

ESTIMATING RESIDENCE TIMES OF HUMPBACK WHALES IN HAWAII

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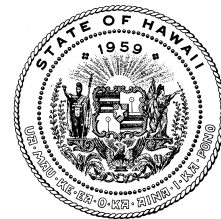
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ABSTRACT

A review of previous literature on humpback whales in the Hawaiian Islands revealed that relatively few whales were identified on more than one day within the same season, but there was little information about the residence times of different classes of whale. We addressed this information gap by examining the sighting histories of individual whales photographed by Kewalo Basin Marine Mammal Laboratory off west Maui and the Kohala Coast of the Big Island from 1976 through 1996. Our analyses of *resighting rate* (the proportion of individual whales identified on more than one day within the same season) showed that (a) overall resighting rates were low (11.94%), (b) resighting rates did not differ significantly among males, mothers, females without calf, and juveniles for the Big Island, Maui, or all data combined, and (c) resighting rates were significantly greater off the Big Island than off Maui. Our analyses of the *resighting intervals* (intervals between first and last identifications within the same season) of all whales identified on more than day showed that (a) most whales (65.98%) had an interval of 2 weeks or less, (b) no juvenile had an interval of more than 4 weeks, and no mother or female without calf had an interval of more than 5 weeks, but some males (N = 10) and adults of unknown sex (N = 2) had intervals of 8 weeks or more, the longest interval being almost 11 weeks (76 days), (c) differences in resighting intervals among classes of whale were not significant overall or for the Big Island, but off Maui resighting intervals for females without calf were significantly shorter than resighting intervals for males and adults of unknown sex, and (d) inter-island resighting intervals tended to be longer than intervals recorded off a single island. Our results suggest that in Hawaii, humpback whales of all classes rarely remain resident in the same locale for long periods. Whales may be more transient off Maui than the Big Island, but it is also likely that differences in the extent of preferred habitat caused sampling differences between these two areas. Resighting rates and resighting intervals of females without calf relative to other whales off Maui and the Big Island suggest that these females may spend more time off the Big Island than off Maui, although further research is required. Finally, inter-island resighting intervals appear to be more representative of residency in the Hawaiian Islands as a whole than are intervals based on resightings of whales in the same location. Future studies combining photo-identification and large-scale satellite telemetry may provide the most precise data on humpback whale residency in the Hawaiian Islands, although obtaining sample sizes sufficient to compare different classes of whale would be financially and logistically challenging.

INTRODUCTION

In the North Pacific, three main wintering areas are utilized by humpback whales. In the eastern North Pacific, humpback whales winter in Mexican waters, specifically in the waters of the southern coast of Baja, California, northern Gulf of California, Revillagigedo Archipelago, and the mainland coast of Mexico including the area around the Islas Tres Marias and the Isla Isabel (Urban & Uguayo 1987). In the western North Pacific, humpback whales winter in Japanese waters, specifically the waters of the Ryukyuan and Bonin Islands (Nishiwaki 1966). However, the main wintering area for the majority of North Pacific humpback whales is in Hawaiian waters, with the most dense concentrations occurring on Penguin Bank and in the “four-island” region between Maui, Lanai, Molokai, and Kahoolawe (Baker & Herman 1981; Herman & Antinaja 1977; Mobley, Bauer, & Herman 1999).

Although the peak period of humpback whale aggregation in Hawaiian waters is typically between January and April, less is known about the length of residency of individual whales. By identifying individual whales from the patterns of pigmentation and scarring on their tail flukes (see Katona et al. 1979), it is possible to calculate minimum residence times by computing the interval between first and last sightings of individual whales within the same winter season. In this report, we review existing literature on residence times of individually-identified humpback whales in the Hawaiian Islands. We then expand on existing knowledge of residency by examining data collected by researchers from Kewalo Basin Marine Mammal Laboratory (KBMML) over 21 winter field seasons in Hawaii. We determine the proportions of whales identified on more than one day within the same season for west Maui and the Kohala Coast of the Big Island, classifying whales into the following categories: male, mother, female without calf, juvenile, and adult of unknown sex. We then examine in detail the intervals between first and last identification within the same season for all these classes of whale for Maui and the Big Island. Finally, because some whales were photographed off both the Big Island and Maui within the same season, we present details of inter-island resighting intervals. Altogether, this represents the most comprehensive analysis to date of humpback whale residency in the Hawaiian Islands.

Review of existing literature

All available literature pertaining to humpbacks in Hawaii was reviewed for examples of repeated sightings of individual whales within a given year. Several previous studies by researchers from KBMML have included information about residency (e.g., Baker & Herman 1984; Mobley & Herman 1985; Gabriele 1992). However, because each of these studies was based on a subset of the data analyzed in the next section of this report, they are not examined individually here.

Darling et al. (1983) identified individual humpback whales off west Maui from 1977-1979. Only 28 of 264 (10.6%) individuals were identified on more than one day within the same season during this time. Of these 28 whales, 26 were identified on dates less than 6 weeks apart. The longest interval between first and last sighting within the same season was 74 days, and the second longest interval was 55 days. The mean of the intervals presented by Darling et al.

(1983) was 20.7 days, but these authors did not distinguish between different classes of whale when presenting within-season resighting intervals.

