Aquatic Mammals 1999, **25.2**, 63–72

Changes over a ten-year interval in the distribution and relative abundance of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters

Joseph R. Mobley, Jr.[1]*, Gordon B. Bauer[2] and Louis M. Herman[3]

[1]*Social Sciences, University of Hawaii-West Oahu, 96-129 Ala Ike, Pearl City, HI 96782, USA*
[2]*Division of Social Sciences, New College of the University of South Florida, 5700 N. Tamiami Trail, Sarasota, FLA 34243, USA*
[3]*Kewalo Basin Marine Mammal Laboratory, 1129 Ala Moana Blvd., Honolulu, HI 96813, USA*

Abstract

Aerial surveys of the wintering population of humpback whales (*Megaptera novaeangliae*) were performed during the 1990 season (Jan–Apr) in the waters adjoining the major Hawaiian Islands using methods consistent with those used in earlier surveys (1977–80). Analysis of these data showed significant increases in both calves and total whales across the intervening period of ten years. Comparisons of number of whales and calves seen on peak flight dates across the five years (1977–80 and 1990) showed significant differences, with numbers of whales and numbers of calves for 1990 revealing the greatest departures from expected frequency. Comparisons of overall encounter rates for both calves (calves/km) and total whales (whales/km) showed significant differences across years, with 1990 rates significantly higher than all previous years. When encounter rates for total whales were compared across years within each of the five major regions (Big Island, Four Island, Penguin Bank, Oahu, and Kauai/Niihau regions), there was a general trend of greater increases moving northwest through the island chain. Together these data suggest that the wintering population may be 'spilling over' from previously preferred habitat (Four Island and Penguin Bank regions) and offer supportive evidence that this endangered population may be recovering.

Introduction

Prohibitions on whaling of North Pacific humpbacks by member nations of the International Whaling Commission were instituted beginning only in 1966, after many years of intensive exploitation. Estimates of the size of the population at that time were approximately 1000 animals, compared with an estimated original abundance of at least 15 000 (Rice, 1978; Johnson & Wolman, 1984). The recovery of the North Pacific population of humpback whales from this depleted status is thus of continuing concern. The humpback is a migratory species, summering in high-latitude highly-productive feeding grounds and wintering in tropical waters around shallow banks, islands, or continental shelves. In winter, most of the activity appears to be related to reproduction (Tyack & Whitehead, 1983; Baker & Herman, 1984; Mobley & Herman, 1985). The wintering population can be divided into eastern, central and western North Pacific regions (Darling & Jurasz, 1983; Darling & McSweeney, 1985; Baker *et al*., 1986; Perry *et al*., 1988). Currently, the majority of the whales appear to winter in the central region comprising the waters around the main Hawaiian Islands. Formal studies of this Hawaiian wintering population began in 1975–76 (Herman & Antinoja, 1977). Aerial studies conducted during the period 1977 through 1980 provided the first complete description of seasonal trends in distribution of the whales and their relative abundance in various areas of the islands (Herman, Forestell & Antinoja, 1980; Baker & Herman, 1981). These surveys were conducted approximately every two weeks, weather permitting, during the months of January through April, covering most of the period when whales are present in Hawaiian waters.

The preferred winter habitats of humpback whales world-wide are shallow tropical or subtropical waters of approximately 100 fathoms (183 m) depth or less in outlying banks, or near islands or continental shelves (Herman *et al*., 1980; Mobley *et al*., 1997; Katona & Whitehead, 1981). During the 1977–80 surveys, three aircraft flew at low

