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Behavioral ontogeny in humpback whale (*Megaptera novaeangliae*) calves during their residence in Hawaiian waters

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ABSTRACT

The ontogeny of behavior in young offspring is a key component of a species life history, influencing short-term survival and life-long future fitness. In this study, we examine the behavioral ontogeny of humpback whale calves during their natal season on the winter breeding grounds. Behavioral data were collected during focal follows for 69 calves. Their relative age was estimated based on the degree of unfurling of the dorsal fin, and analysis of their time budgets revealed that behavior changed as the calves matured. Among the youngest group of calves ($n = 27$), persistent travel accounted for median 85% (interquartile range 34%) of the calves' time budget, they spent little time alone at the surface and the breathing regime included frequent intermittent breaths. Within the oldest group of calves ($n = 26$), time spent traveling dropped to a median 47% (IQR 42%) of the time budget, they spent more time at rest, surfaced alone more frequently, and the breathing regime more closely resembled that of adult humpbacks. We suggest potential functions for these and other components of calf behavior during this period, and review our findings in light of recent discussions on the role of predation pressure as a driving force in mysticete migration.

Key words: humpback whale calves, *Megaptera novaeangliae*, ontogeny, antipredator behavior, calf survival and fitness.

The skills and attributes that young offspring acquire during early ontogeny are generally fitness based (*e.g.*, Estes *et al.* 2003, Gibson and Mann 2008), impacting both short-term survival of the individual (*e.g.*, Fisher and Goldizen 2001, Beauplet

et al. 2005) and long-term population dynamics (Clutton-Brock *et al.* 1987, Lindström 1999). Intraspecific differences in early ontogeny, such as rates of growth and levels of play, are strongly influenced by levels of maternal care and provisioning (*e.g.*, Festa-Bianchet and Jorgeson 1998, Agrawal *et al.* 2001, Sharpe *et al.* 2002). In contrast, interspecific variations in early ontogeny often reflect variable life histories (*e.g.*, Arnould *et al.* 2003). In marine mammals, early behavioral ontogeny is well documented for many pinnipeds (*e.g.*, Guinet *et al.* 2005, Burns and Rehberg 2008), and in the more accessible odontocetes, such as bottlenose dolphin, *Tursiops truncatus* (*e.g.*, Mann and Smuts 1999, Mann and Watson-Capps 2005, Gibson and Mann 2008). By comparison, relatively few studies have focused on the ontogeny of young mysticetes. Notwithstanding, this early ontogeny may shape key aspects of mysticete life history.

Most mysticetes migrate seasonally from high latitude/high productivity feeding areas to low latitude/low productivity breeding areas (*e.g.*, Chittleborough 1965, Rice and Wolman 1971, Payne 1976, Katona and Beard 1990). It is generally accepted that the migration is fitness based, with the energetic advantages of birthing and raising young calves in calm, warmer waters (*e.g.*, Brodie 1975, Clapham 2001) primarily benefiting reproductive females (*e.g.*, Dawbin 1966). However, an alternate hypothesis, originally proposed by Corkeron and Connor (1999), suggests that migration may be an antipredator strategy that minimizes the risk of predation by killer whales (*Orcinus orca*) on baleen whale calves. Several recent publications provide evidence that is pertinent to this hypothesis. Reeves *et al.* (2006) reviewed current evidence, ecological indicators, and anecdotal accounts from the last 200 yr and concluded that killer whales predate baleen whales, including humpbacks, and favor calves as prey. Mehta *et al.* (2007) analyzed long-term rates of scar accumulation in baleen whales and similarly concluded that killer whale predation of baleen whales occurs, with calves on the natal migration being the most frequent targets. Ford and Reeves (2008) compiled 84 accounts of predatory interactions between killer whales and baleen whales and identified a range of aspects of morphology and migratory behavior in baleen whales that function as antipredator strategies. Taken cumulatively, these reports suggest that killer whales predate humpback whales and young humpback whale calves are particularly vulnerable. Migration to warmer waters prior to or immediately following parturition would place the youngest calves out of the habitual range of mammal-eating killer whales (Forney and Wade 2006); however, migration is energetically costly for baleen whale mothers (Lockyer 2007). They rarely feed in the breeding regions (Chittleborough 1965, Payne 1986) yet must accommodate the high energetic costs of lactation (Lockyer 2007) and persist on the breeding grounds later than females without calves (Jones and Swartz 1984, Burnell and Bryden 1997, Craig *et al.* 2003). Whatever the explanation may be, these costs of migration and persistence in breeding regions support the assumption that migration provides some tangible fitness benefit for the mother or her calf.

Where the behavioral ontogeny of baleen whale calves has been documented, periods of play, exercise, and persistent travel characterize specific age stages. For young southern right whales (*Eubalaena australis*) an initial period of almost constant travel is followed by a mid-stage, that comprised of less travel, calf play, and extended rest, and a final short, premigratory period where mother–calf pairs resume rapid travel immediately prior to migration (Taber and Thomas 1982, Thomas and Taber 1984). In gray whales (*Eschrichtius robustus*), the sequence of the behavioral phases is reversed. Early in the season, mother–calf pairs rest and nurse in calm waters. Later in the season, they relocate to deeper waters where currents are stronger. Mothers

accompany their calves into areas of maximum current during tidal changes (Jones and Swartz 1984) and movements during this period also include forays outside the breeding lagoons (Jones and Swartz 1984, Mate *et al.* 2003).

While the basic structure and common components of humpback whale calf behavior within breeding regions, such as echelon travel and calf surface behaviors, have been described (*e.g.*, Glockner and Venus 1983, Glockner-Ferrari and Ferrari 1985), the behavioral ontogeny of humpback whale calves has not been documented. This may be due to the low resight rates of known individuals (Spitz 1999) and the challenges in determining the age of individual calves. Methods used in the other studies, such as resightings of known mother–calf pairs from a high, land-based vantage point (Thomas and Taber 1984), or the assumptions of synchronicity in birthing based on whaling data (Jones and Swartz 1984), are not easily applicable. For humpback whales, land-based observations do not facilitate photo identification of individuals, in Hawaiian waters whales range widely across the breeding region (Cerchio *et al.* 1998), and birthing is asynchronous across a 4- to 6-mo period (Chittleborough 1953, 1958). Although certain morphological features have been used to distinguish humpback whale calves of different relative age (Chittleborough 1953, Darling 1983, Glockner and Venus 1983, Spitz 1999), documentation of these traits requires expensive aerial observations or underwater observation that may impact whale behavior (Constantine 2001, Lundquist 2007).