Glockner and Venus (1983) identified individual humpback whales off west Maui from 1977-1979. When discussing resightings of individual whales, they focused on sightings in different years rather than repeat sightings within the same year. However, from the data that they presented in Appendix Table 2 it is possible to calculate resighting intervals for whales identified on more than one day within the same season. From 1977 – 1979, eight mothers were identified more than once within the same season. The longest resighting interval for a mother was 27 days, and the mean interval for all eight mothers was 12.1 days. One male was identified with an interval of 22 days in 1977 and an interval of 18 days in 1978. Two whales of unknown sex had intervals of 1 and 21 days.

Based on data collected off west Maui from 1977-1981, Glockner-Ferrari and Ferrari (1984) reported that 25% of individually-identified mothers were observed on two or more occasions within the same year. Intervals between successive sightings ranged from 1 to 48 days, with a mean of 13.7 days. Glockner-Ferrari and Ferrari (1985) reported that from 1982-1983 only 9 of 42 (21.4%) mothers were observed more than once within the same season. The longest interval between first and last sighting of a mother during this time was 56 days, and the next longest was 28 days. The mean of all intervals reported for mothers was 16.4 days. Glockner-Ferrari and Ferrari also reported an interval of 45 days for an escort (presumably male) and intervals ranging from 3 to 22 days for three whales of unknown gender.

Cerchio (1998) collected data around Kauai's north, south, and west coasts from 1989-1993. As with the studies conducted off west Maui, he found that few whales were identified more than once within the same season. The percentage of whales identified on more than one day within the same season ranged from 5% in 1989 to 14% in 1992 and 1993. For the 82 whales identified on two different days within the same season, the mean resighting interval was 15 days. For the 19 whales identified on three different days within the same season, the mean interval between first and last sighting was 23 days. For the three whales identified on four different days within the same season, the mean interval between first and last sighting was 37 days. However, the standard deviations in each case were large, indicating that the resighting intervals varied considerably among whales. No information was presented with respect to the classes of whale identified more than once within the same year.

The studies discussed thus far were each focused on a single island location, and any information about residency was restricted to that location. However, some studies have compared data collected off different islands within the same year in order to investigate inter-island movements. These provide some information about residency within the Hawaiian Islands as a whole. The most comprehensive analysis of inter-island movements to date was conducted in a collaborative study by researchers from Moss Landing Marine Laboratories and KBMML (Cerchio et al. 1998). In this study, photographs of humpback whales identified from 1989-1991 off the islands of Kauai and the Big Island were compared. Of 1072 individual whales, only 15 (1.4%) were identified in both locations within the same year. The shortest inter-island resighting interval was 8 days, and the longest was 71 days. Overall, the mean inter-island resighting interval was 33.5 days. Of the 15 whales identified in both locations within the same year, 8 were believed to be male based on their sighting histories, and the remainder were

of unknown sex. These results suggest that males may be more mobile than females within the Hawaiian Islands, although the sample size is relatively small. When the eight known males were considered separately, the mean inter-island resighting interval was 49.8 days. Overall, the inter-island resighting intervals reported in this study are longer than most resighting intervals reported by studies conducted in one location only. This suggests that more representative data on residency within Hawaii as a whole may be produced by comparing data collected in more than one location within the Hawaiian Islands, rather than relying solely on data collected in a single location.

Other data on within-season inter-island movements in Hawaii are meager. Baker and Herman (1981) reported inter-island resighting intervals for five whales that traveled from the Big Island to Maui (mean interval = 26.4 days), for one whale that traveled from Hawaii to Penguin Bank (interval = 25 days), and one whale that traveled from Maui to Oahu (interval = 38 days). Darling and Morowitz (1986) reported that five whales traveled from Maui to the Big Island within the same season, but the resighting interval was documented for only one whale. This whale was first identified on Maui, and was then identified 20 days later on the Big Island. Two days later, the whale was identified once again in Maui waters. Mate et al. (1998) reported that one humpback whale satellite-tagged off Kauai traveled to Oahu in 4 days, while another individual tagged off Kauai spent the next 10 days travelling through the coastal waters of Oahu, Molokai, Lanai, and Maui in addition to visiting Penguin Bank. Finally, Craig (1995) presented details of several inter-island resighting intervals gleaned from the KBMML database. Rather than summarizing those data here, we present them in full in the next section of this report.

In each of the studies reviewed here information about residency was sparse, largely because relatively few whales were identified on more than one day within the same season. This was true for both west Maui and Kauai. Because most studies collected data in the same waters each day, the dearth of resightings within the same year strongly suggests that individual whales are quite mobile and rarely remain resident in the same area for extended periods of time. This suggestion is supported by satellite telemetry of tagged humpback whales: at the most recent Biennial Conference on the Biology of Marine Mammals, Mate (1999) reported that most whales tagged in the Hawaiian Islands did not remain in one area for very long. Although these studies presented some basic data on resighting intervals, in general there was little information regarding possible differences in residency among different classes of humpback whale. This information gap will be addressed in the next section of this report, in which we present data collected over 21 field seasons by researchers from KBMML.

