMs for whale 173787

Whale 173787	Without MFAS	With MFAS	Coef.	SE	*t* value	*p* value
Dive count	138.0	15.0	--	--	--	--
Dive duration (min)	9.9	7.5	-0.27	0.13	-2.1	0.04
Descent rate (m/min)	3.9	6.1	-0.74	0.34	-2.2	0.03
Bottom distance (m)	8.0	37.6	1.55	0.32	4.9	< 0.001
Dive depth SD (m)	3.5	16.7	1.57	0.30	5.3	< 0.001
Maximum depth (m)	34.7	55.5	0.47	0.16	2.9	0.005

behavior, and this whale was far enough away from the training activity for received levels to not exceed 133 dB re 1 µPa (141 dB re 1 µPa²s cSEL), and much of the sound was well below 100 dB re 1 µPa. Therefore, these extreme changes in movement behavior are not likely directly attributable to a behavioral response to the training activity and could simply represent social or breeding behavior (e.g., turning around to join a competitive pod or to chase a female). In fact, although these more rapid movement behaviors occurred in two whales, the only change in behavior that was statistically different in the presence of MFAS was an increase in State 1 behavior, as well as the dive behavior of whale 173787. This animal experienced the highest received levels (up to 158 dB re 1 µPa SPL and 165 dB re 1 µPa²s cSEL at the surface and 167 dB re 1 µPa²s cSEL while diving) and had the closest CPA to a ship just as the sonar went active, when the whale turned around and headed south while enacting the dives seen in Figure 8 (Figure 7). For comparison, humpback whale song has been estimated to have source levels of 151 to 189 dB re 1 µPa (Au et al., 2001, 2006). The first position update following the cessation of MFAS at which time the whale turned and traveled north again for several hours, then turned south one more time. It then crossed the channel between Kaua'i and Ni'ihau at a rapid swim speed in State 4, then briefly received more sonar when it reached Ni'ihau at which time it changed behavior again to State 2.

Other behavioral response studies that have focused on humpback whales or other baleen whale species have found mixed results, although generally most species of baleen whales seem to be less sensitive to noise impacts than other groups of marine mammals (e.g., Miller, 2012; Sivle et al., 2015). In a controlled exposure study using sonar, only half of the 12 exposed humpbacks responded, either to the first or second ramped-up exposure, with only one whale (a female with a young calf) responding to both passes (Wensveen et al., 2017). Half of the whales that responded were in a feeding state with mean received levels of 172 to 173 dB re 1 µPa, while the other half were in a non-feeding state with mean received levels of 167 to 174 dB re 1 µPa. These levels are at least 10 dB higher than those estimated in the present study. However, eight of the whales from the same study were also exposed to killer whale call playbacks. All eight whales changed their heading and increased their speed, and both shallow and deep dives became longer and deeper (Curé et al., 2015). In addition, all five whales that were feeding prior to the killer whale playback stopped feeding during the playback.
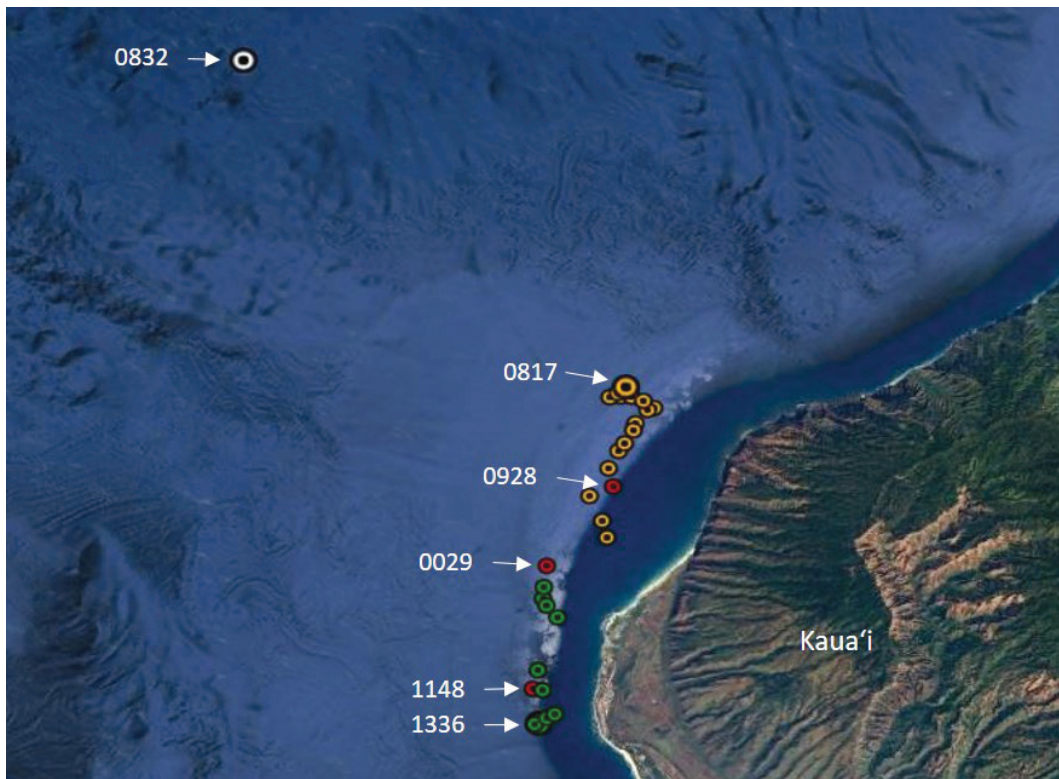
Figure 7. GPS positions of tagged whale 173787 before (in orange), during (in red), and after (in green) the exposure period of MFAS corresponding to the dive profile in Figure 8. Times include the start of the before period (0029 h on 12 February 2018), the last location before the onset of sonar (0817 h), the approximate location of the closest ship when sonar began (0832 h), the first and last locations during the period of sonar (0928 and 1148 h, respectively), and the first location after the sonar ended (1336 h). The whale appears to have followed the shelf break while traveling north along Kaua'i, then it started moving west at the onset of sonar. The exact location of the whale at the onset of sonar is unknown. The whale followed the shelf break south during the period of sonar, then seemed to have turned around and resumed traveling north 2 h after the sonar ended.

