

Habitat preferences by individual humpback whale mothers in the Hawaiian breeding grounds vary with the age and size of their calves

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We investigated whether calf age and calf size influence habitat choice by humpback whale mother–calf pairs in their breeding grounds. During 1997–2008, we conducted focal follows of mother–calf pairs in Hawaiian waters. Tail-fluke identification photographs and calf lengths (measured through videogrammetry) were obtained. Water depth and sea-bed terrain type were derived from GPS data. Identification photographs were matched so that the habitat choices could be established within breeding seasons. Across 72 mother–calf pairs resighted over various intervals within a breeding season, magnitude of depth change between initial and final sightings increased significantly with resighting interval. There was a significant increase from initial depth to final depth for relatively long resighting intervals (27–51 days), but no significant difference for relatively short resighting intervals (2–26 days). Although there was no preference for sea-bed terrain type by mother–calf pairs at their initial sighting, there was a preference for rugged terrain at their final resighting. A resource selection model indicated that the relative probability of a location being used by a mother–calf pair increased (as a function of water depth and rugged sea-bed terrain type) from initial to final sighting; a finding supported by subsequent tests of habitat preference versus availability. For 96 measured calves, calf length and water depth were positively correlated, even when ordinal day of measurement was controlled for statistically; a finding confirmed by a general linear model that simultaneously investigated the relationship between water depth, sea-bed terrain type, number of escorts, ordinal day and calf size. Thus, both calf age and size influence habitat choice by mother–calf pairs in their breeding grounds. The movement of mothers and their maturing calves into deeper waters where they favour rugged sea-bed terrain appears to be part of a suite of behavioural changes during the pre-migratory phase of residency in the breeding grounds.

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In a variety of species in which newborns remain dependent on their mothers beyond parturition, females with offspring often segregate themselves into habitats that are different from those used by females without offspring (e.g. Ciuti, Bongi, Vassale, & Apollonio, 2006; Craig, Herman, Pack, & Waterman, 2014; Lent, 1974; Walker, Parker, & Gillingham, 2006; Wolf, Kauermann, & Trillmich, 2005). For mammals, such segregation may be motivated by predator avoidance (e.g. Ciuti et al., 2006; Main, Weckerly, & Bleich, 1996; Pinard, Dussault, Ouellet, Fortin, & Courtois, 2012; Rachlow & Bowyer, 1998; Walker et al., 2006), access to better food resources (including fresh water for land-dwelling mammals) (Rachlow & Bowyer, 1998), limitations in offspring mobility and activity budgets (Grignolio, Rossi, Bertolotto, Bassano, & Apollonio, 2007), avoidance of harassment by males prospecting for mating opportunities (e.g. Craig et al., 2014; Wolf et al., 2005), or promotion of mother-offspring bonding (Lent, 1974; Mann & Smuts, 1998; Ozoga, Verme, & Bienz, 1982; Schwede, Hendrichs, & McShea, 1993). In some cases, two or more of these factors may exert conflicting pressures. For example, females with recent offspring may relocate to habitats that reduce predation risk to offspring but are also of low productivity, thus compromising their energy intake (e.g. Ciuti et al., 2006). A female's habitat use may also change in relation to her recent offspring's growth, maturation and behaviour as well as her own need to replenish resources or seek mates (e.g. Bon, Joachim, & Maublanc, 1995; Costelloe & Rubenstein, 2015; Grignolio et al., 2007; Jones & Swartz, 1984; Thomas & Taber, 1984). Here, we investigate changes in the habitat use of individually identified humpback whale, *Megaptera novaeangliae*, mothers as a function of the relative age and size of their calves.

Humpback whales are a migratory species with distinct areas for feeding and breeding typically separated by thousands of kilometres (Baker et al., 1986; Chittleborough, 1965; Dawbin, 1966; Katona & Beard, 1990). In summer months, the whales inhabit high-latitude productive waters where they feed on krill and small schooling fish. During winter and spring months, humpbacks of both sexes and all age classes inhabit lower-latitude tropical waters where they calve (females on average produce a single calf every 2–3 years; Baker, Perry, & Herman, 1987; Barlow & Clapham, 1997), rear young and perform behaviours related to mating (summarized in Clapham, 1996, 2000). In these so-called breeding grounds,

feeding (other than by nursing calves) is suspended (Chittleborough, 1965).

A humpback whale calf's habitat use is inextricably linked to that of its mother while in the breeding grounds during its first months of life. As in some ungulate and marsupial (macropod) species, humpback whale offspring exhibit a 'following' (versus a 'hiding') strategy (Fisher, Blomberg, & Owens, 2002; Lent, 1974), typically remaining within 50 m of their mothers during both travel and resting periods (Cartwright & Sullivan, 2009a; Szabo & Duffus, 2008). Of the factors favoured by Fisher et al. (2002) in the evolution of a following strategy in ungulates and macropods, the one that appears most applicable to humpback whales is raising young in an open habitat where hiding is less favoured because of increased predation as well as harassment from conspecifics. Fisher et al. (2002) also promoted the hypothesis that a following strategy is typically associated with delayed weaning because following offspring expend more energy on movement than hiding/sedentary offspring. Humpback whale calves are reared in the open ocean, and weaning occurs after a lactation period of approximately 10.5 months (Chittleborough, 1958). In addition to reducing predation and harassment pressure, following among humpback calves may have evolved to promote the development of muscular myoglobin stores, which are extremely low in neonates but increase significantly by the start of migration to the feeding grounds because following requires more energy than hiding (Cartwright et al., 2016). Muscular myoglobin is important in a humpback's ability to perform the extended aerobic dives typically employed during foraging behaviour and other activities (Kooyman & Ponganis, 1998; Ponganis, 2011; Snyder, 1983).

It has been well established in several populations of humpback whales that mother–calf pairs favour shallow water habitats in the breeding grounds (Betancourt, Herrera-Moreno, & Beddall, 2015; Craig et al., 2014; Ersts & Rosenbaum, 2003; Felix & Botero-Acosta, 2011; Guidino, Llapapasca, Silva, Alcorta, & Pacheco, 2014; Herman & Antinoja, 1977; Smultea, 1994). For example, shore-based observations of humpback whales off Hawaii Island by Smultea (1994) revealed that pods containing a calf occupied waters that were significantly shallower than pods without a calf. Smultea (1994) suggested several potential reasons for the segregation of mother–calf pairs into shallow waters, including avoidance of harassment by sexually active males, avoidance of turbulent waters and avoidance of predators (e.g.

killer whales, *Orcinus orca*, and tiger sharks, *Galeocerdo cuvier*). Recently, Craig et al. (2014) presented substantial evidence to support the harassment avoidance hypothesis, using shore-based theodolite tracking of humpback whales off the west coast of Maui, Hawaii. In addition to demonstrating a significant shallow water preference by pods containing a calf, as compared to noncalf pods, Craig et al. (2014) showed that mother–calf pairs without a male escort occupied significantly shallower waters than those containing one or more male escorts, that the number of males escorting a mother–calf pair decreased progressively with decreasing water depth and that speed of travel (and thus energy expenditure) increased as the number of male escorts increased. Craig et al. (2014) were able to discount predator avoidance and access to sheltered waters as potential explanations for their results; instead they concluded that mothers seek shallow waters to avoid the costs of male harassment.

Sea-bed terrain has also been investigated as a potential factor influencing habitat preferences of humpback whale mother–calf pairs in the breeding grounds. Cartwright et al. (2012) conducted boat-based transect surveys off the west coast of Maui and reported a preference by mother–calf pairs for waters associated with rugged sea-bed terrain rather than flat sea-bed terrain. They attributed this to a generalized preference of mothers for shallow water habitats, noting that the rugged terrain in their study area, composed of ridges of drowned karst reef, tended to be slightly shallower than flat terrain, which was composed of sandy basins (Grigg et al., 2002). However, because the surveys conducted by Cartwright et al. (2012) all took place in March, which is relatively late in the breeding season (Baker & Herman, 1981; Mobley, Bauer, & Herman, 1999), it is possible that many of the calves in the survey sample were beyond the neonate stage. Thus, the findings by Cartwright et al. (2012) may largely reflect habitat preferences of mothers with older calves.

Despite advances in the understanding of some of the factors associated with habitat preferences by humpback whale mother–calf pairs in the breeding grounds, the potential influences of calf age and calf size have not been considered. This is because longitudinal data from individually identified humpback whale mother–calf pairs over the course of the breeding season have rarely been examined with respect to habitat use (Craig & Herman, 2000). In this paper we investigated how individually

identified humpback whale mothers in the breeding grounds vary their habitat use in relation to the relative age and size of their calves.