ESTIMATING RESIDENCE TIMES OF HUMPBACK WHALES IN THE HAWAIIAN ISLANDS, 1976 – 1996

Methods

Humpback whale tail flukes were photographed by KBMML staff between January and April of each year from 1976 through 1996. Photographs were obtained mainly off the Kohala Coast of the Big Island and in the waters of west Maui (see Table 1), but a few photographs (0.6%) were taken around Niihau, Oahu, and Penguin Bank. Each photograph was allocated a unique observation number and assigned to one of five color categories. Each photograph was then compared to all others in the same color category, and all photographs that were found to match were allocated a common “resight” number. This resight number was used to link all photographs of a known individual, so that individual sighting histories could be compiled.

In some cases, the sex of individual whales was determined by observing the genital region directly underwater. More commonly, sex was inferred from social role. An adult observed while escorting a mother and calf was assumed to be male, as was any whale identified as a singer. An adult observed in close proximity to a calf was assumed to be its mother, and therefore female. Biopsy research and underwater observations of the genital region have validated these assumptions (Glockner 1983; Glockner-Ferrari & Ferrari 1985; Clapham et al. 1992; Medrano et al. 1994). When sex was determined, it was applied retrospectively to all previous identifications of an individual.

For the purposes of this study, all sightings of individual whales were assigned to one of five categories: male, mother, female without calf, juvenile, and adult of unknown sex. Juveniles were perceived by experienced observers to be unambiguously small relative to adults, but too large to be calves. In many cases, these would have been yearlings that had recently separated from their mothers.

Residency was examined for these classes of whale by using two measures: resighting rates and resighting intervals. First, the proportion of individual whales identified on more than one day within the same season (resighting rate) was calculated for Maui, the Big Island, and for all data combined. This provides some basic information pertinent to residency: if whales tend to reside in the same area for extended periods of time, they are likely to be photo-identified on more than one day. Conversely, if whales tend to be quite mobile, they are less likely to be photo-identified in the same area on more than one day. Next, the actual resighting intervals of whales identified on more than one day were examined for each class of whale off Maui, the Big Island, and for all data combined. Resighting intervals were calculated by subtracting the date of last identification from the date of first identification within a given season. Finally, because data were collected off Maui and the Big Island within the same season in some years (see Table 1), data on inter-island resighting intervals are presented.

Table 1. Dates and locations of data collection by KBMML in the Hawaiian Islands.

Year	Location	Study Period
1976	Maui	13 March - 16 March
1977	Maui	12 February - 20 April
1978	Maui	1 February - 8 April
1979	Maui	3 February - 31 March
1980	Maui	27 January - 2 April
	Big Island	15 January - 5 April
1981	Maui	11 January - 12 April
	Big Island	21 January - 24 February
1982	Maui	3 January - 28 March
1983	Maui	1 February - 29 March
1984	Maui	26 January - 28 March
1985	Maui	6 March - 6 April
	Big Island	18 January - 12 March
1986	Maui	1 March - 22 April
	Big Island	19 January - 27 February
1987	Maui	23 January - 12 April
1988	Maui	17 March - 16 April
	Big Island	13 January - 10 March
1989	Big Island	7 January - 3 April
1990	Big Island	11 January - 13 April
1991	Big Island	9 January - 15 April
1992	Big Island	11 January - 3 April
1993	Big Island	15 January - 7 April
1994	Big Island	26 January - 19 March
1995	Big Island	23 January - 19 March
1996	Maui	9 January - 17 April

Results

I. Proportion of whales identified on more than one day during the same season.

As with the previous studies reviewed earlier, few whales were identified on more than one day within the same season (Table 2). Overall, only 11.94% of whales were identified on more than one day within the same season. Off Maui, resighting rates were highest for males, followed by mothers, females without calf, adults of unknown sex, and juveniles. However, off the Big Island the highest resighting rate was for females without calf, followed by mothers, males, juveniles, and adults of unknown sex. The differences in resighting rates for males, mothers, females without calf, and juveniles were not significant for the Big Island ($\chi^2 = 1.40$, $df = 3$, $p = 0.71$, $N = 684$), Maui ($\chi^2 = 5.42$, $df = 3$, $p = 0.14$, $N = 947$), or overall ($\chi^2 = 1.71$, $df = 3$, $p = 0.63$, $N = 1652$).

Table 2. Proportion of whales identified on more than one day (resighted) within the same season in the Hawaiian Islands: males, mothers, females without calf, juveniles, and adults of unknown sex.

	Overall *		Big Island		Maui	
	Total no. whales	Percentage resighted	Total no. whales	Percentage resighted	Total no. whales	Percentage resighted
Males	1099	19.75	441	24.94	643	15.09
Mothers	404	17.82	157	25.48	243	12.76
Females without calf	94	17.02	42	28.57	50	6.00
Juveniles	55	14.55	44	18.18	11	0.00
Adults, unknown sex	2853	7.89	1699	9.30	1124	5.25
Total for all whales	4505	11.94	2383	13.76	2071	9.17

* Overall data include a small number of whales identified in other locations within the Hawaiian Islands.

