LRH: MARINE MAMMAL SCIENCE, VOL. **, NO. *, ****

RRH: NOTES

Comparing depth and seabed terrain preferences of individually identified female humpback whales (*Megaptera novaeangliae*), with and without calf, off Maui, Hawaii

Adam A. Pack,[1] Departments of Psychology and Biology, University of Hawaii at Hilo, 200 West Kawili Street, Hilo, Hawaii 96720, U.S.A. and The Dolphin Institute, PO Box 6279, Hilo, Hawaii 96720, U.S.A.; **Louis M. Herman,** The Dolphin Institute, PO Box 6279, Hilo, Hawaii 96720, U.S.A. and Department of Psychology, University of Hawaii at Manoa, 2530 Dole Street, Sakamaki C 400, Honolulu, Hawaii 96822, U.S.A.; **Alison S. Craig,** The Dolphin Institute, PO Box 6279, Hilo, Hawaii 96720, U.S.A. and School of Applied Sciences, Edinburgh Napier University, Sighthill Court, Edinburgh EH11 4BN, Scotland, United Kingdom; **Scott S. Spitz,** The Dolphin Institute, PO Box 6279, Hilo, Hawaii 96720, U.S.A.; **James O. Waterman,** School of Psychology, University of Lincoln, Brayford Pool, Lincoln LN6 7TS, United Kingdom; **Elia Y. K. Herman,** The Dolphin Institute, PO Box 6279, Hilo, Hawaii 96720, U.S.A.; **Mark H. Deakos,** Hawaii Association for Marine Education and Research, Inc., PMB#175 5095 Napilihau Street 109B, Lahaina, Hawaii 96761, U.S.A.; **Siri Hakala**, Pacific Islands Fisheries Science Center, National Oceanic and Atmospheric Administration, 1845 Wasp Boulevard, Building 176, Honolulu, Hawaii 96818, U.S.A.; **Carley Lowe**, Tropical Conservation Biology and Environmental Science Program, University of Hawaii at Hilo, 200 West Kawili Street, Hilo, Hawaii 96720, U.S.A.

Differences in habitat preferences of females with and without dependent offspring have been well documented in several mammalian species (*e.g.*, Main *et al.* 1996, Wolf *et al.* 2005, Ciuti *et al.* 2006, Walker *et al.* 2006, Pinard *et al.* 2012, Craig *et al.* 2014). In some studies, such differences have been reported by observing changes in behavior by individual females. For example, in Alpine ibex (*Capra ibex*) individually identified females had significantly smaller home ranges during summer months when they were with a kid than without (Grignolio *et al.* 2007). Potential factors contributing to a female with offspring segregating from others into a habitat that is different from that which it would occupy when without offspring include predator avoidance (*e.g.*, Main *et al.* 1996, Ciuti *et al.* 2006, Walker *et al.* 2006, Pinard *et al.* 2012), limitations in offspring mobility and activity budgets (Grignolio *et al.* 2007), access to better food resources (including fresh water for land-dwelling mammals) (Rachlow and Bowyer 1998), avoidance of harassment by males prospecting for mating opportunities (*e.g.*, Wolf *et al.* 2005, Craig *et al.* 2014), and/or promotion of maternal-offspring bonding (Lent 1974, Schwede *et al.* 1993).

It has been well established in several populations of humpback whale (*Megaptera novaeangliae*) that at the breeding grounds, groups containing a mother-calf pair favor shallower water habitats than groups without (summarized in Craig *et al.* 2014, see also Guidino *et al.* 2014, Kobayashi *et al.* 2017). There is also some evidence from the Hawaiian breeding grounds that groups containing a mother-calf pair sometimes prefer water associated with rugged seabed terrain to water associated with flat seabed terrain (Cartwright *et al.* 2012, Pack *et al.* 2017). Cartwright *et al.* (2012) found that groups containing a calf off west Maui that were sampled late in the breeding season favored water associated with rugged seabed terrain to flat seabed terrain, but that no such preference existed for pods without a calf. Consistent with this idea, Pack *et al.* (2017) found in these same waters that as a calf ages and grows, the footprint of mother-calf pairs expand from relatively shallow waters, where male density is low, into deeper waters where male density is higher. Accompanying this expansion is a preference for waters associated with rugged seabed terrain. Pack *et al.* (2017)

suggested that acoustic crypsis, which may have evolved to avoid the detection of mother-calf vocalizations by eavesdropping males seeking mating opportunities (Videsen *et al.* 2017), would be enhanced by mother-calf pairs associating with rugged sea-bed terrain because ambient noise levels resulting from snapping shrimp activity tend to be greater over rugged seabed terrain than flat (Knowlton and Moulton 1963).

Of those studies that have investigated differences in humpback whale habitat use in the breeding grounds as a function of calf presence or absence, the vast majority adopted a cross-sectional approach, rather than a longitudinal approach in which known individuals are repeatedly sampled at different times. Although the former approach can be carried out more rapidly than the latter, the disadvantages of a cross-sectional approach are that (1) individuals with calves, which typically have a longer residency period at the breeding grounds than individuals without calves (Craig *et al.* 2001), may be inadvertently sampled multiple times within the same breeding season, thus potentially biasing results towards individual female propensities when with a calf and (2) measures of habitat use of noncalf groups may be biased by including groups that contain either an immature female or no female at all (*e.g.*, Clapham *et al.* 1992, Herman *et al.* 2011, Pack *et al.* 2012). Despite the strength and advantage of longitudinal designs only one study has examined the habitat preferences of the *same* females when they were with *vs.* without a calf. In the Hawaiian Islands, Craig and Herman (2000) found that individually identified females preferred waters off west Maui when they were with a calf, and waters off the north Kohala coast of Hawaii Island when they were without a calf. They suggested that this finding might be due to females with calves preferring shallower waters, since the Maui study area is comprised of more extensive shallow water habitat than the Hawaii Island study area. However, Craig and Herman (2000) adopted a broad approach to habitat preferences, comparing two island locales rather than investigating depth preferences specifically.