In odontocetes, furred or floppy dorsal fins have been used to identify early neonates (*e.g.*, Dearolf *et al.* 2000, Noren *et al.* 2006). This feature was first described by McBride and Kritzler (1951) and has been attributed to the curled position of the calf *en utero* (Etnier *et al.* 2004). Essentially, *en utero*, the fetal dorsal fin is completely furred around the spine (Etnier *et al.* 2004) and the fetus is bent, both laterally and ventrally (Cockcroft and Ross 1990). This facilitates growth *en utero* and accounts for the occurrence of fetal folds at parturition (Cockcroft and Ross 1990). However, this extreme flexibility of the dorsal fin impedes swimming and immediately following parturition and over the next 2 wk the dorsal fin stiffens and straightens (McBride and Kritzler 1951, Etnier *et al.* 2008). In this paper, we demonstrate that the dorsal fin in humpback whale calves straightens with age and can be used to indicate relative age of calves in the breeding region. We use this technique to describe temporal and geographic variations in two age classes of a local Hawaiian calf population and test the hypothesis that behavior of calves changes as they mature. We compare the changes in behavior to patterns described for other baleen whale calves and discuss these results in light of potential fitness benefits for the mother–calf pair.

METHODS

The study was conducted in the near shore waters of the Hawaiian Islands, a primary breeding region for humpback whales of the central North Pacific (Calambokidis *et al.* 2001). Current estimates suggest that the adult population using this region numbers nearly 10,000 (Calambokidis *et al.* 2008) and calves make up to 10% of the population in this area (Mobley *et al.* 1999, Smultea 1994). Data were collected over five winter seasons, using inboard/outboard vessels of 8 m or less, out of Lahaina Harbor, Maui, Hawaii (20°52'N, 156°40'W), between 1999 and 2002, and out of Puako Small Boat Ramp, Hawaii (19°58'N, 155°50'W) in 2003. Sampling was conducted within a 10-km radius of these access points, where all water depths are less than 200 m, and confined to calm waters (Beaufort sea state 2 or less).

Group Selection, Approach, and Monitoring

Our initial direction of travel each day was chosen based on prevailing weather and water conditions, as calm water was required to conduct the behavioral follow and reduced the need to closely approach focal groups. Weather and sea conditions, time and location were noted for all groups containing calves that were encountered in the study area.

Group composition was determined during initial surface sightings. Calves were classified based on size (between one-third and one-half of the length of the adult with which they were most closely associated [Chittleborough 1958]) and the mother based on her proximity to the calf. Other accompanying animals were classed as associated male escorts if synchrony of movement was apparent and they were within three body lengths of the nearest other associated animal (Glockner and Venus 1983, Mobley and Herman 1985, Smultea 1994). Potential groups were approached at speeds of below 12 km/h up to a distance of 300 m. Between 300 m to just above 100 m vessel speed was adjusted to match the speed of the focal group.

Photographic Documentation

For all surface photography we used a Canon EOS A2 35-mm still camera, with a 300-mm lens and Kodak 200 print film (Eastman Kodak Company, Rochester, NY, USA). Photos were scanned, using an HP Photosmart scanner (Hewlett-Packard Company, Palo Alto, CA, USA). Fluke identification photographs of all adult whales were obtained following standard established methods (Katona *et al.* 1979), and used to confirm resightings of individual mothers. Fluke markings in calves are not persistent (Glockner and Venus 1983) so these could not be used for ID purposes. However, the calf was photographed at the surface to document any scars or other external markings, and the angle of persistent furl, or tilt, of the dorsal fin (see Fig. 1). The image was taken from the rear, as close as possible to the 6 o'clock position directly behind the calf, with the calf perpendicular to the water surface. As calves dive they arch slightly and assume a slightly more elevated profile in the water, providing the ideal opportunity to obtain this image. For comparative purposes, we also photographed a selection of mother and escort dorsal fins from the same aspect. Two snorkel divers in the water used a Sony DCR PC 100 (Sony Electronics Inc, Tokyo, Japan) in an Oceanpro housing to videotape the morphology and underwater behavior of the calves. The focal follow was conducted first, followed by surface photography and then underwater documentation to facilitate collecting the behavioral data without disturbing the group for photography.

The Focal Follow

Groups for behavioral follows were selected from within the calmest waters of the study area, away from areas of predictably high levels of vessel traffic. Prior to commencing the follow, the behavioral state and speed of the focal group was monitored for any evidence of response to the vessel, such as continually increasing swimming speeds, increasing frequencies of extended, fluke-up dives, or abrupt cessation of previously observed surface behaviors. Behavior was recorded continuously onto a tape recorder, for 20 min at a distance of 100 m.

If there was no apparent evidence of vessel avoidance, then the group was approached to the maximum distance that allowed for accurate observation of behavior.

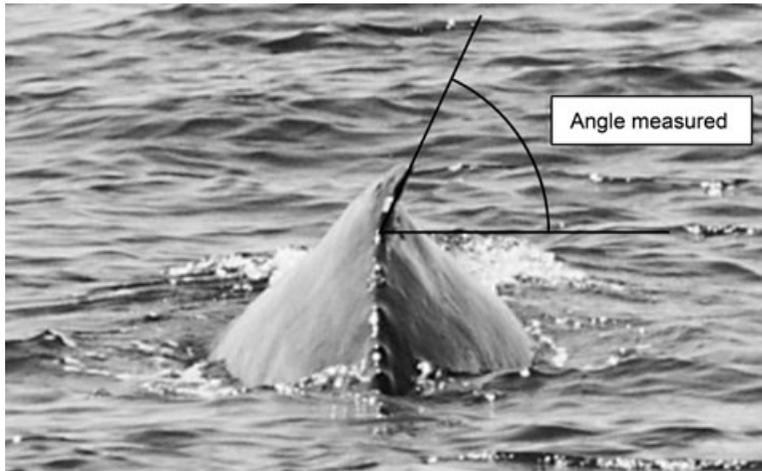


Figure 1. Demonstration of the method used for measuring the angle of the dorsal fin in humpback whale calves. The image of the dorsal fin was taken as close as possible to the 6 o'clock position, to show the whole extent of the calf's dorsal fin, with the calf in an upright position relative to the surface of the water. The angle of the fin relative to the horizontal axis was measured in Adobe Photoshop 7. In "furled" fins the angle of the dorsal fin was $<62^\circ$, in "unfurled" fins the angle was $>72^\circ$.