The proportion of whales identified on more than one day within the same season off the Big Island (13.76%) was significantly greater than the corresponding proportion for Maui (9.17%) ($\chi^2 = 22.27$, $df = 1$, $p < 0.0001$, $N = 4454$). This may suggest that whales in west Maui waters are relatively transient, whereas off the Kohala Coast whales are more likely to linger in the same area. However, there are other potential explanations for this difference. Because the

density of whales is much greater in Maui waters than off the Big Island (Herman et al. 1980; Mobley, Bauer & Herman 1999; Craig 2001), it is possible that a consistently smaller proportion of the population was photographed off Maui than off the Big Island. This would tend to reduce within-season resighting rates off Maui relative to the Big Island. In order to investigate the potential influence of population size on the resighting rates reported here, we compared resighting rates for data collected off Maui in 1987 and 1996. These years were selected because they were the years of greatest research effort off Maui, and they are spaced far enough apart that the population size should have increased significantly over this time period. Based on the 7% annual rate of increase suggested by the aerial surveys of Mobley, Grotfendt, et al. (1999), the population size in 1996 would be about 1.8 times the population size in 1987: i.e., the population would almost have doubled over this time. Table 3 summarizes the proportions of whales identified on more than one day for these two seasons off Maui. The overall resighting rates are very similar: in 1987 8.84% of whales were identified on more than one day and in 1996 the figure was 9.05% ($\chi^2 = 0.00$, $df = 1$, $p = 1.00$, $N = 911$). Thus, an increase in population size appears to have had little effect on the within-season resighting rates of humpback whales identified off west Maui. This suggests that the difference between Maui and the Big Island with respect to the proportion of whales identified on more than one day is not due simply to regional differences in population size.

Table 3. Proportion of whales identified on more than one day (resighted) within the same season off Maui: 1987 and 1996 compared.

	Maui, 1987		Maui, 1996	
	Total no. whales	Percentage resighted	Total no. whales	Percentage resighted
Males	63	17.46	204	13.73
Mothers	31	9.68	91	13.19
Females without calf	10	10.00	6	0.00
Juveniles	3	0.00	4	0.00
Adults, unknown sex	108	3.70	391	5.88
Total for all whales	215	8.84	696	9.05

Another potential explanation for the finding that whales are resighted within the same season more commonly off the Big Island than Maui is that the extent of preferred habitat is

much smaller off the northwest coast of the Big Island than it is off west Maui (Craig & Herman 2000). Humpback whales are typically found in waters less than 183m (100 fathoms) deep (Herman & Antinaja 1977). Almost the entire area between west Maui and the islands of Kahoolawe and Lanai is less than 183 m deep, but off the northwest coast of the Big Island the water deepens to more than 183 m within 5 km of the coastline. Consequently, it is likely that our research vessel consistently sampled a larger proportion of preferred habitat off the Big Island than was possible for Maui. This would tend to increase the probability of identifying whales on more than one day within the same season. However, the possibility that individual whales tend to be more transient in Maui waters than in Big Island waters cannot be discounted.

In addition to the regional difference in overall resighting rates, it appears that the resighting rate of females without calf relative to other whales differed between Maui and the Big Island. Females without calf were the class of whale most likely to be resighted in the same year off the Big Island, whereas they were much less likely than males and mothers to be resighted off Maui (Table 2). It is possible that the behavior of females without calf differs in these two locations. Specifically, it may be that females without calf are less transient off the Big Island than in Maui waters. We have shown previously that individual females identified off Maui and the Big Island in different years were likely to be seen off the Big Island in the years when they had no calf, and off Maui in the years during which they were mothers (Craig & Herman 2000). This would be consistent with the suggestion that females without calf may spend more time in Big Island waters than Maui waters.

II. Resighting intervals of whales identified on more than one day during the same season.

Figure 1 illustrates the intervals between first and last identification for all whales photographed on more than one day during the same season in the Hawaiian Islands. Intervals are expressed in weeks. For example, an interval of 1 represents 1-7 days, 2 represents 8-14 days, and so forth. It is striking that for every class of whale, the majority of individuals had resighting intervals of 2 weeks or less. Overall, 44.98% of whales had an interval of 1 week or less, 65.98% had an interval of 2 weeks or less, 81.04% of whales had an interval of 3 weeks or less, and 89.40% of whales had an interval of 4 weeks or less. No juvenile had an interval of more than 4 weeks, and no mother or female without calf had an interval of more than 5 weeks. However, some males (N = 10) and adults of unknown sex (N = 2) were seen over periods of 8 weeks or more, including one male whose dates of first and last identification were almost 11 weeks (76 days) apart. These data combine all identifications from all locations available in the KBMML database. As such, they include some inter-island resighting intervals. These are presented in detail below.

Figure 1. Intervals between first and last identification of whales photographed on more than one day (all data).

