Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii

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Received February 8, 1993
Accepted February 2, 1994

SMULTEA, M.A. 1994. Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. Can. J. Zool. **72**: 805–811.

Humpback whales (*Megaptera novaeangliae*) were tracked from shore to determine habitat-use patterns in an area relatively undisturbed by human activity near the "Big Island" of Hawaii during the winter 1988 and 1989 calving seasons. The temporal and spatial distributions of whales differed with group size and composition. During afternoon hours, groups containing a calf occurred in water significantly shallower and nearer to shore than did groups without a calf. Late in the breeding season, the same segregation pattern occurred throughout the day. Between-groups distances were significantly greater for groups with a calf than distances between all other groups. The number of whales observed per hour peaked during mid-February, although the relative sighting rates for various group sizes and compositions varied across the breeding season. Adults without a calf may use deep water to facilitate breeding behavior, while maternal females may use shallower water to avoid harassment and injury to calves from sexually active males, turbulent offshore or deep sea conditions, or predators. The predominance of cows with a calf in coastal habitat increases their exposure to expanding human-related development and aquatic activities that could injure, disturb, or displace them.

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Des Rorquals à bosse (*Megaptera novaeangliae*) ont été suivis depuis la côte afin d'étudier leur répartition en hiver dans les divers habitats d'une zone relativement peu perturbée par l'activité humaine, près de la plus grande des îles de l'archipel d'Hawaii, au cours des saisons de mise-bas en 1988 et 1989. Les répartitions temporelle et spatiale des rorquals différaient selon la taille et selon la composition des groupes. Les groupes comptant un baleineau se tenaient dans des eaux relativement moins profondes et plus près de la côte que les groupes sans baleineau durant l'après-midi. Vers la fin de la saison de reproduction, ce type de ségrégation prévalait durant toute la journée. La distance entre les groupes était significativement plus importante lorsqu'il s'agissait de groupes avec baleineau. Le nombre de rorquals observés par heure s'est avéré maximal à la mi-février, mais la fréquence relative des observations de groupes de toutes tailles et de toutes compositions variait durant toute la saison de reproduction. Les adultes sans baleineau utilisent probablement les eaux profondes pour faciliter leur comportement reproducteur, alors qu'il est probable que les femelles se tiennent en eau moins profonde pour éviter le harassement des mâles en rut et les blessures qu'ils pourraient infliger aux baleineaux, et aussi pour échapper aux prédateurs et aux conditions de turbulence qui prévalent dans les eaux profondes du large. La présence des femelles avec leur baleineau en eau peu profonde les expose aux activités humaines qui peuvent leur causer des blessures et les perturber et même les forcer à fuir.

[Traduit par la Rédaction]

Introduction

Approximately 1500 North Pacific humpback whales utilize Hawaiian waters to breed and calve during the winter and spring; an undetermined number of these whales move between the major Hawaiian islands (Baker and Herman 1981; Baker et al. 1986; Darling and Morowitz 1986; Baker and Herman 1987). Recreational water activities such as boating, jet skiing, and parasailing have been increasing in nearshore areas of the Hawaiian islands, and there is evidence that such activity may displace humpback whales, particularly cows with calves, from this habitat (Herman et al. 1980; Glockner-Ferrari and Ferrari 1985, 1990; Salden 1988). Yet, few data on the distribution of humpbacks have been systematically collected on the basis of sex, age, or reproductive class while the whales are at breeding and calving areas. Such information is essential for making sound management decisions for the protection of this endangered species.