This varied with water conditions but in all cases we maintained a minimum distance of 20 m from any associated animals and 50 m from any unaccompanied mother-calf pairs (*e.g.*, Szabo and Duffus 2008). During the focal follow the research vessel maintained a consistent speed and position relative to the group (Nowacek *et al.* 2001, Williams *et al.* 2002). Vessel speed and heading matched the movement of the group and any necessary adjustments were made when the whales were submerged. If a mother-calf pair swam within 50 m of the research vessel, the vessel slowed if previously underway or remained stationary. If behavior continued to follow previous patterns without any signs of interruption the follow continued, but where any coincident changes in behavior were detected, the sample was discontinued. The most frequent occurrences were approaches toward the vessel ($n = 3$ of 149) and escort whales ($n = 5$ of 149).

During the focal follow, all observations of surface behavior were recorded continuously with the calf as the focal animal (Altmann 1974). A designated observer provided an oral description of the focal session data onto a hand-held audio tape recorder throughout the follow. The aim was to obtain a 60-min sample of uninterrupted behavior for each group that contained a calf; however, the follow was terminated if sea conditions changed and exceeded Beaufort sea scale 2, when other vessels approached within 300 m of the focal group or where intermingling of groups led to possible misidentification of individuals. If the sample lasted >30 min prior to the disturbance the shortened sample was used, as long as the onset of the change could be clearly defined and there was no evidence of any coincident change in behavior. Samples lasting <30 min were discarded, as were samples where group composition changed during the follow, as timing of these changes could not be accurately verified.

Table 1. Descriptions of calf surface behaviors and activities.

Behavior	Description
1. Calf travel	Forward, unidirectional relocation at rates > 1.76 km/h.
2. Calf stalled	No evidence of intentional forward movement.
3. Circling intervals	A series of three blows or more, in a circuitous path.
4. Twirling	Repetitious rolling at the surface along the longitudinal axis, frequently through 360°.
5. Pectoral fin slaps	One or both pectoral fins may be raised, waved, and slapped down on the surface. Calf frequently inverted.
6. Tail swish	A rapid lateral movement of the flukes.
7. Tail slap	The flukes are lifted and slapped on the surface of the water.
8. Peduncle throw	The entire peduncle region is raised and thrown down onto or across the surface of the water.
9. Breach	More than one-third of the calf body is propelled above the surface during a straight aerial leap.

Behaviors 1–2 from Taber and Thomas (1984), 3–9 based on descriptions by Glockner and Venus (1983), Glockner Ferrari and Ferrari (1985).

The behavioral state of the calf was monitored continuously and classified using two mutually exclusive behavioral states: travel and stalled. “Travel” was defined as directional forward movement that resulted in a change in location (Thomas and Taber 1984). The minimum rate of movement for travel was 1.852 km/h (*i.e.*, 1 knot as monitored with the onboard GPS); travel below this speed was attributed to drift. Periods with no forward relocation of the mother–calf pair were defined as “stalled” (Thomas and Taber 1984). Circling behavior and vertical movements for breathing was categorized as stalled, as no intentional forward relocation of the pair was evident. Calf surface behaviors were counted throughout the focal follow and the duration of specific behavioral components, such as circling intervals, were timed. Calf respirations were also monitored continuously throughout the sample. Travel, speed and headings were recorded as point samples at 1-min intervals during all surface travel, using the GPS. Definitions of all terms used to describe calf behaviors are provided in Table 1.

When the focal whales were not visible the boat maintained the previous pattern of travel in terms of speed and direction. The whales’ next position when first resighted was described relative to the boat and used to classify out of sight periods during transcription of the tape. When out of sight periods exceeded 10 min these periods were dropped from the data set, as intermittent sightings may have been missed, based on maximum recorded mother–calf dive times (Szabo and Duffus 2008).

Data Analysis

Measurement of the Angle of Furl of the Dorsal Fin— For each animal the angle of tilt, or persistent furl, of the dorsal fin was measured using scanned images of the dorsal fin and Adobe Photoshop 7 software. The single best image was selected based on (1) the photo closest to the 6 o’clock position, (2) the maximum elevation of the calf that allowed the whole extent of the calf’s dorsal fin to be seen, and (3) the required upright position of the calf in the water when the image was taken (see Fig. 1). We determined that images outside the 5–7 o’clock angle were subject to

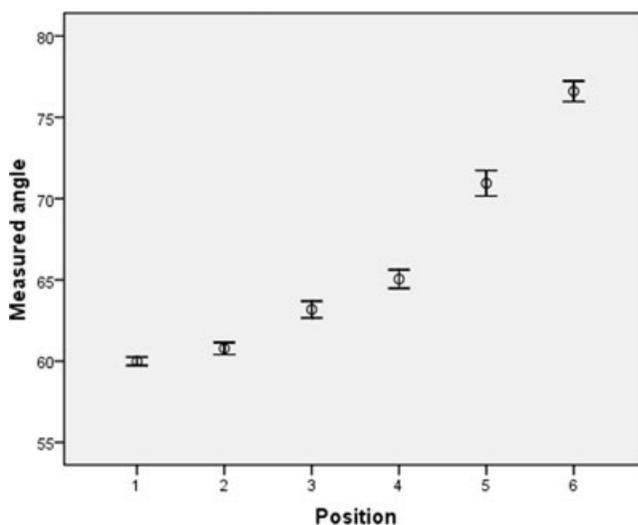


Figure 2. Variation in dorsal fin measurements, according to photographer position, estimated using a fixed model. Simulated measurements were taken using a wooden model, with a “dorsal” offset at 60° , at a height of 20 cm above the ground. Position 1 was directly behind the model, and each successive position was offset by 15° . Error bars show 95% confidence intervals. Measurements are consistent, irrespective of left or right direction of furl.

an exponentially increasing level of variance; actual measurements consistently overestimated the angle of the fin, irrespective of direction of the offset (see Fig. 2). In contrast the variation was $<5^\circ$ within 30° of the 6 o'clock position, *i.e.*, between 5 and 7 o'clock (see Fig. 2). The degree of lens zoom did not influence the accuracy of the measurements, as adjustments could be made within Photoshop to provide a suitably enlarged image from a high-resolution scan. Each selected image was measured three times and the mean angle of the dorsal fin was used in the continuing analysis. The sample of adult dorsal fins was measured using the same protocols.