Here, we adopted a longitudinal approach to compare both water depth and seabed terrain preferences of individually identified female humpback whales off west Maui when they were with and without a calf. Based on the previously described longitudinal study by Craig and Herman (2000) as well as the previously cited cross-sectional studies of depth preferences of calf pods *vs.* noncalf pods, we predicted that individual females with a calf would favor shallower water than when they were without a calf. Regarding seabed terrain preferences, based on the cross-sectional study by Cartwright *et al.* (2012) showing a preference for rugged seabed terrain by groups containing a mother-calf pair but not by groups without a mother-calf pair, we predicted that individual females would prefer rugged seabed terrain when they were with a calf *vs*. without.

North Pacific humpback whales were studied off west Maui in the Au'au, Kalohi, and Pailolo channels of the Hawaiian breeding habitat (Fig. 1). This area is known to contain one of the largest concentrations of humpbacks in Hawaii with all age classes, pod types, and behavioral roles represented, including females with (and without) newborn calves (Herman *et al.* 1980, Mobley *et al.* 1999, Herman *et al.* 2011). Data were collected on 929 d across 12 consecutive breeding seasons from 1997 to 2008, typically from late December to mid-April to cover the period when the majority of humpbacks are found in Hawaii's waters (Baker and Herman 1981, Mobley *et al.* 1999).

Researchers searched for humpback whales from one or two small (<8 m) outboard boats launched daily (or nearly so), mostly from Lahaina harbor but occasionally from one of the other launch ramps along Maui's west coast. Search effort was continuous throughout the day from approximately 0830 to 1700. Whales were approached for close observation as they were sighted, without bias towards any particular type of group or any particular area. At the start of each survey, each member of the crew scanned a different 90° sector of water. If no whale was sighted, the captain attempted to choose a heading that was different from his or her prior survey, sea state permitting. If no whales were sighted by the time the boat either reached the edge of the study area or encountered a high sea state, the boat changed heading and the crew continued its search efforts. An initial GPS location of a focal whale or group of whales was recorded using either a Garmin GPS Map 172 or 172C when the research boat was within approximately 20 m. A focal follow then proceeded. 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 100–300 mm zoom lenses. Tail fluke images of individuals were associated with their behavioral role and group type (*e.g.*, mother in a mother-calf pair either unescorted or escorted by one or more males, nonmaternal female in a competitive group, nonmaternal female in a male-female dyad; see Herman *et al.* (2011) for a detailed description of behavioral roles and group types). Mothers were identified by their consistently close proximity to a calf, and as in previous studies could be assumed to be female from this social role alone even in the absence of other sex determination techniques (*e.g.*, Craig and Herman 2000, Herman *et al.* 2011). This assumption has been validated in the past (*e.g.*, Glockner-Ferrari and Ferrari 1990) and was also validated in the present study when direct examination of the genital region for the presence of a hemispheric lobe was possible (Glockner 1983). At the end of a focal follow, a final GPS location was recorded, the boat motored away from the pod in a pseudo-random direction, and the crew began a new search.

The sharpest and most detailed image of each whale's tail flukes was printed and given a unique observation number as well as a "color" category based on the percentage of white in the ventral portion of its tail flukes (0%, 25%, 50%, 75%, or 100%). The photograph of each whale was then compared to all other photographs within the same and adjacent color categories taken within the same breeding season to determine the number of within-season matches. Once completed, the photograph of each whale was then compared to all other photographs within the same and adjacent color categories taken across different breeding seasons to determine the number of across-season matches. For each match, the date of the resighting was recorded 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. We omitted one sighting of a female accompanied by both a calf and a yearling in the same breeding season.

To extract water depth data at GPS locations, a geographic information system (GIS) model of the study area was constructed using ArcGIS 10.3.1 (Environmental Systems Research Institute). Coastline data from the Hawaii Statewide GIS Program (http://planning.hawaii.gov/gis/download-gis-data/) were included 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. The GPS coordinates at the start of each focal follow were plotted and the Spatial Analyst tool “Extract” - “Extract Values to Points” was used to derive the depth of each pod.