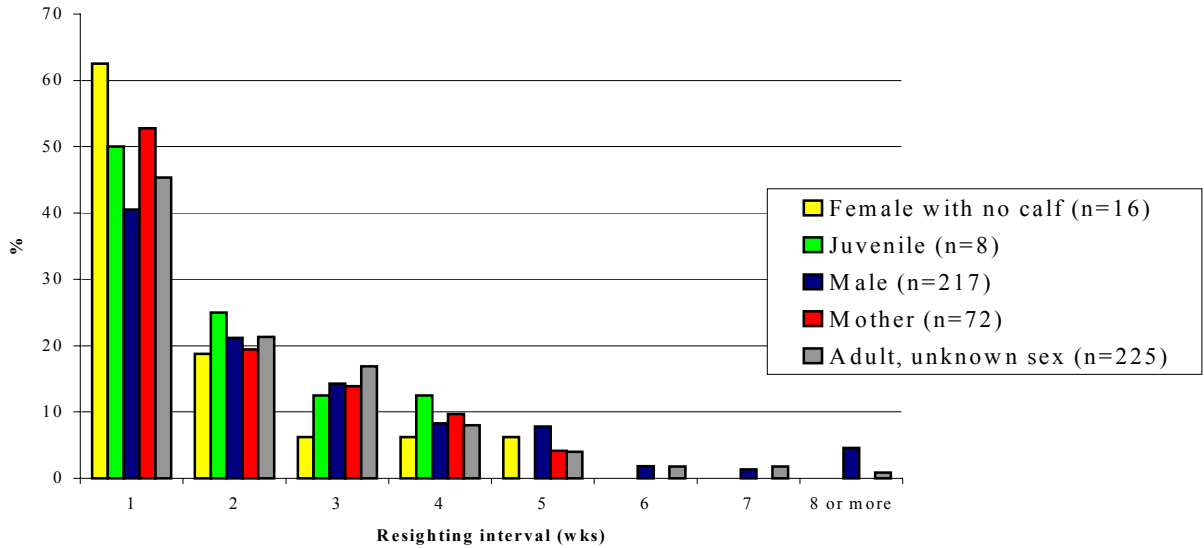


Figure 2 illustrates the intervals, again in weeks, between first and last identification for all whales identified on more than one day within the same season in west Maui waters, and Figure 3 illustrates the corresponding information for the waters off the Kohala Coast of the Big Island. It should be noted that no juvenile was photographed on more than one day within the same season off Maui. Figures 2 and 3 reveal broadly similar trends, with one notable difference: no female without calf had a resighting interval of more than 1 week off Maui, whereas off the Big Island over 40% of females without calf had a resighting interval in excess of 1 week. This is consistent with the suggestion, discussed previously, that females without calf may be less transient off the Big Island than off Maui. The sample size of females without calf in Figure 2 is small (n = 3). However, this is because these females were rarely identified more than once during the same season in Maui waters. A closer examination of the data reveals that of the 50 females without calf that were identified in Maui waters, only three (6.0%) were identified on more than one day. Of these three, none had an interval greater than 3 days. By contrast, of the 42 females identified in Big Island waters, 12 (28.6%) were identified on more than 1 day. Of these 12, eight (66.7%) had resighting intervals greater than 3 days and six (50.0%) had resighting intervals of 7 days or more. The difference in resighting rates of females without calf off Maui as compared to the Big Island was significant ($\chi^2 = 6.95$, $df = 1$, $p = 0.008$, $N = 72$), although it will be recalled that overall resighting rates were higher off the Big Island than off Maui. A comparison of resighting intervals is of limited utility because there are only three data points for Maui, due to the rarity with which females without calf were identified on more than one day in this location. However, a two-tailed Wilcoxon rank sum test showed that even with this minimal sample size, the difference approached statistical significance ($S = 12.00$,

df = 1, p = 0.095). More data are required to permit a definitive conclusion, but these data do suggest that females without calf may spend more time in waters off the Big Island than off Maui.

Figure 2. Intervals between first and last identification of whales photographed on more than one day (Maui).

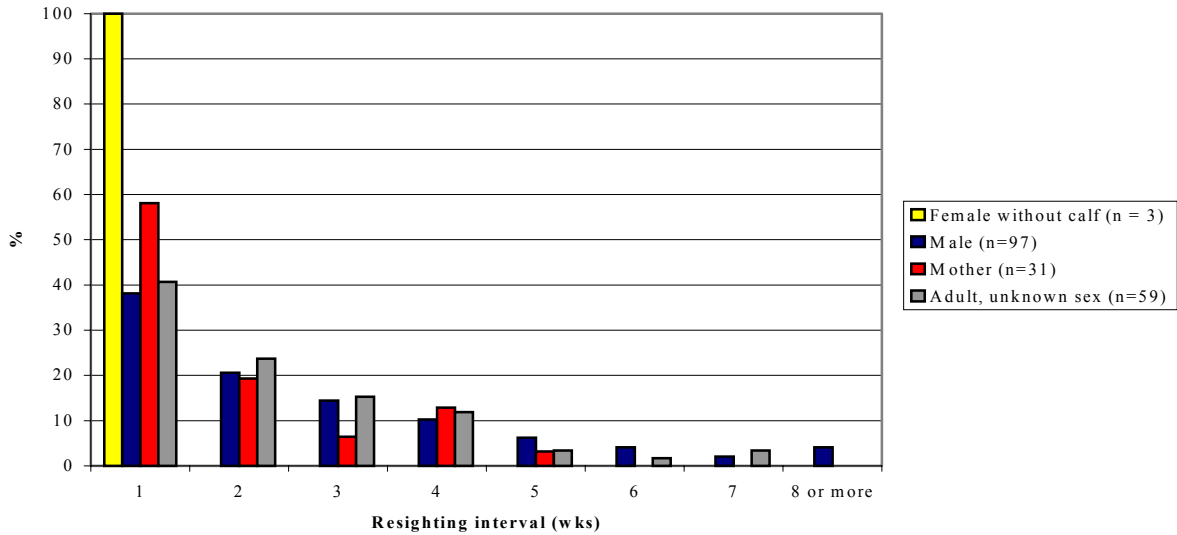


Figure 3. Intervals between first and last identification of whales photographed on more than one day (Big Island).