In another study on their migration route to the Antarctic feeding grounds, Australian humpback whales were exposed to seismic airguns. Limited responses were observed in most of the animals, with the main response being a change in movement behavior exhibited by reduced dive times, reduced southward travel speeds, and some slight movement offshore of the source vessel (Dunlop et al., 2015, 2016). These responses largely occurred above received levels of 140 dB re 1 µPa²s (SEL) and at distances within 3 km (Dunlop et al., 2017). Males were the least affected by the airgun noise, especially while in competitive pods, while females with calves changed their behavior the most (Dunlop et al., 2018).

In Hawai'i, six out of 18 male singing humpback whales exposed to low-frequency active sonar (LFAS) extended the duration of their song during the exposure (Biassoni et al., 2000; Miller et al., 2000). Although nine of the 18 singers also stopped singing during the exposure, four of them did so to join another male, which is a behavior frequently associated with the cessation of song (Darling & Bérubé, 2001; Darling et al., 2006). However, received level was not a good predictor of either response as maximum received levels ranged from 115 to 150 dB re 1 µPa, and these levels occurred across all 18 whales regardless of response (Biassoni et al., 2000). It may be that little response appears to have occurred in the present study because the tagged animals were likely males engaged in breeding behaviors and, therefore, could have been less sensitive to the presence of MFAS. Male humpback whale testes size (Chittleborough, 1955) and testosterone levels (Vu et al., 2015) have both been shown to increase during the breeding season; therefore, it could be that humpback whale behavior on breeding grounds is strongly driven by intrinsic factors
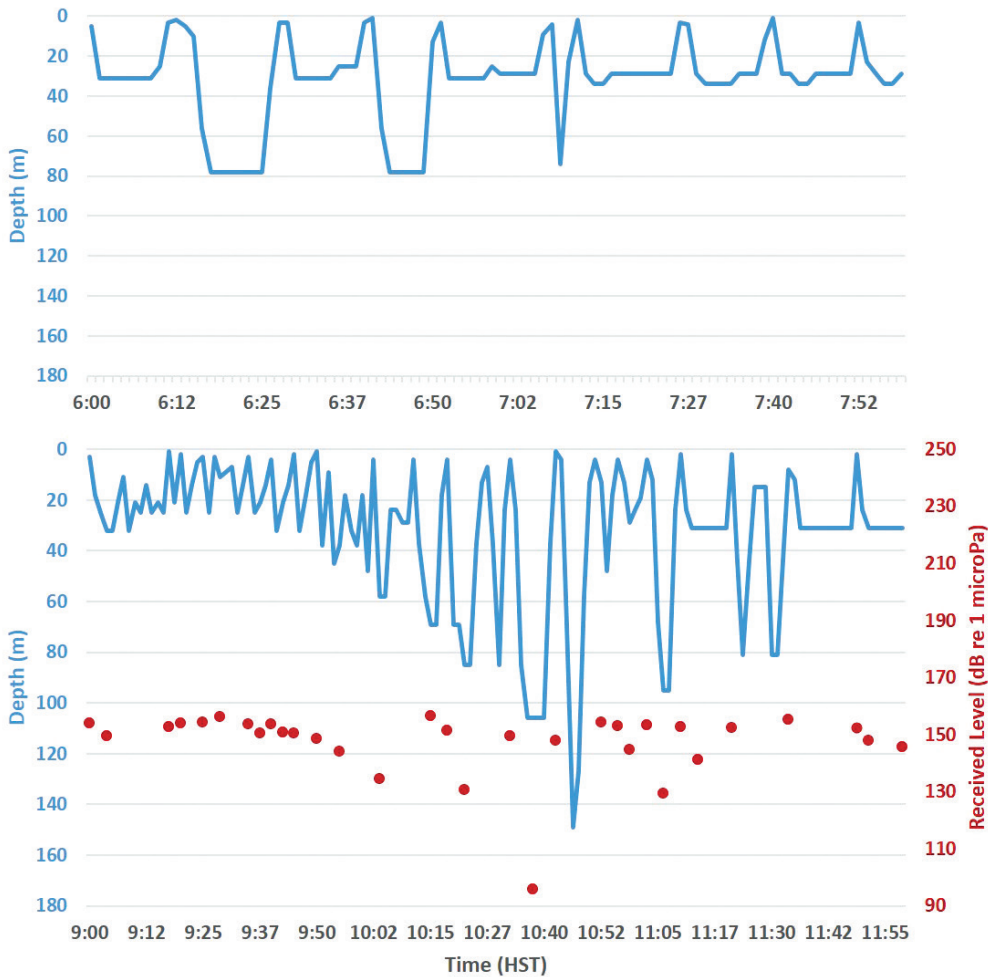
Figure 8. Dive profiles for whale 173787. The top figure is 1.5 h of a typical dive profile for this whale that occurred prior to the MFAS exposure, with several dives to around 30 m with long bottom durations and up-and-down movement while at the bottom. The bottom figure is the 3-h period with MFAS wherein the dives have little bottom time, steep ascent and descent rates, and get deeper with each subsequent dive. These dives are significantly different than the other dives performed by this individual but appear to begin to return to normal before the end of the MFAS period.

such as hormones, while humpback whale behavior on feeding grounds is more susceptible to extrinsic factors such as noise. Alternatively, it could be that the source of the MFAS was far enough away from most of the animals in this study to not be perceived as aversive as most responses in other studies seem to occur at relatively short distances.