Following Cartwright *et al.* (2012), NOAA’s Benthic Terrain Modeler (BTM) (Wright *et al.* 2012) was used to prepare a detailed benthic terrain map. The BTM creates grids of bathymetric position index (BPI), slope, and depth that are combined to generate digital maps of geomorphological features such as slopes, depressions, crests, and flats. Central to the process is the concept of the bathymetric position index: BPI is a second order derivative of the surface that defines the elevation of locations relative to those that surround it. Each cell’s elevation is compared to the mean elevation of those surrounding it (within a user defined rectangle, annulus, or circle). Cells that are lower than those around them are assigned negative BPI values (depressions); cells that are higher than those around them are assigned positive values (crests), and constant slopes (slopes that are >5°) or flat areas (slopes that are ≤5°) are assigned zero BPI values; larger BPI values represent features that differ more dramatically from surrounding areas. These BPI values were classified using a template designed originally by Lundblad *et al.* (2006) for use around American Samoa (an area with very similar benthic topography to 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 classified as either crests, depressions, slopes, or flats. Areas of complex terrain (*i.e.*, crests, depressions, and slopes) were enclosed within a 100 m buffer (to incorporate transitional areas) and merged into a single "rugged" layer. Areas outside this layer were described as "flat." As with Cartwright *et al.* (2012), our classification of "rugged" and "flat" seabed 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. The Analysis tool "Overlay – Spatial Join" was then used to assign a rugged/flat value to each pod based on the GPS location at the start of the focal follow. To examine whether statistically significant differences in habitat use of depth and seabed terrain type reflected actual habitat preferences rather than 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 each analysis according to depth and seabed terrain type. Seabed 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, and >80 m. Using Neu's method for the analysis of utilization-availability data (Neu *et al.* 1974), we compared levels of habitat use to the proportional availability of each habitat type. Chi-square tests, with the Yates correction for continuity where the number of habitat categories was only two, were used to assess whether each habitat type was used in proportion to its availability. Where disproportionate habitat use was identified, Bonferroni corrected 95% confidence intervals were constructed around proportional 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, Neu’s standardized selection indices (that sum to 1.0 within each analysis) were calculated in order 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 seabed terrain type preference was merely an artifact of an association between seabed terrain type and depth, separate Chi-square tests were used to assess seabed terrain type preference within each preferred depth range. All data were organized into Filemaker Pro databases and Microsoft Excel spreadsheets and were analyzed in either SPSS 21 or SAS 9.13.

A total of 1,846 pods with a calf (median pods per breeding season = 150, IQR = 61.75, Q1 = 128.50, Q3 = 190.25), and 2,959 pods without a calf (median pods per breeding season = 232, IQR = 91.50, Q1 = 189.75, Q3 = 281.25) were sighted. The area encompassing GPS locations of these pods was approximately 1,408.22 km^2 and extended from <20 m depth to >400 m (Fig. 1).

Because this area was surveyed without bias towards particular pod types, all resighted females examined here were potentially available for survey when with and without calf throughout the entire area. Thus, although their locations appear clustered in one area (see Fig. 1), this is not a result of any biased sampling protocol, something upon which the Neu's analysis relies, *i.e.*, in order to conduct a valid analysis all areas (in this case depth and terrain zones) must be sampled in proportion to their availability. Furthermore, kernel density estimates were generated for (1) all the whale sightings collected in the course of the study and (2) the first whale sightings of each day to examine for any potential bias in sampling towards particular portions of the study area. A comparison of these density estimates revealed that the first whale sightings of each day were wholly representative of the distribution of all whale sightings. That is, they were not biased towards any particular portion of the study area (from which the day's search may have begun).

Thirty-five females were sighted at least once with a calf and at least once without a calf across all breeding seasons (median number of seasons sighted with a calf = 1.00, IQR = 1.00, Q1 = 1.00, Q3 = 2.00; median number of seasons sighted without a calf = 1.00, IQR = 1.00, Q1 = 1.00, Q3 = 2.00). The maximum number of seasons any female was sighted either with or without a calf was three. Based on the earliest sighting of each female in each reproductive condition (to avoid any bias due to pseudo-replication), individual females were found in significantly shallower water when with a calf (Mdn = 61.28 m, IQR = 20.8 m, Q1 = 50.89 m, Q3 = 71.69 m) than without a calf (Mdn = 70.17 m, IQR = 19.33 m, Q1 = 63.13, Q3 = 82.46 m) (Wilcoxon Signed-rank test: $Z = -3.518$, $n = 35$, $P = 0.0004$; Hodges-Lehmann estimator for depth difference of females in each reproductive condition: HL Mdn = 14.10 m, 95% CI [5.41, 25.21]), with a medium effect size ($r = 0.59$) (Fig. 1). Although all 35 females were judged by eye to be adult-sized at their first sighting, it is possible that some who were initially sighted without a calf (and were not sighted the following year with a calf) were not sexually mature at that time (*e.g.*, see Pack *et al.* 2012). Also, Figure 1 shows three females (Nos. 9, 13, and 28) who were sighted in waters >183 m deep when without calf. Herman *et al.* (1980) and Mobley *et al.* (1999) showed that 90% of humpback whales in the Hawaiian Islands are found within the 100-fathom isobath (*i.e.*, 183 m contour of island shorelines), raising the possibility that these three females were in transit between regions. Therefore, we excluded all females ($n = 9$) from the data set whose maturity could not be verified when sighted initially without calf as well as the three females sighted without a calf in waters greater than 183 m deep and conducted a conservative reanalysis of the remaining 23 females. The results were consistent with those from the previous analysis, confirming that individual adult females were found in significantly shallower water when with a calf (Mdn = 61.64 m, IQR = 22.99 m, Q1 = 50.16 m, Q3 = 73.15 m) than without a calf (Mdn = 69.55 m, IQR = 19.45 m, Q1 = 60.96 m, Q3 = 80.41 m), (Wilcoxon Signed-rank test: $Z = -2.641$, $n = 23$, $P = 0.0083$, HL Mdn = 10.0025, 95% CI 1.830, 18.915), with a medium effect size ($r = 0.55$).