*Phone: 808-454-4716; Fax: 808-453-6176; E-mail: jmobley@hawaii.edu

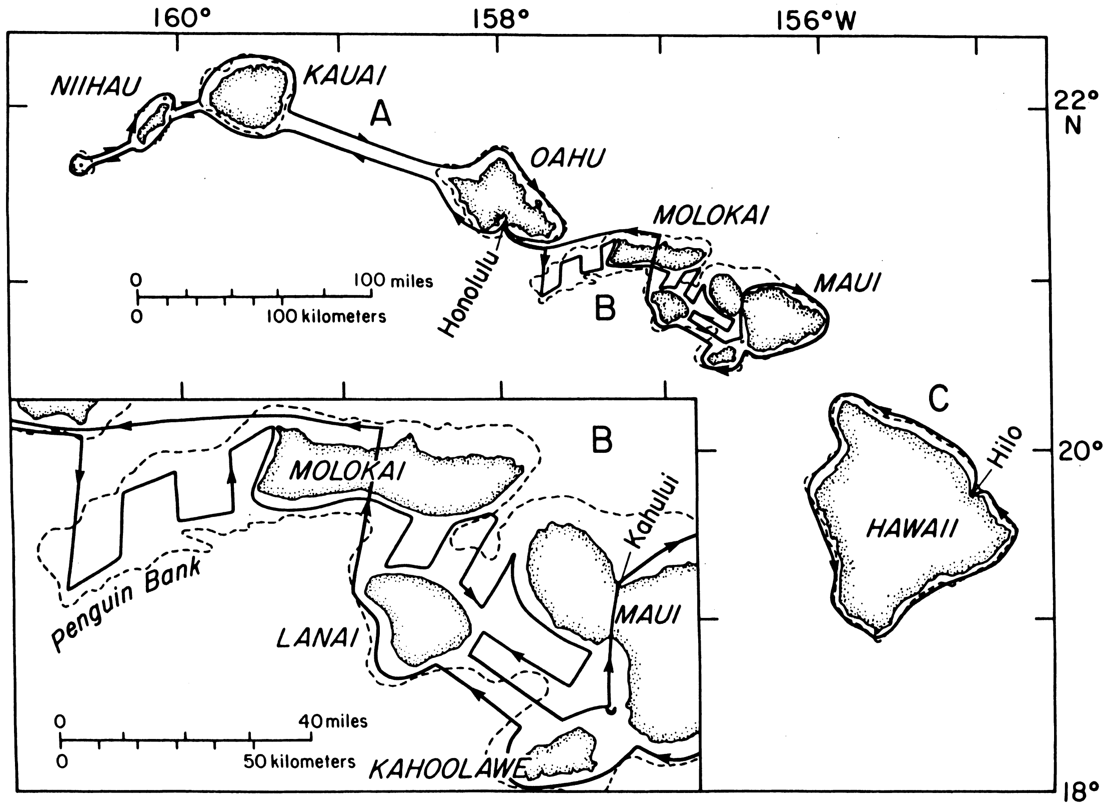

Figure 1. Map of major Hawaiian Islands showing flight paths followed during 1990 season, including: (A) Oahu and Kauai/Niihau regions; (B) Penguin Bank and Four Island regions (detail shown in inset); (C) Big Island region (Note: flight paths for Four Island Region during 1978–79 closely followed those shown here, however 1977 and 1980 flight paths were somewhat discrepant yet covered same general area).

altitudes over assigned areas of the main Hawaiian islands, inspecting all near-shore and shallow-water areas of 183 m or less in depth, as indicated by U.S. Coast Guard navigational charts. The same prescribed flight paths were flown during each survey. The mission was to locate whales, determine numbers, and record behaviors of the whales visually and on camera by orbiting a whale or group of whales until the required data were obtained, or until the whales were no longer visible. Through these methods it was possible to determine the relative numbers of whales in various regions of the Hawaiian islands at a given time, note the changes in these relative numbers seasonally as surveys accumulated over weeks, describe the characteristics of single whales or groups of whales, determine the sizes of the various groups encountered, and note whether a calf was present in a group. Among other findings, these procedures uncovered seasonal peaks in abundance, differences in the density of whales in different regions, the ratio of calves to total whales sighted, spatial organization of groups, and behavioral characteristics (Baker & Herman, 1981; Bauer, 1986). Whales were most abundant in the four-island region, comprising the waters between the islands of Maui, Kahoolawe, Lanai, and Molokai, and in Penguin Bank, a tongue of shallow water extending approximately 24 nm southwesterly from west Molokai. There were few whales around the islands of Oahu, and Kauai, and most of the island of Hawaii except for the northwest coast.

In this paper we report the results of aerial surveys conducted in Hawaiian waters during the 1990 season. These surveys were flown following the procedures of the 1977–80 surveys, and had the same mission. By maintaining procedures and goals constant, it was possible to compare population numbers, characteristics, and trends ten years later with those uncovered earlier. This approach can offer evidence indicating whether the population was stagnant, declining or in a recovery phase.

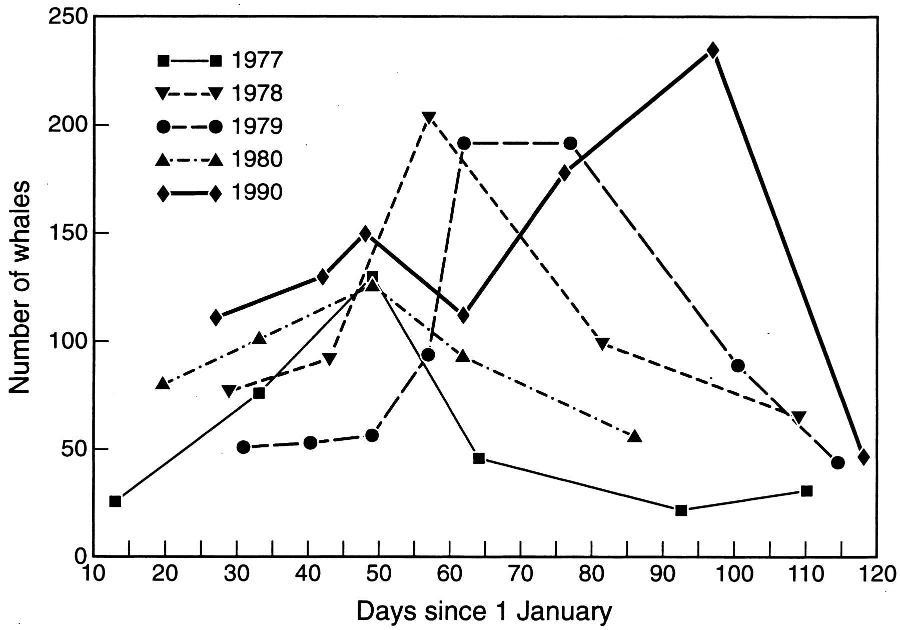

Figure 2. Numbers of total whales seen on each flight date for 1977–80 and 1990 seasons. Points represent totals for all regions, except the following omitted flights: 1977, Big Island on Julian dates 13, 92, 110 and Oahu on Julian date 33; 1979, Big Island on Julian dates 100 and 105; 1980, Big Island on Julian dates 62, 91 and Kauai on 62; Big Island on Julian date 118. Analysis of local trends indicating very low counts on proximate dates suggest that these omissions would not have altered results in any substantive way.

