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Effects of Sex, Seasonal Period, and Sea State on Calf Behavior in Hawaiian Humpback Whales (*Megaptera novaeangliae*)

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Abstract

Ontogeny of behavior in young humpback whale (*Megaptera novaeangliae*) calves likely reflects preparation for adulthood, including courtship and reproductive activities, predator avoidance, and prey capture. Reproductive strategies differ for males and females, with males competing aggressively for females, while females focus their energy on raising calves; thus, certain behaviors may develop differently in each sex. In addition to these forces driving behavioral development, ambient conditions, such as Beaufort sea state, may also impact behaviors by requiring adaptations to different environments, some of which are louder or more energetic. Herein, we examine the roles of sex, seasonal period, and sea state on Hawaiian humpback whale calf behavioral development. We used underwater video recordings to document when calves were (1) at the surface without their mothers, (2) in physical contact with or in close proximity to (within 5 m) of their mothers, (3) playing, (4) milling, (5) interacting with divers, or (6) vocalizing (social sounds). We analyzed footage of 199 groups (1,485.5 min) in which a calf was present using linear mixed effects models. Sex of the calf was determined in 107 groups (64 females, 43 males). Results indicate that males played or were surface active significantly more often than females, and that calves were at the surface without their mothers significantly more often during January and February than March, and significantly more during the end of January than the beginning of February, indicating that spatial proximity to the mother varies. There were no significant findings characterized by sea state though trends were evident. Behavioral differences by calf sex may be attributable to differences by sex in adult social roles—that is, males may need a higher level of fitness and ability to compete for access to females. Greater mother/calf separation midseason may drive development of motor skills, independence, and fitness in preparation for migration.

Key Words: behavior, calf, humpback whale, *Megaptera novaeangliae*, ontogeny, underwater

Introduction

Behavioral ontogeny reflects preparation for adulthood in young animals. Behavioral development is the result of interactions between genetic and environmental (learning) factors. Herein, we used underwater observation to investigate behaviors of first-year humpback calves and how they developed over their first few months of life. We examined if calf sex played a role in ontogenic patterns, how mother/calf spatial relationships changed over time during the first winter, and the presence/absence of calf behaviors (including social vocalizations) in different sea states.

Life History and Distribution

Humpback whales (*Megaptera novaeangliae*) are a cosmopolitan species that migrate seasonally between high-latitude feeding grounds and low-latitude breeding and calving grounds (Chittleborough, 1965; Katona & Beard, 1990). Population numbers in the North Pacific are estimated at 19,594 (Calambokidis et al., 2008), with the Hawaiian population at 10,103 throughout the main islands, 10% of which are calves (Smultea, 1994; Mobley et al., 1999; Calambokidis et al., 2008; Allen & Angliss, 2010). Distribution of humpback whales includes all main Hawaiian Islands (Baker & Herman, 1981), as well as the northwestern islands (Lammers et al., 2011), with the largest numbers occurring off the four-island area of Kaho'olawe, Moloka'i, Lana'i, and Maui (Mobley et al., 1994, 1999).

Humpbacks are present in Hawaiian waters generally between January and May, during which time breeding and calving occur (Glockner & Venus, 1983). Peak occurrence is between late February and early April (Mobley et al., 2000; Carretta et al., 2010), after which the whales, including newborn calves and their mothers, migrate north to feeding grounds (Baker et al., 1987; Clapham, 1996). With some exceptions, calves are typically weaned after 1 y, at which point the female is available to breed.

In the Hawaiian wintering grounds, mother and calf typically remain in close proximity to one another (Glockner & Venus, 1983; Craig et al., 2003). Due to physiological constraints, calves surface to breathe more frequently than their mothers, leaving them alone at the surface and therefore vulnerable to risks such as predation (Whitehead & Moore, 1982; Flórez-González et al., 1994) or boat strikes (Würsig et al., 1984; Dolphin, 1987; Guzman et al., 2012; Stack et al., 2013). Because of calves' reduced physiological capacity to dive and because cows rest at depth, newborn calves typically surface to breathe more frequently than adult whales especially during rest and slow travel (Cartwright & Sullivan, 2009a). Temporal variability in surfacing behavior has been recorded in right whale calves across the breeding season, wherein calves are in close proximity to their mothers during their first several weeks after birth and at the end of the calving season when migration approaches (Thomas & Taber, 1984; Thomas, 1986). In the interim, calves spend time alone at the surface, exhibiting play behavior and emergence of adult-like behaviors (Thomas & Taber, 1984; Thomas, 1986; Cartwright & Sullivan, 2009a). Temporal period may influence development of calf behavior. Calf behavioral development may also be driven by the roles each sex plays in adulthood. Vocal ontogeny also may be influenced by sex or seasonal period, though data for humpback whale vocal development are sparse. Humpback whale calves produce social sounds (Zoidis et al., 2008), which are non-song vocalizations emitted irregularly, often interrupted by silent periods, and do not contain the rhythmic, consistent, and continuous patterning of song. Social sounds do not have a known function but likely have some biological significance that varies in context.

Calf behavioral development patterns, including mother/calf spatial relationships, playing, and vocalizing can be influenced by many factors. To assess early behavioral development, we examined behaviors of first-year humpback whales underwater and within 5 m of the surface in the central North Pacific population that breeds and winters in Hawaiian waters. We considered whether sex, seasonal period, or sea state could be factors influencing early calf behavior development and the presence of calf social sounds.

We theorize that male and female behavior may develop differently based on the roles each sex will play as adults. We also hypothesize that as the season progresses, spatial relations between mothers and calves change and are related to calf development. Last, we consider whether sea state can affect mother/calf spatial proximity and interaction, including vocal interaction (due to an increase in ambient noise conditions; Richardson et al., 1995).