The effects of the proximity of the source vs the received level of the sound is difficult to separate and is a question of interest. For example, Cuvier's beaked whales (*Ziphius cavirostris*) exposed to MFAS within a few kilometers responded at levels between 89 and 127 dB re 1 μPa, while exposure

to distant MFAS at similar received levels (78 to 106 dB re 1 μPa) did not lead to a response (DeRuiter et al., 2013). These whales were located in the Southern California Bight, an area with frequent MFAS occurrence. In contrast, northern bottlenose whales (*Hyperoodon ampullatus*) in a pristine habitat were exposed to LFAS from 1 to 2 kHz at similar received levels (117 to 126 dB re 1 μPa), but those at distances ranging from 0.8 to 28 km responded by avoiding the sound source (Wensveen et al., 2019). Therefore, the role that distance plays in this study conducted in a region of frequent sonar use is unknown but warrants further investigation.

In terms of other baleen whale species, blue whale behavioral responses to MFAS seemed to be associated with behavioral state such that deep feeding and non-feeding whales were more likely to respond than shallow feeding whales (Goldbogen et al., 2013; Friedlaender et al., 2016). However, there may be a frequency component to the likelihood of response as well because foraging blue and fin (*Balaenoptera physalus*) whales were exposed to LFAS at received levels up to 150 dB re 1 µPa with no apparent response (Croll et al., 2001). Gray whales (*Eschrichtius robustus*) were also exposed to LFAS along their southbound migration route off southern California; these whales would avoid the sound source by moving several hundred meters offshore but continued their migration (Buck & Tyack, 2000; Clark & Fristrup, 2001; Ellison et al., 2011). Similar results were obtained for gray whales exposed to industrial drilling noise along the same migration route (Malme et al., 1984). Minke whales appear to be the most sensitive baleen whale, with one whale exposed to sonar demonstrating a prolonged avoidance and aversion response at a received level of 146 dB re 1 µPa within 3 km (Sivle et al., 2015; Kvadsheim et al., 2017), and another minke whale also avoiding the source at 156 dB re 1 µPa at 6 km (Kvadsheim et al., 2017). Minke whales that were acoustically tracked before, during, and after a training event at PMRF were found to shift their distribution north of the activity and appeared to avoid the area around the ships and MFAS (Harris et al., 2018a). These findings point to the roles of species, behavior, source type, and animal experience in the likelihood of a behavioral response to noise.

Given the limited amount of baseline behavior data in these tagged whales, as well as the limited data during periods of MFAS and the inconclusive behavioral results, it is difficult to define any of the movement behavior changes as a behavioral response. In fact, the higher travel speeds occasionally observed may likely be indicative of social or breeding behavior rather than any kind of behavioral response to sonar as they occurred during the peak period of the breeding season and did not co-occur with active sonar. Satellite tags do not produce the level of detail in movement behavior that acoustic tags can provide and, therefore, may not be appropriate for assessment of fine-scale responses. However, satellite tags are being used more widely in both CEEs (e.g., Schick et al., 2019) and opportunistic behavioral response studies (Falcone et al., 2017) as they remain on the animal longer and, thus, can provide longer baseline and post-exposure data. Furthermore, as they do not need to be recovered, the influence of the tracking vessel can be removed from the exposure paradigm. Further tagging work

is planned, which may assist in teasing out the implications of these findings. However, in general, none of the tagged whales spent more than a few days in the waters near Kaua'i after being tagged, and no animals spent any appreciable time actually on the range. Similar results were found by Mate et al. (2019), where few humpback whales crossed the range, and those that did were generally already transiting. Although up to 15% of tagged whales were found in other Navy training areas in Hawai'i, it was still only for a mean of 1 to 4.3 d (Mate et al., 2019). In addition, in both years of this study, only four animals were observed twice over the course of the tagging effort (two animals observed twice in each year), and no whales were observed in both years. Although limited, these findings begin to point to a low likelihood of humpback whales being exposed to sonar at received levels higher than those reported here, or being exposed repeatedly (either within a breeding season or across breeding seasons). Therefore, the impacts of MFAS on the breeding behavior of this population of humpback whales may be minimal and seems unlikely to lead to long-term consequences, although continued monitoring is necessary to make that determination.