Of the earliest sightings of the 35 resighted females, none were unescorted when without a calf compared with 7 when with a calf, 13 were accompanied by a single escort when without a calf compared with 24 when with a calf, and 22 were accompanied by two or more escorts when without a calf compared with only 4 when with a calf. Taken together, individual females when without a calf were significantly more likely to be escorted than when with a calf (Fisher’s exact test, $n = 70$, $P = 0.011$), and were significantly more likely to be found in pods of two or more escorts (Fisher’s exact test, $n = 70$, $P = 0.00001$), findings that corroborate Craig *et al.* (2002). The correlation between the depth of a pod containing a female with a calf and the number of escorts associated with that pod was not significant (Spearman's rho = –0.14, *n* = 35, *P* = 0.437). Likewise, the correlation between the depth of a female without a calf and the number of escorts associated with that female was not significant (Spearman's rho = 0.21, *n* = 35, *P* = 0.225). Thus, the variation in habitat preference that we report here in relation to a female's reproductive state appears to be independent of the number of escorts associated with females in either state, although the relatively low power levels in these analyses of 0.13 and 0.23 respectively suggest that the number of escorts accompanying a female as a contributing factor in female habitat use cannot be completely discounted (*cf*. Craig *et al.* 2014).

With regard to temporal trends in habitat use, the correlation of the depth of a mother-calf pair *vs*. the date of their observation across breeding seasons was not significant, indicating that within the confines of our limited sample the depth preferences of mother-calf pairs were probably relatively stable over time (Spearman's rho = 0.17, *n* = 35, *P* = 0.321). However, a low power level in this analysis of 0.17 suggests the need for further analysis of variations in habitat use over time with a larger sample size than was available in the present study.

The area encompassing GPS locations of the earliest sightings of the 35 females with and without a calf was approximately 530.65 km^2. Excluding areas for which no depth data were available (7.33 km^2 or 1.38% of the total study area), depth ranged from <20 m to 348 m, the area of rugged seabed terrain type was approximately 243.99 km^2 (45.98% of the study area), and the area of flat seabed terrain type was approximately 279.33 km^2 (52.64% of the study area). Table 1 shows the results from the Neu's test for habitat preferences *vs.* habitat availability for individual females when with a calf *vs.* without a calf. When with a calf, female habitat use relative to water depth availability was uneven (Pearson Chi-squared test; χ^2_4 = 67.92, $P < 0.001$): females with a calf preferred depths of 40–79.99 m, responded neutrally to the 20–39.99 m depth range, and avoided all others. Habitat use by females without a calf was also uneven relative to water depth availability (Pearson Chi-squared test; χ^2_4 = 47.04, $P < 0.001$), but depth preferences diverged from those observed when calves were present. When without a calf, females avoided the 20–39.99 m depth range, preferring exclusively the depth range of 60–79.99 m. They also avoided the deepest waters (>80 m range) and responded neutrally to both the <20 m and 40–59.99 m depth ranges. Our findings on depth preferences of females with calf are similar to those of Cartwright *et al.* (2012) for the three shallowest depth ranges: an avoidance of depth ranges of < 20 m, a neutral response to depth ranges of 20–39.99 m (stated range actually 20–40 m), and a preference for depth ranges of 40–59.99 m (stated range actually 40–60 m). They differ, however, with respect to the 60–79.99 m (stated range actually 60–80 m) and >80 m depth ranges: Cartwright *et al.* (2012) reported that mothers responded neutrally to these ranges, whereas we observed a preference for the depth range of 60–79.99 m and an avoidance of >80 m. Our findings on depth preferences when individually identified females were without calf aligned well to those reported for adult-only groups by Cartwright *et al.* (2012) for depth ranges of 20–40 m (avoidance), 40–60 m (neutral), and >80 m (avoidance), but diverged for depth ranges <20 m (avoidance) and 60–80 m (neutral). The slight divergence between Cartwright *et al.*'s (2012) findings regarding depth preferences and those we report here may be due to sampling differences: Possibly, these differences reflect the unique ability of the present study to limit its sampling to single observations of individually identified females when without calf. Also, the extension of our sampling, but not Cartwright *et al.*'s (2012) into the month of April may have been a factor in our finding of a mother-calf preference for 60–79.99 m in addition to 40–59.99 m.