Methods

Data Collection

The study was predominantly conducted in the near-shore waters of northwestern Maui, Hawai'i, in the winters of 2001, 2002, 2005, 2006, 2008, 2009, and 2010; and in 2004, only off northwestern Kaua'i. Studies were not conducted in 2003 and 2007 due to funding limitations; in 2005, data collection occurred off both Kaua'i and Maui. The primary study area in all years but 2004 was located on the leeward side of Maui, between 20° 40' N and 21° 00' N latitude and 157° 35' W and 158° 10' W longitude, including within the Hawaiian Islands Humpback Whale National Marine Sanctuary. On Kaua'i, the study was conducted on the leeward side near Kekaha, north to Polihale State Park, and west out from the northeast tip of Ni'ihau, between 21° 53' N and 21° 58' N latitude and between 159° 36' W and 160° 03' W longitude.

We located humpback whales using random search patterns, transiting slowly (under 10 kts) and performing visual scans for groups with calves. Groups consisted of at least a mother/calf pair, which were sometimes with one or more escorts (an accompanying adult whale; Tyack & Whitehead, 1983). Group composition was determined in the field using group follows (Mann, 1999) and photographic evidence for later confirmation. Group composition was confirmed during nightly video review by a minimum of two experienced research observers using defined protocols. Mothers were identified by confirming the sex of the adult animal closest to the calf when possible either by the diver in the field or from underwater footage. When direct observations were not obtained, the mother was inferred from her social role (Glockner & Venus, 1983; Glockner-Ferrari & Ferrari, 1985) or because she was the adult continually observed in proximity to the calf (Clapham, 1996) as has been supported by biopsy (Craig & Herman, 1997; Craig et al., 2002). No groups with more than one mother/calf pair were encountered. Escorts were identified based on spatial association to the mother/calf pair and on synchrony of movement with the pair but were not included in analysis for this study (Glockner & Venus, 1983; Mobley et al., 1999).

Calves were identified based on size (typically ranging from ¼ to ½ the length of the proximate adult [presumed mother] in closest association; Glockner & Venus, 1983). We generally targeted groups with calves that were older than the neonate stage; if fetal folds were present along the calf's sides or the dorsal fin was not yet erect, we did not study the group. The sex of calves was determined when possible using genital morphology (presence/absence of a hemispherical lobe; True, 1904; Glockner, 1983) either by the diver in the field or during post-processing video review.

Two divers filmed video of each calf. Post-processing video review included comparison of view angles. Sex confirmation was via a direct view of the genitals using lateral approaches by divers and by verifying shots taken of same animals from different angles when possible. Verifying the sex of whales during video review further confirmed roles identified in the field (e.g., mother, escort).

Once a group with a calf was located, we observed the group for up to 30 min via focal group sampling before entering the water (Altmann, 1974; Mann, 1999). We assessed and recorded initial group behavioral state (overall broad-scale behavioral category of the pod upon first approach) and composition (numbers of animals and number of adults with calf). We monitored throughout each encounter to determine if changes occurred. We categorized behavioral state upon first approach into rest, mill, travel, and play (Glockner & Venus, 1983; Thomas & Taber, 1984; Thomas, 1986; Cartwright & Sullivan, 2009a, 2009b). This parameter qualified the predominant state of the calf at first approach and throughout the overall observation bout.

Rest was defined as the state in which the calf was exhibiting little movement, inactive, and generally at depth with its mother except when respiration was necessary; the only movement that resting calves displayed was to travel to the surface to breathe before settling back next to the mother and occasional slow circular movements during respiration bouts in older calves directly above the mother while she rests at depth. *Mill* was defined as swimming slowly with nondirectional movements in a small perimeter and while generally visible at the surface, characterized by almost constant movement; the mother generally rested below the calf perimeter. This behavior is not previously reported in baleen whale calves (i.e., in Taber & Thomas, 1982; Glockner & Venus, 1983; Thomas & Taber, 1984; Thomas, 1986; or Cartwright & Sullivan, 2009a, 2009b) but may have components similar to "stall" as defined in Cartwright & Sullivan (2009a, 2009b). Milling in our study combined viewing the calf both from our underwater perspective and from topside observation. It covers periods when the calf was not engaged in play; was not resting nor in steady, forward motion (travel); and was not circling above the mother as seen during rest. *Travel* was defined when calf and mother (or whole group) were moving generally in a linear direction and at a steady speed, and may be slow or fast (Thomas & Taber, 1984). *Play* is defined as occurring when the calf was continuously rolling, arching, or twirling (rolling on a longitudinal axis combined with stalling [no forward movement]) either under the water surface (usually within 5 m of surface) or at the surface, in which case activities included surface activity such as pectoral fin slaps; tail swishes; tail slaps; peduncle throws; and chin, half, or full body breaching. We further evaluated play based on its aspects of spontaneity (Bekoff, 1972) and purposelessness (Bekoff & Byers, 1981). Play is a locomotor activity. It can include surface active behaviors but also can occur when there is no surface activity.

After a group was assessed, we deployed snorkelers with digital video cameras using two recording systems: one equipped with a single omnidirectional hydrophone (Biomon BM 8263-3c mounted 1 m below the camera) and the other with a two-element hydrophone array. The latter consisted of two HTI MIN-96 hydrophones mounted 1.5 m apart on a bar perpendicular to the optical axis of the camera. Both cameras were mounted inside underwater housings made by Equinox (Galesburg, MI, USA). We collected data following the methods of Zoidis et al. (2008). Divers entered the water and recorded the pod, while attempting to maintain a distance of 10 m or more from the animals. All efforts were made to minimize disturbance and effects of diver presence on the humpback whales.

Topside behavior and fluke photographs were documented using a Canon 10D digital camera and digital video. Data on environmental conditions were recorded, including Beaufort sea state ranging from levels 0 to 3 (observations ceased in conditions greater than a Beaufort 3), average wave height (ground swell; observations ceased in 1.2 m seas), and percent cloud cover.