Acknowledgments

Literature Cited

Abileah, R., Martin, D., Lewis, S. D., & Gisiner, B. (1996). *Long-range acoustic detection and tracking of the humpback whale Hawaii-Alaska migration*. Paper presented at the OCEANS'96, MTS/IEEE, Prospects for the 21st Century conference. https://doi.org/10.1109/OCEANS.1996.572775

Andrews, R. D., Pitman, R. L., & Ballance, L. T. (2008). Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. *Polar Biology*, *31*(12), 1461-1468. https://doi.org/10.1007/s00300-008-0487-z

Au, W. W. L., James, D., & Andrews, K. (2001). High-frequency harmonics and source level of humpback whale

songs. *The Journal of the Acoustical Society of America*, *110*(5), 2770. https://doi.org/10.1121/1.4777702

Au, W. W. L., Pack, A. A., Lammers, M. O., Herman, L. M., Deakos, M. H., & Andrews, K. (2006). Acoustic properties of humpback whale songs. *The Journal of the Acoustical Society of America*, *120*(2), 1103-1110. https://doi.org/10.1121/1.2211547

Bailey, H., Corkrey, R., Cheney, B., & Thompson, P. M. (2013). Analyzing temporally correlated dolphin sightings data using generalized estimating equations. *Marine Mammal Science*, *29*(1), 123-141. https://doi.org/10.1111/j.1748-7692.2011.00552.x

Baird, R. W., Martin, S. W., Manzano-Roth, R., Webster, D. L., & Southall, B. L. (2017). *Assessing exposure and response of three species of odontocetes to mid-frequency active sonar during submarine commanders courses at the Pacific Missile Range Facility: August 2013 through February 2015. Draft Report*. Retrieved from www.cascadiaresearch.org/publications/assessing-exposure-and-response-three-species-odontocetes-mid-frequency-active-sonar

Baker, C. S., & Herman, L. M. (1984). Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Canadian Journal of Zoology*, *62*(10), 1922-1937. https://doi.org/10.1139/z84-282

Biassoni, N., Miller, P. J. O., & Tyack, P. (2000). *Preliminary results of the effects of SURTASS-LFA sonar on singing humpback whales* (WHOI Technical Report, Vol. 6). Woods Hole, MA: Woods Hole Oceanographic Institution. https://doi.org/10.21236/ADA378666

Blackwell, S. B., Nations, C. S., McDonald, T. L., Greene, C. R., Jr., Thode, A. M., Guerra, M., & Macrander, A. M. (2013). Effects of airgun sounds on bowhead whale calling rates in the Alaskan Beaufort Sea. *Marine Mammal Science*, *29*, E342-E365. https://doi.org/10.1111/mms.12001

Blackwell, S. B., Nations, C. S., McDonald, T. L., Thode, A. M., Mathias, D., Kim, K. H., . . . Macrander, A. M. (2015). Effects of airgun sounds on bowhead whale calling rates: Evidence for two behavioral thresholds. *PLOS ONE*, *10*(6), e0125720. https://doi.org/10.1371/journal.pone.0125720

Brown, M., & Corkeron, P. (1995). Pod characteristics of migrating humpback whales (*Megaptera novaeangliae*) off the east Australian coast. *Behaviour*, 163-179. https://doi.org/10.1163/156853995X00676

Buck, J. R., & Tyack, P. L. (2000). Response of gray whales to low-frequency sounds. *The Journal of the Acoustical Society of America*, *107*(5), 2774. https://doi.org/10.1121/1.428908]

Calambokidis, J., Steiger, G. H., Straley, J. M., Herman, L. M., Cerchio, S., Salden, D. R., . . . Balcomb, K. C. (2001). Movements and population structure of humpback whales in the North Pacific. *Marine Mammal Science*, *17*(4), 769-794. https://doi.org/10.1111/j.1748-7692.2001.tb01298.x

Calenge, C. (2006). The package adehabitat for the *R* software: A tool for the analysis of space and habitat use by animals. *Ecological Modeling*, *197*, 516-519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Calenge, C. (2015). *Analysis of animal movements in* R*: The adehabitatLT package*. Auffargis, France: Office National de la Chasse et de la Faune Sauvage Saint Benoist. Retrieved from https://cran.r-project.org/web/packages/adehabitatLT/vignettes/adehabitatLT.pdf

Cerchio, S. (1998). Estimates of humpback whale abundance off Kauai, 1989 to 1993: Evaluating biases associated with sampling the Hawaiian Islands breeding assemblage. *Marine Ecology Progress Series*, *175*, 23-34. https://doi.org/10.3354/meps175023

Cerchio, S., Gabriele, C. M., Norris, T. F., & Herman, L. M. (1998). Movements of humpback whales between Kauai and Hawaii: Implications for population structure and abundance estimation in the Hawaiian Islands. *Marine Ecology Progress Series*, *175*, 13-22. https://doi.org/10.3354/meps175013

Chittleborough, R. (1955). Aspects of reproduction in the male humpback whale, *Megaptera nodosa* (Bonnaterre). *Marine and Freshwater Research*, *6*(1), 1-29. https://doi.org/10.1071/MF9550001

Clapham, P., Palsbøll, P. J., Mattila, D. K., & Vasquez, O. (1992). Composition and dynamics of humpback whale competitive groups in the West Indies. *Behaviour*, *122*(3/4), 182-194. https://doi.org/10.1163/156853992X00507

Clark, C. W., & Fristrup, K. M. (2001). Baleen whale responses to low-frequency human-made underwater sounds. *The Journal of the Acoustical Society of America*, *110*(5), 2751. https://doi.org/10.1121/1.4777574

Costa, D. P., Robinson, P. W., Arnould, J. P., Harrison, A. L., Simmons, S. E., Hassrick, J. L., . . . Crocker, D. E. (2010). Accuracy of ARGOS locations of pinnipeds at-sea estimating using FastLoc GPS. *PLOS ONE*, *5*(1), e8677. https://doi.org/10.1371/journal.pone.0008677