Method

Figure 1 shows the flight paths followed by the aircraft during the 1990 aerial surveys. These paths closely replicated those used during the 1977–80 seasons. However, the flight paths over the four-island region (FIR) during 1977 and 1980 differed somewhat from those flown in 1978, 1979 and 1990. Despite these discrepancies, the paths covered the same general areas of the FIR and represented comparable effort (i.e. comparable flight path distances); thus, the data have been retained for comparison. Flight paths for the remaining regions were identical. Generally, flight paths were chosen to follow the coastlines of the islands at approximately 2–3 km offshore and within the 100 fathom (182 m) isobath. In the case of the extensive shallow water areas of Penguin Bank and the FIR, paths were chosen to obtain maximum coverage of those areas within visual limits of the aircraft.

As during 1977–80, the 1990 aerial surveys were flown in single-engine, high-wing aircraft (Cessna 152 or 172) at an altitude of approximately 500 ft (152 m) and an airspeed of approximately 90–100 knots. Flight paths over areas away from dead reckoning opportunities (Penguin Bank, in particular) were controlled by using VORTAC navigational stations on Oahu and Molokai and digital-display Distance Measuring Equipment (DME).

Seven flights were conducted during 1990, spaced an average of two weeks apart, between Jan 27 and April 28 (Jan 27, Feb 10 and 17, Mar 3 and 17, Apr 7 and 28). A given flight day involved a total of three separate flights (i.e. three separate planes) with near-simultaneous departure times. The schedule of flights for the 1977–79 surveys is described in Baker & Herman (1981). For the 1980 season, a total of five flights were flown (Jan 19, Feb 2 and 18, Mar 3 and 31) (Table 1).

The same criteria used in the earlier series of surveys (1977–80) with regard to canceling flights were also used during the 1990 season (Baker & Herman 1981). Specifically, flights were rescheduled for the next available good weather date when wind speeds exceeded 15 kn, seas were higher than 1.8 m, or cloud ceiling was lower than 455 m.

In addition to the pilot, flights carried two experienced observers and a data recorder.[1] The duties of the data recorder included recording

[1]Big Island flights during 1990 were an exception. A two-seat plane (Cessna 152) was used so the pilot served as the second observer.

Table 1. The number of whales and calves sighted in each indicated region of Hawaii during 1977–80 and 1990 surveys

Region	Year	Total flights	Total whales	Total calves	Flight distance (km) mean	SE
Big Island (Hawaii)	1977	3	55	5	451	0
	1978	5	95	3	451	0
	1979	6	76	4	451	0
	1980	3	85	2	451	0
	1990	6	135	15	451	0
Four Island Region (FIR)	1977	7	164	11	271	10.6
	1978	5	238	19	254	2.2
	1979	8	332	24	233	10.3
	1980	5	158	10	234	2.2
	1990	7	277	32	253	4.8
Penguin Bank	1977	6	96	9	128	0
	1978	6	139	13	128	0
	1979	8	187	13	128	0
	1980	5	158	9	128	0
	1990	7	229	24	128	0
Oahu	1977	5	10	1	165	29.1*
	1978	5	31	0	194	0
	1979	8	88	4	176	18.2*
	1980	5	32	3	165	29.1*
	1990	7	94	9	194	0
Kauai/Niihau	1977	6	45	2	269	0
	1978	5	38	2	269	0
	1979	8	137	8	269	0
	1980	4	23	5	269	0
	1990	7	236	12	252	17.0*

*Note: variation due to one truncated flight.

positions of whales, navigation assistance, and recording voice data onto audio cassette tapes which were later transcribed onto data logs. Observers were responsible for spotting whales. Two of the authors (JM/GB) served on both the earlier (77–80) and later (1990) surveys, which further assured consistency of methods.

When a pod of whales was sighted, the aircraft continued on its path until the sighting location was judged to be perpendicular to the line of flight. The transect was then left in order to orbit the pod sighting to determine its composition in terms of numbers of whales and presence or absence of a calf. When pods were not resighted upon approach, e.g. following a dive, the most conservative estimate of pod size was assigned. Typically, this meant recording such pods as containing one whale. Locations of each pod were noted on data maps using either VORTAC coordinates, visual landmarks, or a combination of both.

In addition to pod information, sea state was noted on a modified Beaufort scale from 0 (calm, flat seas) to 3 (heavy seas). Sea state was noted whenever pods were recorded or when changes occurred.

For regional analyses, the major islands were divided into five regions, consistent with previous reports (Baker & Herman, 1981). These consisted of: (a) the Big Island (Hawaii); (b) Four Island Region (FIR); (c) Penguin Bank; (d) Oahu; and (e) Kauai/Niihau regions.

