

# Estimating the mortality rate of humpback whale calves in the central North Pacific Ocean

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**Abstract:** Sighting histories of individually identified female humpback whales (*Megaptera novaeangliae*) in their winter and summer ranges were used to investigate mortality of North Pacific humpback whale calves. We compiled records collected between 1979 and 1995 by eight independent research groups, which yielded 29 cases where 25 different mothers sighted in Hawai'i were identified later the same year in Alaska. In 7 of 29 cases, a calf sighted with its mother in Hawai'i was missing from its mother's Alaska sighting(s). After investigating many factors, we determined that the largest potential bias would occur in late-autumn observations, when calf absences might indicate weaning or temporary mother-calf separation rather than calf mortality. Our minimal and most robust estimate excluded all mortalities and survivals based on sightings of the mother after October 31; 3 of 20 cases or 0.150 (95% confidence intervals (CI) = 0.032, 0.378). The maximal calf mortality rate, derived from all the available data, was 7 of 29 cases or 0.241 (95% CI = 0.103, 0.434). An intermediate estimate that excluded all cases based on single Alaska sightings and omitted late-season sightings (2 of 11 cases or 0.182; 95% CI = 0.023, 0.518) is perhaps closest to the actual first-year mortality rate for humpback whale calves, although it is compromised by its small sample size. Our results demonstrate both the value and the limitations of using longitudinal data to determine the life-history parameters that are essential for documenting the recovery of endangered populations.

**Résumé :** L'observation suivie de Baleines à bosse (*Megaptera novaeangliae*) femelles identifiées individuellement dans leurs aires d'hiver et d'été a permis d'étudier la mortalité des petits dans la population du Pacifique Nord. Nous avons compilé des données obtenues de 1979 à 1995 par huit groupes indépendants de chercheurs et l'opération a révélé 29 cas où 25 mères différentes aperçues dans les eaux hawaïennes ont été observées de nouveau en Alaska plus tard la même année. Dans 7 des 29 cas, une mère aperçue à Hawaii avec son petit a été revue en Alaska sans son petit. Après avoir examiné plusieurs facteurs, nous avons déterminé que la cause la plus probable d'erreur potentielle était reliée aux observations de fin d'automne, alors que l'absence du petit pourrait s'expliquer par le sevrage ou par la séparation temporaire du petit d'avec sa mère, plutôt que par la mortalité. Notre estimation minimale la plus robuste ne tient pas compte des taux de mortalité et de survie basés sur les observations des mères après le 31 octobre; 3 cas sur 20 ou 0,150 (95 % IC = 0,032, 0,378). Le taux maximal de mortalité des petits, basé sur toutes les données, était de 7 cas sur 29 ou 0,241 (95 % IC = 0,103, 0,434). Une estimation moyenne excluant tous les cas d'observations uniques en Alaska et les observations de fin de saison (2 cas sur 11 ou 0,182; 95 % IC = 0,023, 0,518) est peut être plus près de la mortalité réelle des petits au cours de la première année, bien que les résultats soient compromis par la taille

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insuffisante des échantillons. Nos résultats démontrent la valeur et les limites des données longitudinales pour déterminer les paramètres démographiques essentiels à l'étude de la récupération d'espèces menacées.

[Traduit par la Rédaction]

## Introduction

Population models require estimates of vital rates such as fecundity, adult mortality, and juvenile mortality. Despite its importance in assessing population status, juvenile mortality has not previously been estimated in a humpback whale (*Megaptera novaeangliae*) population. In 1991 and 1996, the National Marine Mammal Laboratory (NMML) convened a two-part workshop to estimate calf mortality and improve existing estimates of birth intervals for female North Pacific humpback whales (Mizroch 1995, 1997). The archive of identification photographs of humpback whale flukes contributed by researchers throughout the North Pacific Ocean and curated at the NMML served as the foundation for these studies.

Humpback whale calves are born over a period of several months on or near the wintering grounds, and migrate back to the feeding areas with their mother (Dawbin 1966; Baker et al. 1987; Clapham 1996). Calf mortality may be inferred when a calf sighted with its mother on the wintering grounds is absent during sightings of its mother on the feeding grounds later that year, because calves typically remain with their mother for at least 10.5 months of lactation (Chittleborough 1958). Weaning begins at approximately 5–6 months of age, when calves begin to feed on fish and other prey (Clapham and Mayo 1990) while still suckling from their mother (van Lennep and van Utrecht 1953). Permanent separation of humpback whale mother–calf pairs typically, but with some exceptions (Clapham and Mayo 1987), occurs some time near the end of the calf's birth year. Separation can take place on their high-latitude feeding grounds (Baraff and Weinrich 1993; Straley 1994; Steiger and Calambokidis 2000), during migration, or after arrival on their winter grounds (Baker and Herman 1984; Glockner-Ferrari and Ferrari 1984; Baker et al. 1987; Clapham and Mayo 1987).

The need for a direct estimate of mortality of North Pacific humpback whale calves is highlighted by the fact that estimated calving rates in the Hawai'i wintering area (0.44–0.73 calves/year per female) (Baker et al. 1987; Glockner-Ferrari and Ferrari 1997; Craig and Herman 2000) tend to be higher than estimates for the southeastern Alaska feeding area (0.37–0.50 calves/year per female) (Baker et al. 1987; Straley 1994). Although these researchers used various methods to estimate calving rates, and each method likely included sources of bias (Baker et al. 1987; Straley 1994), one cause of the differences between calving rates estimated in Hawai'i and Alaska might be calf mortality (Baker et al. 1987).

One would expect the mortality rate for calves to be much higher than that for adults, following the pattern of other mammalian mortality curves (Caughley 1966). The survival rate for adult humpback whales in the Gulf of Maine has been estimated at 0.951 (95% CI = 0.929, 0.969) (Buckland 1990) and 0.96 (SE = 0.0008) (Barlow and Clapham 1997). Using a birth-interval model with sighting data from Gulf of Maine humpback whales, the latter investigators also estimated minimal and maximal likely first-year survival rates.

Their maximal first-year survival rate (0.922) was computed as the square of the estimated adult survival rate, and the minimal estimate as the proportion of identified calves sighted after their first year (0.828). It is important to note that these researchers were attempting to bracket reasonable calf-survival rates and they cautioned against giving their calf-survival estimate much credence (Barlow and Clapham 1997).

This paper describes the use of sighting histories of individually identified females to estimate the mortality rate of humpback whale calves during the first year of life, including the calves' first migration from Hawai'i to feeding grounds in the central North Pacific. The study focused on mothers and calves migrating between Hawai'i and southern Alaska because mark–recapture and genetic studies have demonstrated connections between these regions (Darling and McSweeney 1985; Baker et al. 1986, 1998). A collaborative approach was necessary because no single research group had obtained sufficient data in both winter and summer habitats to estimate calf mortality. One of the principal challenges of the present study was to distinguish mother–calf separation from calf mortality.