To investigate the influence of calf age on habitat selection, we examined whether there were any significant changes in habitat use by individual mother–calf pairs resighted over varying periods of time within a breeding season. To the extent that a resighting of a mother–calf pair within a breeding season reflects the presence of an older calf (compared to an initial sighting), this analysis allowed us to investigate whether habitat use by a humpback whale mother–calf pair changes as the calf within this pair ages. In later stages of calf development, grey whale, *Eschrichtius robustus*, mother–calf pairs relocate into deeper water habitats, with some travelling outside of breeding lagoons (Jones & Swartz, 1984; Mate, Lagerquist, & Urban-Ramirez, 2003; Swartz, 1986). Based on this finding in another mysticete species, we hypothesized that calf age affects the ocean depth used by mother–calf pairs. We predicted that as the time interval between the initial and final sightings of a mother–calf pair increases (reflecting a calf of increasing age), the magnitude of depth change between initial and final sightings would also increase. As a corollary to this hypothesis, we predicted that the probability of mother–calf pairs being located in deeper water would increase from the initial to final sighting.

We next tested for significant changes in association with rough sea-bed terrain as calves aged. Cartwright et al.’s (2012) finding of a preference by humpback whale mother–calf pairs for rugged sea-bed terrain during surveys conducted relatively late in the breeding season suggests that such a preference may largely be reflective of mothers with older calves. Based on this suggestion, we hypothesized that mother–calf pairs would favour rugged sea-bed terrain (relative to its availability) more at their final sighting (i.e. when the calves within these pairs were older) than at their initial sighting, and that the probability of mother–calf pairs being located over rugged sea-bed terrain would increase from the initial to final sighting.

Finally, we measured the body lengths of individually identified calves and determined the water depth and sea-bed terrain type of their location with their mothers. In accordance with our first two hypotheses regarding older versus younger calves, we predicted that larger calves would be located in

deeper waters than smaller calves and that larger calves would be more strongly associated with rugged (as opposed to flat) sea-bed terrain.

Collectively, these hypotheses address two key questions related to humpback whale mother–calf pair habitat use in the breeding grounds: as calves age and grow, do mother–calf pairs favour deeper waters and do they also favour rugged sea-bed terrain?

## METHODS

### *Study Area and Dates*

We studied North Pacific humpback whales in their Hawaiian breeding grounds in the Au’au, Kalohi and Pailolo channels (Fig. 1), an area known to contain the largest coastally based concentrations of humpbacks in Hawaii and a preferred habitat for mother–calf pairs (Craig & Herman, 2000; Herman, Forestell, & Antinoja, 1980; Mobley et al., 1999). Data collection took place on 929 days across 12 consecutive breeding seasons during 1997–2008 (Table 1), typically from late December to mid-April to cover the periods when the majority of humpbacks assume temporary residence in Hawaii’s waters (Baker & Herman, 1981; Mobley et al., 1999).

### *Procedure*

Using one or two small (<8 m) outboard boats launched from Lahaina harbour or occasionally from a nearby launch ramp, we searched for and approached humpback whales on a daily or near-daily schedule, weather and sea state permitting. After the research boat cleared all moored boats outside of the harbour or launch ramp, each member of the crew scanned a different 90° sector of water for sightings of a whale or the ‘blow’ from a whale. If none was sighted, the captain attempted to select a heading that was different from their prior survey, sea state permitting. Search effort was continuous throughout the

day from approximately 0830 hours to 1700 hours. Whales were approached for close observation as they were sighted, without bias towards any particular type of group or any particular area. If no whales were sighted by the time the boat either reached the edge of the study area or encountered a heavy wind line, the captain changed heading and the crew continued its search efforts.

When the research boat was within approximately 20 m of a sighted pod, an initial GPS location was recorded using either a Garmin GPS Map 172 or 172C. A focal follow of the pod then proceeded until all obtainable data (see below) were collected. As individual whales dived or otherwise exposed the ventral surface and trailing edges of their tail flukes, identification images of the unique patterns of these flukes (Katona et al., 1979) were obtained using 35 mm cameras equipped with 300 mm lenses. Tail fluke images of individuals were associated with their social or behavioural roles (e.g. unescorted mother–calf pair, mother–calf pair escorted by one or more males, female without calf in a competitive group of males, female without calf in a male–female dyad; see Herman et al. (2011) for a detailed description of pod types). For each mother–calf pair, the number of male escorts present when the pod was first sighted and any changes in the number of escorts during the focal follow were recorded with a time stamp.

Calf body length was used as a proxy for calf maturity and was measured using an underwater videogrammetric technique (Spitz, Herman, & Pack, 2000; see section below on data processing and analysis for details on the procedure by which calves were measured). During focal follows, if a mother–calf pair was stationary, milling or slow moving, a snorkeller equipped with a Sony DCR-TRV-7 digital video camera in a Jay-Mar VM-6000 underwater housing, as well as a 200–400 kHz hand-held sonar device (Speedtech Depthmate) was deployed and began filming the pod. When the calf's position was perpendicular to the longitudinal axis of the video camera (set to its maximum field of view), the snorkeller measured the distance from the camera to the calf using the sonar device. The exact moment of the distance measurement was recorded on the audio track of the video recording as a distinct click sound made when the sonar device was activated. The measured distance appeared on a screen on the sonar device that was then held in front of the camera as a permanent record of the distance measured at the click sound. Data for additional independent length measurements of a calf were collected when it moved

or swam off and the snorkeller repositioned himself/herself after relocating the calf, or when the snorkeller moved relative to a stationary calf. For each calf measured, the mean of its independent measurements was used to represent its final length.

Once it was determined that all potential data had been collected, the focal follow ended. A final GPS location of the pod was obtained and the boat moved quietly away from the pod in search of a new pod to survey.

#### *Ethical Note*

We conducted this research under National Marine Fisheries Service Permits 941, 707 and 107, and annual State of Hawaii Scientific Permits. The research was approved under University of Hawaii Institutional Animal Care and Use Committee protocols 93-052 through 93-052-9 as well as 99-002.

#### *Data Processing and Analyses*

##### *Determining depth and bottom terrain type from GPS location data*

We constructed a geographic information system (GIS) model of the study area using ArcGIS 10.3.1 (Environmental Systems Research Institute, Redlands, CA, U.S.A.). Coastline data from the Hawaii Statewide GIS Program (<http://planning.hawaii.gov/gis/download-gis-data/>) were incorporated as a vector layer, and depth data from the Main Hawaiian Islands Multibeam Bathymetry Synthesis website (<http://www.soest.hawaii.edu/HMRG/multibeam/bathymetry.php>) were incorporated as a 50 m bathymetric grid. We plotted the GPS coordinates at the start of each focal follow and used the Spatial Analyst tool ‘Extract’ - ‘Extract Values to Points’ to derive the depth of each pod, which we then appended to each positional record.

Following Cartwright et al. (2012), we used NOAA’s Benthic Terrain Modeler (BTM) (Wright et al., 2012) to prepare a detailed benthic terrain map. The BTM allows the user to create grids of

bathymetric position index (BPI), slope and depth that are combined to generate maps of geomorphological features such as slopes, depressions, crests and flats. Central to the process is the concept of bathymetric position: BPI is a second-order derivative of the surface that defines the elevation of locations relative to those that surround it. The BPI algorithm compares each cell's elevation to the mean elevation of the surrounding cells within a user-defined rectangle, annulus or circle. The BTM relies on the creation and combination of both a fine-scale and a broad-scale BPI; with a fine-scale factor, subtle localized topographic features are detected, whereas the use of a broad-scale factor results in the detection of broad-scale topographic features. Cells that are lower than their neighbours are assigned negative BPI values (depressions); higher cells are assigned positive values (crests), and constant slopes (slopes that are  $>5^\circ$ ) or flat areas (slopes that are  $\leq 5^\circ$ ) are assigned zero BPI values; larger numbers represent features that differ more dramatically from surrounding areas. We classified these BPI values using a template/dictionary designed originally by Lundblad et al. (2006) for use around American Samoa (an area whose benthic topography closely resembles that of the study area: an archipelago of mostly submerged volcanoes with a shoreline flanked by reefs that drop off into deep water). Zones were identified as crests, depressions, flats or slopes. Areas of complex terrain (i.e. crests, depressions and slopes) were enclosed within a 100 m buffer (to incorporate transitional areas) and described as 'rugged'; areas outside the buffer were described as 'flat'. As with Cartwright et al. (2012), the classification of rugged and flat terrain closely matched that described in detail by Grigg et al. (2002) as drowned karst (an irregular terrain formed from the dissolution of soluble rocks such as limestone) and sandy submerged basins, respectively. Once the areas were categorized as either rugged or flat, we used the Analysis tool 'Overlay – Spatial Join' to append a rugged/flat value to each pod based on the GPS location at the start of the focal follow.

#### *Determining individual resightings from tail fluke identification photographs*

We printed the clearest photograph of each whale's tail flukes and assigned it a unique observation number as well as a 'colour' category based on the approximate percentage of white in the

ventral portion of its tail flukes as judged by eye (0%, 25%, 50%, 75%, 100%). We then compared the photograph of each mother to all other photographs within the same and adjacent colour categories taken within the same breeding season to determine the number of within-season matches present. For every match, we recorded the date of the resighting along with the presence or absence of a calf, the number of escorts present and the GPS location at the start of the focal follow. Any sightings of a mother accompanied by both a calf and a yearling in the same breeding season ( $N = 1$ ) were omitted. Once within-season matching was accomplished, we matched resighted mothers against each other to identify whether any of these mothers had been resighted within-season in two or more different years. We conducted a correlation analysis on the differences in depth from initial to final sighting for mothers that had within-season resightings in two or more years to determine whether these should be considered as independent observations.