Results

During each year the numbers of whales sighted on each flight increased to a clear peak flight date when the greatest numbers of whales were seen, primarily during the period mid-February to mid-March, followed by a relatively sharp decline (Fig. 2). The year 1990 is somewhat of an anomaly in that the peak occurred relatively late in the season, April 7, but nevertheless is followed by the usual decline as measured on the succeeding flight approximately three weeks later.

Changing peak dates across seasons in conjunction with uneven intervals between flights and unequal numbers of flights (Table 1; Fig. 2) due to postponements and cancellations caused by poor weather conditions make the analysis of data necessarily complex. We therefore present the data in

Table 2. Total whales and calves sighted during 1977–80 and 1990 on peak observation dates

Year	Peak Day	No. Whales	No. Calves
1977	Feb 18	130	6
1978	Feb 26	204	12
1979	Mar 4	192	12
1980	Feb 18	126	5
1990	Apr 7	235	30

three ways: (a) visual inspection of graphic presentation of data; (b) non-parametric analysis of seasonal peak counts; and (c) analysis of covariance, ANCOVA, in which patterns of increasing and decreasing whales across the survey period were statistically controlled. Collectively, these results show that the number of humpback whales increased between the early surveys and 1990.

It can be seen from Figure 2 that during 1990 counts were above 100 whales for each flight except the final one. None of the other years evidences this consistently high count. The second-best year, 1979, shows only two dates with counts over 100, but these were in sharp contrast to numbers observed before and after the peak periods, where counts averaged considerably less than 100.

Differences in sea state can substantially affect sightability of marine mammals and potentially confound comparisons of counts across years (Hammond, 1986; Buckland *et al.*, 1993). Overall sea state conditions were quite good (mean=0.87, SE=0.79) corresponding to an average Beaufort sea state of approximately 2. In addition, careful inspection of the original raw data sheets and summaries further support comparability of sighting conditions between years.

Peak date sightings of total whales were greatest for 1990, 235 whales, representing a 15% increase over the number seen during the next highest year (1978) (Table 2). Chi square analysis indicated the differences in numbers of whales seen on peak dates across years to be significant, with 1990 showing the greatest departure from expected frequency [chi square(4)=36.84, $P<0.001$].

In comparisons of peak dates across years, the greatest number of calves were sighted during 1990, representing a 150% increase over the numbers seen during the next highest years (1978 and 1979) (Table 2). Chi square analysis indicated the differences in numbers of calves across years to be significant, with 1990 representing the greatest departure from expected frequency [chi square(4)=26.16, $P<0.001$].

In order to conduct inferential analyses of differences between years across entire seasons the following steps were executed: (1) counts were converted to encounter rates (number of whales/km surveyed) to control for small differences in survey effort across years (Table 1). Distances were computed from maps of flight paths for each survey date; (2) peak dates were equated by setting them to a value of zero; all other flight dates were counted as negative or positive distances from zero. For example, if the peak flight date were February 27, that date would be coded as zero and flight dates of February 20 and March 6 would be coded as -7 and 7 respectively (assuming it was a non-leap year); (3) analysis of variance (ANOVA) of encounter rates was conducted using a multiple regression/correlation approach in which the model was, 'encounter rate=julian date+(julian date) squared+region+year' (where julian day refers to number of days from Jan 1). Region was used as a control variable, and julian date and (julian date) squared were covariates that accounted for linear and quadratic trends in the seasonal data; (4) analysis of covariance (ANCOVA) was used to partial out the effects of linear and quadratic trends yielding least squares means of encounter rates for each year (Cohen & Cohen, 1983) (Tables 3–4).[2] In this manner comparisons could be made across years by normalizing the major confounding influences and contrasting the least squares means. The results of the ANCOVA procedures were consistent with visual inspection of the distribution of sightings across seasons (Fig. 2) and non-parametric analysis of seasonal peak sighting counts. Where ANOVA results were significant, they are reported, but the focus of the analysis is on planned comparisons of least-squares means using protected t-tests.

There were significant main effects for year [$F(4,136)=4.88$, $P=0.001$] (Fig. 3) and for region [$F(4,136)=22.98$, $P<0.001$]. The year-by-region interaction was not found to be significant. Paired significantly different than all previous years ($P<0.05$). Paired comparisons among the earlier years surveyed (1977–80) revealed only one other significant difference, 1979 rates were significantly greater than those during 1977 ($P<0.03$).

Although the year by region interaction was not significant, likely due to insufficient statistical power (Cohen, 1988), noticeably different trends in the data, measured as counts (Table 1) or least squares means (Table 3), begged closer inspection of regional differences. When the patterns of increases in encounter rates are examined across the five regions, there is a trend for the increases to get larger moving northwestward across the island

[2]The co-variates and years did not interact, indicating homogeneity of regression, and thus permitting analysis of least-square means (Cohen & Cohen, 1983).