Seabed terrain type preferences were investigated by comparing the proportional use *vs*. availability of each terrain type within each of the preferred depth ranges (*i.e.*, females with a calf: 40–59.99 m and 60–79.99 m; females without a calf: 60–79.99 m) (Table 2). No seabed terrain type preferences were observed for individual females when either with or without a calf; seabed terrain type use was in proportion to availability within preferred depth ranges (females when with a calf: Pearson Chi-squared test; 40–59.99 m, χ_1^2 = 0.295, P = 0.587, N.S.; 60–79.99 m, χ_1^2 = 0.449, P = 0.503, N.S.; females when without a calf: Pearson Chi-squared test; 60–79.99 m, χ_1^2 = 0.340, P = 0.560, N.S.). The lack of a preference for rugged seabed terrain by individual females with a calf (which did not support our hypothesis) is different from the finding of Cartwright *et al.* (2012) that pods containing a female with a calf favored rugged bottom terrain to flat bottom terrain, and also different from Pack *et al.* (2017) who demonstrated that mothers of older and larger calves are likely to be found in waters associated with rugged seabed terrain. It is possible that the difference in seabed terrain preferences between these previous studies and the current study is a function of the relatively low power in the current analyses, which for a large effect size was calculated at 0.44 and 0.52 for seabed terrain preferences at 40–69.99 and 60–79.99 respectively for females when with calf, and 0.59 at 60–79.99 for females when without calf. However, it is likely that this apparent discrepancy is related to the timing and duration of sampling. The whale surveys by Cartwright *et al.* (2012) were all performed in the month of March, which is relatively late in the breeding season (Baker and Herman 1981, Mobley *et al.* 1999) and may therefore be unrepresentative of habitat preferences over the breeding season as a whole, whereas our sampling was more evenly distributed across the entire breeding season. Of the initial sightings of the 35 females when with a calf, 16 occurred in the months of January and February (relatively early in the season) and 19 occurred in the months of March and April (relatively late in the season). Although Pack *et al.* (2017) demonstrated that mothers of older and larger calves, often observed later in the breeding season, are likely to be found in waters associated with rugged seabed terrain, they also found that mothers of younger and smaller calves, often observed earlier in the season, do not exhibit this preference. Thus, in the current study, it is conceivable that the mother-calf pair sightings that occurred early in the season which amounted to nearly half of the sample reduced the significance of any preferences for rugged seabed terrain if such a preference is characteristic of females with calf late in the breeding season, as suggested by Pack *et al.* (2017).

Overall, our study has enriched the understanding of female humpback whale habitat use on the breeding grounds. Although earlier studies using cross-sectional approaches consistently indicated a general preference by humpback whale groups containing a calf for shallow water habitats compared to non-calf groups, these studies could not control for oversampling individual mother-calf pairs or distinguish between those noncalf groups containing mature females, immature females, and no females. By using a longitudinal approach we have shown for the first time that when *individual* mature females are with a calf they favor shallower water than when they are without a calf. This is consistent with Craig and Herman's (2000) finding that *individual* females tended to prefer Maui waters to Hawaii Island waters when with a calf, but directly demonstrates the importance of water depth even within a single island locale. Thus, as in other mammalian species in which an individual female's habitat preferences change when she has dependent offspring (*e.g.*, Grignolio *et al.* 2007), individual humpback whale females vary their habitat use based on their reproductive condition.

As described earlier several factors may potentially underlie a female’s tendency to modify her habitat use when with recent offspring. Recently, Craig *et al.* (2014) investigated the factors associated with the preference of maternal female humpback whales for shallow water habitats. Because humpback whales of all age classes other than newborn calves fast on the breeding grounds Craig *et al.* (2014) were able to eliminate access to better food resources as a motivating factor. Likewise, they found little evidence to support predator avoidance as a significant factor. What Craig *et al.* (2014) did find was both a positive linear correlation between the depth occupied by a mother-calf pair and the number of male escorts in their company, and a positive linear correlation between the number of escorts associated with a mother-calf pair and the speed with which that pod traveled. These findings supported the hypothesis that maternal humpback whales favor shallow water habitats to avoid male harassment, which for a mother-calf pair can be energetically costly.

Given the importance of shallow-water habitats to humpback whale mother-calf pairs, concerns have been raised in Hawaii since the early 1980s about a reduction in the number of mother-calf pairs in the Au’au channel along the west Maui shoreline, possibly in association with increasing levels of vessel traffic. For example, the number of mother-calf groups sighted by Glockner-Ferrari and Ferrari (1985, 1990) within 0.4 km of the west Maui shoreline in 1983 (17.2%) was less than half that in 1981. Nearly 30 yr later, Cartwright *et al*. (2012) reported that only 1.2% of 86 mother-calf groups surveyed were within 0.4 km of the same shoreline. Although striking, these temporal trends should be approached with some caution because the surveys of Glockner-Ferrari and Ferrari (1985, 1990) were not systematic and the later systematic surveys by Cartwright *et al.* (2012) were restricted to late in the breeding season when many calves are larger and older and will have expanded their footprint into deeper waters (Pack *et al.* 2017). Furthermore, in the current study, no trend was apparent in our correlation analysis of mother-calf depth versus date across years from 1997 to 2008. However, this analysis may have been constrained by the relatively low sample size. Future studies should examine historical changes in mother-calf pair habitat use in Maui waters from 1997 to 2008 more comprehensively, and compare these findings to data from new surveys that extend over the entire breeding season. In the meantime, the current findings taken together with recent studies in the same area (Cartwright *et al.* 2012, Craig *et al.* 2014, Pack *et al.* 2017), reinforce the importance of both shallow water and deeper water habitats to female humpbacks off west Maui depending on their reproductive condition as well as on the age and size of their calves.

ACKNOWLEDGMENTS

This research was conducted 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. This work was supported through contributions from members of The Dolphin Institute (TDI), TDI participants, Earthwatch volunteers, LeBurta Atherton, The Homeland Foundation, the Robles Foundation, the Seto Foundation, and the LeBurta Atherton Foundation. We are grateful to the many volunteers, interns and students that assisted in data collection, processing and analysis. We also thank Rachel Cartwright, Kristen LaBonte, and Miguel A. Llapapasca for their suggestions regarding the Neu’s analysis, and the three anonymous reviewers for their comments on an earlier version of this manuscript. Coauthor Louis M. Herman passed away during the final stages of the production of this paper. Dr. Herman first described shallow water preferences for mother-calf pairs in Hawaiian waters (Herman and Antinoja 1977). This paper is dedicated to his memory and enduring legacy.