To verify the change in the dorsal fin with age, a group of five calves that exhibited known neonate traits was selected. Each calf in this group exhibited two or more verified neonate traits; these comprised persistent fetal creases (Eberhardt and Norris 1964, Darling 1983), ($n = 2$ of 5), pale body color (Chittleborough 1953), ($n = 3$ of 5), an indentation behind the blowhole, consistent with descriptions of a neck indentation (McBride and Kritzler 1951), ($n = 3$ of 5), and verifiable small body length ($<1/3$) relative to the mother ($n = 4$ of 5), (Glockner and Venus 1983, measured as per Spitz *et al.* 2000). These references all relate to humpback whale calves, except for the indentation behind the blowhole (McBride and Kritzler 1951, Cockcroft and Ross 1990) and the time sensitive estimate of persistence of fetal creases (Eberhardt and Norris 1964). Five calves with the most erect fins that had been documented extensively underwater were selected for comparison and underwater footage was examined for evidence of the listed neonate traits. The length of the body relative to the mother and the dorsal fin measurements for this group were compiled and compared to the group with documented neonate traits. Resights of the same calf, based on the confirmed re-identification of the mother and spanning intervals of

>7 d, were also compiled and measured to determine whether the dorsal fin changed over the 7-d time interval in these re-identified calves.

Transcription of Taped Observations of Behavior

The behavioral tapes were transcribed against a stopwatch, with a verified timed count at the start of each tape to ensure accuracy. Using predominant activity sampling (PAS, Hutt and Hutt 1970), calf behavior was classified either as travel or stalled for each 1-min time block of the sample. When behavior changed during out-of-sight periods, the distance traveled was divided by the minimum rate of travel (1.7 km/h, *i.e.*, 30 m/min) to provide a minimum estimate of time spent traveling. The remaining portion of the out-of-sight period was classified as stalled. Other extended behaviors, such as periods of persistence at the surface and calf circling intervals, were also classified using PAS. Changes in direction of travel of $>90^\circ$ either within a single surfacing interval or across a maximum of three successive surfacings were counted and recalculated as changes in direction per traveling hour. Surface activities were recorded as events within 1-min time blocks and expressed as event frequencies per hour. Calves' breathing regimes were classified based on the time between consecutive breaths. Breath intervals >60 s were classified dives as per Chu (1988), in order to allow comparisons with existing published data. Shorter breath intervals were subdivided into intermittent breaths (30–60 s) or short (<30 s) breaths, as a review of the frequency distribution for all blows recorded in this study revealed a clear increase in blow frequencies below the 30-s point.

Statistical Analysis

Data were analyzed using SPSS version 16 software (SPSS Inc, Chicago, IL, USA). Nonparametric tests were used for nonnormal data sets, or data sets where variances were unequal; otherwise parametric tests were applied. Results were interpreted as significant at the 0.05 alpha level or less, with Bonferroni corrections incorporated to correct for multiple testing.

We used an independent samples *t*-test to compare the dorsal fin measurements of the calves exhibiting neonate traits with those where neonate traits were absent ($n = 5$ in each group). The sample size for changes in resighted calves across a 7-d interval ($n = 2$) was too small to warrant statistical testing. Maximum dive times were obtained for all calves from the focal follow data ($n = 69$) and dorsal fin measurements were also available for all the calves in this group. Although no studies have yet documented changes in the breathing regimes of mysticete neonates, several other studies have verified that maximum dive times increase as other young marine mammals mature (*e.g.*, Mann and Smuts 1999, Noren *et al.* 2001, Arnould *et al.* 2003). We compared maximum dive times and the angle of the dorsal for this group of 69 calves, using correlation tests. As the breathing regime may be influenced by activity (Sumich 1983) we then repeated this analysis using only calves that traveled throughout the sample period ($n = 11$).

As calf dorsal fin measurements when categorized by month had equal variances, we used an ANOVA test followed by a *post hoc* Tukey test to determine the precise nature of the variation between months. For comparisons of dorsal fin measurements by island we truncated the data to represent equivalent sighting periods for each island, and compared the data sets using an independent samples *t*-test. Dorsal fin

measurements were also categorized according to group association; again variances were equal, and an ANOVA test was used to detect any significant variation between groups. However, power in this analysis was low due to unequal sample sizes. Therefore we ascribed calves into three different dorsal fin measurement classes and retested the data to detect any association between class and composition. To construct the classes, the maximum variation either between successive measurements, or due to displacement from the 6 o'clock position when photographed (5°), was doubled and used as a 10° buffer across the mid-point of the data set; calves with dorsal fins that measured $\leq 62^\circ$, subsequently defined as "furled," were assigned to class 1; those above the buffer, ($\geq 72^\circ$) subsequently referred to as "unfurled," were assigned to class 2. Those calves with dorsal fin measurements within the 10° buffer (*i.e.*, 62° – 72°) were assigned to the buffer group. We then ran a chi-squared test of association between class and group composition.

For the behavioral analysis only those calves in mother–calf only or mother–calf with a single escort group were used, because multiple male associations affect calf behavior (Cartwright 1999). Calf behavior was widely variable, so median values and interquartile ranges were used to describe central tendencies for nonnormal data and for percentile or proportional data. To reduce dimensionality in the data set, elements of the behavioral regime were incorporated into a smaller number of representative factors using a principal component analysis. The resulting factors were used to compare the behavior of calves in the furled group, class 1, to behavior of calves in the unfurled group, class 2, using ANOVA tests. Variations in patterns of travel and rest, surface persistence, activity, and the structure of the breathing regime were tested.