#### *Examining how depth differences from initial to final sighting relate to calf age*

For each mother–calf pair for which GPS data were available for both the initial sighting and the final sighting, we derived depth using a GIS for each sighting and calculated the resighting interval (i.e. number of days from initial sighting to final sighting). We then examined the relationship between the magnitude of the difference in depth from the initial to final sighting (i.e. the depth at the final sighting minus the depth at the initial sighting) and the resighting interval (a proxy for calf age). Following this, we split the maximum resighting interval so that depth at the initial and final sightings could be compared for relatively short (2–26 days) and relatively long (27–51 days) resighting intervals. Finally, because Craig et al. (2014) found a positive relationship between the water depth at which mother–calf pairs were found and the number of escorts in their company, for each mother–calf pair we found in deeper water at their final resighting, we compared the number of escorts at both sightings to examine whether there was any skew towards an increased number of escorts at the final sighting compared to the initial sighting.

### *Modelling habitat preferences at initial and final sightings*

We used logistic regression to estimate a resource selection function (RSF) by comparing the environmental characteristics (depth and sea-bed terrain type) of used locations to those of available locations for each mother–calf pair, while controlling for number of escorts, ordinal day and resighting interval. We investigated how those characteristics related specifically to the relative probability of use at initial versus final sighting. We generated 1000 random locations per used location (within the minimum convex polygon encompassing all used locations) using a GIS; this encompassed the full study area, excluding any terrestrial land within the polygon boundary. We used a generalized linear mixed model (GLMM) with binary response variable (1 = used, 0 = available), binomial error distribution and logit link to compare habitat selection at initial and final sightings. We included a random intercept for each mother–calf pair to account for the nonindependence associated with repeated sampling of the same units. The RSF model was fitted using the ‘glmer’ command of the ‘lme4’ package (Bates, 2010) within the R platform (Version 3.3.2) (R Core Team, 2015) and estimated using Laplace approximation as recommended by Bolker et al. (2009). Models were checked visually for evidence of collinearity between predictors by plotting all continuous variables against each other; no collinearity problems were observed. We assessed the significance of the full RSF model by comparison to a corresponding null model (i.e. an intercept-only model with no independent variables) using a likelihood ratio test (LRT) ('anova' function in the 'stats' package; R Core Team, 2015) with test set to 'Chisq' (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We determined the significance of the individual fixed effects (independent variables) based on the Wald  $z$  statistics and  $P$  values provided by 'glmer'. All statistical tests were two tailed with  $\alpha$  set to 0.05.

Visual inspection of residual plots did not reveal any obvious violations of model assumptions. In addition to the LRT, which evaluated how well the model fit our data, we also evaluated the model's predictive accuracy. This was carried out using  $k$ -fold cross-validation, testing predictive performance using area under the curve (AUC) (Boyce, Vernier, Nielsen, & Schmiegelow, 2002). This procedure partitions the original data set into  $k$  bins and performs  $k$  iterations of training and validation in which a different bin is held out each time for validation while the remaining  $k - 1$  bins are used to train the model.

As recommended by Boyce et al. (2002), we used 10 folds ( $k = 10$ ) to evaluate the predictive performance of the RSF model. The AUC of a receiver operating characteristic (ROC) curve represents the relative proportions of correctly and incorrectly classified predictions over a range of threshold levels by plotting true positives versus false positives for a binary classifier system. As defined by Swets (1988), models can be classed as follows: (1) noninformative ( $AUC=0.5$ ); (2) less accurate ( $0.5 < AUC \leq 0.7$ ); (3) moderately accurate ( $0.7 < AUC \leq 0.9$ ); (4) highly accurate ( $0.9 < AUC < 1$ ); and (5) perfect ( $AUC=1$ ).

#### *Determining preferred habitat relative to available habitat*

To examine whether statistically significant differences in use of depth and sea-bed terrain type reflected actual habitat preferences, and were not simply artefacts of habitat availability, we employed an approach similar to that used by Cartwright et al. (2012) and Guidino et al. (2014). We subdivided the study area for analysis according to depth and sea-bed terrain type. Sea-bed terrain type was categorized as either rugged or flat, and depth was categorized as follows: <20 m, 20–39.99 m, 40–59.99 m, 60–79.99 m, >80 m. Using Neu's method for the analysis of utilization–availability data (Neu, Byers, & Peek, 1974), we compared levels of habitat use to the proportional availability of each habitat type. Where disproportionate habitat use was identified, Bonferroni-corrected 95% confidence intervals were constructed around observed use estimates and compared to expected use estimates in order to identify which habitat types were used disproportionately to their availability (i.e. which habitat types were responsible for the statistical significance in the chi-square statistic). This allowed the designation of habitat as either avoided (95% confidence interval of the observed proportion of sightings in each habitat type was entirely below the expected proportion of sightings), preferred (95% confidence interval of the observed proportion of sightings in each habitat type was entirely above the expected proportion of sightings), or neutral (95% confidence interval for the observed sightings contained the expected proportion). Lastly, we calculated Neu's standardized selection indices to provide standardized estimates of habitat use based on habitat availability. These values sum to 1.0 within each analysis and can be used to compare the strength of selection between habitat categories. A single chi-square test was sufficient to

examine depth preferences, however, in order to rule out the possibility that any observed sea-bed terrain type preference was merely an artefact of an association between sea-bed terrain type and depth, we used separate chi-square tests to assess sea-bed terrain type preference within each preferred depth range.

### *Measuring calf length*

Digital images from video recordings of each calf were captured along with their respective sonar distance measurements on an Apple computer using either Adobe Photoshop or Adobe OnLocation software. An image suitable for measurement required the calf's body to be positioned horizontally in the  $X$ - $Y$  plane (and not angled into the  $Z$  plane), and the tip of the rostrum and tail fluke notch to be clearly visible. All suitable images were measured with Adobe Photoshop software using standard photogrammetric principles as described in Spitz et al. (2000). Each suitable image of a calf was displayed on the computer screen. The distance from the camera to the whale measured by the sonar device at the moment that image was captured, and the calibrated angle of view of the video camera lens at a fixed focal length (the widest angle of the camera lens was used throughout) allowed for the calculation in metres of the field of view of the camera at the measured distance. The field of view filled the horizontal dimension of the software window (720 pixels). The  $X$ - $Y$  coordinates of the tip of the rostrum and the fluke notch were measured in pixels, and calf image length ( $L_i$ ) was calculated in pixels using the formula  $((X_1 - X_2)^2 + (Y_1 - Y_2)^2)^{1/2}$ . The calf's true length in metres was then expressed as  $(F \times L_i)/720$ , where  $F$  is the field of view of the camera at the sonar-measured distance (in metres).

Validation of the accuracy and precision of the videogrammetric technique was provided by Spitz et al. (2000) using objects of known length, including a 6.10 m pipe, which approximates the length of an older but not yet weaned calf (Clapham, Wetmore, Smith, & Mead, 1999). The differences between the measured mean lengths at three distances and the true pipe length were consistently small (i.e.  $\leq 6$  cm), and length measurements had high precision ( $\leq 1.5\%$  variation) (Spitz et al., 2000). This videogrammetric technique has been used previously to measure the body lengths of humpback whale calves (Pack et al., 2009), as well as noncalves in various behavioural roles (Herman et al., 2013; Pack et al., 2009, 2012;

Spitz, Herman, Pack, & Deakos, 2002).

#### *Examining how calf size relates to water depth and sea-bed terrain type*

For each calf measured, we calculated the ordinal day of measurement and derived both water depth and sea-bed terrain type at the start location of the focal pod using a GIS (see above). We then conducted correlation analyses to examine the relationship between calf length and water depth, between calf length and ordinal day, between ordinal day and water depth, as well as between calf length and water depth when ordinal day was partialled out. Calf length was also correlated against number of escorts and sea-bed terrain type. Following this, we used a general linear model (GLM) with calf size as the response variable, Gaussian error distribution and identity link to simultaneously investigate the relationship between calf size, water depth, terrain type, number of escorts and ordinal day. We assessed the significance of the fixed effects by comparing the full model against models without each effect, using likelihood ratio chi-square tests ('Anova' function in the 'car' package (Fox & Weisberg, 2011). All statistical tests were two tailed with  $\alpha$  set to 0.05.

#### *Data organization and statistical analysis tools*

We organized all data into Filemaker Pro databases and Microsoft Excel spreadsheets, and analysed the data using SPSS 22 (IBM, Armonk, NY, U.S.A.), SAS 9.13 (SAS Institute Inc., Cary, NC, U.S.A.) or R 3.3.2 (R Foundation for Statistical Computing, Vienna, Austria). Since depth data were not normally distributed, we computed medians and interquartile ranges (IQR) and conducted nonparametric analyses (excepting the GLMM analysis). Chi-square tests with  $df=1$  were performed with Yates' correction for continuity.