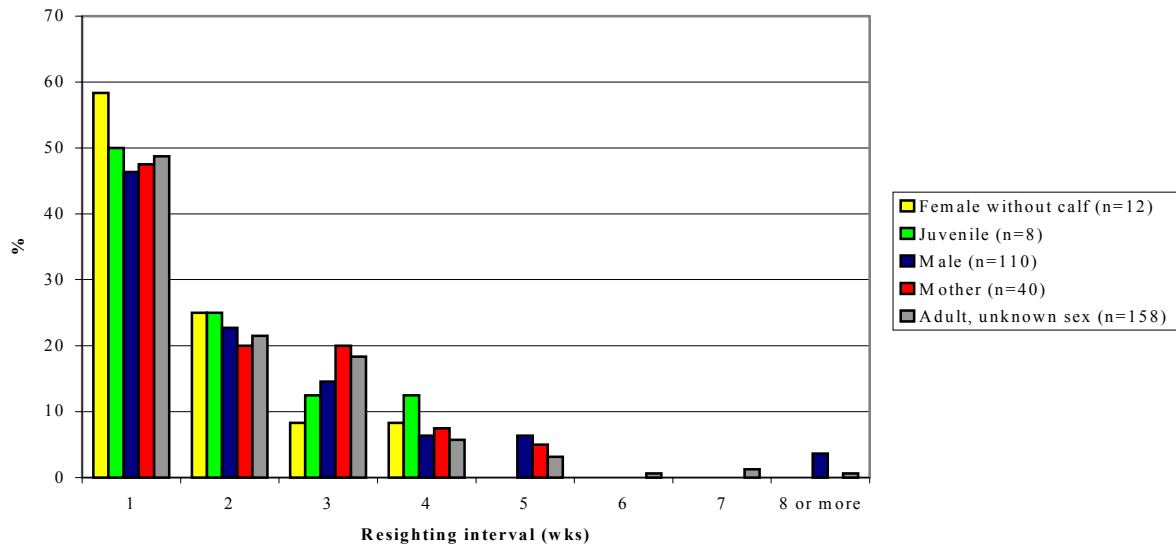


Table 4 summarizes the resighting intervals (in days) for each class of whale identified on more than one day within the same season. Data are presented separately for Maui and the Big Island. Rather than calculating mean intervals and standard deviations, we calculated median intervals and interquartile ranges. With skewed distributions, as are evident in Figures 1-3, medians are more representative of the data than are means, and interquartile ranges are the appropriate measure of variability.

Table 4. Median intervals (in days) between first and last identification for all males, mothers, females without calf, juveniles, and adults of unknown sex identified on more than one day during the same season off the Big Island, Maui, and overall.

	Location	Median (days)	Interquartile range	Minimum	Maximum	N
Males	Big Island	8.0	13.0	1	76	110
Mothers	Big Island	8.5	13.5	1	35	40
Females without calf	Big Island	6.5	10.0	1	23	12
Juveniles	Big Island	6.5	10.5	1	28	8
Adults, unknown sex	Big Island	8.0	13.0	1	57	158
All whales	Big Island	8.0	13.0	1	76	328
Males	Maui	13.0	20.0	1	64	97
Mothers	Maui	5.0	12.0	1	33	31
Females without calf	Maui	2.0	2.0	1	3	3
Juveniles	Maui	-	-	-	-	-
Adults, unknown sex	Maui	10.0	15.0	1	45	59
All whales	Maui	10.0	17.0	1	64	190
Males	Overall	11.0	17.0	1	76	217
Mothers	Overall	7.0	12.5	1	35	72
Females without calf	Overall	5.0	10.5	1	31	16
Juveniles	Overall	6.5	10.6	1	28	8
Adults, unknown sex	Overall	8.0	14.0	1	65	225
All whales	Overall	9.0	15.0	1	76	538

Note: Overall data include a small number of whales identified at other locations within the Hawaiian Islands.

For all classes of whale the intervals were very variable, as indicated by the relatively high interquartile ranges. For the Big Island, mothers had the longest median interval (8.5 days), followed by males and adults of unknown sex (8 days), and then females without calf and juveniles (6.5 days). In the case of Maui, males had the longest median interval (13 days), followed by adults of unknown sex (10 days), mothers (5 days), and females without calf (2 days). No juvenile was identified on more than 1 day off Maui. When all data were combined, males had the longest median interval (11.0 days), followed by adults of unknown sex (8 days), mothers (7 days), juveniles (6.5 days), and females without calf (5 days).

The differences in resighting intervals among classes of whale were not significant overall (Kruskal-Wallis, $F_{[4,533]} = 1.92$, $p = 0.106$) or for the Big Island (Kruskal-Wallis, $F_{[4,323]} = 0.34$, $p = 0.851$), but were significant in the case of Maui (Kruskal-Wallis, $F_{[3,186]} = 2.96$, $p = 0.034$). A Dunn test (Zar 1984) revealed that off Maui, resighting intervals for females without calf were significantly shorter than resighting intervals for males and adults of unknown sex. This is consistent with the suggestion that females without calf are more transient off Maui than off the Big Island, although again it should be noted that only three females without calf were identified on more than one day off Maui.