We approached and studied groups that included a calf (regardless of calf behavioral state or any other factors), across multiple years, and off two island habitats. This ensured that our data would be from a representative sample of all mother/calf groups within the study area and time. Whale behavior may be unavoidably altered by introducing foreign stimuli, such as boats in proximity, other commonly used research techniques (e.g., tags suction-cupped to or embedded in the animals or biopsy darts), or divers in the water, but all efforts were made to reduce influencing behavior during observations.

Data Processing

We reviewed underwater video of mother/calf groups from eight field seasons in Hawai'i using a modified one-zero behavioral sampling methodology based on Altmann (1974) and Mann (1999). We developed an ethogram detailing specific movements, spatial relationships, and interactions below (at depth) and at or near the surface for mother and calf. Behaviors addressed herein were assessed for the calf in 30 s increments during video review. Groups with less than 30 s of usable video time were not included in the analyses. We examined activities and coded behaviors on our specifically designed ethogram when calves were at depth, 5 m below the water surface, and when at the surface alone in order to elucidate calf behaviors and potentially their ontogeny.

We recorded presence/absence of behaviors in all 30 s segments that were indicative of the following, which were our dependent variables:

1. Calves at the surface alone (included codes for unaccompanied calves at or < 5 m from the surface without mother and with no other humpback whales in view within at least 15 m)
2. Mothers/calves in close proximity (included codes for calf lingering/resting underneath its mother, mother/calf in physical contact, or calf in a nursing position)
3. Calves playing (included codes for calf play and calf surface active when part of play)
4. Calves milling
5. Calves interacting with divers (included codes for calf approaching, looking at, lingering in front of, returning to look at, or contacting diver; all calf-initiated behaviors)

We also documented as the 6th dependent variable the number of social sounds recorded per group using techniques described in Zoidis et al. (2008).

The dependent variables coded "calf mill" and "calf play" in a 30 s segment (#4 above) is different than broad-scale milling or playing as an overall calf behavioral state as described above in "Data Collection." Mill and play can both be an overall activity during an entire observation bout or, at a finer scale, an action the calf engages in during a 30 s increment. For example, a short-term milling bout can occur in the midst of an overall resting period.

Distance between mother, calf, and diver and the depths of animals were estimated in mother body lengths (Glockner & Venus, 1983), assuming an average body length of approximately 13 m for a Hawaiian mother humpback whale (Spitz et al., 2000). The margin of error was approximately ± 2 m based on the standard deviation (SD) and range of measured body lengths of 26 mother whales (Spitz et al., 2000).

Data Analysis

To enable categorical analysis by seasonal period with adequate sample sizes, we divided the breeding/calving study seasons into five 2-wk periods across years. We categorized these into seasonal periods as follows: Period 1 = January 1-15; Period 2 = January 16-31; Period 3 = February 1-14; Period 4 = February 15-28; and Period 5 = March 1-15. To minimize the potential for pseudo-replication and to increase sample independence, we aggregated results from each encounter and took precautions to include encounters with new groups (calves not observed previously) based on standard humpback whale fluke identification for adults (Katona et al., 1979), and other identifying characteristics on the animals' bodies as seen by divers and noted during nightly video review.

We divided the six dependent behavioral variables by the number of 30 s segments in the encounter to give us the average number of times the behaviors occurred per 30 s segment for each calf. We ran a correlation on environmental factors (Beaufort sea state, wave height, and percent cloud cover) and found that all three were correlated with each other. We discuss only Beaufort sea state in our analyses using the first four levels of that variable (Beaufort 0 to 3) because it was reported most consistently of the three throughout the years of our study. We used linear mixed effects models (LMEMs) to test the effects of sex, seasonal period, Beaufort sea state, and the interactions on each of the six dependent behavioral variables. We included group composition (mother/calf, mother/calf/escort, or mother/calf/escort + other adults), overall calf behavioral state (general state of behavior upon approach and during an observation bout as defined above which included rest, mill, travel, and play), and number of boats within 1 km of the group during the encounter as covariates in the model. We used likelihood ratio tests to compare null models (models with only random effects included) to the LMEMs to confirm validity of the latter. Validity was confirmed only when LMEMs differed significantly from the null models. We performed post-hoc Wilcoxon Mann-Whitney tests with Bonferroni corrections (to account for multiple comparisons) to determine how the fixed effects influenced the dependent variables. All analyses were done in *R*, Version 2.15.1 (2011 R Foundation for Statistical Computing).

Results for comparison of sex, seasonal period, and Beaufort sea state by the six dependent behavioral variables are shown in Table 1; they are expressed as boxplots for presentation if significant (Figures 1 & 2). We calculated mean (± SD) frequency of 30 s segments in which behaviors occurred by sex, seasonal period, and/or Beaufort sea state (Table 2). Nonsignificant findings are included in the "Discussion" section.

Results

We analyzed underwater digital video recordings of 199 humpback whale groups in which a calf was present (1,485.5 min; mean = 7.5 ± 9.0 min per group; range = 1.0 to 53.5 min; Table 1). Scatterplots showed similar distributions of frequency of occurrence of each behavior for short durations and for long durations; therefore, we included groups with as little as 1 min of footage. All video was used in the comparisons by seasonal period, though not all was used for comparisons by sex (due to recordings that resulted in undetermined sex identifications) or by Beaufort sea state, which was not recorded during all years (Table 1).

Significant differences were found by sex and seasonal period individually when compared with occurrence of surface activity/play and time the calves spent at the surface without their mothers, respectively (Table 1). No significant differences were found by the interaction of sex and seasonal period or by weather with any variables.

We found 51 of the 199 calves in this study were never at the surface alone (26%). Of the 148 that did surface alone, sex was known for 15 of them (12 females, 3 males).

Sex

We were able to determine calf sex in 107 of the 199 groups (64 females, 43 males) and to document behaviors in 2,228 30 s segments (1,114 min of tape; females = 1,207 segments, males = 1,021 segments; range of 30 s segments for females = 2 to 76, range of 30 s segments for males = 2 to 107). The most commonly exhibited overall calf behavioral state was resting: 65% of the male calves and 70% of female calves predominantly rested. The remaining calves predominantly milled (21% of the males, 22% of the females), travelled (7% of the males, 6% of the females), and played (7% of the males, 2% of the females).