## Materials and methods

### Field methods

Field studies on humpback whales in the central North Pacific Ocean were conducted independently by eight research groups from 1979 to 1995 (Table 1). Researchers collected individual identification photographs of humpback whales in two of their principal winter and summer habitats in the North Pacific, including the wintering grounds in the Hawaiian islands (Fig. 1) and the two best known feeding areas: southeastern Alaska extending south to northern British Columbia, and Prince William Sound (Fig. 1).

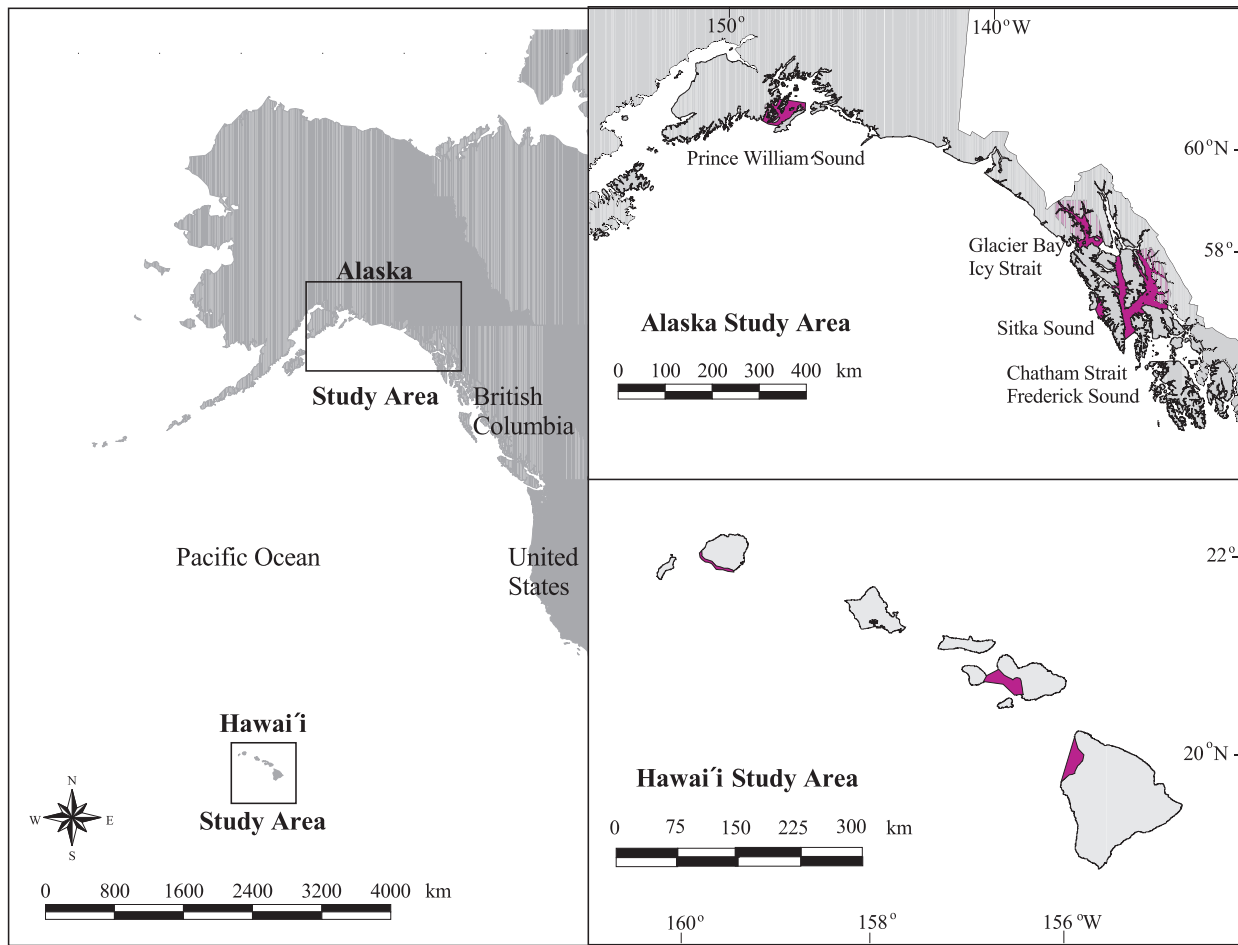
### Individual identification

Researchers approached whales in motorized vessels and photographed the ventral surface of the flukes of each whale (Fig. 2), using a 35-mm SLR (single-lens reflex) camera equipped with a telephoto lens and black and white print or color slide film. Researchers took field notes that described each whale encounter, including the presence or absence of a calf, number of whales in the group, date, time, location, and behavior. We defined a whale *sighting* as an encounter during which individual identification photographs and supporting information were obtained. Research groups independently documented and compiled sighting histories for individual whales, using the stable natural markings visible in photographs of the ventral flukes (Katona et al. 1979; Jurasz and Palmer 1981) and other parts of the body (Glockner 1983).

### Determining age–sex classes

At the start of the study, participants discussed their research methods, with particular emphasis on their criteria for determining if a whale was a "mother" or a "calf," and agreed on the following standards. We determined age-classes of whales according to the following body-size criteria: calves are typically 4–4.5 m in length at birth (Chittleborough 1958; Clapham et al. 1999), grow to 7–8 m in length by late summer (Straley 1994), and attain body lengths of 8–10 m at independence (Clapham et al. 1999). Based

**Fig. 1.** Map of Alaska and Hawai'i study areas (shaded).



**Table 1.** Study areas and dates of fieldwork in the North Pacific Ocean.

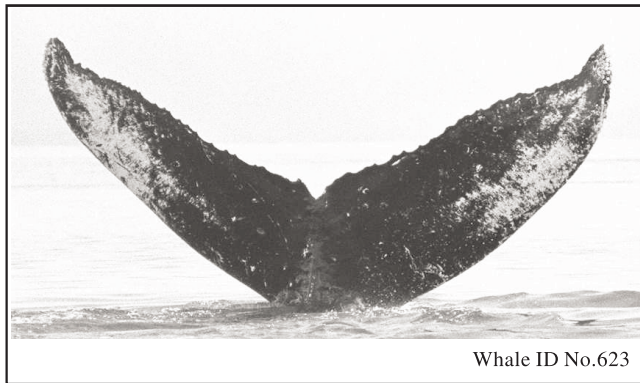
Research group	Region	Month(s)	Year(s)
KBMML	All main Hawaiian Islands	January–April	1981
	Maui and Hawai'i, HI	January–April	1982–1994
	Glacier Bay, Icy Strait, and Frederick Sound, SE Alaska	July–August	1981–1984
CWS	Maui, HI	February–May	1979–1990, 1995
MLML	Kauai, HI	January–April	1989–1993
HSU	Frederick Sound, SE Alaska	July	1989
WCWRF	Maui and Hawai'i, HI	January–April	1979–1981
	Frederick Sound, SE Alaska	June–September	1981–1985
JSI	Northern SE Alaska, excluding Glacier Bay and Icy Strait	November–March	1979–1984
		Year-round	1985–1995
NGOS	Prince William Sound, Alaska	June–September	1980–1995
GBNP	Glacier Bay and Icy Strait, SE Alaska	June–August	1982–1995