While on the breeding and calving grounds, humpback whales occur primarily in water less than 180 m in depth (Dawbin 1966; Winn et al. 1975; Herman and Antinoja 1977; Herman et al. 1980). Trends observed on the wintering grounds in Hawaii and the Caribbean suggest that segregation may exist within this parameter: humpback cows with a calf appear to predominate in shallow, generally sheltered or coastal water, while adults occur mostly in deeper, more exposed water (Herman et al. 1980; Whitehead and Moore 1982; Glockner-Ferrari and Ferrari 1985; Mattila and Clapham 1989). Most studies have arbitrarily categorized "preferred" habitat, however (e.g., "inshore" versus "offshore" areas, geographical regions). Although such information is generally useful, it may be biased by habitat classifications that are not necessarily biologically important to whales. Refined systematic assessment is needed of spatiotemporal factors influencing humpback distribution, particularly in Hawaii.

Study results conflict regarding the distribution of humpback cows with a calf in Hawaiian waters. Glockner-Ferrari and Ferrari (1985, 1990) and Salden (1988) reported a progressive decrease in the percentage of cows with a calf in the nearshore waters off western Maui (Fig. 1), based on nonsystematic vessel surveys from 1977 to 1988; they associated this apparent displacement with increased human activity in coastal waters. In contrast, no significant change in the mean location of humpbacks relative to distance from shore, including groups with a calf, was found between the

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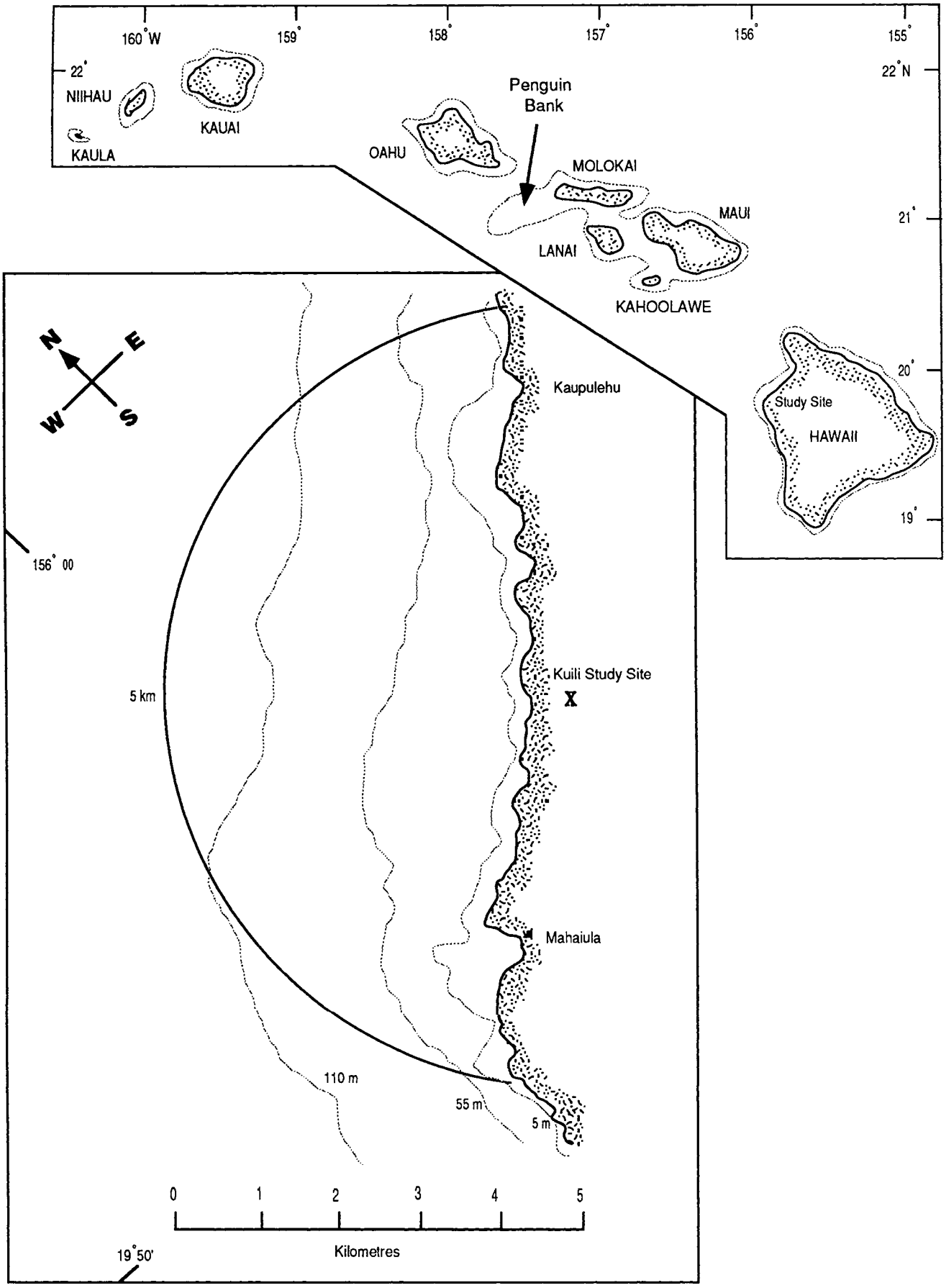