## **RESULTS**

Across all breeding seasons, data were collected on a total of 1846 pods with a calf and 2959

pods without a calf (Table 1). The area encompassing GPS locations of these pods was approximately 1408.22 km<sup>2</sup> and extended from <20 m depth to >400 m (Fig. 1). To identify any bias in sampling towards particular portions of the study area, we generated kernel density estimates for (1) all of the whale sightings collected in the course of the study and (2) the first whale sightings of each day. A comparison of these density estimates indicated that the first whale sightings of each day were wholly representative of the distribution of all whale sightings, i.e. they were not biased towards any particular portion of the study area (from which the day's search may have begun). The duration of focal follows varied depending on several factors including pod type and the type of data collected. For mother–calf pods in which both tail fluke identification images and calf size were obtained ( $N = 96$ ), median focal follow duration was 68.04 min (IQR = 44.54 min).

#### *Preferences of Water Depth and Sea-bed Terrain Type in Relation to Relative Calf Age*

Seventy-nine mothers were resighted with their calf one or more times within a breeding season. For 72 of these mother–calf pairs, a GPS location from which depth could be derived was recorded at the start of a focal follow for both the initial and final sightings. The 72 mother–calf pairs represented 58 mothers that were resighted within a single breeding season and seven mothers that were resighted within two different breeding seasons (i.e. with a different calf in each). For the latter, the minimum and maximum across-season resighting intervals (i.e. including the first and final year sighted) were respectively 3 years and 12 years (median = 9 years, IQR = 3 years). These across-season resightings of individual mothers with different calves were considered to be independent observations because comparison of the data on the difference in depth from initial to final sighting obtained from each mother showed no significant correlation between the sightings featuring the first versus second calf (Spearman rank-order correlation:  $r_s = 0.036$ ,  $N = 7$ ,  $P = 0.939$ ). Therefore, we considered the total sample size of 72 mother–calf pairs to be independent. The time interval (resighting interval) from the initial to the final sighting for these mother–calf pairs ranged from 2 to 51 days, and the area encompassing their GPS

locations was approximately 246.42 km<sup>2</sup>. Excluding areas for which no depth data were available (3.94 km<sup>2</sup>), depth ranged from <20 m to 171 m and the area of rugged sea-bed terrain was approximately 85.31 km<sup>2</sup> or 34.62% of the total study area.

As predicted, there was a significant positive linear relationship between a mother–calf pair’s resighting interval (median resighting interval = 14.00 days, IQR = 13.50 days,  $N = 72$ ), and the magnitude of difference in water depth from their initial to final sighting (median difference in water depth = 3.31 m, IQR = 21.37 m,  $N = 72$ ) (Spearman rank-order correlation:  $r_s = 0.36$ ,  $N = 72$ ,  $P = 0.002$ ) (Fig. 2). Also, there was a significant increase from initial water depth (median water depth = 55.27 m, IQR = 29.67 m) to final water depth (median water depth = 67.37 m, IQR = 17.04 m) for relatively long resighting intervals (27–51 days) (Wilcoxon signed-ranks test:  $Z = -2.353$ ,  $N = 12$ ,  $P = 0.019$ ), but no significant difference between initial water depth (median water depth = 67.79 m, IQR = 23.85 m) and final water depth (median water depth = 64.03 m, IQR = 19.73 m) for relatively short resighting intervals (2–26 days) (Wilcoxon signed-ranks test:  $Z = -0.611$ ,  $N = 60$ ,  $P = 0.541$ ). However, the median ordinal day at initial sighting for relatively short resighting intervals (median ordinal day = 66 days, IQR = 35.5 days) was significantly later in the breeding season than for relatively long resighting intervals (median ordinal day = 34.5 days, IQR = 22.25 days) (Mann–Whitney  $U$  test:  $Z = -3.416$ ,  $N = 72$ ,  $P = 0.001$ ). Overall, both of these analyses indicate that as a mother’s calf aged, there was a tendency for her and her calf to be found in deeper water. These findings cannot be explained by a positive association between water depth and the number of escorts in association with a mother–calf pair, as was found in Craig et al. (2014). Of the 72 resighted mother–calf pairs, 44 were found in deeper water at their final sighting, 16 with fewer escorts than at their initial sighting, 18 with the same number of escorts and 10 with a greater number of escorts. These mother–calf pods showed no significant skew towards an increased number of escorts at final as compared to initial sighting (Pearson chi-square test:  $\chi^2_2 = 2.36$ ,  $P = 0.307$ ). Therefore, the number of escorts did not have a confounding effect on the results we report here.

### *Mother–Calf Resource Selection Model*

We used the relationship between mother–calf locations, sighting (initial versus final), water depth and sea-bed terrain type to create a resource selection function; number of escorts, ordinal day and resighting interval were all held constant during model estimation. The results of this model relate the relative probability of a location being used to the environmental characteristics present there. The final model predicted mother–calf occurrence significantly better than the null model (likelihood ratio test set to chi-square:  $\chi^2_{10} = 22.519$ ,  $P = 0.013$ ) and returned a validation score (AUC of ROC curve) of 0.59, suggesting that caution be taken when generalizing these findings to other breeding grounds and/or populations, especially those with depth and sea-bed terrain characteristics that differ significantly from those in our study area.

There was a significant interaction between water depth and sighting (Wald  $z$  test:  $z = 2.866$ ,  $P = 0.004$ ) (for full model results see Appendix, Table A1), indicating that the probability of a location being used by a mother–calf pair (as a function of water depth) changed significantly between the initial and final sightings. At initial sighting the probability of use declined with depth (i.e. shallow waters were ‘preferred’), while at final sighting the probability of use increased with depth. There was also a significant interaction between sea-bed terrain type and sighting (Wald  $z$  test:  $z = 1.965$ ,  $P = 0.049$ ), indicating that the probability of a location being used by a mother–calf pair (as a function of sea-bed terrain type) also changed significantly between initial and final sightings. At initial sighting the probability of use was largely unrelated to terrain type, however, at final sighting the probability of use increased dramatically in association with rugged sea-bed terrain. No significant effects were observed for the control variables; number of escorts, ordinal day or resighting interval (see Appendix, Table A1).

### *Neu’s Test for Habitat Preferences versus Availability*

Table 2 shows the results from the Neu’s test for habitat preferences versus habitat availability

with respect to depth for mother–calf pairs on their initial and final sightings within the same season. At initial sighting, habitat use was uneven relative to water depth availability (Pearson chi-square test:  $\chi^2_4 = 115.91$ ,  $P = < 0.0001$ ). Mother–calf pairs at initial sighting avoided the deepest waters ( $>80$  m), preferring water depths of 40–59.99 m and 60–79.99 m. Areas of  $<20$  m and 20–39.99 m depth were responded to neutrally. Habitat use of mother–calf pairs at their final sighting was also uneven relative to water depth availability ( $\chi^2_4 = 132.46$ ,  $P \leq 0.0001$ ). As at their initial sighting, mother–calf pairs at their final sighting avoided the deepest waters ( $>80$  m), preferred depth ranges of 40–59.99 m and 60–79.99 m, and responded neutrally to depth ranges of 20–39.99 m. However, in contrast to their initial sighting, mother–calf pairs at their final sighting also avoided depth ranges of  $<20$  m.

We investigated sea-bed terrain type preferences by comparing the proportional use versus availability of each terrain type within each of the depth ranges for which mother–calf pairs showed preferences (i.e. 40–59.99 m and 60–79.99 m). At initial sighting, mother–calf pairs were neutral in their use of sea-bed terrain type within the preferred depth ranges (Pearson chi-square test: 40–59.99 m:  $\chi^2_1 = 0.249$ ,  $P = 0.618$ ; 60–79.99 m:  $\chi^2_1 = 0.940$ ,  $P = 0.332$ ; see Table 3). At final sighting, again sea-bed terrain type was used neutrally within the preferred depth range of 60–79.99 m ( $\chi^2_1 = 0.719$ ,  $P = 0.396$ ; Table 3), but within the preferred depth range of 40–59.99 m there was a preference for rugged terrain ( $\chi^2_1 = 9.980$ ,  $P = 0.002$ ; Table 3), which was used disproportionately in relation to its availability. Thus, we confirmed our prediction that mother–calf pairs should favour waters associated with rugged sea-bed terrain more at their final sighting (when calves are older) than at their initial sighting.