Table 3. Least square mean encounter rates (whales/km) and standard errors (in parentheses) of whales by year and region

Region	Year 1977	1978	1979	1980	1990
Big Island	0.0439	0.0461	0.0270	0.0612	0.0470
	(0.0141)	(0.0107)	(0.0096)	(0.0137)	(0.0108)
Four Island	0.0964	0.1965	0.1705	0.1317	0.1748
	(0.0340)	(0.0402)	(0.0314)	(0.0402)	(0.0366)
Penguin Bank	0.1100	0.1690	0.1734	0.2147	0.3111
	(0.0536)	(0.0519)	(0.0451)	(0.0577)	(0.0527)
Oahu	0.0034	0.0209	0.0688	0.0374	0.0907
	(0.0235)	(0.0228)	(0.0178)	(0.0229)	(0.0208)
Kauai/Niihau	0.0270	0.0297	0.0626	0.0210	0.1268
	(0.0181)	(0.0197)	(0.0155)	(0.0218)	(0.0181)
Total Whales:	370	541	820	456	971
Mean Encounter Rates:	0.0508	0.0909	0.0994	0.0928	0.1527
	(0.0162)	(0.0162)	(0.0134)	(0.0177)	(0.0155)

Table 4. Least square mean calf encounter rates (calves/km) and standard errors (in parentheses) by year and region

Region	Year 1977	1978	1979	1980	1990
Big Island	0.0034	0.0011	0.0015	0.0015	0.0059
	(0.0010)	(0.0007)	(0.0007)	(0.0010)	(0.0008)
Four Island	0.0058	0.0136	0.0126	0.0069	0.0210
	(0.0031)	(0.0036)	(0.0028)	(0.0036)	(0.0033)
Penguin Bank	0.0041	0.0146	0.0125	0.0093	0.0366
	(0.0061)	(0.0059)	(0.0052)	(0.0066)	(0.0060)
Oahu	− 0.0002	− 0.0015	0.0026	0.0048	0.0095
	(0.0032)	(0.0031)	(0.0024)	(0.0031)	(0.0028)
Kauai/Niihau	0.0010	0.0014	0.0038	0.0046	0.0064
	(0.0016)	(0.0017)	(0.0014)	(0.0019)	(0.0016)
Total Calves:	28	33	53	29	92
Mean Encounter Rates:	0.0022	0.0057	0.0063	0.0053	0.0163
	(0.0018)	(0.0018)	(0.0015)	(0.0020)	(0.0017)

Note: Negative values for least squares means reflect very low real encounter rates and are an artifact of statistical procedures, i.e., they do not represent real values less than zero.

chain (Fig. 5). The binomial probability of deriving four points (beyond the initial point) approaches significance (P=0.06). Analysis of Kauai/Niihau encounter rates across years showed these increases to be significant [F(4,23)=5.06, P<0.01], with 1990 encounter rates greater than all previous years (P<0.05). Protected t-tests indicate that 1990 encounter rates for Oahu were greater than in 1977 or 1978 (P<0.05) and greater for Penguin Bank than in 1977. Comparisons among the earlier years (1977–80) were not significantly different.

The same ANCOVA procedures were used for analyzing changes in calf rates. Calf sightings across years also showed a significant main effect for year [F(4,136)=8.40, P<0.001] with calf rates during 1990 significantly greater than all previous years (P<0.001) (Fig. 4). Again the year-by-region interaction was not significant. Calf rates among the earlier years (1977–80) were not significantly different.

Interestingly, increases in calf encounter rates showed a different pattern than for total whales, i.e. increases were greater in the more southeasterly part of the Island chain (Table 4). Calf sightings increased significantly around the Big Island, F(4,16)=6.81, P=0.002, with 1990 greater than all

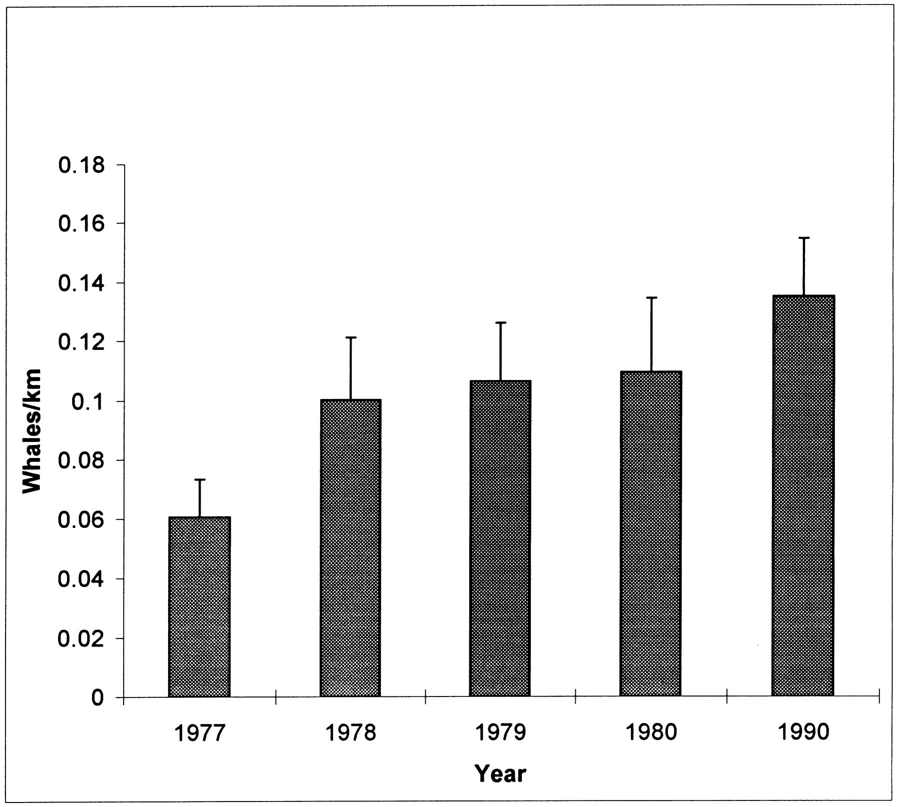

Figure 3. Encounter rates for total whales (whales/km) showing standard errors, for each survey year.