Males played significantly more than females regardless of seasonal period (Table 1). No other significant differences between sex and the dependent behavioral variables were detected ($p > 0.05$). Males exhibited play behavior 0.10 ± 0.15 of the time (99.5 of 1,021 30 s segments), whereas

Table 1. Sample size, minutes of footage, and results of linear mixed effects models (LMEMs) and Pairwise Wilcoxon statistical tests; males played significantly more often than females (LMEM: $p = 0.036$, Pairwise Wilcoxon: $p = 0.039$). Calves were at the surface without their mothers significantly more often during Periods 1 through 4 than Period 5 (1 v 5: $p = 0.009$, 2 v 5: $p < 0.001$, 3 v 5: $p = 0.034$, 4 v 5: $p < 0.001$), and more often during Period 2 than 3 ($p = 0.011$; LMEM: $p < 0.001$). There were no significant differences by Beaufort sea state.

Attribute	*n*	Minutes of footage	Comparison	LMEM *p*	Wilcoxon Z	Wilcoxon *p*
Sex			Surface activity/ play	0.036		
Females	64	603.0	F v M		15.81	0.039
Males	43	510.5				
Total	107	1,113.5				
Seasonal period			Calf at surface	< 0.001		
1 (Jan 1-15)	4	5.5	1 v 5		47.26	0.009
2 (Jan 16-31)	34	286.0	2 v 3		3.68	0.011
			2 v 5		6.59	< 0.001
3 (Feb 1-14)	52	340.5	3 v 5		2.84	0.034
4 (Feb 15-28)	49	302.5	4 v 5		5.31	< 0.001
5 (March 1-15)	60	551.0				
Total	199	1,485.5				
Beaufort			No significance	> 0.05		
0	13	50.0				
1	66	510.5				
2	64	584.5				
3	30	236.5				
Total	173	1,381.5				

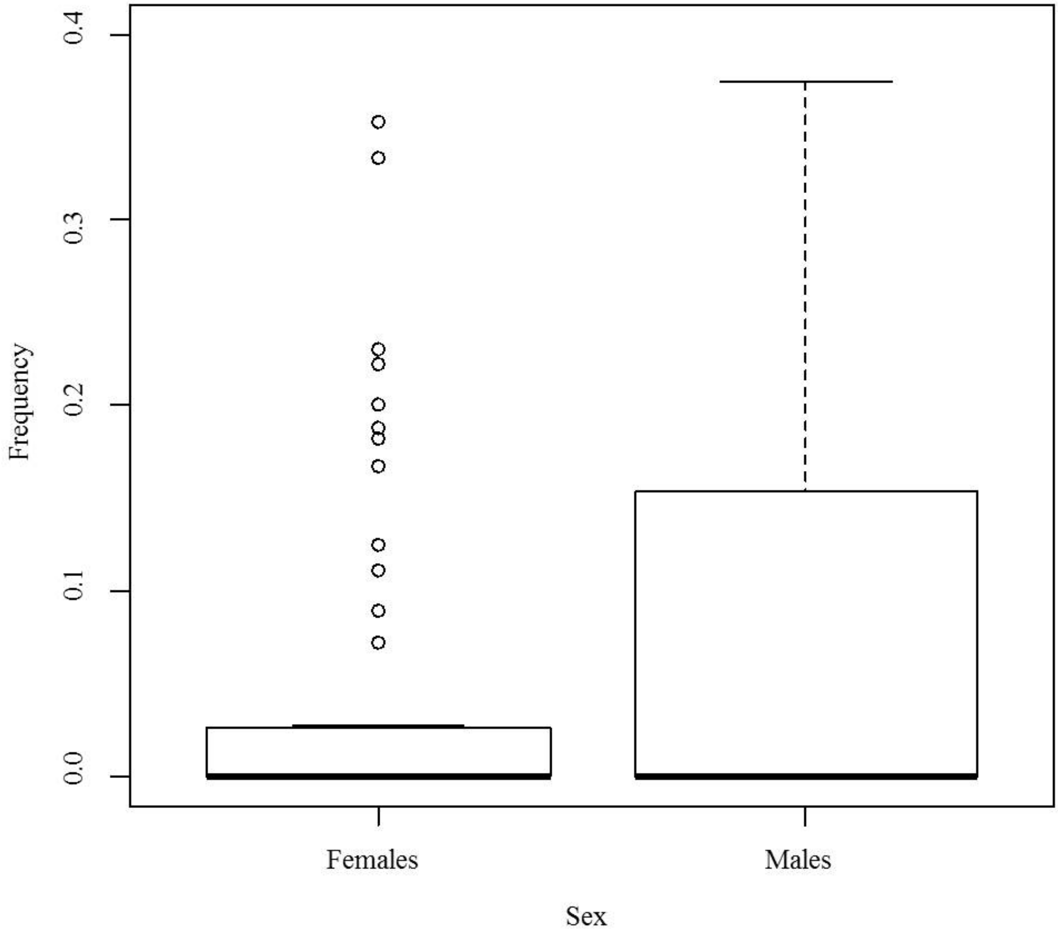

Figure 1. Average frequency of 30 s segments in which calves played by sex; males were surface active/played significantly more than females (see Table 1). The horizontal line through the box shows the median, the bottom of the box shows the 25th percentile of the data, and the top of the box shows the 75th percentile. Y-axis is from 0.0 to 0.4. The error bars show the minimum and maximum of all data.

females played only 0.05 ± 0.10 of the time (57 of 1,207 30 s segments) (see Table 2 & Figure 1).