#### *Preferences of Water Depth in Relation to Calf Size and Sea-bed Terrain Type*

##### *Correlation results*

During 1998–2007, the lengths of 96 calves were measured (range 3.77–7.62 m, median = 5.64 m, IQR = 1.25 m,  $N = 96$ ) in waters ranging in depth from 24.86 m to 202.09 m (median = 64.00 m, IQR

= 17.81 m,  $N = 96$ ). Seven of the calves were measured at the initial sighting of the 72 mothers that were resighted within season, and five were measured at the final sighting. The remaining 84 calves that were measured were from mothers that were not resighted within season. Ordinal day of calf measurement ranged from 7 days to 124 days (median = 73.5 days, IQR = 41.75 days,  $N = 96$ ). There was a significant positive linear correlation between calf length and water depth (Spearman rank-order correlation:  $r_s = 0.391$ ,  $N = 96$ ,  $P < 0.0001$ ) (Fig. 3). There was also a significant positive correlation between calf length and ordinal day (i.e. longer calves were found later in the season) ( $r_s = 0.236$ ,  $N = 96$ ,  $P = 0.021$ ; Fig. 4). Importantly, the correlation between calf length and water depth remained significant even when ordinal day was partialled out for all calves ( $r_s = 0.391$ ,  $N = 96$ ,  $P < 0.0001$ ). Thus, our prediction that larger calves would be found in deeper waters than smaller calves was confirmed. Furthermore, the correlation between ordinal day and water depth was not significant ( $r_s = 0.049$ ,  $N = 96$ ,  $P = 0.637$ ), indicating that it was not the case that regardless of calf size, mother–calf pairs would be found in deeper water as the season progressed. Likewise, the correlation between calf size and number of escorts was not significant ( $r_s = 0.094$ ,  $N = 96$ ,  $P = 0.365$ ), indicating that, as in our earlier analysis of calf age versus depth differences, number of escorts was not a confounding variable. In terms of sea-bed terrain type, the correlation with calf size just missed significance ( $r_s = 0.194$ ,  $N = 96$ ,  $P = 0.059$ ).

### *GLM results*

The results of the GLM confirmed the correlation analyses of calf size versus ordinal day and depth: there were significant positive relationships between both ordinal day and calf size, and water depth and calf size, indicating that larger calves were observed later in the season ( $\chi^2_1 = 7.469$ ,  $P = 0.006$ ), and that larger calves were associated with deeper water ( $\chi^2_1 = 14.026$ ,  $P < 0.001$ ). In addition, the relationship between calf size and sea-bed terrain type indicated that, on average, calves observed over rugged sea-bed terrain were approximately 0.3 m (SE = 0.15) longer than calves observed over flat terrain, but this relationship narrowly missed the  $\alpha = 0.05$  level for statistical significance ( $\chi^2_1 = 3.549$ ,  $P$

= 0.060).

## DISCUSSION

Our results enhance and broaden the understanding of the dynamics of habitat use by humpback whale mother–calf pairs in the Hawaiian breeding grounds by demonstrating for the first time that the preferences of individual mother–calf pairs for both water depth and sea-bed terrain type vary systematically within a breeding season. As a mother’s residency in the breeding grounds extends, and her calf becomes older, their mother–calf pair ‘footprint’ expands into deeper waters and they are more likely to be found over rugged sea-bed terrain. The expansion of a mother–calf pair’s footprint into deeper waters with increasing calf age was seen most dramatically with relatively long resighting intervals. However, because the median ordinal day at initial sighting for relatively short resighting intervals occurred later in the breeding season than for relatively long resighting intervals, this could indicate that many of the short resighting intervals were due to sampling the tail end of a longer residency period for these mothers (i.e. when they had already relocated to deeper waters) and/or may reflect the influence of time of the season on habitat use, as was demonstrated regarding calf size. To the extent that calf size reflects calf maturity, corroborative evidence of the relationship between relative calf age and water depth was shown by the positive linear correlation between calf length and water depth. Importantly, our GLMM and GLM analyses not only confirmed our findings but also revealed that they remained robust even when other potentially confounded variables were controlled for. Overall, our findings indicate that like mothers in several terrestrial following species (Grignolio et al., 2007), as well as in hider species in which young are transitioning to a following strategy (e.g. Costelloe & Rubenstein, 2015), humpback whale mothers in Hawaiian waters adjust their habitat choices as their calves age and grow.

### *Potential Benefits of Shallow Water Habitats for Mothers with Young Calves*

The residency period of humpback mothers in the breeding grounds tends to be longer than that of females without a calf (Craig, Herman, & Pack, 2001). Presumably the extension of a mother's residency in the breeding grounds is beneficial to the survival of her calf, despite the costs associated with the depletion of maternal energy reserves while fasting (Christiansen, Dujon, Sprogis, Arnould, & Bejder, 2016; Clapham, 2001; Herman, 2016). Craig et al. (2014) reported that during their residency in Hawaiian waters, maternal female humpback whales favour shallow water habitats to avoid energetically costly associations (as reflected in greater travel speeds) with male humpbacks (i.e. escorts) prospecting for mating opportunities. They also speculated that additional costs of association with escorts include potential injury to the calf and/or mother–calf separation. As noted by Smultra (1994), in cetaceans the segregation of mothers and their newborns from males may promote mother–offspring bonding through avoidance of mistaken imprinting, forced separation of mother and offspring, disruption of nursing, or injury by attending males. For example, Mann and Smuts (1998) described attempts by three inexperienced female bottlenose dolphins, *Tursiops aduncus*, to abduct neonates from their mothers, which resulted in the mothers rapidly retrieving their infants and behaving aggressively towards these females. The first and second weeks of a neonate bottlenose dolphin's life appear to represent a sensitive imprinting period characterized by a dramatic increase in the rate of maternal signature whistle production (Fripp & Tyack, 2008). In humpback whales, there is no evidence that suggests active harassment by other females of mother–calf pairs in the breeding grounds, although as noted earlier, male escorts associated with mother–calf pairs may be viewed as a form of harassment (Craig et al., 2014). The potential for disruption in bonding between a mother and her calf by such male harassment is supported through anecdotal evidence. Pack, Herman, Craig, Spitz, and Deakos (2002) reported the temporary separation of a mother and her calf when a pair of males sequestered the mother, with one of the males attempting copulation. Also, we have recorded instances of a calf, after surfacing alone to breath, returning to the escort instead of its mother, followed by the mother rapidly retrieving the calf (Pack,

n.d.). While in theory a calf may be at risk of injury from an escort, we have never observed escorts physically injuring a calf, although some researchers have observed occasions where a mother appears forced to ‘carry’ an apparently stressed and exhausted calf on its back after being chased and crowded by multiple competing escorts (Cartwright & Sullivan, 2009b; Darling, Jones, & Nicklin, 2006). Another potential cost of being escorted would be disruption of nursing. During our study we observed calves nursing in the presence of escorts, including one calf that nursed on four separate occasions in the presence of two competing escorts. Thus, the presence of escorts does not necessarily prevent nursing from occurring, but it is possible that the frequency or duration of nursing bouts (e.g. Videsen, Bejder, Johnson, & Madsen, 2017) may be affected.

Humpback whale mothers on the breeding grounds not only segregate themselves (and their calves) into areas with relatively low male density, they also appear to actively avoid encounters with other mother–calf pairs and other females (Darling, 2001). This tactic may reduce the chance of mistakenly suckling the wrong calf and promote the mother–calf bond, as observed in many ungulate species (Lent, 1974). Misplaced parental investment has been documented in baleen whales: Frasier, Hamilton, Brown, Kraus, and White (2010) reported that two North Atlantic right whale, *Eubalaena glacialis*, calves switched between mothers and stayed with their ‘adopted’ mothers until weaning. Further fine-scale behavioural study of humpback whale mothers and their calves in relation to habitat use and potential involvement in bonding in the breeding grounds would be helpful in better understanding this issue.

#### *Potential Benefits of Expanding the Habitat Footprint into Deeper Waters*

Compared to juveniles and mature females without a calf, humpback whale mother–calf pairs are on average one of the last social groupings to depart the breeding grounds for high-latitude feeding grounds (Craig, Herman, Gabriele, & Pack, 2003; Dawbin, 1966). The expansion of a humpback whale mother–calf pair’s habitat footprint into deeper waters with increasing residency and calf age, as well as

calf size, may coincide with preparation for departure from the breeding grounds. For example, in southern right whales, *Eubalaena australis*, Best and Rüther (1992) reported evidence suggesting that mothers with larger calves may depart their South African breeding grounds earlier than mothers with smaller calves. However, Thomas and Taber (1984) reported that the timing of emigration of southern right whale mother–calf pairs from the breeding grounds at Peninsula Valdes, Argentina, was independent of calf age and size, as well as the length of time since parturition. Instead, they suggested that the timing of emigration was likely due to seasonal factors. Our finding that the ordinal day on which humpback whale calves were measured was unrelated to the depth of water in which they and their mothers were located argues against seasonal factors alone being associated with the expansion of a mother–calf pair's habitat footprint into deeper waters. Instead, we found that this habitat change was most closely associated with the size and age of the calf. Nevertheless, considering that in Hawaii calf births appear to occur throughout the breeding season (Pack et al., 2009), and also that there is a significant decrease in the number of mother–calf pairs (and other groups) in the breeding grounds in April (e.g. Craig et al. 2002; Herman & Antinoja, 1977; Pack & Herman 2007), it is likely that there is a threshold time of the year, which our data may not have captured, at which humpback whale mothers depart the breeding grounds regardless of the size and age of their calves.