**Note:** KBMML, Kewalo Basin Marine Mammal Laboratory; CWS, Center for Whale Studies; MLML, Moss Landing Marine Laboratory; HSU, Humboldt State University; WCWRF, West Coast Whale Research Foundation; JSI, J. Straley Investigations; NGOS, North Gulf Oceanic Society; GBNP, Glacier Bay National Park; HI, Hawaiian Islands.

on this information, but in the absence of empirical length measurements, we defined a *calf* as a whale less than 1 year old, identified primarily by its size (less than 9 m in length) but also by its grayish body coloration and close, consistent affiliation with a particular adult whale, considered to be its *mother*. Researchers primarily used behavioral observations to determine the sex of adult whales. We termed any adult whale identified in a persistent, close

association with a calf at some point in its sighting history a *female*. We refer to a female as a mother only in the years when she was sighted with a calf. In Hawai'i, researchers presumed that any solitary whale observed singing was *male*, as was an adult whale "escort" in close association with a mother and calf (Herman and Antinofa 1977), based on the use of underwater sexing techniques pioneered by Glockner (1983). Underwater photographs of the geni-

**Fig. 2.** Sample fluke-identification photograph.



tal region (Glockner and Venus 1983) and molecular genetic techniques (Lambertsen et al. 1988; Baker et al. 1998) were used to confirm or determine the sex of a small number of whales.

### Compiling sighting histories of individual whales

Researchers contributed identification photographs and sighting histories of known females to the North Pacific humpback whale photographic archive at the NMML (Mizroch et al. 1990). During the first phase of the calf-mortality workshop we created a photographic catalog of known Hawai'i females and distributed it to researchers working in Alaska and British Columbia, who independently matched their entire photographic catalogs (each containing 150–400 whales) with it. NMML researchers independently used computer-aided matching (Mizroch et al. 1990) to compare the catalog of Hawaiian females to the approximately 12 000 photographs in the archive.

The matching procedure resulted in a cross-matched list of known females in the central North Pacific. From this list we extracted the subset of females that were identified in both Hawai'i and on the feeding grounds and distributed it to participating researchers. These researchers then submitted sighting data on these females, including calf presence, to be compiled into multiyear winter and summer sighting histories. We verified and error-checked the resulting data base. If we detected any discrepancies concerning a particular data point (i.e., questionable identification as a female or ambiguity about the presence of a calf), that record was excluded from our analyses.

### Estimating calf mortality

To estimate calf mortality, we calculated the proportion of mothers identified with a calf in Hawai'i but without a calf in all of their Alaska sightings that year. The resulting sample size was small, but we recognized that increasing the sample of known calf survivals by adding females sighted in Alaska with a calf but not sighted with a calf in Hawai'i would have introduced bias into the calf-mortality estimate (Appendix). We also calculated a calf mortality estimate after removing all cases in which the first Alaska sighting of the mother occurred after October 31. We agreed on the October 31 criterion on the assumption that some calves could be at least 10 months of age and weaned by that date.

The estimate we present here is based on longitudinal data on the fate of individual animals, no assumptions being made about the age structure of the population. Our calf-mortality estimate excludes neonatal mortality that occurred before the mother was observed in Hawai'i and calf mortality associated with the death of mothers. We assumed that adult mortality in this population over a 8-month period was likely to be sufficiently low (Buckland 1990) that the latter factor would cause only a negligible negative bias in the calf-mortality estimate. We could not effectively assess the

potential effects of the mother's or the calf's age during migration on the calf-mortality rate.

### Investigating potential sources of bias

Participants in the calf-mortality workshop recognized the need to examine and test the assumptions inherent in our methods and predict how violations of these assumptions would bias the calf-mortality estimate. We evaluated and tested the two main assumptions of this study: (1) that the presence or absence of a calf can be determined accurately and (2) that the probability of identifying a female in Alaska after she has been identified with a calf that year in Hawai'i is independent of whether she lost her calf. Specifically, we statistically evaluated three factors: (i) the rates at which we misclassified mothers, calves, or their companions (due to observer error or whale behavior); (ii) whether the sighting probabilities of mothers with a calf differed from those of females without a calf, owing to geographic segregation or other aspects of behavior; and (iii) the possibility that calves may have been weaned and permanently separated from their mother prior to her first sighting in Alaska.

### Statistical analysis

We calculated the 95% confidence limits of the calf-mortality proportions according to Zar (1984). We used Fisher's exact test to examine hypotheses about  $2 \times 2$  contingency tables. Non-parametric statistics (Spearman's rank-order correlation coefficient, Mann-Whitney  $U$  and Kolmogorov-Smirnov tests) were used in situations where the samples were not normally distributed or had unequal sample sizes and heterogeneous variances.

## Results

### Description of data set

The sighting data base comprised 2179 sightings of 314 individually identified females between 1979 and 1995. Of these females, 87 were sighted in both Hawai'i and Alaska in the same year. In only 29 of these same-year cases (involving 25 individuals), the female was identified in Hawai'i with a calf and sighted later the same year in Alaska (Tables 2, 3), giving us the opportunity to detect calf mortality. None of the Hawai'i females were identified in the same year in British Columbia, although we compared photographs from that area.

### Calf-mortality rate

Seven of the 29 Hawai'i mothers were sighted without their calf in Alaska, giving an estimated calf-mortality rate of 0.241 (95% CI = 0.103, 0.434). One female, No. 256, had a calf in 1986 that survived the migration to Alaska but was lost during July or August (Table 2; Baker et al. 1987). The remaining deaths could have occurred on the wintering grounds, during migration, or at some time during the feeding season prior to the mother's first sighting. Female 6902 appears twice in Table 2, with calf mortalities in 1991 and 1993. Note that in 3 cases of calf survival, females 623, 1192, and 17208 were each sighted once without their calf in Alaska (Table 3) but were later sighted with the calf again.

We designed this study to measure calf mortality during migration and the early feeding season. However, the data set of same-year mothers contained several Alaska mothers who were not sighted until autumn (Tables 2, 3). Basing the calves' ages on their Hawai'i-to-Alaska sighting intervals, only one of the calves presumed to have died (the calf of

**Table 2.** Sighting data for the 7 observed cases of humpback whale (*Megaptera novaeangliae*) calf mortality.

Case No.	Female ID No.	Research groups <sup>a</sup>	Date of last Hawai'i sighting	Date of first Alaska sighting	With calf in Hawai'i? <sup>b</sup>	With calf in Alaska? <sup>b</sup>	Hawai'i-to-Alaska sighting interval
1	586	KBMML, KBMML	Mar. 22, 1984	Aug. 15, 1984	Yes (1)	No (1)	146
2	3280	CWS, JSI	Mar. 31, 1986	Dec. 11, 1986	Yes (1)	No (2)	255
3	256	KBMML, GBNP/JSI	Mar. 3, 1986	June 11, 1986	Yes (1)	Yes (3), No (4)	100
4	1168	CWS/KBMML, JSI	Apr. 4, 1987	Dec. 23, 1987	Yes (2)	No (1)	263
5	1192	CWS, JSI	Mar. 8, 1988	Oct. 10, 1988	Yes (1)	No (3)	216
6	6902	MLML, JSI	Apr. 9, 1991	Dec. 9, 1991	Yes (2)	No (3)	244
7	6902	MLML, JSI	Apr. 14, 1993	Feb. 5, 1994	Yes (1)	No (1)	297

<sup>a</sup>The research group(s) in Hawai'i followed by the group(s) in Alaska. For abbreviations of research-group names see Table 1.