III. Inter-island resighting intervals.

Despite the fact that data were collected off both Maui and the Big Island during the same season in 5 years (Table 1), almost all whales identified on more than one day were observed in only one location within a given season. However, there were several instances of movements between different islands within the same season (see Table 5). Fourteen whales were identified initially off the Big Island and subsequently off Maui, and one was identified initially off Maui and subsequently off Niihau. Although the data may appear to suggest a northwesterly direction of travel, the apparent direction of movement of whales in many cases is likely to be a result of the timing of data collection in each location (see Table 1). Of the fifteen whales, eight were known to be male, one was known to be female, and the remaining six were of unknown sex. Overall, the mean inter-island resighting interval was 36.2 days. When males alone were considered, the mean interval was 35.5 days, and for whales of unknown sex the mean interval was 38.0 days. The only female in this data set had an inter-island resighting interval of 31 days, and was unaccompanied by a calf.

Table 5. Resighting intervals of whales identified off more than one Hawaiian Island within the same season.

Whale	Sex	First identification		Second identification		Interval (days)
		Location	Date	Location	Date	
4	Unknown	Big Island	23 Jan 1980	Maui	26 Feb 1980	34
6	Male	Big Island	1 Mar 1988	Maui	27 Mar 1988	26
8	Unknown	Big Island	6 Feb 1980	Maui	1 Mar 1980	24
23	Male	Big Island	12 Feb 1980	Maui	1 Mar 1980	18
48	Male	Big Island	10 Mar 1988	Maui	12 Apr 1988	33
68	Female	Maui	7 Mar 1981	Niihau	7 Apr 1981	31
96	Unknown	Big Island	31 Jan 1980	Maui	26 Feb 1980	26
152	Unknown	Big Island	30 Jan 1981	Maui	10 Mar 1981	39
433	Male	Big Island	13 Feb 1981	Maui	3 Apr 1981	49
498	Male	Big Island	5 Mar 1988	Maui	21 Mar 1988	16
979	Unknown	Big Island	3 Mar 1988	Maui	13 Apr 1988	41
1019	Male	Big Island	21 Feb 1988	Maui	12 Apr 1988	51
1026	Unknown	Big Island	19 Jan 1988	Maui	24 Mar 1988	64
1031	Male	Big Island	18 Feb 1988	Maui	15 Apr 1988	57
1043	Male	Big Island	19 Feb 1988	Maui	24 Mar 1988	34

Note: These data were previously presented in Baker and Herman (1981) and Craig (1995).

Discussion

Resighting rates

Overall, the results showed that only 11.94% of whales were identified on more than one day within a single season. Thus, the vast majority of whales were identified on only one day during the winter reproductive season. This is consistent with the studies reviewed earlier, and by considering the results of all studies together we can conclude that this is true for all locations within Hawaii in which whales have been studied intensively: west Maui, the Kohala Coast of the Big Island, and the north, south, and west coasts of Kauai. Similar findings have been reported from the winter grounds of the North Atlantic. For example, Mattila et al. (1994) reported that only 15.8% of humpbacks were identified on more than one day within the same season at Samana Bay, Dominican Republic, and Mattila et al. (1989) reported that only 9.1% of humpbacks were identified on more than one day on Silver Bank. If humpback whales on the winter grounds tended to reside in the same area for protracted periods, resightings of whales within the same season would be much more common than they are for Hawaii and other winter grounds. Thus, all available data on within-season resighting rates suggest that humpback whales on the winter grounds do not tend to reside in the same area for long periods, and may be quite transient at the local level. It should be noted that this apparent transience is very different from the residency behavior of humpback whales in the summer feeding grounds, where whales are often resighted in the same location many times throughout the feeding season (Clapham 2000). For example, Baker et al. (1985) reported that 54% of whales identified in southeastern Alaska in 1982 were sighted on more than one day, and Clapham et al. (1993) reported that 77.3% of whales identified in the Gulf of Maine between 1979 and 1988 were resighted on more than one day during the same year.

When we compared resighting rates for Maui and the Big Island, we found that significantly more whales were identified on more than one day off the Big Island than off Maui. This may indicate that humpback whales are more transient in west Maui waters than off the Kohala Coast of the Big Island. However, there are other potential explanations, as discussed previously. It is possible that the difference in resighting rates off Maui and the Big Island is related to regional differences in population density. However, although the population size of humpback whales in Hawaii appears to be increasing annually at a rate of 7% (Mobley, Grotefendt, et al. 1999), a comparison of overall resighting rates off Maui in 1987 and 1996 showed very little difference. Consequently, it is unlikely that the difference in resighting rates between Maui and the Big Island is due simply to differences in population density. However, it is possible that the regional difference in resighting rates was due to differences in the extent of preferred habitat. Because the extent of preferred habitat is much greater in the west Maui region than off the northwest coast of the Big Island (e.g., see Craig & Herman 2000), it is probable that our research boat consistently sampled a greater proportion of preferred habitat off the Big Island than off Maui. This would tend to increase the probability of identifying individual whales on more than one occasion. However, the possibility remains that humpback whales are indeed more transient off west Maui than off the Big Island.

We presented a comprehensive analysis of resighting rates for the following classes of whale: males, mothers, females without calf, juveniles, and adults of unknown sex. Off Maui, resighting rates were highest for males, followed by mothers, females without calf, adults of unknown sex, and juveniles. Off the Big Island, the highest resighting rate was for females without calf, followed by mothers, males, juveniles, and adults of unknown sex. When all data were combined, the highest resighting rates were for males, followed by mothers, females without calf, juveniles, and adults of unknown sex. However, statistical analysis revealed that there were no significant differences in resighting rates between these classes of whale for Maui, the Big Island, or all data combined.