To assess vessel impact, behavioral data collected during the habituation period were compared to aspects of behavior monitored during the focal follow. We used the Wilcoxon signed-rank test to compare paired data on speed during the habituation period to speed during the follow, and the proportion of time spent in travel in the first and final 10 min of the follow. In this second analysis, we hoped to detect any evidence of switches in behavioral state due to the presence of the vessel in closer proximity. Additionally, we ran power analyses to ensure that sample sizes were sufficient for all nonsignificant outcomes using an estimated power of 0.8, and a medium effect size (equivalent to one-half of one SD) as adequate to ensure that chances of type 2 error were within acceptable limits.

RESULTS

Changes in the Morphology of the Dorsal Fin as an Indicator of Relative Age

Dorsal fin measurements were obtained for 123 of 149 different calves encountered. Photo-identifications of the mothers were used to confirm resightings of calves and where calves were resighted ($n = 7$), measurements of the calf's dorsal fin on the first sighting only were included in the data set. Calf dorsal fin measurements ranged from 29° for dorsal fins that were furled (curled over) to 90° for entirely unfurled dorsal fins; the mean angle was 68° (SD 13), mean variation between the three measurements of each selected image was 1.9° (SD 1.8). The mean angle of the dorsal fin of adult dorsal fins examined ($n = 12$) was 87° (SD 2.3).

For the five calves with documented neonate traits the mean dorsal fin angle was 44° (SD 4.9), compared to 79° (SD 5.4) for the second group of five calves,

where neonate traits were absent and all calf body lengths were $>1/3$ of the mother's length. The difference between the dorsal fin measurements for the two groups was significant (independent samples *t*-test; $t = -10.820$, $df = 8$, $P < 0.001$).

Unfortunately, within-season resights of individual mother-calf pairs were infrequent ($n = 7$ over the course of the study) and generally over a very short period of 1 or 2 d ($n = 5$ of 7). Only two resights were on separate occasions of over 7 d apart, with reliable dorsal fin documentation obtained on both days. For the first resighted calf, the dorsal fin furl measurement increased by 13° from 54° to 67° across a 15-d period (21 January to 25 February 2001). For the second resighted calf the dorsal fin furl increased by 8° from 62° to 70° across a 7-d period (20–27 February 2003). However, data on both maximum dive time and dorsal fin measurement were available for 69 calves and there was clear evidence of a strong, positive correlation between these factors (Spearman's $\rho = 0.597$, $P < 0.001$). When we repeated this analysis using only those calves that traveled for 100% of the observation period ($n = 11$), the trend remained significant (Pearson's correlation coefficient = 0.641, $P = 0.034$).

Variation in Dorsal Fin Measurement with Month of Sighting, Island Location, and Group Composition

When categorized by month of sighting ($n = 123$ calves measured) the mean measurement of calf dorsal fins increased significantly between January, February, and March, but then stayed relatively constant for April (see Table 2; Levene's

Table 2. Variation in the angle of the dorsal furl in calves, classified by group composition.

Category	<i>n</i>	Mean dorsal fin furl (°)	SD (°)	Minimum (°)	Maximum (°)
Month of sighting ^a					
January	19	55	13	29	86
February	32	65	14	41	89
March	59	72	10	48	90
April	13	70	10	51	86
Island location ^b					
Maui	50	67	13	41	89
Island of Hawaii	46	71	11	43	88
Group composition ^c					
Mother/calf alone	20	67	14	29	89
Mother, calf, single escort	91	67	13	38	90
Mother, calf, multiple escorts	12	75	13	43	89

^aDifferences were significant between January, February and March; using ANOVA (Levene's statistic = 1.771, $P = 0.156$; ANOVA $F = 10.749$, $df = 3$, $P < 0.001$).

^bDifferences between islands truncated to include sightings within the same time periods for both islands (27 January to 27 March annually) were not significant; using an independent two samples *t*-test ($t = -1.868$, $df = 94$, $P = 0.065$).

^cDifferences between group compositions were not significant; using a chi-squared test of association ($\chi^2 = 6.730$, $df = 4$, $P = 0.151$, $n = 123$).

statistic = 1.771, $P = 0.156$; ANOVA $F = 10.749$, $df = 3, 119$, $P < 0.001$). A *post hoc* Tukey test indicated that the significant differences occurred between January, February, and March. January sightings included a very small number of calves ($n = 2$ of 19) with dorsal fin measurements $>72^\circ$ (class 2 calves). Similarly, April sightings included a small number of calves ($n = 3$ of 13) with dorsal fin measurements $<62^\circ$ (class 1 calves). There was no evidence of significant variation in dorsal fin measurements when classified by island (Maui *vs.* Island of Hawai'i) across equivalent time periods (see Table 2; independent samples *t*-test; $t = -1.868$, $df = 94$, $P = 0.065$; power = 0.75; sample size of harmonic mean 47.9 with a medium (6°) effect size). Additionally, there was no indication of significant variation between the mean dorsal fin measurements classified by group composition (see Table 2; Levene's test statistic = 0.268, $P = 0.765$, ANOVA $F = 2.363$, $df = 2$, $P = 0.099$). Although the power of this analysis was low, due to unequal sample sizes (power = 0.4, based on harmonic mean sample size of 21.4, with medium effect size [6°]), within-group variation was high, indicating calves of each class were represented in each group type. When calves were grouped into classes based on dorsal fin measurements, a chi-squared test of association also indicated there was no evidence of association with group composition ($\chi^2 = 6.730$, $df = 4$, $P = 0.151$, $n = 123$); sample size >109 , power analysis >0.8 , based on a medium (6°) effect size (Cohen 1992).

Behavioral Analysis

Behavioral samples were completed for 149 calves. Of these, 69 were for calves in unaccompanied mother-calf pairs or pairs accompanied by a single escort, and included reliable dorsal fin documentation. This comprised 64.0 h of recorded behavior, with a mean sample time for behavioral focal follows of 55.7 (SD 8.8) min.