FIG. 1. Study area of western Hawaii. Inset: The Hawaiian islands, including 183-m (100-fathom) depth contours.

islands of Maui and Lanai (Fig. 1) based on aerial and vessel surveys between 1976 and 1991 (Forestell et al. 1991). Aerial surveys in 1990 also indicated that humpback groups with a calf near Maui were not located differently from adult groups (Forsyth et al. 1991). The issue of habitat selection needs clarification.

Base-line information on whale distribution is needed prior to the introduction of potential human-related disturbance that may alter habitat-use patterns. The west coast of the "Big Island" has been relatively undisturbed by human activities compared with western Maui, yet many areas are proposed or slated for development, including construction or expansion of hotel resorts and marinas (County of Hawaii Planning Department 1992). Detailed descriptions of seasonal abundance and distribution of whales near the Big Island are limited or outdated, however.

Based on observations in relatively pristine, coastal water of the Big Island, this study set out to test the hypothesis that humpback groups containing a calf occur in different locations than non-calf groups, and obtained base-line data on the temporal and spatial distribution and abundance of humpbacks according to group size and sex–age composition.

Methods

Study area

Land-based observations were made from the Kuili cinder cone on the west coast of the Big Island, Hawaii (Fig. 1). The observation station was located 104.2 m above sea level and approximately 300 m from shore. The study area encompassed the coastal waters within a 5-km radius of the land station and a depth range of 0 – 128 m (mean 56 m, SD = 32.0 m, $n = 112$ samples at 0.5-km^2 intervals); water depth increased with increasing distance from shore ($r^2 = 0.88$, $p < 0.001$) (Fig. 1). The seabed consisted of coral and sand. Nearshore water of the study area provided a lee from the predominant northeast trade-winds. Surface water temperatures in Hawaii remain near 25°C (77°F) from November to March and extend downward 50 – 80 m (Gosline 1965). Observations were made from 9 February to 29 March 1988 and from 20 January to 5 April 1989, dates coinciding with the known seasonal occurrence of the majority of humpbacks in Hawaii during the breeding – calving season (Herman and Antinoja 1977; Baker and Herman 1981).

Group classification

Observations were made on humpback whales of the North Pacific population wintering near Hawaii. An observational "group" was defined as a single whale or two or more whales within 10 body lengths (approximately 150 m) of one another characterized by synchronized surfacing patterns (Mobley and Herman 1985). Whales were categorized as belonging to one of the following social groups (described by Tyack 1981; Baker and Herman 1984; Mobley and Herman 1985; Silber 1986): cow–calf pair; cow–calf with escort (an accompanying (generally mature male) whale); cow–calf pair with two or more escorts; single adult; two adults (dyad); or a group of more than two adults. All non-calf whales were "adults," since subadults other than calves could not be reliably distinguished from adults. Groups were tracked with a theodolite and binoculars for at least one sequence of surfacings to determine pod composition.