<sup>b</sup>Numbers in parentheses are numbers of sightings.

**Table 3.** Sighting data for the 22 observed cases of calf survival.

Case No.	Female ID No.	Research groups <sup>a</sup>	Date of last Hawai'i sighting	Date of first Alaska sighting	With calf in Hawai'i? <sup>b</sup>	With calf in Alaska? <sup>b</sup>	Hawai'i-to-Alaska sighting interval
1	121	WCWRF/CWS, KBMML	Feb. 3, 1981	July 16, 1981	Yes (2)	Yes (1)	163
2	722	KBMML, CSB	Mar. 10, 1981	July 15, 1981	Yes (1)	Yes (3)	127
3	168	WCWRF, KBMML	Apr. 6, 1981	Aug. 7, 1981	Yes (1)	Yes (2)	123
4	623	KBMML/CWS, JSI/GBNP	Apr. 18, 1982	July 1, 1982	Yes (1)	Yes (15)	74
5	369	KBMML, NGOS	Feb. 26, 1983	July 13, 1983	Yes (1)	Yes (1)	137
6	447	CWS/KBMML, NGOS	Mar. 23, 1983	July 7, 1983	Yes (3)	Yes (3)	106
7	623	CWS, WCWRF/KBMML	Apr. 6, 1985	July 20, 1985	Yes (1)	No (1), Yes (2)	105
8	262	CWS, JSI	Feb. 27, 1986	Dec. 3, 1986	Yes (1)	Yes (1)	279
9	839	KBMML/CWS, NGOS	Apr. 17, 1986	June 19, 1986	Yes (1)	Yes (1)	63
10	249	KBMML, JSI/GBNP	Mar. 17, 1986	Aug. 30, 1986	Yes (1)	Yes (2)	166
11	273	KBMML, CSB/JSI	Feb. 21, 1987	Sept. 9, 1987	Yes (1)	Yes (1)	200
12	1192	KBMML, JSI	Apr. 3, 1987	Dec. 28, 1987	Yes (1)	Yes (3), No (1)	269
13	8335	CWS, JSI	Mar. 30, 1988	Aug. 6, 1988	Yes (1)	Yes (2)	129
14	17208	CWS, JSI	Apr. 23, 1988	Oct. 27, 1988	Yes (1)	No (1), Yes (5)	187
15	128	CWS, JSI	Jan. 31, 1989	Dec. 3, 1989	Yes (2)	Yes (1)	306
16	130	CWS, JSI	Mar. 21, 1989	Nov. 30, 1989	Yes (1)	Yes (1)	254
17	731	MLML, JSI	Mar. 26, 1989	Dec. 3, 1989	Yes (1)	Yes (1)	252
18	622	KBMML, HSU	Apr. 2, 1989	July 6, 1989	Yes (2)	Yes (1)	95
19	6698	CWS, NGOS	Apr. 12, 1989	July 6, 1989	Yes (1)	Yes (4)	85
20	737	KBMML, JSI	Feb. 9, 1993	Oct. 12, 1993	Yes (4)	Yes (1)	245
21	722	KBMML, GBNP	Feb. 24, 1993	July 7, 1993	Yes (2)	Yes (1)	133
22	717	KBMML, JSI	Mar. 28, 1993	Aug. 12, 1993	Yes (1)	Yes (1)	137

<sup>a</sup>The research group(s) in Hawai'i followed by the group(s) in Alaska. For abbreviations of research-group names see Table 1.

<sup>b</sup>Numbers in parentheses are numbers of sightings.

mother 6902, which was at least 10 months of age) was known to have been old enough to be fully weaned by the date of its mother's first sighting. The calf-mortality estimate excluding calves that could have been weaned (i.e., all mortalities and survivals based on sightings of the mother after October 31) was 3 out of 20, or 0.150 (95% CI = 0.032, 0.378).

Reliance on single Alaska sightings to determine calf presence leaves the calf-mortality estimate vulnerable to mistaking temporary mother-calf separation for mortality. We removed all mortality and survival cases based upon single Alaska sightings of the mother, leaving 4 mortalities out of 14 cases, or 0.286 (95% CI = 0.084, 0.581). To minimize the potential effects of both weaning and temporary mother-calf separation, we also computed an estimate omitting post-October 31 sightings as well as all the remaining mortalities and survivals that were based upon single Alaska sightings,

resulting in 2 calf mortalities out of 11 cases, or 0.182 (95% CI = 0.023, 0.518).

In contrast, a potential negative bias could result if any of the "surviving" calves (Table 3) died after we saw last them in midsummer. To compensate, we computed an estimate omitting the 9 calf survivals that were last identified before September 1, resulting in a calf-mortality rate of 7 out of 20 cases, or 0.350 (95% CI = 0.154, 0.592). However, based on the low calf-mortality rate (1 out of 29 cases; Table 2) detected on the feeding grounds, we suspect that this is an overestimate of calf mortality.

**Investigating bias: frequency of mother or calf misidentification**

The remainder of our analyses examined the possibility that violations of our two main assumptions affected the calf-mortality estimate. Our first main assumption, that calf

**Table 4.** Contingency of Alaska sighting on calf presence in Hawai'i.

	Sighted in Alaska	Sighted in Alaska	Total
No. of females with calf in Hawai'i	27 (10.9)	219 (89.0)	246
No. of females without calf in Hawai'i	13 (14.6)	76 (85.4)	89
Total	40	95	335

**Note:** Numbers in parentheses are percentages. No significant difference using Fisher's exact test,  $p = 0.4189$ .

presence can be determined accurately, requires correct identification of both mother and calf.

#### *Misidentifications of mothers*

Misidentifications of females were detectable in our data base because any whale that had been identified as a mother by any research group was added to the catalog of presumed females. Other research groups included their sightings of this whale in the data base regardless of whether or not their data indicated that the whale was female. We used each whale's long-term sighting history to discern whether it was male or female. In the sighting histories of the 314 presumed females, we found that 293 (93%) were identified solely as female, 5 (1.6%) were identified as female except at 1 sighting, 9 (2.9%) were apparently males identified once as a female, and 7 (2.2%) were not resolvable. Seven of the 9 misidentifications of males as mothers occurred in Hawai'i, out of a total of 726 sightings, an error rate of 0.9%. Two of the misidentifications occurred in Alaska, out of a total of 969 sightings, an error rate of 0.2%.

All but 1 of the mothers (No. 586) in the list of calf mortalities (Table 2) has been observed as a mother in other years. Taken together with the low error rates described above, this suggests that misidentification of mothers was not a large source of positive bias in the calf-mortality estimate.