Costa, D. P., Schwarz, L., Robinson, P., Schick, R. S., Morris, P. A., Condit, R., . . . Kilpatrick, A. M. (2016). A bioenergetics approach to understanding the population consequences of disturbance: Elephant seals as a model system. In A. N. Popper & A. Anthony (Eds.), *The effects of noise on aquatic life II: Advances in experimental medicine and biology* (Vol. 875, pp. 116-169). New York: Springer. https://doi.org/10.1007/978-1-4939-2981-8_19

Craig, A. S., Herman, L. M., Pack, A. A., & Waterman, J. O. (2014). Habitat segregation by female humpback whales in Hawaiian waters: Avoidance of males? *Behaviour*, *151*(5), 613-631. https://doi.org/10.1163/1568539X-00003151

Croll, D. A., Clark, C. W., Calambokidis, J., Ellison, W. T., & Tershy, B. R. (2001). Effect of anthropogenic low-frequency noise on the foraging ecology of *Balaenoptera* whales. *Animal Conservation*, *4*, 13-27. https://doi.org/10.1017/S1367943001001020

Curé, C., Sivle, L. D., Visser, F., Wensveen, P. J., Isojunno, S., Harris, C. M., . . . Miller, P. J. O. (2015). Predator sound playbacks reveal strong avoidance responses in a fight strategist baleen whale. *Marine Ecology Progress Series*, *526*, 267-282. https://doi.org/10.3354/meps11231

Darling, J. D., & Bérubé, M. (2001). Interactions of singing humpback whales with other males. *Marine*

Mammal Science, *17*(3), 570-584. https://doi.org/10.1111/j.1748-7692.2001.tb01005.x

Darling, J. D., Jones, M. E., & Nicklin, C. P. (2006). Humpback whale songs: Do they organize males during the breeding season? *Behaviour*, *143*(9), 1051-1101. https://doi.org/10.1163/156853906778607381

DeRuiter, S. L., Southall, B. L., Calambokidis, J., Zimmer, W. M., Sadykova, D., Falcone, E. A., . . . Tyack, P. L. (2013). First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. *Biology Letters*, *9*(4), 20130223. https://doi.org/10.1098/rsbl.2013.0223

Douglas, D. C., Weinzierl, R., Davidson, S. C., Kays, R., Wikelski, M., & Bohrer, G. (2012). Moderating Argos location errors in animal tracking data. *Methods in Ecology and Evolution*, *3*(6), 999-1007. https://doi.org/10.1111/j.2041-210X.2012.00245.x

Dujon, A. M., Lindstrom, R. T., & Hays, G. C. (2014). The accuracy of Fastloc-GPS locations and implications for animal tracking. *Methods in Ecology and Evolution*, *5*(11), 1162-1169. https://doi.org/10.1111/2041-210X.12286

Dunlop, R. A., Noad, M. J., McCauley, R. D., & Cato, D. H. (2018). *BRAHSS: The behavioral responses of migrating humpback whales to air guns: Results*. Paper presented at the 3rd Programme Review Meeting of the E&P Sound & Marine Life Joint Industry Programme, The Hague, the Netherlands.

Dunlop, R. A., Noad, M. J., McCauley, R. D., Kniest, E., Paton, D., & Cato, D. H. (2015). The behavioural response of humpback whales (*Megaptera novaeangliae*) to a 20 cubic inch air gun. *Aquatic Mammals*, *41*(4), 412-433. https://doi.org/10.1578/AM.41.4.2015.412

Dunlop, R. A., Noad, M. J., McCauley, R. D., Kniest, E., Slade, R., Paton, D., & Cato, D. H. (2016). Response of humpback whales (*Megaptera novaeangliae*) to ramp-up of a small experimental air gun array. *Marine Pollution Bulletin*, *103*(1-2), 72-83. https://doi.org/10.1016/j.marpolbul.2015.12.044

Dunlop, R. A., Noad, M. J., McCauley, R. D., Scott-Hayward, L., Kniest, E., Slade, R., . . . Cato, D. H. (2017). Determining the behavioural dose-response relationship of marine mammals to air gun noise and source proximity. *Journal of Experimental Biology*, *220*(16), 2878-2886. https://doi.org/10.1242/jeb.160192

Ellison, W. T., Southall, B. L., Clark, C. W., & Frankel, A. S. (2011). A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. *Conservation Biology*, *26*(1), 21-28. https://doi.org/10.1111/j.1523-1739.2011.01803.x

Falcone, E. A., Schorr, G. S., Watwood, S. L., DeRuiter, S. L., Zerbini, A. N., Andrews, R. D., . . . Moretti, D. J. (2017). Diving behaviour of Cuvier's beaked whales exposed to two types of military sonar. *Royal Society Open Science*, *4*(170629), 1-21. https://doi.org/10.1098/rsos.170629

Friedlaender, A. S., Hazen, E. L., Goldbogen, J. A., Stimpert, A. K., Calambokidis, J., & Southall, B. L. (2016). Prey-mediated behavioral responses of feeding blue whales in controlled sound exposure experiments. *Ecological Applications*, *26*(4), 1075-1085. https://doi.org/10.1002/15-0783

Gailey, G., Sychenko, O., McDonald, T., Racca, R., Rutenko, A., & Bröker, K. (2016). Behavioural responses of western gray whales to a 4-D seismic survey off northeastern Sakhalin Island, Russia. *Endangered Species Research*, *30*, 53-71. https://doi.org/10.3354/esr00713