Data collection

A surveyor's theodolite (Lietz/Sokkisha Model DT20E, ±10 s precision, 30 power magnification) was used to track whales as described by Tyack (1981). Theodolite-measured declination angles were converted to distance from the land station through application of a computer program (Rusconi and Hawkinson 1991) that utilized trigonometric calculations corrected for curvature of the earth. Only whale groups within 5 km of the land station were tracked, based on distance conversions made in the field. Using the theodolite information, the initial positions of all groups were plotted on nautical charts. The water-depth used in analysis was determined by interpolating between charted depths nearest the plotted group location. "Between-groups" distance was the distance between plotted whale groups observed within a scan period when at least one calf was present in the study area.

Land-based observations were conducted on 6 days per week by two or three people equipped with 10 × 50 or 8 × 40 power binoculars. Scan sampling (Altmann 1974) was used to document whale distribution. For each scan, the observation field was divided into two equal sections ("left" and "right") covering approximately 90° each as described by Bauer (1986). A scan was defined as a consecutive search of the two sections totaling 30 min, beginning alternately on the left and right sections. Four scans were conducted each day at 2-h intervals, alternating every other day on the following schedule: 07:00, 09:00, 11:00, and 13:00 on day 1 and 11:00, 13:00, 15:00, and 17:00 on day 2. Scans were conducted only during a Beaufort No. 3 or less (wind speed <21 km/h, occasional whitecaps) and a visibility rating of "good" (glare or haze in <5% of the study area) or better to ensure consistent observation conditions (Reilly et al. 1983). It was assumed that distance from shore did not significantly affect sightability of whales within the study area, based on the results of vessel-based verification of observations from land (Smultea 1991, 1992), other land-based studies (Reilly et al. 1983; Bauer 1986; Helweg 1989), and the observation that calves spend more time at the surface than other whales (Bauer 1986), thereby increasing the likelihood of their being spotted.

Analysis

General linear model, fixed-effects, multivariate analysis of variance (MANOVA) for unbalanced data (Zar 1984) was used to analyze distribution data. The water depth associated with each whale group location was selected as the dependent variable rather than distance from shore, since the two measures were highly correlated for whale locations ($r^2 = 0.81$, $p < 0.001$) and because water depth appears to be a better indicator of humpback location than proximity to shore (Herman et al. 1980; Whitehead and Moore 1982; Mattila et al. 1989) (however, for distance from shore summary statistics see Smultea 1991, 1992). The dependent variable was tested against the following independent variables: period of day (morning (before 12:00) versus afternoon (after 12:00)), fortnight (2-week periods based on the Julian calendar, beginning 1 January) (Mobley and Herman 1985), and year. Scan times were combined into diurnal and fortnightly periods for analysis to increase sample size and test power. The following social groups were compared using the aforementioned independent variables: groups containing a calf, and groups of one, two, and more than two adults. The number of whales accompanying a calf did not influence distribution ($F = 0.31$, $p < 0.75$, $r^2 = 0.01$). Therefore, all groups containing a calf (henceforth "group with calf") were pooled for further analysis. Each group was treated as an independent sample, and five known resightings were excluded from the analysis.

One- and two-factor analyses of variance were used to assess the effects of group type and fortnight on between-groups distances. A Bonferroni-protected t test utilizing least squares means was used to determine which variables of interest contributed to significant ($p \leq 0.05$) MANOVA differences. Seasonal-abundance data were analyzed according to fortnightly periods. To compensate for differential effort across the breeding season and years, the number of whales and groups observed per hour was used as an index of comparison to assess relative abundance.