other years ($P<0.003$) except 1977 ($P<0.08$). The FIR showed a main effect for year, $F(4,25)=3.27$, $P<0.03$, with 1990 encounter rates higher than 1977 and 1980 ($P<0.01$). Penguin Bank had significantly more sightings in 1990, $F(4,25)=3.83$, than each of the previous survey years ($P<0.02$). For Oahu, increases were found to be significant using planned comparisons with 1990 encounter rates greater than 1977 or 1978 ($P<0.04$). Kauai/Niihau showed only a significant increase between 1990 and 1977 ($P<0.03$). In contrast to the increases noted for 1990, no significant effects for increases in calf sightings were found between any of the previous years.

Discussion

The data and analyses presented here suggest that the Hawaiian wintering population has increased over a relatively short 10–13 yr intervening period. This finding was supported by increases in the numbers of whales and calves seen on peak flight dates, as well as increases in overall encounter rates of whales and calves. Numbers of calves in particular showed a dramatic increase from the 1977–80 to the 1990 data. When the calf encounter rate for 1990 is compared to the mean encounter rate for 1977–80, the difference represents a 214% increase, as compared to only a 72% increase for total whales.

The evidence for increases on the Hawaiian wintering grounds reinforce the possibility that the North Pacific population of humpback whales may be recovering. This interpretation must be treated with caution, however, as the population is still likely only a fraction of its original pre-exploitation abundance. The 1990 surveys occurred only 24 years after the international moratorium on the hunting of humpback whales established in 1966. Additionally, the fact that humpback whale females appear to have calves at intervals of 2.7 yrs (Baker, Perry & Herman, 1987) suggests that the initial stages of recovery should be a slow process.

The patterns of increase were not uniform throughout the five regions. Though comparisons with 1990 data demonstrated an overall increase, there was a general pattern of larger increases

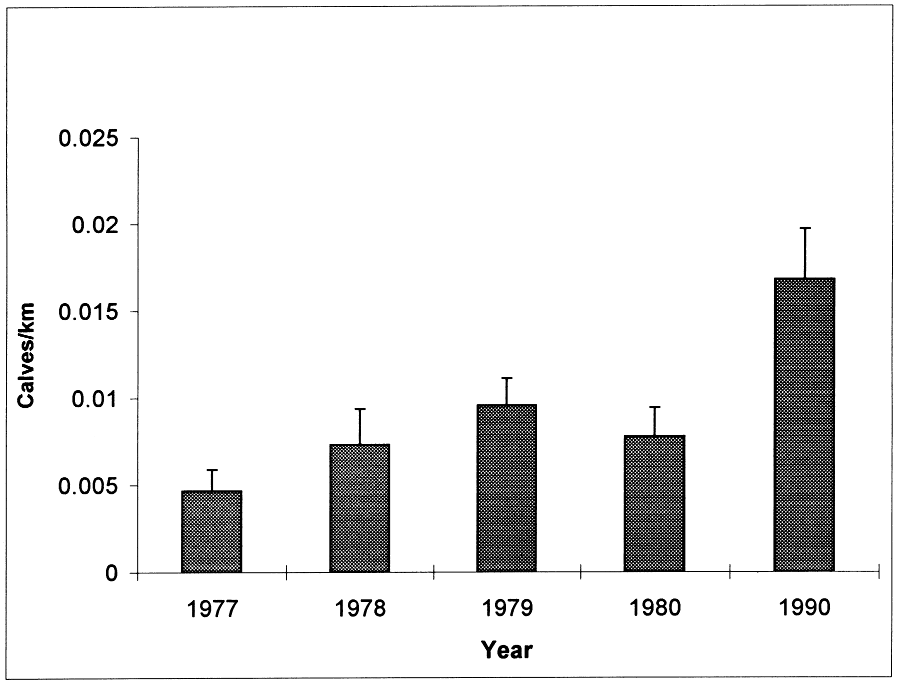

Figure 4. Encounter rates for calves (calves/km) showing standard errors, for each survey year.