Seasonal Period
We analyzed five 2-wk segments (January through mid-March) for 199 groups and 2,971 30 s segments (1,485.5 min of video; Table 1). The amount of time that calves were within 5 m of the surface without their mothers was significantly influenced by seasonal period (LMEM: $p < 0.001$). Calves were within 5 m of the surface without their mothers significantly more during Periods 1 through 4 than during Period 5, and significantly more during Period 2 than Period 3 (Table 1). Calves were within 5 m of the surface without their mothers 0.69 ± 0.24 of the time during Period 1 (7.5 out of 11 30 s segments), 0.58 ± 0.29 during Period 2 (334/572), 0.35 ± 0.35 during Period 3 (236/681), 0.46 ± 0.34 during Period 4 (278/605), and 0.13 ± 0.15 during Period 5 (143/1,102) (see Table 2 & Figure 2).

Beaufort Sea State
Beaufort sea state was recorded for 173 groups and 2,762 30 s segments (1,381 min of video; Table 1). There were no significant findings related to sea state.

Discussion

Our findings demonstrate that aspects of behavior of Hawaiian humpback whale calves are influenced by the sex of the calf and the seasonal period. No significant differences were found by

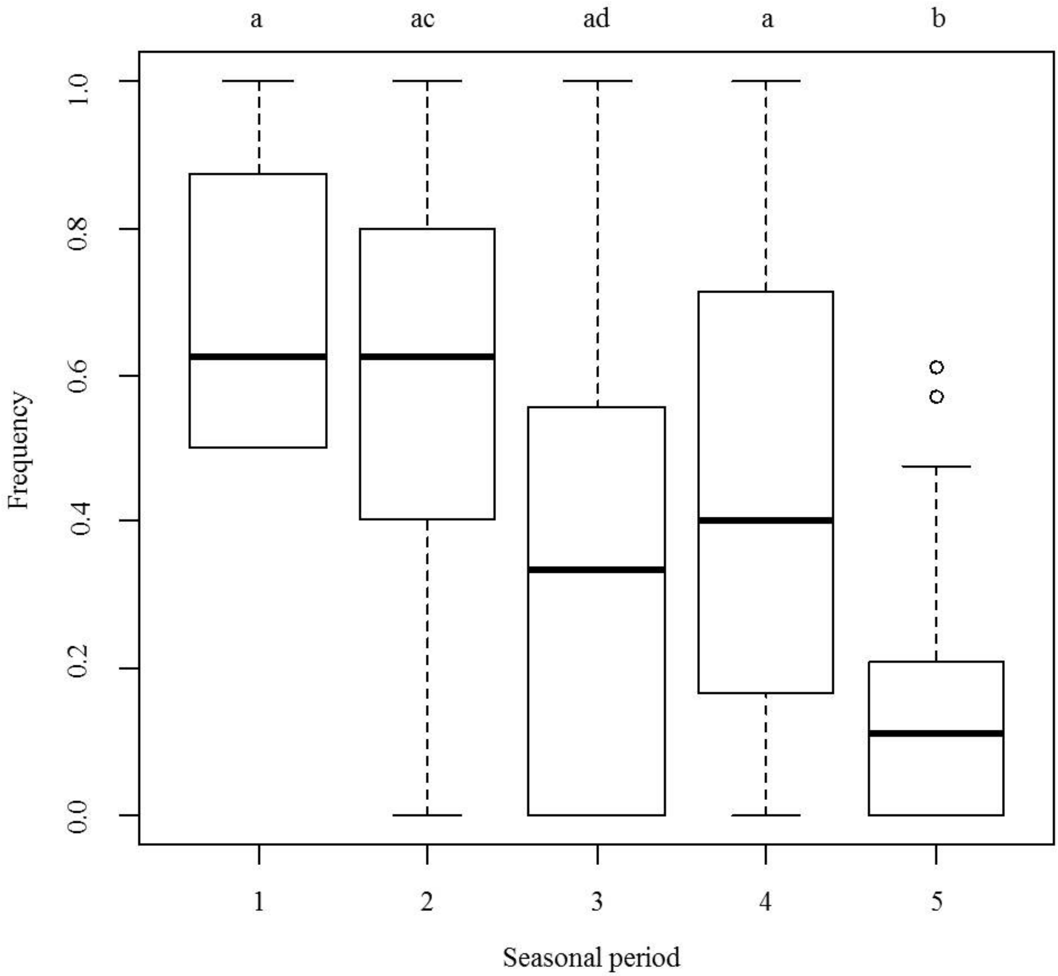

Figure 2. Average frequency of 30 s segments in which calves were at the surface without their mothers by seasonal period; calves were at the surface alone significantly more often during Periods 1 through 4 (denoted by a) than Period 5 (b), and during Period 2 (c) than Period 3 (d) (for *p* values, see Table 1).

the interaction of sex and seasonal period or by weather with any other variables. Several nonsignificant trends in behavior were present by the independent variables, which, with a higher sample size of coded behaviors, may prove significant. Trends in calf behavior, such as seasonal- and sex-influenced patterns, can provide insight into calf behavioral development. This study assessed both behavioral changes and developmental pattern changes that may reflect ontogenic development in mother/calf behaviors. These patterns may be a prerequisite for humpback whale migration, which warrants young animals adjusting to changing habitats in different oceanographic regions. It also entails the development of physical abilities to allow them to survive in new and hazardous environments. Aspects of behavioral development, both physical and social, for young migratory baleen whales are multifaceted and complex, and they change as the calves mature.

Sex

Male calves were surface active or played significantly more than females. This could be a result of preparation for the differing roles of males and females in adulthood. Male and female adult humpbacks display different behaviors, particularly on the breeding and calving grounds.