Expansion of a humpback whale mother–calf pair's habitat footprint into deeper waters may also promote the development of muscular myoglobin stores in the calf through enhanced physical exertion, an important preparation for migration along deep migratory routes (e.g. Mate, Gisinier, & Mobley, 1998). In cetaceans and other marine mammal species, muscular myoglobin is a key contributor to the ability to perform the extended aerobic dives typically used during foraging behaviour and other activities (Kooyman & Ponganis, 1998; Ponganis, 2011; Snyder, 1983). In a recent study, Cartwright et al. (2016) showed that although muscular myoglobin levels in humpback whale neonates are extremely low, they increase significantly by the commencement of migration. Cartwright et al. (2016) suggested that high levels of activity during humpback whale calf ontogeny (Cartwright & Sullivan, 2009a) may enhance the production of myoglobin stores. If so, then a mother's movement into deeper waters, which has been

shown by Craig et al. (2014) to be associated with increased energetic demands on her and her calf (due to a higher probability of being escorted by one or more males and the consequent increased rate of travel), may be beneficial to a calf at a certain point in its ontogeny through greater facilitation of the development of myoglobin stores than would occur by remaining in shallow waters until the commencement of migration.

Ovulation, although less likely to occur in mothers than in sexually mature females without calf (Chittleborough, 1958, 1965), may be an additional factor that promotes the expansion of a mother's habitat footprint with her calf into deeper waters since this may facilitate finding a suitable mate. However, there may be a selective advantage to a mother whose postpartum ovulation is delayed until her current calf has reached a certain level of maturity and the mother–calf bond has been solidified. The greater energetic costs associated with lactation than pregnancy notwithstanding (Dawbin, 1966; Lockyer, 1984), a lactating female that conceives early in her residency will face greater energetic demands than a nonpregnant lactating female, and energetic constraints may thus promote a premature departure from the breeding grounds to commence feeding. Such a departure could compromise the survival prospects of the current calf. Mortality of calves born in Hawaii has been estimated at approximately 18% within the first 9 months, based on sightings of individual mothers initially with their calf in Hawaii but later without their calf on two or more occasions in the Alaskan feeding grounds prior to 31 October (by which point weaning may have occurred) (Gabriele et al., 2001). Perhaps more importantly, if a mother ovulates too early in her residency, consorting with one or more males during the mating process would expose her and her calf to energetic costs that could put the calf at risk (Craig et al., 2014). Thus, female tactics, both behavioural and physiological, to avoid male harassment and impregnation early in a mother's residency on the breeding grounds would have fitness benefits. In accordance with this, Craig et al. (2002) showed that male humpbacks were more likely to associate with nonmaternal females (i.e. those with a higher reproductive potential) than with maternal females (also see Herman et al., 2011), at least until the late breeding season when there were fewer nonmaternal females present on the breeding grounds. These authors raised the possibility that this phenomenon may be due not only to male preferences but also to

the behaviour of females, which appears to fit well with the current findings of a mother's movements into deeper waters as her calf matures.

#### *Potential Benefits of Associating with Rugged Sea-bed Terrain*

Cartwright et al. (2012) surveyed humpback whales during 2008–2010 in many of the same waters as the current study and reported a significant preference of humpback whale mother–calf pairs for rugged sea-bed terrain. We found that this was not the case for mothers at their initial sighting, and was true only of mothers at their final within-season sighting, within the preferred 40–59.99 m depth range, when their calves were relatively older. However, the surveys of Cartwright et al. (2012) all took place in March, which is relatively late in the breeding season (Baker & Herman, 1981; Mobley et al., 1999). Although Cartwright et al. (2012, page 12) acknowledge that their overall results 'highlight key areas currently used by maternal females during the latter portion of the season...', because no comparison was made with maternal females during earlier portions of the season, this inference remained untested until the current study. Our finding that, from initial to final sighting, mothers changed their selection response to rugged terrain from neutral to preferred (within the preferred 40–59.99 m depth range) is consistent with the proposal by Cartwright et al. (2012), and suggests that many of the mother–calf pairs they surveyed were probably late in their residency and contained relatively mature calves.

The possible benefits mothers derive from associating with rugged sea-bed terrain once their calves are older (and their own fat reserves are more depleted) may be explained in part by changes in the behaviour of mother–calf pods and tactics used to avoid males. Cartwright and Sullivan (2009a), using the angle of furl of a calf's dorsal fin as a proxy for its stage of maturity, found that the behaviour of humpback whale calves at the youngest stage is usually characterized by persistent travel. Our findings that mothers are found in shallower water with younger calves more often than with older calves and that they show no sea-bed terrain preference suggest that for mothers of younger calves, sea-bed terrain type is less important than simply segregating into shallow water where the density of male humpback whales is

relatively low (Craig et al., 2014).

In contrast, at a later stage of calf development, Cartwright and Sullivan (2009a) found that calves engaged in relatively more resting behaviour than earlier in their development. Given our finding that mothers with older calves tend to be found in deeper water where the density of male humpback whales is relatively high (Craig et al. 2014), associating with a particular sea-bed terrain type may be advantageous to the extent that it facilitates resting behaviour and avoidance of male humpbacks. Cartwright et al. (2012) reported that singing male humpbacks and dyads (which are composed primarily of male–female pairs or male–male pairs; Pack et al., 2012), showed a slight preference for sandy, flat sea-bed terrain. Possibly then, a mother of a relatively older calf seeks waters associated with rugged sea-bed terrain as a tactic to promote rest (and energy conservation) by attempting to continue to avoid areas preferred by males when located in deeper waters. Another potential benefit of rugged sea-bed terrain to mothers and calves is that this type of terrain may facilitate acoustic crypsis, making it less likely that mother–calf vocalizations will be detected by eavesdropping males seeking mating opportunities. Videsen et al. (2017) showed that the intensity of vocalizations produced by mother–calf pairs is considerably lower than that of other humpback whale vocalizations, and speculated that this results from strong selection pressure to reduce the likelihood of detection by male humpback whales or predators. Such acoustic crypsis would in theory be enhanced in areas of rugged sea-bed terrain because the ambient noise due to snapping shrimp activity tends to be louder over such terrain than it is over sandy bottoms (Knowlton & Moulton, 1963). Our finding that mothers with older calves tended to select rugged terrain may reflect an increase in the benefits of acoustic camouflage from male humpbacks at a time when males are more likely to seek and escort females with calves due to the increasing rarity of females without calves as the breeding season progresses (Craig et al., 2002). While intriguing, further investigation into each of these hypotheses is clearly warranted, including how a mother of an older calf balances the need for rest with the other requirements associated with calf myoglobin development.

## *Conclusions*

In response to the need for isolation, both fallow deer, *Dama dama*, and white-tailed deer, *Odocoileus virginianus*, females with fawns appear to reduce their home range size (Ciuti et al., 2006; Nixon, Hansen, & Brewer, & Chelsvig, 1992; Ozoga et al., 1982; Scanlon & Vaughan, 1985). Our findings suggest that this is also true of humpback whale mother–calf pairs on the breeding grounds, at least during the earliest stages of a neonate’s life. We found that both calf age and size were associated with habitat choice in the Hawaiian breeding grounds, with younger and smaller calves located with their mothers in shallower waters, and older and larger calves located with their mothers in deeper waters. The gradual movement of mother–calf pairs into deeper waters in close coordination with a fasting mother’s increasing residency and the maturation of her calf appears to be part of a suite of behavioural changes expressed prior to migration back to the feeding grounds.

Humpback whale calves typically remain with their mothers for approximately 12 months (Baraff & Weinrich, 1993; Chittleborough, 1965; Clapham & Mayo, 1987). Birthing, although rarely witnessed in humpback whales, is thought to occur primarily in the early weeks of the breeding season (Nishiwaki, 1959). However, in Hawaiian waters evidence of calves at or near neonate size across the breeding season (Fig. 4), as well as calves possessing neonate physical characteristics (furled dorsal fin and fetal folds) (Cartwright & Sullivan, 2009a) likely reflect a wide range of dates on which birthing occurs. As a consequence, at any point during the breeding season, these waters are likely to contain mothers with calves of varying maturity. Our findings indicate that in Hawaii during the humpback whale breeding season, both shallow- and deep-water habitats are important for mothers depending upon the age and size of their calves. These same waters are also shared by numerous vessels engaged in a variety of activities including whale watching (Cartwright et al., 2012; Pack & Herman, 2007). Recently, Lammers, Pack, Lyman, and Espiritu (2013) showed that humpback whale calves are particularly vulnerable to vessel collisions in Hawaiian waters, with the majority of collisions reported in the same region as the present study. These findings warrant extreme vigilance while navigating through this region during the

humpback whale breeding season to avoid collisions with whales. They also suggest an avenue for future research into whether vessels in close proximity to mothers with neonates in shallow waters lead to the premature abandonment of this refuge for deeper waters.