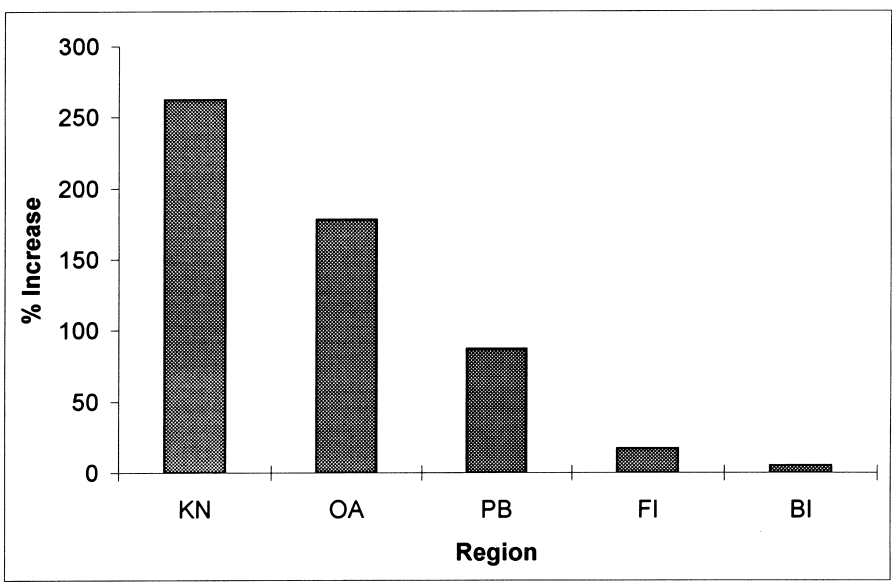

Figure 5. Percent increases in encounter rates (mean of 1977–80 compared to 1990) across regions.

moving northwesterly through the island chain, with Kauai showing nearly a four-fold increase in encounter rates. As such, these data suggest a 'spill-over' of whales from former preferred habitat (Penguin Bank and FIR, Herman *et al.*, 1980; Baker & Herman, 1981). What factors may have produced this change? Regression to the mean may have influenced the change data, in that extremely low measured densities such as were found in the Kauai/Niihau area in 1977–80 would be expected to gravitate upward. However, the increasing trend in the high density area of Penguin Bank, where statistical regression would be expected to generate lower encounter rates, suggests that other explanations are needed.

Prey availability is presumably not a factor, since examinations of whales harvested in breeding waters typically show little or no food in their stomachs (e.g. Dawbin, 1966; Tomilin, 1967). Rather, the behavior and local movements of whales on the wintering grounds are presumably controlled by factors related to reproductive success (Tyack & Whitehead, 1983; Baker & Herman, 1984; Mobley & Herman, 1985). Findings by Frankel *et al.* (1995) of regular spacing between humpback whale singers may indicate a constraint on habitat usage. However, reports from the Silver Bank region in the Caribbean where minimum spacing is considerably less suggests that these distances may be density-dependent (Whitehead, 1981).

If the wintering population is indeed spilling over from the FIR and Penguin Bank regions, then why is the calf distribution not changing in a similar fashion? Calf rates for Kauai/Niihau, where there was an overall substantial increase in whale sightings, were the second lowest observed among the five regions during 1990 (Table 4). Wilson (1975) noted: 'The single most widespread response to increased population density throughout the animal kingdom is restlessness and emigration (p. 83).' Further, the population members responsible for expanding beyond the limits of over-crowded habitats are typically juveniles and subordinate individuals (Christian, 1970; Calhoun, 1971). This observation could explain the low percentages of pods with calf seen around Kauai/Niihau, suggesting that it is primarily the non-reproductive members of the population which are occupying this region.

The changes in distribution and relative abundance support the need for long-term studies of absolute abundance using consistent methods. More sophisticated aerial surveys based on traditional line transect techniques designed to produce estimates of absolute abundance are ongoing (e.g. Mobley, Forestell & Grotefendt, 1997). These studies will also assess the stability of the 'spillover' effects reported for the 1990 data. Other techniques, such as the application of mark-recapture models to individual identification photographs (e.g. Cerchio, 1998), offer the potential for further clarification of these trends. For example, some of the increase in humpback whale counts on these surveys might be attributable to longer durations of residency, rather than just increases in absolute abundance. Mark-recapture methods can contribute to removing this ambiguity.

Acknowledgements

Funding for the 1990 season was provided by the University of Hawaii Sea Grant College Program under Institutional Grant No. NA89AA-D-SG063 from NOAA Office of Sea Grant, Dept. of Commerce, as well as by private contributions. This is Sea Grant Publication No. UNIHI-SEAGRANT-JC-91-01. We also gratefully acknowledge the contributions of the following survey staff: Brooks Bays, Nina Forsyth, Adam Frankel, Sharene Fuchigami, David Helweg, Harriet Helweg, Michael Hoffhines, and Hilary Maybaum. We would also like to thank Julianne Misiewicz for all of her assistance in data coding and management. Additional funding was provided by the Hawaii Humpback Whale National Marine Sanctuary and the New College Faculty Development Fund in 1996 and 1997 to complete this manuscript. Finally, we thank Jeff Laake of the National Marine Mammal Laboratory in Seattle for his helpful suggestions regarding data analysis and William Friedl for his insightful review of the manuscript.

References

Baker, C. S. & Herman, L. M. (1981) Migration and local movement of humpback whales (*Megaptera novaeangliae*) through Hawaiian waters. *Can. J. Zool.* **59,** 460–469.

Baker, C. S. & Herman, L. M. (1984) Aggressive behavior between humpback whales, *Megaptera novaeangliae*, wintering in Hawaiian waters. *Can. J. Zool.* **62,** 1922–1937.