Results

A total of 536 groups comprising 950 whales were observed during 270 scans totaling 135 h in the winters of 1988 and 1989 (Table 1). The location of whales relative to water depth was dependent on fortnight and group type during both study years ($F = 2.70$, $p < 0.005$, $r^2 = 0.13$). Bonferroni-protected

TABLE 1. Summary of 1988 and 1989 observation efforts and humpback whale sightings

	1988	1989	Total
Effort			
No. of observation days	42	50	92
No. of scans	110	160	270
No. of scan hours	55	80	135
Sightings			
No. of whales	427	523	950
No. of groups	246	290	536
No. of single whales	115	126	241
No. of dyad groups	67	96	163
No. of three or more adult groups	18	23	41
No. of groups with a calf			
Unescorted cow–calf pairs	21	15	36
Cow–calf pairs escorted by one adult	24	21	45
Cow–calf pairs escorted by two or more adults	1	9	10
Total	46	45	91

TABLE 2. Summary statistics (depth in metres, mean ± SD) for humpback whale locations, based on group type and period of the day

	Group type			
Period of the day	Group with a calf	1 adult	2 adults	>2 adults
Morning (before 12:00)	63±3.8 (n = 44)	72±2.0 (n = 142)	69±2.7 (n = 80)	72±6.2 (n = 19)
Afternoon (after 12:00)	56±3.6*†‡ (n = 47)	66±2.2§ (n = 99)	71±2.7 (n = 83)	70±5.3 (n = 22)

*$p < 0.05$ compared with groups of 1 adult during the afternoon.
†$p < 0.005$ compared with groups of 2 adults during the afternoon.
‡$p < 0.10$ compared with groups of >2 adults during the afternoon.
§$p < 0.05$ compared with groups of 1 adult during the morning.

t tests also indicated significant relationships between period of day and location of some group types.

Groups with a calf (n = 91) occurred in water significantly shallower than groups of one and two adults during the afternoon ($p < 0.05$) (Table 2). The same segregation pattern occurred throughout the day at the end of the breeding season (11 March to 7 April) ($p < 0.005$) (Table 3). However, the location of groups with a calf was independent of the absence (n = 22 scans) or presence (n = 69 scans) of one or more adult groups in the study area, regardless of fortnight ($F = 0.27$, $p < 0.60$, $r^2 = 0.01$).

Between-groups distances were significantly greater for groups with a calf (mean 2560 m, SD = 1344 m, n = 158) than for all other groups (mean 2170 m, SD = 1188 m, n = 128) ($F = 6.59$, $p < 0.01$, $r^2 = 0.02$). For groups with a calf, this distribution was independent of both fortnight and group type ($F = 1.50$, $p < 0.15$, $r^2 = 0.01$).

Single adults were the only non-calf group that appeared to significantly shift distribution patterns. They were observed in shallower water during the afternoon than the morning ($p < 0.05$) (Table 2). In addition, they occurred in shallower water than adult dyads from 26 February to 10 March ($p < 0.01$) (Table 3).

TABLE 3. Summary statistics (depth in metres, mean ± SD) for humpback whale locations, based on group type and fortnightly period

	Group type			
Fortnightly period	Group with a calf	1 adult	2 adults	>2 adults
15–28 Jan.	— (n = 0)	77±4.1 (n = 25)	69±4.1 (n = 26)	66±9.2 (n = 5)
29 Jan – 11 Feb.	64±11.9 (n = 2)	66±5.0 (n = 17)	66±5.2 (n = 16)	64±9.4 (n = 5)
12–25 Feb.	67±4.4 (n = 23)	67±2.2 (n = 87)	75±2.4 (n = 71)	76±6.0 (n = 12)
26 Feb. – 10 Mar.	73±4.4 (n = 22)	61±3.2* (n = 43)	77±4.2 (n = 24)	75±5.5 (n = 14)
11–24 Mar.	56±3.8† (n = 29)	72±2.9 (n = 52)	76±4.5 (n = 21)	73±10.3 (n = 4)
25 Mar. – 7 Apr.	39±5.3‡ (n = 15)	73±5.0 (n = 17)	56±9.2 (n = 5)	74 (n = 1)

*$p < 0.01$ compared with groups of 2 adults during the same fortnightly period.
†$p < 0.005$ compared with groups of 1 and 2 adults during the same fortnightly period.
‡$p < 0.005$ compared with groups of 1 adult during the same fortnightly period.