Garrigue, C., Zerbini, A. N., Geyer, Y., Heide-Jørgensen, M-P., Hanaoka, W., & Clapham, P. (2010). Movements of satellite-monitored humpback whales from New Caledonia. *Journal of Mammalogy*, *91*(1), 109-115. https://doi.org/10.1644/09-MAMM-A-033R.1

Goldbogen, J. A., Southall, B. L., DeRuiter, S. L., Calambokidis, J., Friedlaender, A. S., Hazen, E. L., . . . Tyack, P. L. (2013). Blue whales respond to simulated mid-frequency military sonar. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1765), 20130657. https://doi.org/10.1098/rspb.2013.0657

Guéguen, L. (2001). Segmentation by maximal predictive partitioning according to composition biases. In O. Gascuel & M. F. Sagot (Eds.), *Computational biology. JOBIM 2000: Lecture notes in computer science* (Vol. 2066, pp. 32-44). Berlin, Germany: Springer. https://doi.org/10.1007/3-540-45727-5_4

Guéguen, L. (2009). Computing the likelihood of sequence segmentation under Markov modelling. *ArXiv*, *0911*(3070), 1-36. https://doi.org/arXiv:0911.3070

Harris, C. M., Martin, S. W., Martin, C., Helble, T. A., Henderson, E. E., Paxton, C. G., & Thomas, L. (2018a, September). *Quantifying behavioral responses of minke whales to sonar activity during Navy training exercises*. Paper presented at the 6th International Meeting on the Effects of Sound in the Ocean on Marine Mammals, The Hague, the Netherlands.

Harris, C. M., Thomas, L., Falcone, E. A., Hildebrand, J., Houser, D., Kvadsheim, P. H., . . . Blanchard, J. (2018b). Marine mammals and sonar: Dose-response studies, the risk-disturbance hypothesis and the role of exposure context. *Journal of Applied Ecology*, *55*(1), 396-404. https://doi.org/10.1111/1365-2664.12955

Heaney, K. D., & Campbell, R. L. (2016). Three-dimensional parabolic equation modeling of mesoscale eddy deflection. *The Journal of the Acoustical Society of America*, *139*(2), 918-926. https://doi.org/10.1121/1.4942112

Henderson, E. E., Helble, T. A., Ierley, G. R., & Martin, S. W. (2018a). Identifying behavioral states and habitat use of acoustically tracked humpback whales in Hawaii. *Marine Mammal Science*, *34*(3), 701-717. https://doi.org/10.1111/mms.12475

Henderson, E. E., Aschettino, J., Deakos, M., Alongi, G., & Leota, T. (2018b). *Satellite tracking of migrating humpback whales in Hawai'i* (TR 3106). Retrieved from https://apps.dtic.mil/dtic/tr/fulltext/u2/1056602.pdf

Herman, L. M., Pack, A. A., Rose, K., Craig, A., Herman, E. Y., Hakala, S., & Milette, A. (2011). Resightings of humpback whales in Hawaiian waters over spans of 10-32 years: Site fidelity, sex ratios, calving rates, female

demographics, and the dynamics of social and behavioral roles of individuals. *Marine Mammal Science*, *27*(4), 736-768. https://doi.org/10.1111/j.1748-7692.2010.00441.x

Højsgaard, S., Halekoh, U., & Yan, J. (2006). The *R* package geepack for generalized estimating equations. *Journal of Statistical Software*, *15*(2), 1-11. https://doi.org/10.18637/jss.v015.i02

Højsgaard, S., Halekoh, U., & Yan, J. (2016). *Generalized Estimating Equation package (Version 1.2-1):* R. Retrieved from https://cran.r-project.org/web/packages/gee

Horton, T. W., Holdaway, R. N., Zerbini, A. N., Hauser, N., Garrigue, C., Andriolo, A., & Clapham, P. (2011). Straight as an arrow: Humpback whales swim constant course tracks during long-distance migrations. *Biology Letters*, *7*(5). https://doi.org/10.1098/rsbl.2011.0279

Horton, T. W., Hauser, N., Zerbini, A. N., Francis, M. P., Domeier, M. L., Andriolo, A., . . . Nasby-Lucas, N. (2017). Route fidelity during marine megafauna migration. *Frontiers in Marine Science*, *4*, 422. https://doi.org/10.3389/fmars.2017.00422

Jeanniard-du-Dot, T., Holland, K., Schorr, G. S., & Vo, D. (2017). Motes enhance data recovery from satellite-relayed biologgers and can facilitate collaborative research into marine habitat utilization. *Animal Biotelemetry*, *5*(1), 17. https://doi.org/10.1186/s40317-017-0132-0

Johnston, D. W., Chapla, M. E., Williams, L. E., & Mattila, D. K. (2007). Identification of humpback whale *Megaptera novaeangliae* wintering habitat in the northwestern Hawaiian Islands using spatial habitat modeling. *Endangered Species Research*, *3*, 249-257. https://doi.org/10.3354/esr00049

Jonsen, I., & Patterson, T. (2019). *Fit continuous-time state-space models for filtering Argos satellite (and other) telemetry data (Version 0.2.1):* R. Retrieved from https://rdrr.io/github/bmcclintock/crwHMM/man/fit_ssm.html

Kennedy, A. S., Zerbini, A. N., Vásquez, O. V., Clapham, P., & Adam, O. (2014). Local and migratory movements of humpback whales (*Megaptera novaeangliae*) satellite-tracked in the North Atlantic Ocean. *Canadian Journal of Zoology*, *92*, 8-17. https://doi.org/10.1139/cjz-2013-0161