Variations in Calf Behavior According to the Furl of the Dorsal Fin

Behavior was compared between class 1 ($n = 26$) and class 2 ($n = 27$) calves. The mean dorsal fin measurement for class 1 calves was 53° (SD 7.1) *vs.* 79° (SD 5.3) for class 2 calves. Full details of calf behavior within each class are provided in Table 3. Overall, the results indicated that prominent aspects of the time budget, the frequency of certain surface activities and the structure of the calf's breathing regime varied between the two classes. Class 1 calves spent more time traveling and surface activities included twirls, tail slaps, and tail swishes. In addition, the breathing regime featured shorter dives, more frequent intermittent breaths and less clustered short breaths. For class 2 calves more time was spent stalled and solitary calf circling intervals were more frequent. For these calves mean dives were longer, intermittent breaths were less frequent and short breath intervals were more closely clustered.

A single PCA factor was used to represent the time budget, comprising percentage time spent traveling or stalled, time the calf was alone at the surface, the frequency and duration of circling intervals, and speed of travel. All these features had values within the rotated component matrix of over ± 0.6 . The mean value of the factor increased significantly between the class 1 and class 2 calves (ANOVA $F = 7.054$, $df = 1$, $P = 0.011$, $\alpha/k = 0.025$). This reflected the reduction in percentage of time spent traveling and in speed of travel between classes 1 and 2, as these were negative values in this component. Time spent stalled, time the calf spent at the surface, and

Table 3. Time budgets and behavior of class 1 and class 2 calves. (Mean + SD provided for normally distributed statistics, median + IQR for all non normal, percentage and proportional data sets).

Components of the calves behavioral regime	Class 1 (<i>n</i> = 26)	Class 2 (<i>n</i> = 27)
Total observation time (min)	1,410	1,550
Mean duration of observations (min)	54.2 (SD 9.2)	57.4 (SD 8.1)
Travel periods		
Time spent traveling (%)	85.5 (IQR 34.2)	47.0 (IQR 42)
Estimated speed when traveling (km/h)	4.4 (SD 2.1)	3.7 (SD 2.0)
Course changes per hour	0 (IQR 2.2)	0 (IQR 0)
Stalled periods		
Total time stalled (%)	14.5 (IQR 34.2)	53.0 (IQR 42.0)
Calf alone at surface (%)	4.0 (IQR 22.5)	11.7 (IQR 10.0)
Mother and calf at surface (%)	0 (IQR 5.5)	3.0 (IQR 8.3)
Circling intervals per hour	0 (IQR 3)	5 (IQR 3)
Duration of circling intervals (min)	0 (IQR 1.2)	1.2 (IQR 0.8)
Breathing regime		
Mean total breathing frequency (per hour)	88.3 (SD 20.8)	76.5 (SD 15.5)
Length of maximum dives (s)	178 (SD 73)	281 (SD 89)
Mean duration of extended dives (>60 s)	120 (SD 49)	175 (SD 55)
Mean duration of short breath intervals (<30 s)	16 (SD 3.0)	14 (SD 2.2)
Mean no. of extended dives (per hour)	12 (SD 4.3)	13 (SD 2.7)
Mean no. of intermittent blows (per hour)	22 (SD 13.2)	11 (SD 8.5)
Proportion of between dive blows <i>vs.</i> all blows	61.6 (IQR 20.9)	68.2 (IQR 9.5)
Proportion of intermittent blows <i>vs.</i> all blows	23.4 (IQR 15.2)	12.5 (IQR 10.7)
Proportion of extended dives <i>vs.</i> all blows	14.3 (IQR 10.2)	17.6 (IQR 5.9)

the number and duration of calf circling intervals were all represented by positive coefficients in the rotated matrix and these increased between class 1 and class 2 calves. A second factor, representing changes in direction, did not vary significantly between classes (ANOVA $F = 1.784$, $df = 1$, $P = 0.189$, $\alpha/k = 0.025$). The time budgets of calves in class 1 and class 2 are shown in Figure 3.

Total surface activity within classes was broken down into specific types of activity. A hierarchical cluster analysis revealed some groupings of specific behaviors such as tail slaps and tail swishes, while twirling and breaching emerged as clearly distinct surface activities. Variation in these two activities was therefore investigated independently. Twirling was the commonest behavior, seen in 42 of the 69 calves, breaching was the most variable, but no significant variation in frequency between

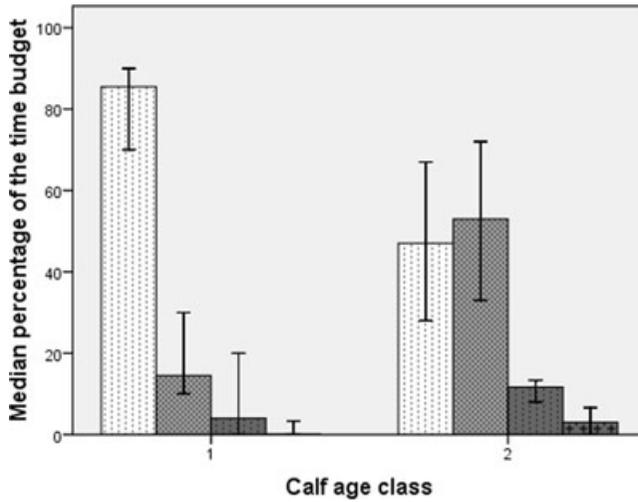


Figure 3. Time budgets of class 1 and class 2 calves. Bars represent median percentages of the time budget. Differences between the time budgets of class 1 and class 2 calves, when components were compiled into a single PCA component, were significant (ANOVA $F = 7.054$, $df = 1$, $P = 0.011$). Error bars indicate 95% confidence intervals.

the two classes was detected (one-way ANOVA test; Levene's statistic = 0.609 and 0.150 for twirling and breaching, respectively, $P = 0.439$ and 0.700 ; ANOVA $F = 0.221$, $df = 1$, $P = 0.64$ for twirling and $F = 0.102$, $P = 0.751$ for breaching). Mean event frequency of tail slaps and tail swishes decreased from 3.2 (SD 5.1) events per hour for class 1 calves to 0.4 (SD 0.9) events per hour for class 2 calves; a single PCA component representing both activities decreased significantly between classes (Levene's statistic = 3.739, $P = 0.059$; ANOVA $F = 8.242$, $df = 1$, $P = 0.006$, $\alpha/k = 0.0166$).