The observed distribution of whale group types was not related to Beaufort number within a Beaufort range of 0–3 ($F = 1.13$, $p < 0.50$, $r^2 = 0.00$). There was also no significant relationship between the location of whales, Beaufort number, and time of day ($F = 0.39$, $p < 0.90$, $r^2 = 0.01$), although Beaufort number increased in the afternoon (generally from Beaufort 1 to 2) ($\chi^2 = 85.8$, $p < 0.001$). Beaufort 2 or less (no whitecaps) occurred during 76% of the 270 scans.

Abundance of social groups

The largest number of groups and individuals observed per hour occurred from 12 to 25 February for both 1988 and 1989, after which the sighting rate declined (Fig. 2). The relative sighting rate of whales based on group size and composition varied across the study period, however. Groups of two and more than two adults generally decreased in relative abundance after the peak period of whale abundance, whereas the proportion of single adults remained fairly constant at 40–50% of all sightings (Fig. 2). In contrast, the relative proportion of groups with a calf increased across the breeding season, as generally did the proportion of escorted cow–calf pairs (Fig. 3). Overall, more cow–calf pairs were escorted by at least one adult (n = 55) than not (n = 36), and calves composed 9.6% of all whales sighted. The earliest calf sighting for either study year occurred on 1 February 1989.

Discussion

Groups with a calf occurred predominantly in shallower, more nearshore waters than adult groups. They may be located differently from other whales for various reasons, including reduction of interactions with conspecifics. For example, behavioral studies indicate that cows with a calf avoid contact with other whales (Tyack 1982; Tyack and Whitehead 1983; Mobley et al. 1988). Avoidance of harassment from males was cited as a major factor influencing habitat segregation by gray whale (*Eschrichtius robustus*) cow–calf pairs during the winter breeding seasons (Jones and Swartz 1984), and similar segregation occurs among southern right whales (*Eubalaena australis*) (Payne 1986). Conspecific encounters could result

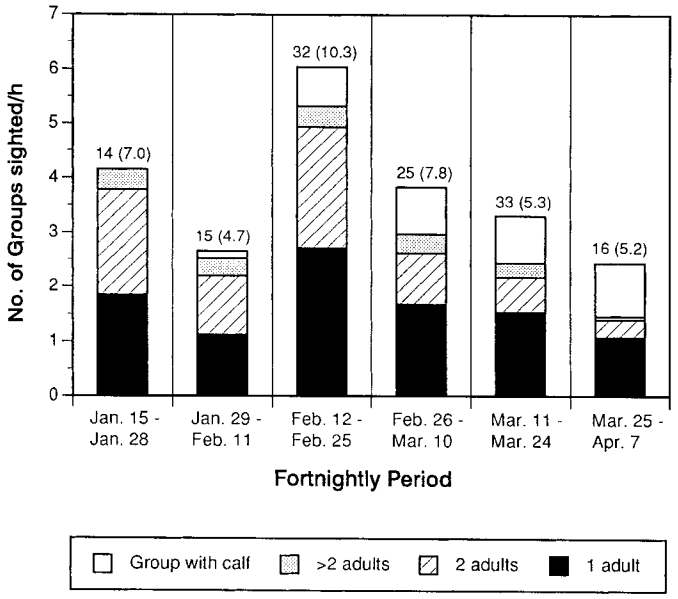

FIG. 2. Hourly sighting rates of humpback whale group types across fortnights for the 1988 and 1989 observation periods combined. The total hours of effort per fortnight are shown above the bars, followed by the number of individuals observed per hour in parentheses.