Kvadsheim, P. H., DeRuiter, S., Sivle, L. D., Goldbogen, J., Roland-Hansen, R., Miller, P. J. O., . . . Southall, B. L. (2017). Avoidance responses of minke whales to 1-4 kHz naval sonar. *Marine Pollution Bulletin*, *121*(1-2), 60-68. https://doi.org/10.1016/j.marpolbul.2017.05.037

Lagerquist, B. A., Mate, B. R., Ortega-Ortiz, J. G., Winsor, M., & Urbán-Ramirez, J. (2008). Migratory movements and surfacing rates of humpback whales (*Megaptera novaeangliae*) satellite tagged at Socorro Island, Mexico. *Marine Mammal Science*, *24*(4), 815-830. https://doi.org/10.1111/j.1748-7692.2008.00217.x

Lam, F-P. A., Kvadsheim, P. H., Miller, P. J., Tyack, P. L., Ainslie, M. A., Curé, C., . . . Dekeling, R. P. (2016). Controlled sonar exposure experiments on cetaceans in Norwegian waters: Overview of the 3S-project. In A. N. Popper & A. Anthony (Eds.), *The effects of noise on aquatic life II: Advances in experimental medicine and biology* (Vol. 875, pp. 589-598). New York: Springer. https://doi.org/10.1007/978-1-4939-2981-8_711

Lockyer, C. (1984). Review of baleen whale (Mysticeti) reproduction and implications for management. *Report of the International Whaling Commission*, *6*, 27-50.

Luque, S. P. (2007). Diving behavior analysis in *R*. *R News*, *7*, 8-14.

Malme, C. I. Miles, P. R., Clark, C. W., Tyack, P., & Bird, J. E. (1984). *Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whale behavior – Phase II: January 1984 migration* (Report 5851). Prepared by Bolt Beranek & Newman Inc., Anchorage, AK, for U.S. Minerals Management Service.

Manzano-Roth, R., Henderson, E. E., Martin, S. W., Martin, C., & Matsuyama, B. M. (2016). Impacts of U.S. Navy training events on Blainville's beaked whale (*Mesoplodon densirostris*) foraging dives in Hawaiian waters. *Aquatic Mammals*, *42*(4), 507-518. https://doi.org/10.1578/AM.42.4.2016.507

Marschner, I., & Donoghoe, M. W. (2018). *Fitting Generalized Linear Models (Version 1.2.1):* R. Retrieved from https://cran.r-project.org/web/packages/glm2

Martin, S. W., Martin, C. R., Matsuyama, B. M., & Henderson, E. E. (2015). Minke whales (*Balaenoptera acutorostrata*) respond to navy training. *The Journal of the Acoustical Society of America*, *137*(5), 2533-2541. https://doi.org/10.1121/1.4919319

Martin, S. W., Martin, C., Matsuyama, B. M., Alongi, G., Henderson, E. E., Helble, T. A., & Ierley, G. R. (2018). *Baleen whales acoustically derived behaviors with potential responses to U.S. Navy sonar training*. Paper presented at the 6th International Meeting on the Effects of Sound in the Ocean on Marine Mammals, The Hague, the Netherlands.

Mate, B., Gisiner, R., & Mobley, J. (1998). Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. *Canadian Journal of Zoology*, *76*(5), 863-868. https://doi.org/10.1139/z98-008

Mate, B., Palacios, D. M., Baker, C. S., Lagerquist, B., Irvine, L., Follett, T., . . . Winsor, M. (2019). *Humpback whale tagging in support of marine mammal monitoring across multiple Navy training areas in the Pacific Ocean: Final report for the Hawaiian breeding area in Spring 2018, including historical data from previous tagging efforts*. Retrieved from https://www.navy-marinespeciesmonitoring.us/files/1915/5484/0269/Mate_et_al_2018_Humpback_Whale_Tagging_on_US_West_Coast_Summer-Fall_2017.pdf

Miller, P. J. (2012). The severity of behavioral changes observed during experimental exposures of killer (*Orcinus orca*), long-finned pilot (*Globicephala melas*), and sperm (*Physeter macrocephalus*) whales to naval sonar. *Aquatic Mammals*, *38*(4), 362-401. https://doi.org/10.1578/AM.38.4.2012.362

Miller, P. J., Biassoni, N., Samuels, A., & Tyack, P. L. (2000). Whale songs lengthen in response to sonar. *Nature*, *405*(6789), 903. https://doi.org/10.1038/35016148

Miller, P. J., Kvadsheim, P. H., Lam, F-P., Tyack, P. L., Curé, C., DeRuiter, S. L., . . . Hooker, S. K. (2015). First indications that northern bottlenose whales are sensitive to behavioural disturbance from anthropogenic noise. *Royal Society Open Science*, *2*(6), 140484. https://doi.org/10.1098/rsos.140484

Noad, M. J., & Cato, D. H. (2007). Swimming speeds of singing and non-singing humpback whales during migration. *Marine Mammal Science*, *23*(3), 481-495. https://doi.org/10.1111/j.1748-7692.2007.02414.x

Norris, T. F., McDonald, M., & Barlow, J. (1999). Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. *The Journal of the Acoustical Society of America*, *106*(1), 506-514. https://doi.org/10.1121/1.427071