#### *Misidentifications of calves*

Misidentifications of non-calves as calves in Hawai'i would have inflated the calf-mortality estimate because the "calf" would be unlikely to have accompanied the female in her Alaska sightings later that year. Calves in Hawai'i are quite small, often less than 5 m in length, and therefore not easily mistaken for juveniles or adults. We did not detect any errors or ambiguities of this type in our Hawai'i field observations, although there were 2 cases in which yearlings were mistakenly coded as a calf in the data base. Although calves on the Alaska feeding grounds can be up to 8 m in length, and can be difficult to distinguish using the size difference alone, we detected no apparent errors in calf identification in Alaska. In 3 cases of calf mortality, the female was either alone or her companion was a known adult, therefore calf misidentification could not have been a factor. In 3 cases, group sizes varied but we found no indication of an unattended calf in or near the group. In the final case (No. 3; Table 2) there were numerous sightings of female 256 after her own calf disappeared, during which time she primarily accompanied another known mother-calf pair (Baker et al. 1987).

#### **Sighting bias associated with female reproductive status**

Our second main assumption was that Hawai'i mothers would have an equal probability of being sighted in Alaska regardless of whether or not their calf died. We investigated whether the sighting probabilities for a particular female in

Alaska depended on whether she had a calf during her Hawai'i sightings that year. Using the 335 cases in which females were sighted in either Hawai'i or Alaska in a given year, we found that of the 246 females sighted with a calf in Hawai'i, 27 (10.9%) were sighted the same year in Alaska (Table 4). Of the 89 females sighted without a calf in Hawai'i, 13 (14.6%) were sighted later that year in Alaska. Mothers with a calf were more than twice as likely to be sighted in Hawai'i ( $n = 246$ ) as non-mothers ( $n = 89$ ), but their Alaska sightings did not appear to be related to their reproductive status. We could not reject the null hypothesis that the proportion of females sighted in Alaska was equivalent regardless of whether or not they had a calf in Hawai'i (Fisher's exact test,  $p = 0.42$ ). Because Alaska sightings of females did not appear to depend on whether or not they had a calf in Hawai'i, we concluded that if a female lost a calf she would be no more or less likely to be sighted in Alaska.

#### **Dependence of sighting probability on calf presence**

If mothers with calves were geographically separated from other females, or behaved differently in a way that affected our ability to identify them, the calf-mortality estimate could be non-representative of the population. For Alaska and Hawai'i, we chose the single year with the largest number of sightings and tested the null hypothesis that mothers with a calf were resighted on the same number of days as females without a calf. Multiple sightings of a female within the same day were not used in this analysis.

#### *Alaska*

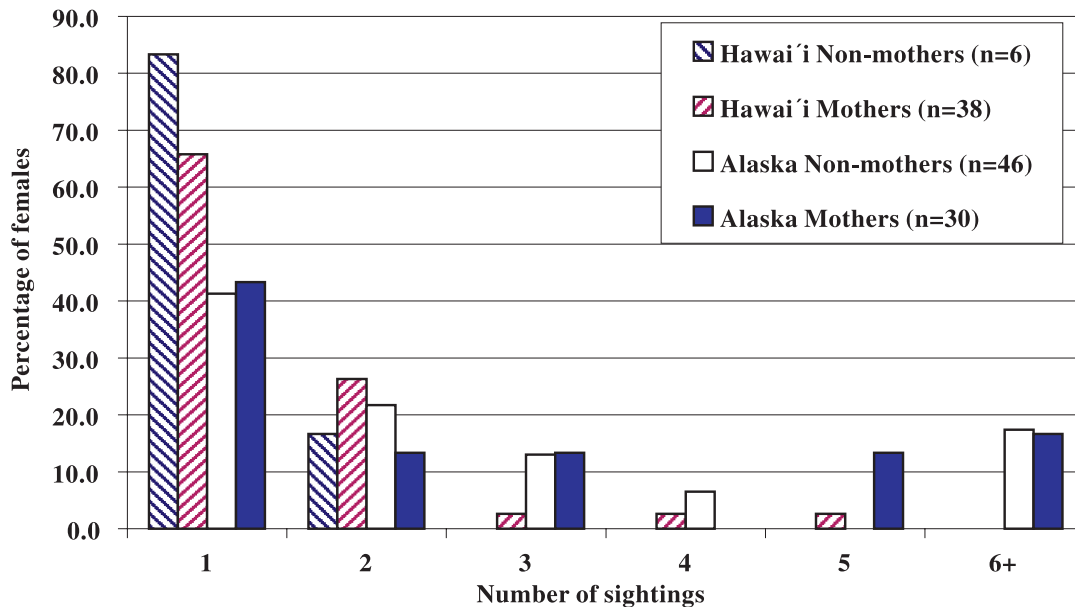
There were 314 sightings of 76 different females in Alaska in 1992. Females with and without a calf were sighted between 1 and 30 times, although females were typically sighted on only one occasion (42%), regardless of whether or not they had a calf (Fig. 3). There was no statistically significant difference between the distributions of the number of resightings per season of mothers with a calf and non-parous females in Alaska (Kolmogorov-Smirnov test,  $\chi^2 = 1.155$ ,  $df = 2$ ,  $p > 0.99$ ).

To investigate the potential effect of single sightings on calf-mortality estimation, we investigated the rates at which single sightings of females occurred in the calf-mortality (3/7, or 43%) and -survival (12/22, or 55%) records. There appear to be a larger proportion of survivals based on single sightings, but they are not statistically distinct from one another (Fisher's exact test,  $p = 0.6817$ ), and the proportion of mortalities based on single sightings is very close to the 42% calculated for the population as a whole (Fig. 3).

#### *Hawai'i*

There were 64 sightings of 45 different females in Hawai'i in 1989. Most females were sighted on only one or two occasions, regardless of whether or not they had a calf (Fig. 3),

**Fig. 3.** Number of within-season sightings of mothers and non-mothers in Alaska and Hawai'i. Alaska sightings were drawn from 1992 and Hawai'i sightings from 1989, the year with the most data for the respective region.



**Table 5.** Sightings of Hawai'i females before and after calving.

Case No.	Female ID No.	Research group <sup>a</sup>	Region <sup>b</sup>	Date of photograph	Calf present?
1	10827	WCWRF	HI	Feb. 29, 1980	No
	10827	WCWRF	HI	Mar. 11, 1980	Yes
2	5288	WCWRF	HI	Jan. 31, 1981	No
	5288	WCWRF	HI	Feb. 16, 1981	Yes
3	34633	MLML	HI	Feb. 12, 1991	No
	34633	MLML	HI	Mar. 21, 1991	Yes
4	256	KBMLL	HI	Mar. 5, 1988	No
	256	GBNP	SE Alaska	June–September 1988	Yes

<sup>a</sup>For abbreviations of research-group names see Table 1.