The breathing regime was represented by a series of three PCA components. One of these (comprising the mean length of dives, the proportion of intermittent breaths per hour and mean length of short breaths) showed significant variation between age classes (Levene's statistic = 1.117, $P = 0.296$; ANOVA $F = 10.933$, $df = 1$, $P = 0.002$). The mean value of the component decreased between class 1 and class 2 calves. Mean length of dive was a negative value in this component, this increased between class 1 and class 2 calves while the proportion of intermittent breaths (a positive integer) decreased between class 1 and class 2 calves. Thus, class 1 calves made shorter dives than class 2 calves, and took more frequent, single intermittent breaths. For class 2 calves, mean dive times lengthened, class 2 calves took fewer single, intermittent breaths between extended dives and short breaths of <30 s were slightly more clustered. Notably, the mean total breathing frequency, which included all breath intervals, was consistent between the age classes. This suggests a change in the structure of the breathing regime, rather than a change in overall breathing frequency (full details are provided in Table 3).

Observations during the focal follows confirmed that the mother and calf were within one calf body length during 98% of all surfacings. Underwater observations confirmed that during calf circling activities the mothers were invariably at rest below their calf. Furthermore, calves did not move vertically up and down in the

water column without surfacing and based on our observations mother–calf pairs usually surfaced prior to a change in state from stalled to travel.

Statistical Assessment of Vessel Impact

Mean travel speed during the 20-min habituation period was 4.1 km/h (SD 1.5); this fell slightly to 3.9 km/h (SD 1.0) during the focal follow but this difference was not significant (Wilcoxon signed-rank test, $Z = -1.070$, $P = 0.285$). Associated power for this analysis was 0.89, based on a sample size of 42 traveling groups. Similarly, the proportion of time each calf spent in travel during the first 10 *vs.* the final 10 min of the follow did not vary significantly ($Z = -1.420$, $P = 0.156$). Here power increased to 0.98, as the full sample size of 69 calves was used (see Howell 1999—power analysis of sample size for paired samples).

DISCUSSION

This study demonstrates a field technique that can be used to distinguish between two age classes of humpback whale calves within the Hawaiian calf population. Applying this technique, our results indicate that there is moderate synchrony in calf age across the winter season, little variation in relative calf age between island regions, and all age classes of calves are equally represented in different group associations. Our results also suggest that at least some of the wide variability in humpback whale calf behavior in Hawaiian waters may be attributable to relative calf age. The youngest cohort of humpback whale calves, distinguished in this study by the persistent furl of the dorsal fin, characteristically spent much of their time in persistent travel and took frequent breaths, while older calves spent more time at rest or circling alone at the surface and had greater breath holding capacity. We suggest that each of these distinct regimes may potentially promote the ontogeny of attributes that enhance calf fitness, and maximize the calves' chances of successfully completing the natal migration to the feeding grounds.

While numerous authors cite floppy or folded dorsal fins as a distinguishing neonate trait (*e.g.*, Dearolf *et al.* 2000, Noren *et al.* 2001), very few report the changes seen in the dorsal fin as neonates mature. Results from this study demonstrate that in humpback whale calves furled dorsal fins coincided with other known characteristics of early neonates. In contrast, neonate traits were absent in calves where the dorsal fins were closer to erect, or unfurled. In measurements of two resighted calves, dorsal fin measurements indicated that the dorsal fins unfurled toward the erect position over time, and differences could be quantified using this technique. Additionally, the angle of the dorsal fin increased with increasing breath-holding capacity and the latter is a known indicator of ontogeny in other cetacean neonates (*e.g.*, Mann and Smuts 1999, Noren *et al.* 2001, Arnould *et al.* 2003). This combined evidence suggests that the angle of the dorsal fin increases, *i.e.*, the dorsal fin straightens, as humpback whale calves mature. In comparison, the degree of variation ($\sim 2^\circ$ – 3°) among measured adult dorsal fins was consistently small. Some adult dorsal fins appear to “wobble” slightly when the animal surfaces, but this observation is most likely attributable to the surrounding blubber, as the underlying muscles are stiff (Etnier *et al.* 2008). We did not observe any such equivalent waiver in calf dorsal fins; however, there is inevitably some individual variation in morphological features and this may affect the degree of accuracy of this method. Notwithstanding, the general

approach described here appears to provide a way to discriminate between younger and more mature humpback whale calves within this breeding region.

The general trend of increasing mean angle of the calves' dorsal fins between January and March is consistent with a predictable rise in mean calf age across the winter season. Parturition prior to arrival in Hawaii, as suggested by Glockner and Venus (1983) and Spitz (1999), would explain the early-season sightings of small numbers of mature calves. Late season sightings of younger calves support Chittleborough's (1958) reports of postpartum ovulation or second ovulations after natal mortality; based on an 11-mo gestation (Chittleborough 1953, 1958) conception in March or April would result in a relatively late birth the following year. Alternatively, these observations could reflect temporal variation in patterns of breeding and parturition, as high levels of variation in feeding site origin (Stevick *et al.* 2006, Calambokidis *et al.* 2008) could result in different lengths of migration and different arrival times for females. Whatever the explanation, these younger late born calves may warrant further study, as late births in ungulate populations are associated with higher mortality (Guinness *et al.* 1978).

As no significant difference in relative calf age emerged between the different island locations this may suggest a relatively homogenous calf population, at least between the two areas studied. Additionally, there was no significant difference in relative calf age when classified according to group composition. Indeed, all age classes of calves were found in groups in which single and multiple escorts accompanied the mother-calf pair. This suggests that although females with calves become more attractive to males as the season progresses (Craig *et al.* 2002), the attractiveness of the female may not be strongly influenced by the relative age of any existing calf.