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## Appendix

**Table A1**

Summary of results from generalized linear mixed model for mother–calf resource selection function model (initial vs final sightings)

Variable	$\beta$	SE	$z$	$P$
Intercept	-5.472	0.491	—	<b>&lt;0.001</b>
First sighting*depth	-0.021	0.008	-2.708	<b>0.007</b>
Final sighting*depth	0.032	0.011	2.866	<b>0.004</b>
First sighting*rugged terrain	-0.239	0.911	-0.262	0.793
Final sighting*rugged terrain	2.308	1.174	1.965	<b>0.049</b>
First sighting*depth*rugged terrain	0.002	0.013	0.163	0.871
Final sighting*depth*rugged terrain	-0.024	0.017	-1.408	0.159
Number of escorts	-0.002	0.084	-0.021	0.983
Ordinal day	0.001	0.087	0.015	0.988
Resighting interval	0.000	0.083	0.001	0.999
<b>Random effects</b>		<b>Variance</b>		<b>SD</b>
Mother–Calf pair	0	0		

Statistically significant ( $\alpha=0.05$ )  $P$  values are shown in bold.

**Table 1**

Boat survey effort for mother–calf pods (1997–2008)

Season	First date	Final date	No. days	Total no. pods	No. mother–calf pods
1997	8-Jan-97	15-Apr-97	82	485	215
1998	8-Jan-98	19-Apr-98	80	585	203
1999	3-Jan-99	17-Apr-99	92	532	182
2000	6-Jan-00	14-Apr-00	85	478	193
2001	27-Dec-00	16-Apr-01	84	395	154
2002	2-Jan-02	21-Apr-02	80	336	108
2003	29-Dec-02	8-May-03	74	268	85
2004	30-Dec-03	28-Apr-04	71	313	128
2005	6-Jan-05	17-Apr-05	65	384	167
2006	30-Dec-05	15-Apr-06	75	382	146
2007	5-Jan-07	8-May-07	72	339	135
2008	6-Jan-08	16-Apr-08	69	308	130
<b>Total</b>			<b>929</b>	<b>4805</b>	<b>1846</b>

**Table 2**

The proportional use versus availability of each depth range by mother–calf pairs on their initial and final sightings

Mother–Calf pair	Depth range (m)	Area (km <sup>2</sup> )	Counts (N groups)		Observed proportions <sup>1</sup> (95% CIs)	Expected proportions <sup>1</sup>	Inference <sup>2</sup>	Neu's standardized selection index <sup>2</sup>
			Expected	Observed				
<b>Initial sighting</b>	<20	34.7	1.9	1	0.014 (-0.023, 0.05)	0.027	Neutral	0.062
	20–39.99	66.7	3.7	6	0.083 (-0.003, 0.169)	0.052	Neutral	0.193
	40–59.99	135.4	7.6	21	0.292 (0.15, 0.433)	0.105	Preferred	0.332
	60–79.99	196.0	11.0	36	0.500 (0.344, 0.656)	0.152	Preferred	0.393
	>80	854.1	47.8	8	0.111 (0.013, 0.209)	0.664	Avoided	0.020
<b>Final sighting</b>	<20	34.7	1.9	0	0	0.027	Avoided	0
	20–39.99	66.7	3.7	3	0.042 (-0.021, 0.104)	0.052	Neutral	0.105
	40–59.99	135.4	7.6	25	0.347 (0.199, 0.495)	0.105	Preferred	0.432
	60–79.99	196.0	11.0	36	0.500 (0.344, 0.656)	0.152	Preferred	0.441
	>80 m	854.1	47.8	8	0.111 (0.013, 0.209)	0.664	Avoided	0.022

<sup>1</sup> Proportions have been rounded and may not total 1.

<sup>2</sup> Neu's indices provide standardized estimates of habitat use, based on habitat availability. Depth ranges were classified as 'preferred' (where the 95% CIs of the observed proportion of sightings in each habitat type were entirely above the expected proportions based on habitat availability)

and as ‘avoided’ (where the 95% CIs of the observed proportions were entirely below the expected counts). In all other (neutral) regions, the 95% CIs of observed proportions included the expected proportions.

**Table 3**

The proportional use versus availability of each sea-bed terrain type (flat versus rugged) within each of the depth ranges for which mother–calf pairs showed preferences (i.e. 40–59.99 m and 60–79.99 m, Table 2) at their initial and final sightings

Mother–Calf pair	Depth range (m)	Sea-bed terrain	Area (km <sup>2</sup> )	Counts (N groups)		Observed proportions <sup>1</sup> (95% CIs)	Expected proportions <sup>1</sup>	Inference <sup>2</sup>	Neu's standardized selection index <sup>2</sup>				
				Expected	Observed								
<b>Initial sighting</b>	40–59.99	Flat	98.3	15.3	16	0.762 (0.554, 0.97)	0.729	Neutral	0.543				
	40–59.99	Rugged	36.5	5.7	5	0.238 (0.03, 0.446)	0.271	Neutral	0.457				
	60–79.99	Flat	134.6	24.8	26	0.722 (0.555, 0.889)	0.690	Neutral	0.539				
	60–79.99	Rugged	60.5	11.2	10	0.278 (0.111, 0.445)	0.310	Neutral	0.461				
<b>Final sighting</b>	40–59.99	Flat	98.3	18.2	11	0.440 (0.218, 0.662)	0.729	Avoided	0.226				
	40–59.99	Rugged	36.5	6.8	14	0.560 (0.338, 0.782)	0.271	Preferred	0.774				
	60–79.99	Flat	134.6	24.8	22	0.611 (0.429, 0.793)	0.690	Neutral	0.414				
	60–79.99	Rugged	60.5	11.2	14	0.389 (0.207, 0.571)	0.310	Neutral	0.586				

<sup>1</sup> Proportions have been rounded and may not total 1.

<sup>2</sup> Neu's indices provide standardized estimates of habitat use, based on habitat availability. Depth ranges were classified as 'preferred' (where the 95% CIs of the observed proportion of sightings in each habitat type were entirely above the expected proportions based on habitat availability)

and as ‘avoided’ (where the 95% CIs of the observed proportions were entirely below the expected counts). In all other (neutral) regions, the 95% CIs of observed proportions included the expected proportions.