<sup>b</sup>HI, Hawaiian islands.

although a few mothers were sighted up to 5 times. Again, we could not reject the hypothesis that Hawai'i mothers with a calf were resighted as frequently as non-parous females (Kolmogorov–Smirnov test,  $\chi^2 = 0.638$ ,  $df = 2$ ,  $p > 0.99$ ). Thus, we found no evidence in Hawai'i or Alaska that our ability to identify females was affected by behavioral differences between mothers and females without a calf.

**Frequency of mothers sighted without their calves**

Observer error or other circumstances that would cause researchers to fail to detect a calf when it was with its mother in Hawai'i would reduce the sample size available for the calf-mortality estimate, but the estimate would remain unbiased. In contrast, failure to detect a calf accompanying its mother in Alaska would positively bias the calf-mortality estimate. We examined the relevant data for both areas.

*Hawai'i*

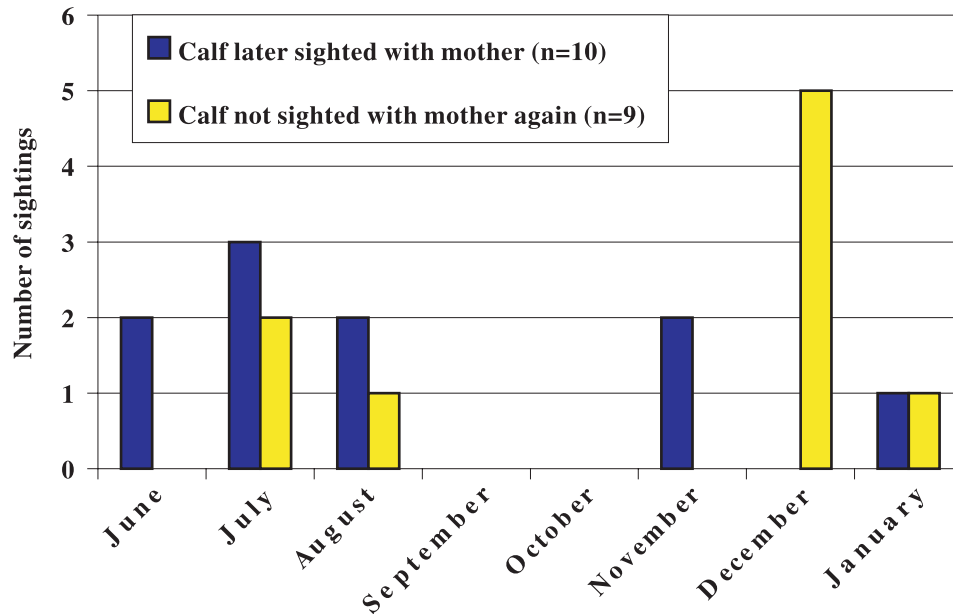
No Hawai'i females were sighted with a calf and later without a calf in Hawai'i. However, 4 females (3.4%) were first sighted in Hawai'i with no calf and later sighted with a calf (Table 5) compared with 112 mothers with 2 or more Hawai'i sightings that were with their calf on every sighting.

The 4 cases of calf absence indicate either that the observers missed a calf that was present or that they encountered the female prior to parturition. Three of these females were later sighted in Hawai'i with a calf, while 1 female (No. 256) was not sighted with a calf until that summer in Alaska. We surmise that female 256's only 1988 Hawai'i sighting occurred prior to parturition, because it appears unlikely that an undetected calf was present during the 35-min encounter under good observational conditions, in which both adults in the pod were photographically identified. Female 256 was sighted on 15 different days with her calf between June and September 1988 in southeastern Alaska, during which researchers noted the calf's small size and possible late-season birth. These infrequent sightings of Hawai'i mothers with and without their calves during a season suggest that missing a calf which was present in Hawai'i or sighting a female prior to parturition was rare.

*Alaska*

We used the entire data base to investigate the likelihood of sighting a female without her calf in Alaska during years in which she was known to have a calf (excluding the presumed mortalities included in Table 2). Using data on

**Fig. 4.** Temporal distribution of Alaska sightings of mothers without their calves. Cases in which the calf was later sighted with its mother indicate a temporary separation. Cases in which the calf was not sighted again may indicate a temporary separation, permanent separation, or mortality.



mothers sighted at least twice in a given year, we found 668 sightings of mothers who were with their calf on every sighting, and 19 sightings of mothers whose calf was not present or not detected by the observer. In 10 of these cases, mothers were sighted with their calf, then without their calf, then with their calf again (Fig. 4), yielding a 1.4% probability (10 out of 687) of missing a calf that is known to have been alive. In an additional 9 cases, the calf was sighted with its mother once or more, but was absent on the mother's final sighting (Fig. 4). In these 9 cases we do not know whether their separation was temporary or permanent, or indicates mortality. Although these data appear to suggest that mothers without their calf on their final sighting tended to be sighted after November 1, statistical analysis revealed no significant difference in the timing of sightings of the two groups of mothers (Fisher's exact test,  $p = 0.18$ ). Note that the Alaska sightings in January are encounters with mothers and their near-yearling calves, not mothers with neonates.

The above result is similar to what we found when we investigated the number of days that elapsed between the last Hawai'i sighting and the first Alaska sighting for the 7 mothers that lost their calves compared with the 22 mothers that did not lose their calves (Fig. 5). In 4 out of the 7 mortalities (57%), the mother's first Alaska sighting did not occur until at least late November. In comparison, only 6 of the 22 survivals (27%) were documented in late November or later. Late-season sightings seem to be overrepresented in the mortalities compared with survivals; however, the difference is not statistically significant (Fisher's exact test,  $p = 0.1581$ ). Similarly, the interval between the last Hawai'i sighting and the first Alaska sightings of the mothers associated with the 7 calf mortalities (mean = 217 days, SE = 26.4 days) was larger but not significantly different from than those associated with the 22 surviving calves (mean = 165 days, SE = 16.5 days) and 24 non-mothers (mean = 166 days, SE = 16.6 days;  $F_{[50]} = 2.06$ ,  $p = 0.14$ ).

#### Influence of birth interval on the calf-mortality estimate

If calf mortality was linked to reproductive interval, females with short birth intervals would be overrepresented in a longitudinal study because researchers would have had more opportunities to detect calf mortality. In 4 calf-mortality cases, we could not determine the birth interval prior to mortality, but for the 3 females sighted in the year prior to calf mortality, their birth intervals were 2 years (No. 256), 2 years (No. 6902), and 1 year (No. 1192). Based on these limited data, we assumed that the birth intervals for the 23 females were not systematically different from those for the remainder of the population.