Baker, C. S., Herman, L. M., Perry, A., Lawton, W. S., Straley, J. M., Wolman, A. A., Kaufman, G. D., Winn, H. E., Hall, J. D., Reinke, J. M. & Ostman, J. (1986) Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Mar. Ecol. Prog. Ser.* **31,** 105–119.

Baker, C. S., Perry, A. & Herman, L. M. (1987) Reproductive histories of female humpback whales (*Megaptera novaeangliae*) in the North Pacific. *Mar. Ecol. Prog. Ser.* **41,** 103–114.

Bauer, G. B. (1986) The behavior of humpback whales in Hawaii and modifications of behavior induced by human interventions. Ph.D. thesis, University of Hawaii at Manoa, Honolulu.

Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L. (1993) Distance sampling: Estimating abundance of biological populations. Chapman and Hall, New York.

Calhoun, J. B. (1971) Space and the strategy of life. In: A. H. Esser (ed.). *Behavior and environment: the use of space by animals and men*, pp. 329–387. Plenum Press, New York.

Cerchio, S. (1998) Estimates of humpback whale abundance off Kauai, 1989–1993: evaluation of biases associated with sampling the Hawaiian population. *Mar. Ecol. Prog. Ser.* **175,** 23–34.

Christian, J. J. (1970) Social subordination, population density, and mammalian evolution. *Science* **168,** 84–90.

Cohen, J. (1988) Statistical power analysis for the behavioral sciences. Erlbaum, Hillsdale, NJ.

Cohen, J. & Cohen, P. (1983) Applied multiple regression/correlation analysis for the behavioral sciences. Erlbaum, Hillsdale, NJ.

Darling, J. D. & Jurasz, C. M. (1983) Migratory destinations of North Pacific humpback whales (*Megaptera novaeangliae*). In: R. Payne (ed.). *Communication and behavior of whales*. Westview Press, Boulder, CO.

Darling, J. D. & McSweeney, D. J. (1985) Observations on the migrations of North Pacific humpback whales (*Megaptera novaeangliae*). *Can. J. Zool.* **63,** 308–314.

Dawbin, W. H. (1966) The seasonal migratory cycle of humpback whales. In: K. S. Norris (ed.). *Whales, dolphins, and porpoises*, pp. 145–171. University of California Press, Berkeley, CA.

Frankel, A. S., Clark, C. W., Herman, L. M. & Gabriele, C. M. (1995) Spatial distribution, habitat utilization, and social interactions of humpback whales (*Megaptera novaeangliae*) off Hawai'i, determined using acoustic and visual techniques. *Can. J. Zool.* **73,** 1134–1146.

Hammond, P. S. (1986) Line transect sampling of dolphin populations. In: M. M. Bryden & R. Harrison (eds). *Research on dolphins*, pp. 251–279. Clarendon Press, Oxford.

Herman, L. M. & Antinoja, R. (1977) Humpback whales in the Hawaiian breeding waters: population and pod characteristics. *Sci. Rep. Whales Res. Inst., Tokyo* **29,** 59–85.

Herman, L. M., Forestell, P. H. & Antinoja, R. C. (1980) The 1976/77 migration of humpback whales in Hawaiian waters: composite description. Marine Mammal Commission Report No. MMC-77/19.

Johnson, J. H. & Wolman, A. A. (1984) The humpback whale, *Megaptera novaeangliae. Mar. Fish. Rev.* **46,** 30–37.

Katona, S. & Whitehead, H. P. (1981) Identifying humpback whales using their natural markings. *Polar. Rec.* **20,** 439–444.

Mobley, J. R. Jr., Forestell, P. H. & Grotefendt, R. A. (1997) Preliminary results of 1993 and 1995 aerial surveys of Hawaiian waters. In: P. M. Payne, B. Phillips & E. T. Nitta (eds). Report of the workshop to assess research and other needs and opportunities related to humpback whale management in the Hawaiian Islands, April 1995, pp. 1–8. Kaanapali, Maui, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-OPR-11.

Mobley, J. R. Jr. & Herman, L. M. (1985) Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. *Can. J. Zool.* **63,** 762–772.

Perry, A., Mobley, J. R., Baker, C. S. & Herman, L. M. (1988) Humpback whales of the central and northeastern Pacific: Photographic identification catalog. Sea Grant Publications, Sea Grant College Program, Honolulu, Hawaii.

Rice, D. W. (1978) The humpback whale in the North Pacific: distribution, exploitation, and numbers. In: K. S. Norris & R. Reeves (eds). Report on a workshop on problems related to humpback whales (*Megaptera novaeangliae*) in Hawaii, pp. 29–44. Report to the U.S. Marine Mammal Commission, Washington, DC.

Tomilin, A. G. (1967) Cetacea. In: *Mammals of the USSR and adjacent countries, Vol. 9*. Israel Programs for Scientific Translations, Jerusalem.

Tyack, P. & Whitehead, H. (1983) Male competition in large groups of wintering humpback whales. *Behaviour* **83,** 132–154.

Whitehead, H. P. (1981) The behaviour and ecology of the humpback whale in the northwest Atlantic. Ph.D. thesis, Univ. of Cambridge, Cambridge.

Wilson, E. O. (1975) Sociobiology: the new synthesis. Harvard Univ. Press, Cambridge.