Adult females show greater parental investment and expend energy on calving and raising young, whereas males spend the winter competing for sexually mature females, with both aggressive and passive displays (e.g., Tyack & Whitehead, 1983;

Table 2. Average (± SD) frequency of 30 s segments in which each behavior or event occurred by sex, seasonal period, and Beaufort; significant groups are denoted by subscript letters. Males (denoted by $_b$) played significantly more often than females ($_a$; $p = 0.039$). Calves were at the surface without their mothers significantly more often during Periods 1 through 4 ($_c$) than Period 5 ($_d$; 1 v 5: $p = 0.009$, 2 v 5: $p < 0.001$, 3 v 5: $p = 0.034$, 4 v 5: $p < 0.001$), and more often during Period 2 ($_e$) than 3 ($_f$; $p = 0.011$). There were no significant differences by Beaufort sea state. Sample sizes are provided in Table 1.

Attribute	Calf at surface w/o mother	Mother/calf in close proximity	Calf surface active/play	Calf mill	Calf/diver interaction	Calf social sounds
Sex						
Females	0.36 ± 0.32	0.25 ± 0.27	$0.05 \pm 0.10_a$	0.10 ± 0.11	0.10 ± 0.13	0.18 ± 0.26
Males	0.47 ± 0.30	0.25 ± 0.26	$0.10 \pm 0.15_b$	0.07 ± 0.11	0.14 ± 0.22	0.10 ± 0.19
Seasonal period						
1	$0.69 \pm 0.24_c$	0.40 ± 0.22	0.00 ± 0.00	0.40 ± 0.13	0.06 ± 0.13	0.00 ± 0.00
2	$0.58 \pm 0.29_{ce}$	0.18 ± 0.26	0.07 ± 0.14	0.06 ± 0.11	0.07 ± 0.18	0.10 ± 0.15
3	$0.35 \pm 0.35_{cf}$	0.23 ± 0.24	0.04 ± 0.12	0.10 ± 0.14	0.07 ± 0.13	0.18 ± 0.27
4	$0.46 \pm 0.34_c$	0.20 ± 0.25	0.05 ± 0.12	0.07 ± 0.10	0.07 ± 0.16	0.10 ± 0.24
5	$0.13 \pm 0.15_d$	0.30 ± 0.28	0.06 ± 0.12	0.08 ± 0.11	0.11 ± 0.16	0.06 ± 0.14
Beaufort						
0	0.25 ± 0.31	0.40 ± 0.35	0.08 ± 0.15	0.17 ± 0.13	0.25 ± 0.30	0.17 ± 0.28
1	0.30 ± 0.33	0.22 ± 0.25	0.06 ± 0.15	0.08 ± 0.12	0.07 ± 0.14	0.09 ± 0.18
2	0.38 ± 0.34	0.23 ± 0.22	0.05 ± 0.11	0.06 ± 0.09	0.09 ± 0.16	0.07 ± 0.15
3	0.38 ± 0.31	0.23 ± 0.33	0.12 ± 0.08	0.06 ± 0.13	0.04 ± 0.06	0.08 ± 0.19

Baker & Herman, 1984; Helweg & Herman, 1994; Craig et al., 2002). Aggressive displays include bubble blasts, head lunges, physical bumping and pushing, and charges and strikes. Passive displays include singing and escorting, which can turn into aggressive displays when challenged. Because of this disparity between the sexes in terms of future parental investment, males and females utilize different strategies to further their reproductive success over the course of their lives.

Sex-specific traits are evident in other polygynous adult mammals, including terrestrial animals. Development of larger bodies, greater fighting abilities, and the subsequent benefits of a higher social status are part of the success in male mating access in ungulates (Clutton-Brock et al., 1982) as compared to sex-specific traits in adult ungulate females which show greater parental investment in the care and protection of their offspring (Geist, 1971; Jakimchuk et al., 1987; Main & Coblentz, 1990). Young male elephant calves have different nursing behaviors than female calves which, in turn, optimize their size later in life. Size is an important component of future mating success of polygynous adult bull elephants (Lee & Moss, 1986). Male humpback calves spending more time in play (more locomotor activity) indicates that humpback whale behavioral gender divergence begins early.

In mammals, play at an early age has been suggested as critical to the development of social and motor skills (Bekoff, 1984). Play patterns and behaviors often mimic techniques to escape from predators, to capture prey, and to acquire mates (Byers & Walker, 1995). Play is an important tool in sensory, motor, cognitive, and social development as it mimics real-life scenarios such as predator avoidance, prey capture, and intraspecific interactions, including fighting. It helps develop social skills (Bekoff, 1984) and the skills necessary for survival and successful reproduction (Fagen, 1981; Byers & Walker, 1995). Play's role in development is supported by two hypotheses: (1) the motor-training hypotheses and (2) the social-relationship hypothesis (Byers & Walker, 1995; Spinka et al., 2001). Both these hypotheses have been presented to suggest that play behavior is a preparatory tool for adulthood. The motor-training hypothesis suggests play is geared toward developing motor skills needed as adults. Because it is important for males but not females to develop fighting skills, male calves may engage in at-surface play behavior to a greater extent than female calves.

The social-relationship hypothesis suggests play is geared toward learning to interact with individuals and with groups of specific social demographics the animals will encounter as adults (Byers & Walker, 1995; Spinka et al., 2001). In terrestrial species, such as ungulates (lambs), primates (olive baboons and rhesus monkey), and the Norway rat, the ontogeny of play has been studied in order to evaluate play and the role of social dynamics as well as the role of gender or natural selection (e.g., Sachs & Harris, 1978; Chalmers, 1980; Meaney et al., 1981). Sexual differences have been documented in play behavior of young in species with differing gender reproductive strategies as adults (Spinka et al., 2001). Infant male gorillas, for example, exhibit a higher incidence of certain play behaviors and play initiation than females (Maestripieri & Ross, 2004).

The role of play in the development of young male humpbacks is likely influenced by both the motor-training and the social-relationship hypotheses. Although calves play solitarily in the Hawaiian wintering grounds (as compared to Hervey Bay, Australia, where mother/calf pairs engage with other mother/calf pairs; Gibson et al., 2009), play results in indirect social benefits by developing the locomotor skills necessary to fulfill adult social roles. Furthermore, surface active and play behaviors, such as twirling, rolling, breaching, and charging, may lead to the development of behaviors that will physically prepare males for male-male competition, as seen in competitive groups (where males perform these behaviors to displace challenging escorts), and mate acquisition.