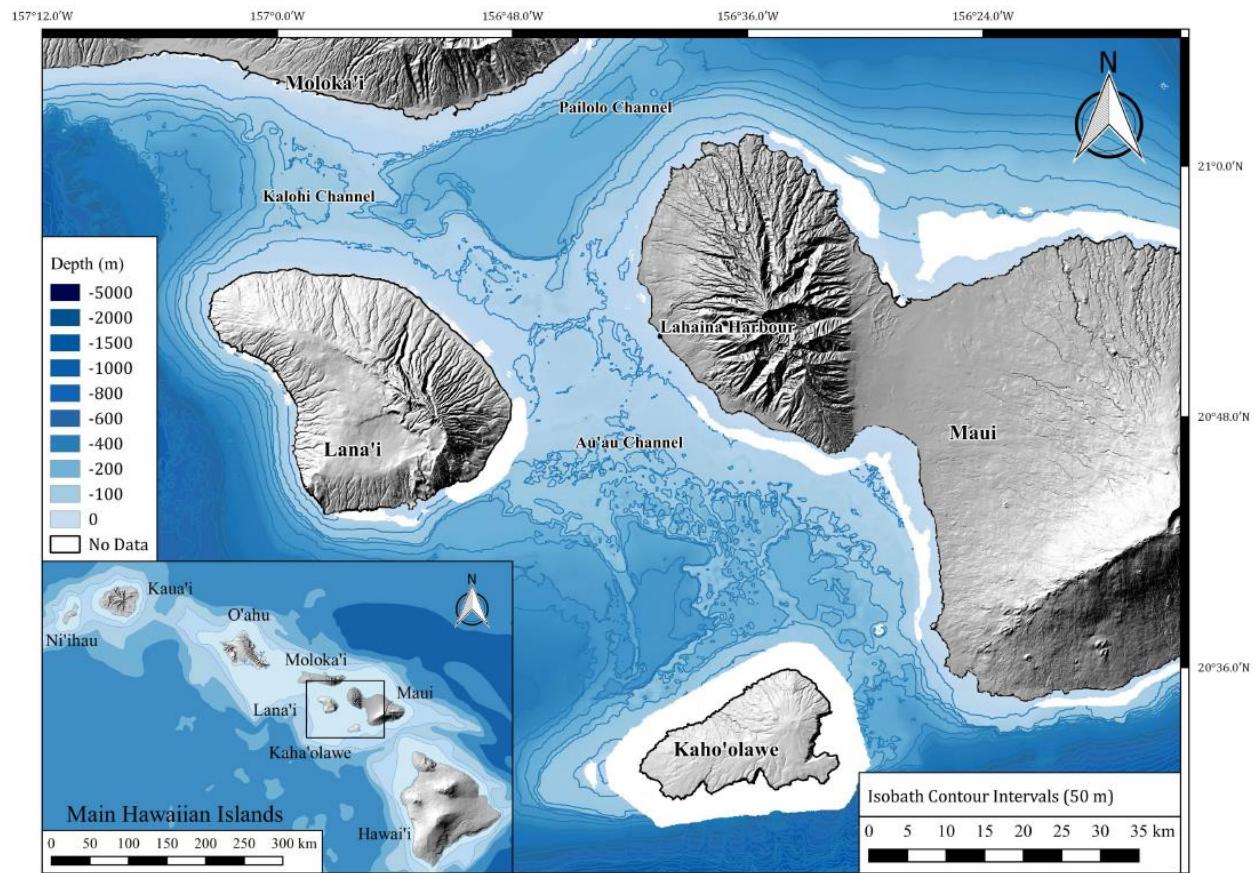
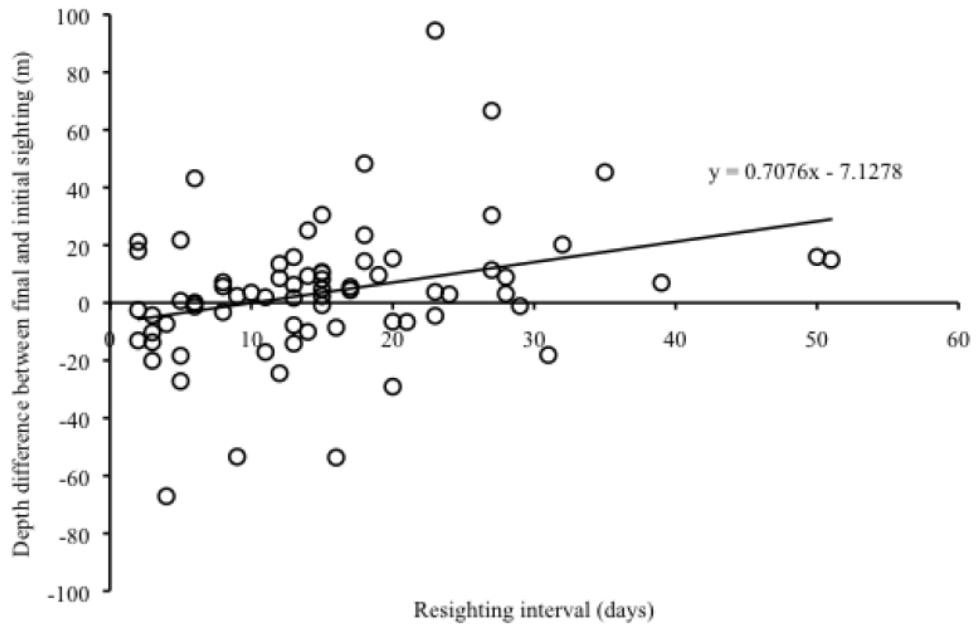
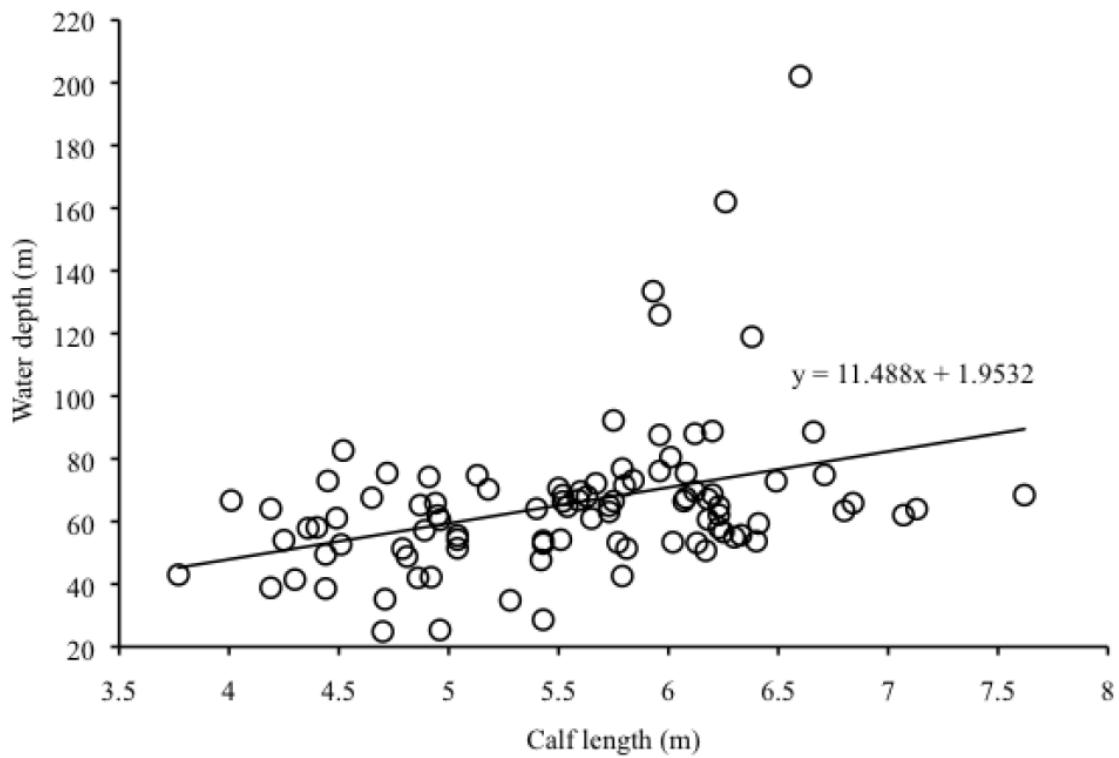


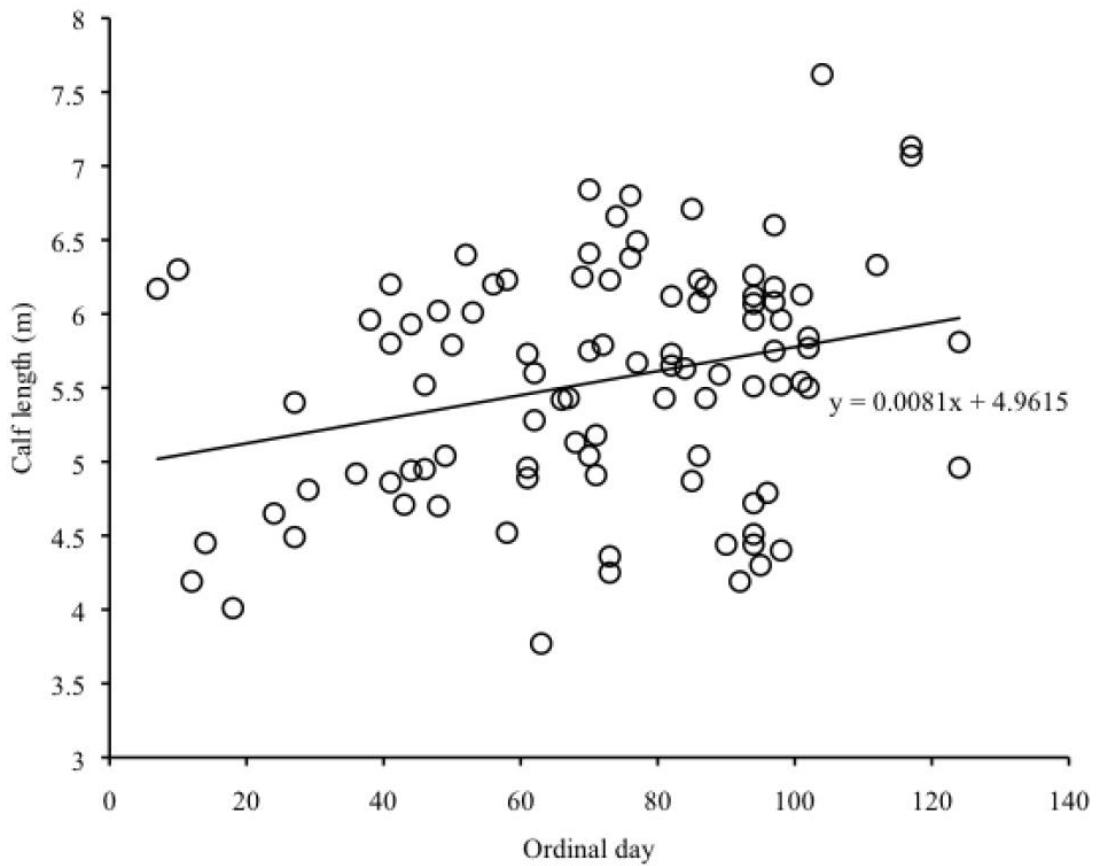
Figure 1. Study area in the Hawaiian Islands.



**Figure 2.** Scatter plot of the maximum resighting interval of 72 humpback whale mother–calf pods versus the difference in depth from their initial to final sighting. The trend line and equation fitting the data are shown (Spearman rank-order correlation:  $r_S = 0.36$ ,  $N = 72$ ,  $P = 0.002$ ).



**Figure 3.** Scatter plot of the measured lengths of 96 humpback whale calves versus the depth of the water each occupied at the start of a focal follow. The trend line and equation fitting the data are shown (Spearman rank-order correlation:  $r_s = 0.391$ ,  $N = 96$ ,  $P < 0.0001$ ).



**Figure 4.** Scatter plot of the lengths of 96 humpback whale calves measured using underwater videogrammetry as a function of ordinal day of measurement (1 January = ordinal day 1). The trend line and equation fitting the data are shown (Spearman rank-order correlation:  $r_s = 0.236$ ,  $N = 96$ ,  $P = 0.021$ ).