The resighting rate of females without calf relative to the resighting rates of other classes of whale was quite different off the Big Island as compared to Maui. Off the Big Island, females without calf were the class of whale most likely to be identified on more than one day, whereas off Maui females without calf were much less likely to be resighted than were males and mothers. As was noted earlier, the suggestion that these females may spend more time off the Kohala Coast of the Big Island than off west Maui is consistent with our previous research showing that individual females are likely to be identified off Maui in the years during which they have a calf and off the Big Island in the years when they have no calf (Craig & Herman 2000).

Resighting intervals

Our analysis of resighting intervals for whales identified on more than one day within the same season showed that for the majority of whales (65.98%), 2 weeks or less elapsed between first and last identification within the same season. Moreover, 81.04% of whales had intervals of 3 weeks or less, and 89.40% of whales had intervals of 4 weeks or less. The longest interval between first and last identification for any whale was exhibited by one male whose dates of first and last identification were almost 11 weeks (76 days) apart. This interval is 2 days longer than the longest interval previously reported for humpback whales in the Hawaiian Islands (Darling et al. 1983). No mother or female without calf had an interval in excess of 5 weeks, and no juvenile had an interval greater than 4 weeks. However, 10 males and two adults of unknown sex had intervals of 8 weeks or more.

When resighting intervals were considered separately by island, the trends were generally similar for Maui and the Big Island. However, there was a difference in the resighting intervals of females without calf in the two locations. Off Maui, no female without calf had a resighting interval of more than 3 days. By contrast, off the Big Island 50.0% of all females without calf that were identified on more than one day had intervals of 7 days or more. This again suggests that females without calf may spend more time in waters off the Big Island than off Maui, although more data are required before a definitive conclusion can be reached.

Resighting intervals for all classes of whale were very variable. Off the Big Island, mothers had the longest median interval, followed by males and adults of unknown gender, and finally by females without calf and juveniles. However, statistical analysis indicated that the differences between these classes of whale were not significant. It should be noted that the variability of intervals within each class of whale would reduce the chance of finding significant

differences between classes. Off Maui, males had the longest median interval, followed by adults of unknown sex, mothers, and females without calf. In this case, statistical analysis indicated that the resighting intervals of females without calf were significantly shorter than the resighting intervals of males and adults of unknown sex. Again, this is consistent with the suggestion that females without calf are relatively transient in Maui waters.

Overall, biological considerations predict that females without calf should spend little time in Hawaiian waters as compared to males and mothers. The absence of an exploitable food resource in the winter grounds and the rarity of feeding during most of the migration mean that wintering humpback whales must subsist on stored energy reserves for extended periods of time (Nishiwaki 1959; Chittleborough 1965; Dawbin 1966). Male humpback whales are likely to remain on the winter grounds for as long as their energy reserves allow, in order to maximize their mating opportunities. However, after a female without a calf has become pregnant there is no need to remain on the winter grounds. Given that she will have to face the extreme energetic demands of lactation while she herself is not feeding the following winter, her best strategy is probably to return to the feeding grounds and begin accumulating energy reserves as soon as possible. In the years when a female has a calf, however, she presumably remains on the winter grounds until such time as her calf is sufficiently mature and robust to survive the migration back to the high-latitude feeding grounds. Juveniles are unlikely to remain in the winter grounds for extended periods of time because they are physiologically incapable of reproducing, and because their smaller body size will restrict their ability to accumulate stored energy reserves (Calder 1984).

Inter-island resighting intervals

There were fifteen cases in which individual whales were identified off more than one island within the same season. Of these fifteen whales, eight were known males, six were of unknown sex, and only one was a known female. Overall, the mean inter-island resighting interval for these whales was 36.2 days. The mean inter-island resighting interval for males only was 35.5 days, and the mean interval for whales of unknown sex was 38 days. The interval for the only female (without a calf) in this data set was 31 days. The most notable aspect of these intervals is that they tend to be longer than the resighting intervals reported for whales identified off only one island during the same season. For example, off the Big Island only 4 of 110 (3.6%) males had a resighting interval of 35 days or more, and only 3 of 158 (1.9%) adults of unknown sex had a resighting interval of 38 days or more. In the case of Maui, only 11 of 97 (11.3%) males had a resighting interval of 35 days or more, and only 3 of 59 (5.1%) whales of unknown sex had a resighting interval of 38 days or more. This underlines the fact that resighting intervals provide only minimum estimates of residency, and suggests that inter-island resighting intervals are more representative of residency in the Hawaiian Islands as a whole than are intervals based on resightings of whales in the same location.

Directions for future research

While providing the most comprehensive analysis to date of humpback whale residency on the winter grounds, our study has raised some interesting issues that should prompt further research. The finding that inter-island resighting intervals tend to be longer than resighting intervals recorded off a single island suggests a need for more studies comparing data collected simultaneously in different locations throughout Hawaii. The possibility that whales, especially females without calves, may be more transient in west Maui waters than in the waters off the Kohala Coast of the Big Island merits further investigation. Future studies combining photo-identification with large-scale satellite telemetry would provide the most precise data on residency. However, obtaining a sample size sufficient to allow statistical comparison of different classes of whale would be financially and logistically challenging.

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