LITERATURE CITED

Baker, C. S., and L. M. Herman. 1981. Migration and local movement of humpback whales (*Megaptera novaeangliae*) through Hawaiian waters. Canadian Journal of Zoology 59:460–469.

Cartwright, R., B. Gillespie, K. LaBonte, T. Mangold, A. Venema, K. Eden and M. Sullivan. 2012. Between a rock and a hard place: habitat selection in female-calf humpback whale (*Megaptera novaeangliae*) pairs on the Hawaiian breeding grounds. PLOS ONE 7(5):e38004.

Ciuti, S., P. Bongi, S. Vassale and M. Apollonio. 2006. Influence of fawning on the spatial behaviour and habitat selection of female fallow deer (*Dama dama*) during late pregnancy and early lactation. Journal of Zoology 268:97–107.

Clapham, P. J., P. J. Palsboll, D. K. Mattila and O. Vasquez. 1992. Composition and dynamics of competitive groups in the West Indies. Behaviour 122:182–194.

Craig, A. S., and L. M. Herman. 2000. Habitat preferences of female humpback whales *Megaptera novaeangliae* in the Hawaiian Islands are associated with reproductive status. Marine Ecology Progress Series 193:209–216.

Craig, A. S., L. M. Herman and A. A. Pack. 2001. Estimating

Residence times of humpback whales in Hawaii. Report to the Hawaiian Islands Humpback Whale National Marine Sanctuary. Office of National Marine Sanctuaries, National Oceanic and Atmospheric Administration. National Oceanic and Atmospheric Administration, U.S. Department of Commerce and the Department of Land and Natural Resources, State of Hawaii. 22 pp.

Craig, A. S., L. M. Herman and A. A. Pack. 2002. Male mate choice and male-male competition coexist in the humpback whale (*Megaptera novaeangliae*). Canadian Journal of Zoology 80:745–755.

Craig, A. S., L. M. Herman, A. A. Pack and J. O. Waterman. 2014. Habitat segregation by female humpback whales in Hawaiian waters: Avoidance of males? Behaviour 151:613–631.

Glockner, D. A. 1983. Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment. Pages 447–464 *in* R. Payne, ed. Communication and behavior of whales. Westview Press, Boulder, CO.

Glockner-Ferrari D., and M. Ferrari. 1985. Individual identification, behavior, reproduction, and distribution of humpback whales, *Megaptera novaeangliae*. Report No. MMC-83/06 NTIS PB85-200772, U.S. Marine Mammal Commission, Washington, DC.

Glockner-Ferrari D., and M. Ferrari. 1990. Reproduction in the humpback whale (*Megaptera novaeangliae*) in Hawaiian waters 1975–88: the life history, reproductive rates and behaviour of known individuals identified through surface and underwater photography. Report of the International Whaling Commission (Special Issue 12):161–169.

Grigg, R., E. Grossman, S. Earle, S. Gittings, D. Lott and J. McDonough. 2002. Drowned reefs and antecedent karst topography, Au'au Channel, S.E. Hawaiian Islands. Coral Reefs 21:73–82.

Grignolio, S., I. Rossi, E. Bertolotto, B. Bassano and M. Apollonio. 2007. Influence of the kid on space use and habitat selection of female Alpine ibex. Journal of Wildlife Management 71:713–719.

Guidino, C., M. A. Llapapasca, S. Silva, B. Alcorta and A. S. Pacheco. 2014. Patterns of spatial and temporal distribution of humpback whales at the southern limit of the Southeast Pacific breeding area. PLOS ONE 9(11):e112627.

Herman, L. M., and R. C. Antinoja. 1977. Humpback whales in the Hawaiian breeding waters: Population and pod characteristics. Scientific Reports of the Whales Research Institute, Tokyo 29:59–85.

Herman, L. M., P. H. Forestell and R. C. Antinoja. 1980. Study of the 1976/77 migration of humpback whales into Hawaiian waters: Composite description. Report No. MMC-77/19. U.S. Marine Mammal Commission, Washington, DC.

Herman, L. M., A. A. Pack, K. Rose, A. Craig, E. Y. Herman, S. Hakala and A. Milette. 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 27:736–768.

Katona, S. K., B. Baxter, O. Brazier, S. Kraus, J. Perkins and H. Whitehead. 1979. Identification of humpback whales by fluke photographs. Pages 33–44 *in* H. E. Winn and B. L. Olla, eds. Behavior of marine animals: Current perspectives in research. Volume 3. Cetaceans. Plenum Press, New York, NY.

Knowlton, R. E., and J. M. Moulton. 1963. Sound production in the snapping shrimps Alpheus (Crangon) and Synalpheus. Biological Bulletin 125:311–331.

Kobayashi, N., H. Okabe, I. Kawazu, *et al*. 2017. Distribution and local movement of humpback whales in Okinawan waters depend on sex and reproductive status. Zoological Science 34:58–63.

Lent, P. C. 1974. Mother-infant relationships in ungulates. Pages 14–55 *in* V. Geist and F. Walther, eds. The behaviour of ungulates and its relation to management. Volume 1. The papers of an International Symposium, Calgary, Canada, 2–5 November 1971. International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.