When comparing behaviors by sex, while not significant, trends indicate male calves were at the surface without their mothers and interacted with the divers more often than females. These behaviors show developing independence and boldness, both important for fitness for males, who will be competing for females as adults. Females milled and emitted social sounds more often than males, which may build social vocal repertoire and contact communication skills when female calves later become mothers. Northern right whale mothers vocalize to their calves when they become separated, presumably to reunite (Parks & Tyack, 2005). Both sexes were in close proximity to their mothers with equal frequency.

The role of adult male humpbacks on the breeding grounds is primarily to out-compete other males for breeding opportunities (Clapham et al., 1992). Increasing fitness via greater physical activity, swimming at the surface, and motor development from a young age may give certain males advantages over others (Cartwright & Sullivan, 2009a). This development is useful in order for a male to become the primary escort of a female; it is also useful for a challenging male (a secondary or joining escort) that may be more likely to approach and compete with the primary escort if the challenging male has developed greater risk-taking abilities. In contrast, the role of the female in adulthood is to rear and wean calves (Clapham, 1996). Although males compete for females, the choice of mate is made by the females (Clapham, 1996), and they do not compete with other females for adult males. Thus, playing to mimic competitive or aggressive displays is likely not as crucial to females in behavioral development as it appears to be for males. We would predict that because it is more important for adult male humpback whales to develop fighting skills than for females, that male calves would exhibit risk-taking behavior to a greater extent than female calves; male humpback calves staying at the surface alone engaging in visible (e.g., surface active or play) behaviors is an example of risk-taking behavior.

Seasonal Period

Spatial distances between calves and mothers varied, with different proximities evident by seasonal period. Calves were at the surface alone significantly more during January and February than during March, and significantly more during the end of January than the beginning of February, indicating humpback calf spatial patterns are not distinctly linear as time progresses. Overall, our findings for calves alone at the surface were consistent with Cartwright (2005); 26% of calves from our study were never at the surface alone compared with 25% of calves from Cartwright's study.

In addition to developmental behavior patterns by sex, other baleen whales such as southern right whales (*Eubalaena australis*) and some bottlenose dolphins (*Tursiops* sp.) have distinct temporal regimes in their development (Taber & Thomas, 1982; Thomas & Taber, 1984; Gubbins et al., 1999) and exhibit mother/calf spatial patterns where proximity varies.

Young humpback whale calves associate closely with their mothers, benefitting from their vigilance and protection (Szabo & Duffus, 2008). In general, behavioral development in a variety of young mammals follows a pattern of increasing independence with age (Lee & Moss, 1986; Cousse et al., 1994; Schwede et al., 1994; Miles & Herzing, 2003; Gibson & Mann, 2008; Stanton et al., 2011). Newborn dolphin and whale calves spend most of their time within a body length or two of their mothers, but as they age, this distance increases while time spent close to their mothers decreases (Taber & Thomas, 1982; Mann & Smuts, 1999). In a study of one captive gray whale (*Eschrichtius robustus*) calf (Wisdom et al., 2001), an opposite sequence of behavioral phases was noted wherein the calf was being rehabilitated and showed a pattern of less activity from February 1997 through March 1998. While it is possible that this pattern is typical of gray whale calves in the wild, it is difficult to directly compare this calf's behavioral development to that of wild gray whale calves or young of other baleen whale species.

The pattern of changing spatial proximity is seen in southern right whale calves from birth until they prepare to migrate. Neonate calves are in close proximity to their mothers; then, as they grow, during their mid-seasonal period, they gain independence and are at the surface without their mothers. Just before migration, they once again return to swimming in close proximity to their mothers (Taber & Thomas, 1982; Thomas & Taber, 1984; Thomas, 1986). Humpback whale calves in our study exhibit this same general pattern. While the initial proximity noted in right whales between mother and calf at the surface was not significant in our study, it was a nonsignificant trend (a higher sample size could reveal significance in comparisons with Period 1). It is noteworthy that humpback whale calves were in close proximity to their mothers most often during the first and last periods, Periods 1 (40% of the time) and 5 (30% of the time), compared with ~20% during the three middle periods when they are more distant, following the same pattern of right whale calves, a similar baleen whale species.

As the first season of life progresses, calves grow and develop their motor abilities. Generally, mother/calf proximity increases across the breeding season until Period 5. Both in right and humpback whales, calves linger at the surface without their mothers for longer periods of time as the weeks progress until just prior to commencing migration, an energetically costly period (Craig & Herman, 1997). In right whales, calves in Period (stage) 1 seldom separate from their mothers (Taber & Thomas, 1982), which is similar to our findings that in the earliest seasonal period, neonate humpback whale calves typically spent the most amount of time in proximity to their mothers. In Periods 2, 3, and 4, calves spent less than a quarter of their time in proximity to their mothers. These are also the periods in which they circled above the mother (at depth) during bouts of separation, similar to right whale calves, perhaps to practice increased separations, greater spatial distances, and increasing independence while maintaining an awareness of the mother's position. More time spent engaged in more constant locomotor activity at the surface while the calf is "away" from the mother likely increases the fitness of the calf and promotes development of motor skills. Right whale calves in these interim periods also spent time alone at the surface, exhibiting play behavior, improving coordination, and developing the muscle strength necessary for migration (Thomas & Taber, 1984; Thomas, 1986).

The trends evident in baleen whale calf behavior with regards to mother/calf spatial proximity may demonstrate an ontogenic pattern comprised from a suite of factors. Development of mother/calf spatial relationships over time that show a distinct beginning, middle, and end pattern likely reflect calves' growth patterns and interrelated survival requirements. Greater fitness and expanded locomotor skills are useful both for the northern migration, where long periods of travel are required and predator avoidance and prey capture abilities are necessary, and for survival into adulthood, where increased fitness may offer an advantage for successful mating or calf rearing. In March, as humpbacks start preparing for migration, calves' respiration rates were more similar to those of their mothers (they were able to hold their breath longer), indicative of greater fitness.