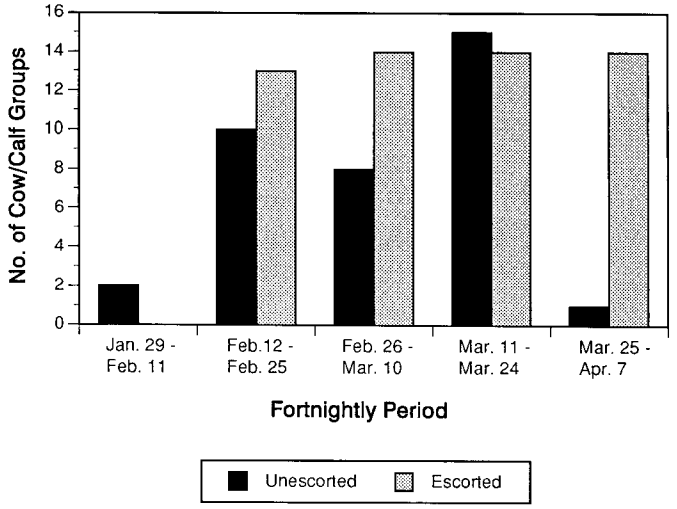

FIG. 3. Relative sighting frequency of unescorted and escorted humpback whale cow–calf pairs across fortnights for the 1988 and 1989 observation periods combined.

in premature social interactions of the calf, increased energy expenditure, interruption of nursing bouts, mistaken imprinting or nursing attempts, separation of calves from cows, or even injury to calves (Herman et al. 1980; Whitehead and Moore 1982; Jones and Swartz 1984; Thomas and Taber 1984). Moreover, segregation is a common strategy exhibited by females with infants in many ungulate species (Lent 1974) believed to have a common ancestry and to show similarity in breeding systems with baleen whales (Slijper 1966; Darling 1983).

Segregation by maternal humpbacks during the afternoon and the late breeding season coincided with periods of increased courting and aggression by adults, activities that cows with a calf may attempt to avoid spatiotemporally. For example, surface-active behaviors increase during the afternoon (Bauer 1986; Helweg 1989), including at the study area in 1988 (Greenberg 1988). Cow–calf pairs are also escorted more frequently in the afternoon (Helweg 1989), suggesting that males may court postpartum females later in the day. Harassment of maternal females by males may also increase near the end of the breeding season, when the availability of nonparturient estrous females decreases and the proportion of adult males and escorted cows with a calf increases (Dawbin 1966; Herman et al. 1980; Mobley and Herman 1985). Approximately 14% of maternal females may ovulate about 1 month after parturition (Glockner-Ferrari and Ferrari 1990), representing a breeding opportunity for males. The relatively few cows with a calf occurring in deep water could represent postpartum–estrous females with older calves.

Cow–calf use of shallow habitat may discourage courting males, which may select deep water to avoid collisions with the sea floor (Jones and Swartz 1984) or coral in shallow regions of the study area, a tactic previously suggested for the probable female in large surface-active groups (Glockner-Ferrari and Ferrari 1985; Mattila et al. 1989). Moreover, adults may attract other adults to their locations in deep water, since they frequently join one another (Tyack 1982; Mobley and Herman 1985; Mobley et al. 1988). In addition, Bauer (1986) noted that net group size increased among whales farther from shore.

Inshore shallow water may provide protection for calves from potential predators found mostly in deeper Big Island waters, such as various sharks (Tinker and DeLuca 1973), killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*), and pygmy killer whales (*Feresa attenuata*) (Chittleborough 1953; Perryman and Foster 1980; Minasian et al. 1987; D. McSweeney, personal communication). Shallow water, especially near surf zones, may be used to confound the echolocation abilities of odontocetes and minimize the vulnerability of calves from below (Würsig and Würsig 1980; Thomas and Taber 1984).