Behavioral differences according to relative calf age were quite pronounced. Persistent travel characterized class 1 calves and the furled dorsal fins and shorter dive times of calves in this group support the assumption that this is the youngest cohort of calves within the sample. Persistent travel has been documented for early cetacean neonates in other studies, such as southern right whales (Thomas and Taber 1984) and bottlenose dolphin (Mann and Smuts 1999). In captive settings, continual movement and the almost complete cessation of sleep in both neonates and their mothers has been documented throughout the first month following parturition (Lyamin *et al.* 2005). Previous authors (*e.g.*, Norris *et al.* 1977, Thomas and Taber 1984) have suggested that this early traveling behavior in neonates could stimulate the production of muscle myoglobin. Levels in neonates are generally very low compared to adults (Noren *et al.* 2001) and increases in muscular myoglobin levels coincide with the onset of mobility and exercise (Thorson and Le Boeuf 1994, Burns *et al.* 2007). In humans, intense training leads to increased levels of muscle myoglobin, and training under hypoxic conditions further enhances these gains (Vogt *et al.* 2001). Increased effort is required for swimming in cetacean neonates (Noren *et al.* 2006); during underwater observations in this study, class 1 calves maintained a persistent and frequent fluke beat while swimming. Still, at this point, a causative link between exercise and the production of myoglobin has yet to be established. Other factors, such as predation pressure on young naïve calves or the mothers' motivation to seek out mates and maximize her future reproductive success, also provide plausible explanations for persistent travel. Additionally, younger calves, or females with younger calves, could be more sensitive to the presence of vessels. However, the similarities between our results and those from other studies that were not vessel based (*e.g.*, Thomas and Taber 1984, Lyamin *et al.* 2005), combined with the analysis

of vessel impact data included in this study, provide support for our assertion that our observations reflect natural patterns of behavior and were not induced or amplified by the presence of the research vessel.

Class 2 calves spent less time traveling, more time at rest and swimming speeds were slower. These calves had more erect dorsal fins and longer dive times and were presumed to comprise the more mature cohort when compared to the class 1 calves. Among class 2 calves the frequency and duration of circling increased and during circling periods the mother remained resting below. Vessel habituation of the mother or her calf could be a contributory factor here; however, this switch in behavior also correlates with land-based observations for maturing southern right whale calves (Thomas and Taber 1984) and observations of young odontocetes in wild (Mann and Smuts 1999) and captive settings (Lyamin *et al.* 2005). As suggested by these authors, this alteration in behavior may reflect the changing physiological priorities of the mother–calf pair during this period. Stored maternal fat resources represent the sole source of energy for both the mother and her calf while in breeding regions and maternal costs of lactation increase through the lactation period as the proportion of lipid in the milk rises (Oftedal 1997). As metabolic costs in adult marine mammals represent 40% maintenance and 60% locomotion costs (Williams 1999), switching from travel to rest would conserve energy in both the mother and the calf. In general, when young animals are less active metabolic rates decline (Arnould *et al.* 2003) and energy is preferentially allocated to growth (Sibly and Calow 1986). Low activity rates may therefore enhance calf growth rates, and larger body size has a wide range of associated benefits for the calf. These include reduced costs of travel on the upcoming migration (Williams 1999), increased breath holding capacity (Schreer and Kovacs 1997), reduced risk of predation during migration (Chittleborough 1953), and enhanced reproductive success (Spitz *et al.* 2002).

Despite the constraints of a finite energy supply, surface activity was common in calves of both classes. This type of behavior fits definitions of play, as a functional component of early ontogeny that facilitates the development of motor skills and maneuverability (Bekoff 1984). In this data set, twirling, where the calf rolled along its longitudinal axis, was the most frequent calf surface behavior in calves of all ages, and this may be an effective antipredator behavior. Killer whales often attack baleen whales by ramming forcefully into their undersides (Ford *et al.* 2005) and in five of 15 accounts of predatory interactions between humpback and killer whales reported by Ford and Reeves (2008), humpback whales, including calves, used rolling as a method of defense. Tail flukes and pectoral fins were additionally used as weapons, thus proficient motor skills and movements of the fins and flippers developed during surface activities, such as breaching, tail slaps, and tail swishes, though energetically costly (Whitehead 1985), may prove to be a good antipredator investment. Current findings indicate that between 15% and 20% of the humpback calf population in the central North Pacific, and up to 40% of the humpback calf population in Mexican breeding grounds may interact with killer whales while on the breeding grounds or during the natal migration (Dolphin 1987, Mehta *et al.* 2007, Steiger *et al.* 2008). However, as scarring is mostly mild (Mehta *et al.* 2007), this suggests that at least some attacks are sublethal and calves can potentially deflect these predatory events. Enhanced motor skills could thus provide a selective advantage and when coupled with larger calf body size resulting from rest and persistence on the breeding grounds, these attributes could justify the costly persistence of lactating mothers in breeding regions. Larger body size may advertise greater handling time to potential predators,

as well as increased breath holding capacity. This latter trait would offset the threat of drowning, a strategy that is also often employed by killer whales when attacking mysticete calves (Ford and Reeves 2008).

The description of behavioral ontogeny in humpback whale calves provided here closely resembles those reported for other baleen whale calves in breeding regions that are collectively classed as "fight species" by Ford and Reeves (2008), namely, right and gray whales. These three species typically attempt to defend themselves when attacked by killer whales, calves are targeted preferentially (Mehta *et al.* 2007) and in all three there are also distinct sequential phases of travel and rest along with functional play activities during early ontogeny. This convergence lends support to the hypotheses originally proposed by Corkeron and Connor (1999) that, along with other potential functions, migration may incorporate an antipredator strategy that reduces calf vulnerability to killer whale predation. Warm, calm waters characterize breeding regions and may promote proximate mechanisms such as growth that enhance ultimate attributes such as predator avoidance and future fitness. Sublethal predators can dramatically alter the behavior of their marine mammal prey even if they rarely kill them (Wirsing *et al.* 2008). In this context, costly maternal lingering in areas like Hawaii, where risks of killer whale predation are low (Mobley *et al.* 2001, Baird *et al.* 2006), appears justifiable and warrants consideration as a possible factor that may shape the migratory behavior of mysticetes.

Finally, when taken cumulatively, the findings of this study further highlight the importance of breeding regions in the life history of humpback whales, underscoring the need for careful management and protection of these critical regions.

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