Lundblad, E. R., D. J. Wright, J. Miller, E. M. Larkin, R. Rinehart, D. F. Naar and T. Battista. 2006. A benthic terrain classification scheme for American Samoa. Marine Geodesy 29:89–111.

Main, M. B., F. W. Weckerly and V. C. Bleich. 1996. Sexual segregation in ungulates: New directions for research. Journal of Mammalogy 77:449–461.

Mobley, J. R., G. B. Bauer and L. M. Herman. 1999. Changes over a ten-year interval in the distribution and relative abundance of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. Aquatic Mammals 25:63–72.

Neu, C. W., C. R. Byers and J. M. Peek. 1974. A technique for analysis of utilization-availability data. The Journal of Wildlife Management 38:541–545.

Pack, A. A., L. M. Herman, A. S. Craig, *et al*. 2017. Habitat preferences by individual humpback whale mothers in the Hawaiian breeding grounds vary with the age and size of their calves. Animal Behaviour 133:131–144.

Pack, A. A., L. M. Herman, S. S. Spitz, *et al.* 2012. Size assortative pairing and discrimination of potential mates by humpback whales in the Hawaiian breeding grounds. Animal Behaviour 84:983–993.

Pinard, V., C. Dussault, J. P. Ouellet, D. Fortin and R. Courtois. 2012. Calving rate, calf survival rate, and habitat selection of forest dwelling caribou in a highly managed landscape. Journal of Wildlife Management 76:189–199.

Rachlow, J. L., and R. T. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): Maternal trade-offs. Journal of Zoology 245:457–465.

Schwede, G., H. Hendrichs and W. McShea. 1993. Social and spatial organization of female white-tailed deer, *Odocoileus virginianus*, during the fawning season. Animal Behaviour 45:1007–1017.

Videsen, S. K. A., L. Bejder, M. Johnson and P. T. Madsen. 2017. High suckling rates and acoustic crypsis of humpback whale neonates maximise potential for mother-calf energy transfer. Functional Ecology 31:1561–1573.

Walker, A. B., K. L. Parker and M. P. Gillingham. 2006. Behaviour, habitat associations, and intrasexual differences of female Stone’s sheep. Canadian Journal of Zoology 84:1187–1201.

Wolf, J. B., G. Kauermann and F. Trillmich. 2005. Males in the shade: Habitat use and sexual segregation in the Galapagos sea lion (*Zalophus californianus wollebaeki*). Behavioral Ecology and Sociobiology 59:293–302.

Wright, D. J., M. Pendleton, J. Boulware, *et al.* 2012. ArcGIS Benthic Terrain Modeler (BTM), v. 3.0, Environmental Systems Research Institute, NOAA Coastal Services Center, Massachusetts Office of Coastal Zone Management. Available at http://esriurl.com/5754.

Received: 29 April 2017

Accepted: 19 January 2018

Figure 1. Study area in the Hawaiian Islands, showing locations of 35 resighted females (numbered) at their earliest sighting when with a calf (white circles) and their earliest sighting without a calf (gray circles) between 1997 and 2008. The star indicates the position of Lahaina harbor, from where nearly all surveys were launched. The dotted line indicates the area bounded by the initial GPS sightings of all pods containing a calf (n = 1,846) and not containing a calf (n = 2,959).

---

[1] Corresponding author (e-mail: pack@hawaii.edu).

Table 1. The proportional use versus availability of each depth range by individual females when with a calf *vs*. without a calf.