The location of groups with a calf when alone in the study area did not differ significantly from when adults were present. This suggests that cows with calf may not actually be "alone" and may be responding to conspecific sounds from beyond the study area but undetected by observers, as humpbacks respond to intraspecific vocalizations 9–10 km away (Tyack 1982; Tyack and Whitehead 1983). Calm, warm, shallow water may also be important in minimizing energy expenditure for cows and calves (Brodie 1977; Whitehead and Moore 1982), as the study area generally provided a sheltered lee from the predominant tradewinds. Other unevaluated factors may also influence the distribution of groups with a calf, such as calf maturity, predation rates, ocean-bottom topography, currents, water clarity, or anthropogenic underwater noise.

Distributional differences among single adults were unclear, particularly as I could not determine their gender or sexual maturity. However, significant differences in the mean depth location of single adults between morning (72 m) and afternoon (66 m) were minimal and believed to be of no discernible biological significance.

Abundance trends of social groups

Observations suggest that regional segregation of reproductive classes may occur and change over time in Hawaii. For example, the Big Island's importance as a nursery

area may be increasing. I observed a higher proportion of groups with a calf in 1988 and 1989 (17% of 536) than has been previously reported over similar dates from 1977 to 1980 (10% of 111) (Bauer 1986) and in 1988 (9% of 275) (Helweg 1989). Furthermore, I sighted relatively fewer (9% of 536) groups larger than two adults (with or without a calf) during 1988 and 1989 compared with 1977–1980 at the Big Island (16% of 111), Maui (29% of 926), and Penguin Bank (35% of 159) (Bauer 1986) (Fig. 1). These observations indicate that the Big Island may be a less competitive area for females than other Hawaiian islands or less utilized for aggressive courting activities characteristic of groups of more than two adults (Tyack and Whitehead 1983; Baker and Herman 1984). However, within-season trends in the relative abundance of group types were generally consistent with other studies: as the relative abundance of breeding groups decreased, the proportion of groups with calf increased, reflecting the departure of most adults and the prolonged stay of cows with calf (Dawbin 1966; Mobley and Herman 1985).

Management implications

Humpback cows with calf may occur in shallower, more nearshore waters than adult groups during certain diurnal and monthly periods for a combination of the aforementioned reasons, perhaps foremost to minimize encounters with sexually active males, according to the results of other behavior studies. Such habitat is probably important for successful nursing and calf rearing. Although management action has been recommended to protect humpback whale calving areas (National Marine Fisheries Service 1991), minimal systematic data describe the qualities that define such habitat. Furthermore, systematic examination of the effects of development on the use of coastal habitat by humpback whales is also lacking. Yet, if the probability of successful humpback calving and calf rearing is greater in coastal waters than in deep offshore waters, increasing human use of these areas could affect the viability of the North Pacific humpback whale population by displacing pregnant or maternal females.

This study lends insight into the general environmental requirements of humpback whales, corroborating and refining studies indicating the predominant occurrence of calves in shallow, protected waters of the breeding grounds. The results provide baseline data from one of the few remaining relatively pristine areas of the Hawaiian calving grounds useful for monitoring potential changes in the distribution of wintering humpbacks relative to increasing human use of coastal waters. Such knowledge is essential in improving management schemes to conserve humpback whales throughout their marine habitat.

Acknowledgments

This research was supported by the Marine Mammal Commission, Cetacean Society International, American Cetacean Society (National/San Pedro, Monterey, and Los Angeles chapters), Hawaii Audubon Society, Moss Landing Marine Laboratories, and the David and Lucille Packard Foundation. I am grateful for the encouragement and advice of Bernd Würsig and the field assistance of Ellen Purcell, Janet Biondi, Marci Greenberg, and Eric Dorfman. Dan McSweeney of the West Coast Whale Research Foundation helped coordinate project logistics. Steven Katona, Gregory Silber, Mason Weinrich, and two anonymous reviewers provided constructive comments on the manuscript. This represents contribution No. 36 of the Marine Mammal Research Program, Texas A&M University, Galveston.

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