Pack, A. A., Herman, L. M., Craig, A. S., Spitz, S. S., Waterman, J. O., Herman, E. Y., . . . Lowe, C. (2018). Comparing depth and seabed terrain preferences of individually identified female humpback whales (*Megaptera novaeangliae*), with and without calf, off Maui, Hawaii. *Marine Mammal Science*, *34*(4), 1097-1110. https://doi.org/10.1111/mms.12495

Richlen, M., Davis, M., Cooper, M., & Brown, B. (2017). *COMPASS – A survey toolkit for marine species data collection: Annual progress report*. Retrieved from https://www.navymarinespeciesmonitoring.us/files/9115/3081/8282/Richlen_et_al._2018_-_COMPASS_2017_-_Final.pdf

Robertson, F. C. (2014). *Effects of seismic operations on bowhead whale behavior: Implications for distribution and abundance assessments* (Unpublished doctoral dissertation). The University of British Columbia, Vancouver, BC. Retrieved from UBC Theses and Dissertations.

Robertson, F. C., Koski, W. R., Thomas, T. A., Richardson, W. J., Würsig, B., & Trites, A. W. (2013). Seismic operations have variable effects on dive-cycle behavior of bowhead whales in the Beaufort Sea. *Endangered Species Research*, *21*(2), 143-160. https://doi.org/10.3354/esr00515

Scales, K. L., Schorr, G. S., Hazen, E. L., Bograd, S. J., Miller, P. I., Andrews, R. D., . . . Falcone, E. A. (2017). Should I stay or should I go? Modelling year-round habitat suitability and drivers of residency for fin whales in the California current. *Diversity and Distributions*, *23*(10), 1204-1215. https://doi.org/10.1111/ddi.12611

Schick, R. S., Bowers, M., DeRuiter, S., Friedlaender, A., Joseph, J., Margolina, T., . . . Southall, B. L. (2019). Accounting for positional uncertainty when modeling received levels for tagged cetaceans exposed to sonar. *Aquatic Mammals*, *45*(6), 675-690. https://doi.org/10.1578/AM.45.6.2019.675

Sivle, L. D., Kvadsheim, P. H., Curé, C., Isojunno, S., Wensveen, P. J., Lam, F-P. A., . . . Miller, P. J. O. (2015). Severity of expert-identified behavioural responses of humpback whale, minke whale, and northern bottlenose whale to naval sonar. *Aquatic Mammals*, *41*(4), 469-502. https://doi.org/10.1578/AM.41.4.2015.469

Sivle, L. D., Wensveen, P. J., Kvadsheim, P. H., Lam, F-P. A., Visser, F., Curé, C., . . . Miller, P. J. O. (2016). Naval sonar disrupts foraging in humpback whales. *Marine Ecology Progress Series*, *562*, 211-220. https://doi.org/10.3354/meps11969

Southall, B. L., Nowacek, D. P., Miller, P. J. O., & Tyack, P. L. (2016). Experimental field studies to measure behavioral responses of cetaceans to sonar. *Endangered Species Research*, *31*, 293-315. https://doi.org/10.3354/esr00764

Southall, B. L., Moretti, D., Abraham, B., Calambokidis, J., DeRuiter, S., & Tyack, P. (2012). Marine mammal behavioral response studies in southern California: Advances in technology and experimental methods. *Marine Technology Society Journal*, *46*(4), 48-59. https://doi.org/10.4031/MTSJ.46.4.1

Stimpert, A. K., DeRuiter, S. L., Southall, B. L., Moretti, D. J., Falcone, E. A., Goldbogen, J. A., . . . Calambokidis, J. (2014). Acoustic and foraging behavior of a Baird's beaked whale, *Berardius bairdii*, exposed to simulated sonar. *Scientific Reports*, *4*, 7031. https://doi.org/10.1038/srep07031

Tyack, P., & Whitehead, H. (1982). Male competition in large groups of wintering humpback whales. *Behaviour*, *83*(1), 132-154. https://doi.org/10.1163/156853982X00067

U.S. Department of the Navy. (2011). *Pacific Missile Range Facility (PMRF) cultural landscape* (Final Report). Prepared for Commander Navy Region Hawaii by TEC Inc. – Joint Venture. Retrieved from https://www.cnic.navy.mil/regions/cnrh/installations/pacific_missile_range_facility_barking_sands/about/history

U.S. Department of the Navy. (2017). *Criteria and thresholds for U.S. Navy acoustic and explosive effects analysis (Phase III)*. San Diego, CA: Space and Naval Warfare System Command, Pacific.

Vu, E. T., Clark, C., Catelani, K., Kellar, N. M., & Calambokidis, J. (2015). Seasonal blubber testosterone concentrations of male humpback whales (*Megaptera novaeangliae*). *Marine Mammal Science*, *31*(3), 1258-1264. https://doi.org/10.1111/mms.12191

Wensveen, P. J., Isojunno, S., Hansen, R. R., von Benda-Beckmann, A. M., Kleivane, L., van IJsselmuide, S., . . . Curé, C. (2019). Northern bottlenose whales in a pristine environment respond strongly to close and distant Navy sonar signals. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1899), 20182592. https://doi.org/10.1098/rspb.2018.2592

Wensveen, P. J., Kvadsheim, P. H., Lam, F-P. A., von Benda-Beckmann, A. M., Sivle, L. D., Visser, F., . . . Miller, P. J. O. (2017). Lack of behavioural responses of humpback whales (*Megaptera novaeangliae*) indicate limited effectiveness of sonar mitigation. *Journal of Experimental Biology*, *220*, 1-12. https://doi.org/10.1242/jeb.161232