Newborns initially need to surface more often than their mothers both to breathe more frequently and to gain muscle tissue (Cartwright & Sullivan, 2009a), and they need to swim more constantly with their mothers due to the newborn's reduced capacity to be buoyant (Thomas & Taber, 1984). Swimming constantly is likely a form of practice or learning (Thomas & Taber, 1984); it also increases fitness (Cartwright & Sullivan, 2009a). Seasonal Periods 2 through 4 in which more solitary movements at the surface are observed likely contribute in other ways to the impending migration (i.e., increasing coordination, continuing to build muscle, and improving general motor skills through activities at the surface; Thomas & Taber, 1984). In addition, it may enhance investigative time away from the mother along with the emergence of adult-like behaviors such as surface activity or faster swimming that an adult might use in competitive groups or in pursuit of prey (Fish, 1993). Results from Stanton et al. (2011) suggest that temporary separations allow dolphin calves to build and strengthen their social networks. Humpback whales have different social development than dolphins, but similarities may reflect that the humpback whale calf's separation time also leads to social skills later in adulthood.

Calves resume remaining close to their mothers in preparation for migration in Period 5. This "premigration" period, similar to that documented in southern right whales (Taber & Thomas, 1982), interrupts the independence activities likely in order to allow a return to coordinated movements with the mother that would be vital for survival in the long migration northward.

Surprisingly, nonsignificant trends show that calves were at the surface without their mothers more in higher sea states than in lower sea states. Consistent with that trend, calves were within 5 m of their mothers nearly twice as often in a sea state 0 than in the higher three sea states. These findings are unexpected because calm conditions provide the least amount of ambient disturbance and therefore would seem to provide the safest conditions for calves venturing away from their mothers. This finding confounds the idea that calves would stay in proximity to the mother for protection. It may be that curiosity (especially in older calves) outweighs caution and may be triggered by the increase in wave action and ambient noise that accompany higher sea states. It is also possible that the conditions present in higher sea states (higher wave height and wind chop) allow for greater muscular and respiratory development as a result of longer duration swimming at higher speeds in rougher waters (Fish, 1993). Calves also were surface active or playing more often in sea state 3 than in the three lower sea states. Perhaps, like dolphins playing in the wake of boats, higher sea states provide a more stimulating environment for surface activity than flat seas. Calves milled, were interested in the diver(s), and emitted social sounds two to three times more in sea state 0 than in the other three sea states. The latter could be due to an increase in masking which occurs at higher sea states from ambient noise negating social sounds which attenuate quickly (Zoidis et al., 2008). Also, although not significant, the occurrence of calf social sounds was higher in the beginning of February than during any other period.

Ecological and behavioral studies have long been conducted by observing organisms in their natural environment (Connor & Smolker, 1985; Herzing, 1996, 1997; Dudzinski, 1998); the most well-known may be those of Goodall (e.g., Van Lawick-Goodall, 1986) with chimpanzees and Fossey (e.g., Fossey, 1976) with gorillas. Although an obvious limitation to entering an animal's habitat is that it may disrupt natural behaviors, it allows for greater observation and depth of study in marine mammals (e.g., Glockner & Venus, 1983; Similä & Ugarte, 1993) that otherwise would only be viewed when they surface. Underwater observation, when done inconspicuously and with minimally invasive techniques, can provide a unique and comprehensive viewpoint on whales and their behaviors despite the limitations of presenting an external stimulus that may alter behavior (Glockner & Venus, 1983; Glockner-Ferrari & Ferrari, 1985; Similä & Ugarte, 1993; Spitz et al., 2000; Zoidis et al., 2008; Cartwright & Sullivan, 2009a, 2009b; Pack et al., 2009). Additionally, some habituation to human activity is likely (as noted for dolphins in the Bahamas; Dudzinski, 1996, 1998), particularly in Maui, which is a high traffic recreation area due to the presence of vessels, snorkelers, and paddleboarders who may not be aware humpbacks are resting nearshore.

Individual variations in maternal care have been documented in dolphins (Hill et al., 2007). Off Maui, certain humpback whale individuals are known from many study years (M. Ferrari, pers. comm., 4 February 2010) and typically remain undisturbed by the presence of a diver; while other mothers with calves are skittish either because they are inexperienced (Mann & Smuts, 1999) or because they are unhabituated to divers. Likewise, some calves are cautious of a diver and maintain a large berth and close proximity to their mother; others are bold and approach and investigate divers, leaving the mother for longer periods of time; and some appear to ignore the divers. Last, increasing our sample size of calves in this study would strengthen our results and potentially allow detection of significance where there are currently nonsignificant trends. Better methodologies to definitively and precisely age calves within their first few months of life will also greatly enhance a more refined examination at the ontogeny of this species.

Conclusion

Continued data collection on humpback whale calves will increase our knowledge of calf activity during each of the five periods of development examined in this study which, consistent with the goals of the Humpback Whale Recovery Plan (National Marine Fisheries Service [NMFS], 1991), may present more significant trends to aid in understanding humpback whale ontogeny and endangered species management. Tagging research will allow us to collect data for longer periods and during nighttime hours, which, in turn, will provide a more complete understanding of calf activity budgets and allow us to investigate diel patterns. Broadening the scope of this study to other parts of the Hawaiian Islands, specifically the northwestern Hawaiian chain, or to the Caribbean will allow us to determine if trends are unique to the population living in the main Hawaiian Islands or can be extrapolated to broader regions. Additional parameters such as assessing effects, if any, of escort presence on mother or mother/calf behavior/spatial distances are part of our future goals. Understanding humpback whale calf behavior is necessary to allow for proper management in order to adhere to the goals of species recovery.

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