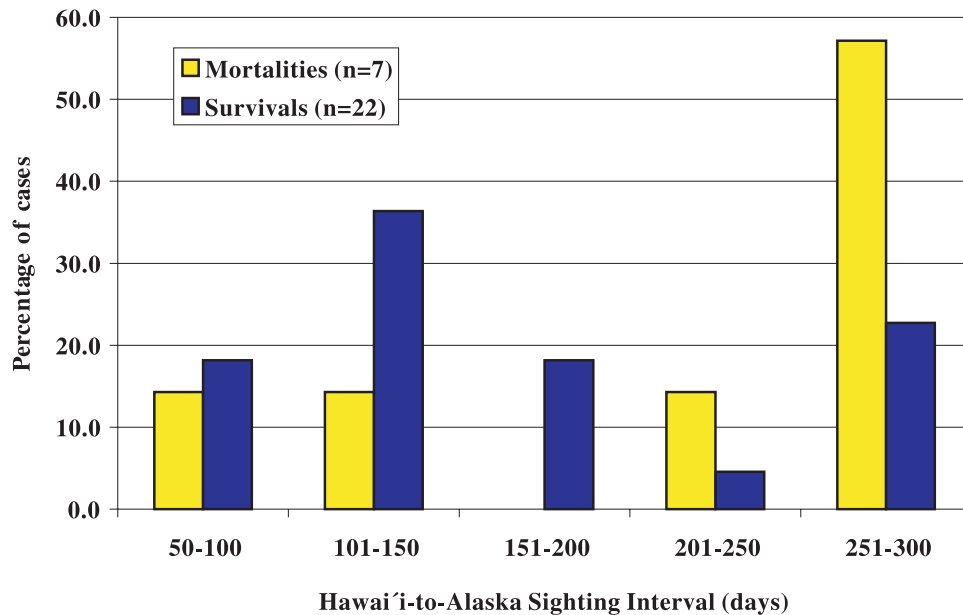
One female was notable for her yearly birth cycle. Female 1192 was observed in Hawai'i or Alaska with a calf each year between 1987 and 1991, with only 1 known mortality, although the fate of her 1990 calf is unknown because she was not sighted in Alaska that year (Straley 1994; D. Glockner-Ferrari, unpublished data). Female 1192 was observed with a calf in Hawai'i and Alaska in 1987 (Table 3). In March 1988, this female was observed with a calf in Hawai'i 62 days after her last sighting in southeastern Alaska in January 1988. She was not sighted again until October 1988 in southeastern Alaska, unaccompanied by the calf, which would have been approximately 8 months of age. Female 1192 was also observed with a calf in Alaska in November 1989 (Straley 1994), indicating successful reproduction in the year following the presumed mortality. If the October absence of her 1988 calf was a case of true mortality, the sighting record of female 1192 (Tables 2, 3) suggests that she may have ovulated and conceived post partum, after the death of the calf (Chittleborough 1958).

#### Discussion

We computed a point estimate of calf mortality using the



**Fig. 5.** Temporal distribution of Hawai'i-to-Alaska sighting intervals for mothers in cases of calf mortality or calf survival. Sighting data for each mother are summarized in Tables 2 and 3.



entire data set (0.241; 95% CI = 0.103, 0.434) and a less biased estimate that excluded all November through February mortalities and survivals because calf absences could have been attributable to weaning rather than mortality (0.150; 95% CI = 0.032, 0.378). The estimate that attempted to account for the potential positive bias which could have resulted from undetected midsummer mortalities among the surviving calves seemed unrealistically high (0.350; 95% CI = 0.154, 0.592), and excluding these data was perhaps unjustified in light of the low number of calf mortalities (1 out of 29 cases) that we detected during summer. We also attempted to compensate for the potential effects of temporary mother-calf separation by excluding all cases that depended on single Alaska sightings. However, removing all of these sightings did not seem warranted, given that we could not detect a statistically significant difference between the rates at which single sightings occurred in records of mortality versus survivals. And finally, although the estimate that omitted all mortalities and survivals based upon single Alaska sightings, as well as late-season sightings (0.182; 95% CI = 0.023, 0.518), was plausible, its small sample size and correspondingly wide 95% confidence intervals made it less than ideal. Nevertheless, this point estimate may be the closest approximation to the actual mortality rate of humpback whale calves in their first year, midway between a minimal estimate of 0.150 and a maximal estimate of 0.241.

#### Likely sources of bias

Based on our analyses, we do not believe that we violated either of our main methodological assumptions. First, we found no evidence that the reproductive status of a female in Hawai'i affected the probability of her subsequent resighting in Alaska that year (Table 4). From this we inferred that we met the assumption that the probability of identifying a female in Alaska after she had been identified with a calf that year in Hawai'i is independent of whether she was still with her calf. Second, misidentification of mothers or calves also appeared to have a negligible effect on the calf-mortality es-

timate, especially since all but 1 of the females in the mortality list (Table 2) has been identified as a mother in other years.

We also failed to detect any effect of reproductive status on the number of times that a female was resighted in Alaska or Hawai'i (Fig. 3). However, the comparatively small sample sizes of females without a calf in Hawai'i (Table 4, Fig. 3) suggest that mothers were photographed more often than other females.

Given our incomplete understanding of the weaning process, we could not dismiss the potential positive bias due to temporary or permanent mother-calf separation. Although we cannot be certain whether calves that were missing in the late season, and included in the presumed mortalities (Table 2) or in general (Fig. 4), were dead or just separated from their mother, two factors led us to believe that the potential positive bias of weaning and temporary mother-calf separation affected the calf-mortality estimate. First, long sighting intervals appear to be overrepresented in the mortalities compared with the survivals (Fig. 5). Although the difference was not statistically significant, small sample sizes may have resulted in low statistical power of this test. Second, sightings of mothers without their calf on the final sighting tended to occur later in the season (Fig. 4), although again this result was not statistically significant. The results of these two analyses may indicate that calves become progressively more independent as weaning continues, culminating in permanent separation. Given that humpback whale calves are born over a period of months, one might also expect that an increasing number of calves would be old enough to be weaned in late fall and early winter.

The fact that none of the 3 late-season females with calf mortalities (Nos. 3280, 1168, and 6902) have been sighted elsewhere in southeastern Alaska (J. Straley, unpublished data) seems to indicate that they spend a considerable proportion of their feeding season in unstudied areas in the Gulf of Alaska or elsewhere before arriving in Sitka Sound in autumn (Straley 1994). The sighting intervals for these females

(Table 2) are substantially longer than the few published Alaska-to-Hawai'i sighting intervals, ranging from 36 to 117 days (Baker et al. 1985; Gabriele et al. 1996; Calambokidis et al. 1997), which suggests that they include more than just migration. Finally, the predominance of late-season females amongst the calf mortalities might instead reflect a change in migratory behavior for females that have lost a calf. It seems plausible that a female who lost a calf on the feeding grounds might stay in Alaska later to maximize her food intake prior to her next pregnancy.

#### Population-level implications of the calf-mortality rate

Our point estimates of 0.150 and 0.241 could account for some of the reported variability in calving rates in winter and summer habitats, although other factors have almost certainly played a role as well. Our point estimates of calf mortality are slightly higher than the average first-year mortality rate of 0.13 computed by Barlow and Clapham (1997), but comparable to their estimated maximal rate (0.17) in the Gulf of Maine. This similarity makes sense, given that their maximal rate was based upon sightings of known-age whales after their first year of life.