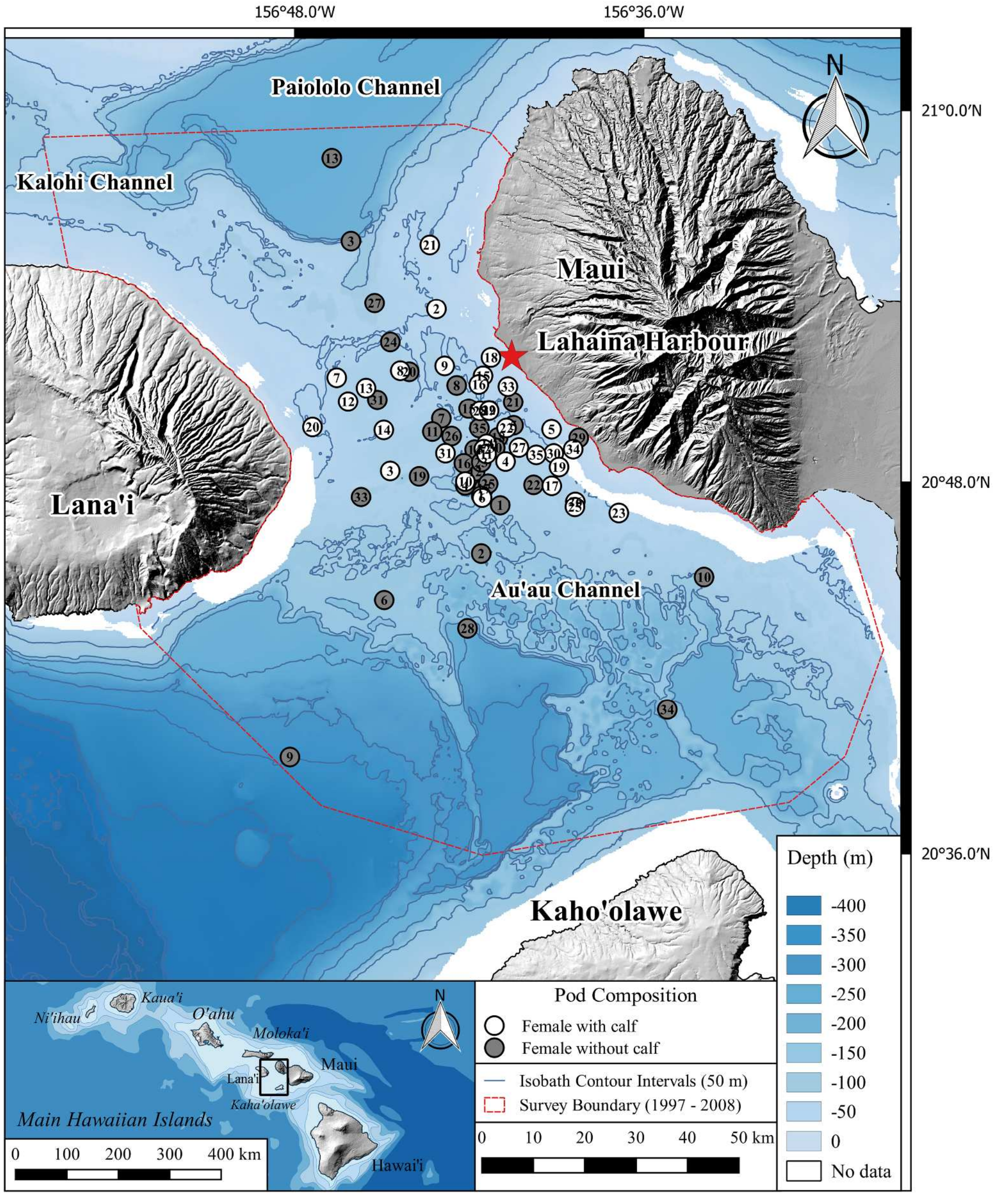
Female	Depth range (m)	Area (km^2)	Counts		Observed proportions (Oi)[a] and 95% CI	Expected proportions (Pi)[a]	Inference	Neu's standardized selection index[a]
			Expected	Observed				
With a calf	< 20	34.7	0.9	0	0	0.027	Avoided	0
	20–39.99	66.7	1.8	4	0.114 (−0.028–0.256)	0.052	Neutral	0.250
	40–59.99	135.4	3.7	13	0.371 (0.156–0.587)	0.105	Preferred	0.400
	60–79.99	196.0	5.3	16	0.457 (0.235–0.679)	0.152	Preferred	0.340
	>80	854.1	23.2	2	0.057 (−0.046–0.161)	0.664	Avoided	0.010
Without a calf	< 20	34.7	0.9	1	0.029 (−0.046–0.103)	0.027	Neutral	0.159
	20–39.99	66.7	1.8	0	0	0.052	Avoided	0
	40–59.99	135.4	3.7	6	0.171 (0.003–0.340)	0.105	Neutral	0.245
	60–79.99	196.0	5.3	19	0.543 (0.321–0.765)	0.152	Preferred	0.537
	>80	854.1	23.2	9	0.257 (0.062–0.452)	0.664	Avoided	0.058

[a] Proportions have been rounded and may not total 1. Neu's indices provide standardized estimates of habitat use, based on habitat availability. Depth ranges were classified as preferred (where 95% CI's of observed counts (Oi) were entirely above the expected counts based on habitat availability (Pi) and avoided (where 95% CI's of observed counts were entirely below the expected counts). In all other (neutral) regions, 95% CI of observed counts included the expected count.

Table 2. The proportional use versus availability of each terrain type (flat *vs*. rugged) within each of the depth ranges for which females in each reproductive state showed a preference (with a calf: 40–59.99 m and 60–79.99 m; without a calf: 60–79.99 m, Table 1).

Female	Depth range (m) and terrain	Area (km^2)	Counts		Observed proportions (Oi)[a] and 95% CI	Expected proportions (Pi)[a]	Inference	Neu's standardized selection index[a]
			Expected	Observed				
With a calf	40–59.99 Flat	98.3	9.5	10	0.769 (0.507–1.031)	0.729	Neutral	0.553
	40–59.99 Rugged	36.5	3.5	3	0.231 (-0.031–0.493)	0.271	Neutral	0.447
	60–79.99 Flat	134.6	11.0	12	0.750 (0.508–0.992)	0.690	Neutral	0.574
	60–79.99 Rugged	60.5	5.0	4	0.250 (0.008–0.492)	0.310	Neutral	0.426
Without a calf	60–79.99 Flat	134.6	13.1	14	0.737 (0.511–0.963)	0.690	Neutral	0.557
	60–79.99 Rugged	60.5	5.9	5	0.263 (0.037–0.489)	0.310	Neutral	0.443

[a] Proportions have been rounded and may not total 1. Neu's indices provide standardized estimates of habitat use, based on habitat availability. Depth ranges were classified as preferred (where 95% CI's of observed counts (Oi) were entirely above the expected counts based on habitat availability (Pi) and avoided (where 95% CI's of observed counts were entirely below the expected counts). In all other (neutral) regions, 95% CI of observed counts included the expected count.



243x290mm (300 x 300 DPI)