Our calf-mortality estimate has important implications for models of the rate of increase for the central North Pacific stock of humpback whales. Although juvenile mortality is generally considered not to have a profound effect on rates of increase in cetacean populations (Reilly and Barlow 1985; Brandao et al. 2000), it seems unlikely that the North Pacific population, with calf-mortality rates of 0.150–0.241, could attain a rate of increase in excess of 10% (Brandao et al. 2000) as reported for southern hemisphere humpback whale populations (Paterson and Paterson 1989; Bryden et al. 1990; Best 1993; Bannister 1994). Notably, the models used by Brandao et al. (2000) only considered juvenile mortality rates of 1 and 12%, somewhat lower than those indicated by our analyses. Our results seem to be more consistent with the estimated rates of population increase reported for California and Hawai'i, which range from 5 to 8% (Steiger and Calambokidis 2000; J.R. Mobley, personal communication). A greater understanding of other relevant population parameters is needed before the recovery rate of the North Pacific stock can be confidently determined (National Marine Fisheries Service 1991), particularly in light of differences in apparent recovery rates.

Although this calf-mortality estimate is based on a large-scale and long-term data-collection effort by eight research groups over the course of 16 years, it has relatively wide confidence intervals, owing to the small sample size available for the study. The most promising way to increase the sample size would be to cover the feeding areas more comprehensively, documenting a much higher proportion of Hawai'i mothers on their feeding grounds (Table 4). of Potential biases could further be evaluated by obtaining longitudinal, within-season data on individual mother–calf pairs in order to fully document the weaning process. Our results highlight the need to maintain and support the long-term studies that made the calf-mortality estimate possible, because these longitudinal studies are often the only source of data for estimating population parameters. Limited information is available on the causes of the calf mortalities observed during field studies in Alaska and Hawai'i (Straley 1994; Glockner-Ferrari

and Ferrari 1997) or the analysis of stranding reports in Hawai'i (Mazzuca et al. 1998). The lack of specific information on causes of mortality and the remaining unknown population parameters should not be allowed to hinder the development and implementation of conservation measures that target vulnerable members of the population, such as mothers and calves.

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This study would not have been possible without the data-collection efforts of numerous field staff working with each participating research group, and others who helped analyze the fluke-identification photographs constituting the females' sighting histories. We thank the following people for their participation in the calf-mortality workshops: Jay Barlow, Stephen T. Buckland, John Calambokidis, Suzanne Harkness, Rod Hobbs, Elizabeth A. Mathews, Mike Osmond, Dan Salden, Gretchen Steiger, Allen A. Wolman, Jorge Urban, and Judy Zeh. Tom Norris was instrumental in helping with the Moss Landing Marine Laboratories fieldwork in Kauai. The Center for Whale Studies thanks the Wallace Alexander Gerbode Foundation, the David and Lucile Packard Foundation, and members of the Center for Whale Studies. The Center for Field Studies (Earthwatch) provided funding for the University of Hawai'i field efforts. For assistance with Alaska fieldwork we thank Ken Krieger and Bruce Wing of the National Marine Fisheries Service Auke Bay Laboratory, John Straley, Jim and Carol Greenough, K.J. Metcalf, and Biological Journeys. Mary Beth Moss, Doug DeMaster, Suzanne Harkness, and Susan Rickards made comments on the manuscript that improved the final product. Sue Moore deserves special thanks for her editing contributions and for helping this large collaborative project keep its momentum. Tania M. Lewis made the study-area map. Sonja Kromann of the NMML Library cheerfully provided the numerous scientific articles necessary to provide the background of this paper. Glacier Bay National Park and Preserve provided logistical and financial support that enabled this manuscript to be completed. The comments of two anonymous reviewers improved the final manuscript. All field research was conducted under scientific research permits issued by the NMFS.

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**Appendix.** Mathematical explanation of the need to use Hawai'i and Alaska sightings of females for estimating calf mortality.

When one considers females that are seen in Hawai'i and Alaska (but are not necessarily identified as females) and that gave birth to a calf (whether detected or not), there are four situations that could occur, depending on whether or not the calf was observed in Hawai'i or in Alaska, as summarized in the following table.

	Frequency of females	
	Without calf detected in Hawai'i	With calf detected in Hawai'i
Without calf detected in Alaska	$n_{nn}$	$n_{pn}$
With calf detected in Alaska	$n_{np}$	$n_{pp}$

Frequency  $n_{nn}$  is not observable because no calf was observed in either place, but the other frequencies are. It does not matter why the calves were not detected (i.e., because they were not there or because they were missed).

Let  $\alpha_H$  be the probability of detecting a calf in Hawai'i,  $\alpha_A$  the probability of detecting a calf in Alaska,  $s$  the calf-survival rate, and  $N$  the true number of females seen in Hawai'i and Alaska that gave birth to a calf, then the following expected frequencies,  $E$ , result:

	Expected frequency of females	
	Without calf detected in Hawai'i	With calf detected in Hawai'i
Without calf detected in Alaska	$E_{n_{nn}} = N(1 - \alpha_H)(1 - \alpha_A)s$	$E_{n_{pn}} = N\alpha_H(1 - \alpha_A)s$
With calf detected in Alaska	$E_{n_{np}} = N(1 - \alpha_H)\alpha_A s$	$E_{n_{pp}} = N\alpha_H\alpha_A s$

If data from females with a calf detected in Hawai'i are used, the expected value of the proportion with a calf detected in Alaska is

$$E\left(\frac{n_{pp}}{n_{pn} + n_{pp}}\right) = \frac{N\alpha_H\alpha_A s}{N\alpha_H} = \alpha_A s$$

showing that the proportion is an unbiased estimate of calf survival multiplied by the probability of detecting a calf in Alaska. If this probability is not equal to 1 (that is, some Alaska calves are missed), calf survival is underestimated.

If data from females without a calf detected in Hawai'i and in Alaska could somehow be determined (giving the value  $n_{nn}$ ), the expected value of the proportion with an Alaska calf detected (for those females with no calf detected in Hawai'i) is

$$E\left(\frac{n_{np}}{n_{nn} + n_{np}}\right) = \frac{N(1 - \alpha_H)\alpha_A s}{N(1 - \alpha_H)} = \alpha_A s$$

the same as before. The same thing happens if the two data sets are pooled.

Now, if the data are pooled but the value of  $n_{nn}$  is not known, the expected proportion of females with calves in Alaska detected is

$$\begin{aligned} E\left(\frac{n_{pp} + n_{np}}{n_{pn} + n_{pp} + n_{np}}\right) &= \frac{N\alpha_A s}{N\alpha_H + N(1 - \alpha_H)\alpha_A s} \\ &= \alpha_A s \left[ \frac{1}{\alpha_H + (1 - \alpha_H)\alpha_A s} \right] \\ &\geq \alpha_A s \end{aligned}$$

showing that calf survival multiplied by detection is overestimated. Only if all calves are detected in Hawai'i ( $\alpha_H = 1$ ) would this estimate be unbiased. Therefore, bias is created when Hawai'i data in which calf status is uncertain or misleading (not detecting a calf that is later detected in Alaska, for whatever reason) are used, because the affected females cannot be identified later in Alaska.