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## **An overview of humpback whale research in Hawaiian waters and a summary of early attempts to estimate whale abundance**

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### **Abstract**

Since the cessation of major commercial whaling operations for humpback whales in the North Pacific in 1966, the Hawaiian Islands, the principal mating and calving grounds for this population have witnessed a resurgence in the numbers of whales assuming temporary residency each winter and spring season. As such, this area has also served as a central resource for studying humpback whale behavior and biology in the breeding grounds. Efforts to estimate humpback whale abundance in Hawaiian waters have employed several different methods including vessel and aerial-based surveys as well as mark-recapture techniques using sighting and resighting data of photo-identified individuals. These efforts stretch back to the mid to late 1970s when boat-based and aerial-based surveys estimated less than 1000 humpbacks in Hawaiian waters. Mark-recapture studies from 1977-1983 compared with 1989-1993 revealed a steady increase in the estimated numbers of humpbacks from between 1000-2000 to between 4000-5000, respectively. A positive trend in humpback whale abundance was also witnessed from aerial surveys conducted around all the main Hawaiian Islands between 1993-2000. Throughout these studies, several potential biases were identified that may have impacted estimates of abundance. Currently, more than 10,000 humpbacks are estimated to visit Hawaiian waters each year with an estimated annual rate of increase of 6% based on the most recent mark-recapture study from 2004-2006. It is proposed that abundance estimates be updated.

### **Introduction**

The Hawaiian Islands are the principal breeding grounds for North Pacific humpback whales (*Megaptera novaeangliae*) (Calambokidis et al., 2008). Each winter and spring, humpback whales of both sexes and all age classes assume temporary residency in Hawaiian waters for purposes of calving, mating and participating in behaviors and social interactions related to breeding activities (Craig et al., 2003; Herman et al., 2011). Commercial whaling during the first six decades of the 20<sup>th</sup> century had a devastating impact on the population of North Pacific humpback whales, reducing their numbers to between 1000 and 1400 individuals from an estimated original population of perhaps 13,000-15,000 individuals (Rice, 1978; Gambell, 1976; Johnson & Wolman, 1985). It is unclear whether humpback whales have always been present in Hawaiian waters (Herman, 1979). However, the first scientific surveys of humpback whales in these waters in the mid-1970s estimated less than 1000 individuals present (Herman & Antinaja, 1977; and as cited in Darling & Morowitz, 1986, Wolman & Jurasz, 1977; Rice & Wolman, 1978; and Rice & Wolman, 1979). Currently, more than 10,000 humpbacks complete an annual migration into Hawaiian waters, based on abundance estimates of approximately 10,103 individuals (excluding calves) or 55% of the North Pacific population that were generated from the 2004-2006 SPLASH (Structures of Populations, Levels of Abundance, and Status of Humpbacks) project (Calambokidis et al., 2008). This project, which used photo-identification mark-capture techniques to provide abundance estimates, also reported an estimated annual rate of population increase of 6%. The purpose of the current report is to provide a brief overview on what has been established studying humpback whales in Hawaiian waters since the 1970s

including a history of research efforts to estimate humpback whale abundance prior to the most recent estimates provided through the SPLASH project.

Pioneering studies of humpback whales in Hawaiian waters in the mid-1970s focused on establishing their presence, estimating of their abundance and mapping their distribution. Based on boat and aerial surveys, between approximately 250 and 800 whales were estimated to assume residence in Hawaiian waters between 1976-1979 (Herman & Antinaja, 1977; and as cited in Darling & Morowitz, 1986, Wolman & Jurasz, 1977; Rice & Wolman, 1978; and Rice & Wolman, 1979). The majority of humpbacks were found within the 100 fathom isobath (183-m contour around the main Hawaiian Islands) with the greatest concentrations of whales and calves occurring in two areas, between the islands of Maui, Molokai, Lanai and Kahoolawe (the “four-island” region) and across Penguin Bank, a shallow tongue extending approximately 25 nm southwest from Molokai (Herman & Antinaja, 1977; Herman et al., 1980). Also established was the presence of a third whale often accompanying a mother-calf pair, termed “escort” (Herman & Antinaja, 1977) and later identified as a male, presumably prospecting for a receptive female (Glockner, 1983).

Because of its clear and relatively calm coastal waters with easy access to humpback whales, Hawaii became one of the “hot beds” for research on humpback whale behavioral ecology in the breeding grounds starting in the 1970s and 80s with early studies describing their social organization, migratory patterns, behavior, social interactions, song, and other forms of communication (see Herman, 2016 for a comprehensive summary). These studies revealed peak times in abundance (between early-mid February and mid-March) that coincided with peaks in aggressive activities, that abundance appeared to peak earlier off Hawaii Island than Maui, and that aggressive behaviors in male-male competition over single females within competitive groups followed a progressive path of escalation (Baker & Herman, 1981,1984). In addition, research established the interactions between singing males and other groups (Tyack, 1981), that affiliations, other than that of a mother and her calf, tended to be transient (Mobley & Herman, 1985), and that mature females produced calves on average every two to three years (Baker et al., 1987). Various studies also established the connectedness of individually identified humpback whales in the Hawaiian breeding grounds to feeding grounds off Alaska (e.g., Baker et al., 1986). In the Hawaiian breeding grounds, the presence of numerous males “singing” asynchronously across the breeding season as well as other characteristics led Herman and Tavorlga (1980) to propose that the humpback whale mating system was similar in many ways to a lek mating system (see also Clapham, 1996; Herman, 2016). In order to better understand the function of humpback whale song and other non-song vocalizations, research into the responses of humpbacks to playback of song as well as other natural and non-natural sounds characterized part of the research effort in the mid-1980s. These studies revealed that playback of song lead to few whales approaching the sound source compared to playback of social sounds from highly active competitive groups or a humpback feeding call recorded in Alaskan waters by Baker (1985) (Mobley et al., 1988, see also Tyack, 1983). Also, Silber (1986) conducted early work characterizing non-song vocalizations (social sounds) in the breeding grounds (see also Zoidis et al., 2008 for recent findings on calf vocalizations). Later work on song revealed the distribution, movements and spacing characteristics of singers (Frankel et al., 1995), established diurnal and seasonal trends of singing favoring relatively more song in evening hours and during peak periods of whale abundance (Au et al., 2000), and described the acoustic characteristics of song

(Au et al. 2006). Studies on singing behavior showed singers being joined by other individual males (Darling & Berube, 2001), that joiners sometimes formed apparent coalitions with singers (Darling et al., 2006), and that song similarity could serve as an attractant to male singers (Darling et al., 2012). Research in Hawaii in the 1990s and 2000's continued to focus heavily on describing the behavioral ecology of humpbacks. Studies demonstrated diurnal and seasonal variations in humpback behavior and pod characteristics (Helweg & Herman, 1994), a male-biased sex ratio of photo-identified whales in the breeding grounds (Craig & Herman, 1997), the preference of Maui waters by individual females when with calf, and waters off Hawaii Island when without calf (Craig & Herman, 2000), residency characteristics in the breeding grounds and migratory timing into and out of the breeding grounds as a function of age-class, sex, and reproductive state (Craig et al., 2001, 2003), the preference of male escorts for associating with females without calf (i.e. those with a higher reproductive potential) over females with calf (Craig et al. 2002), calf mortality rates of approximately 18% (Gabriele et al., 2001), adult survival rates (Mizroch et al., 2004), the behavioral ontogeny of calves (Cartwright & Sullivan, 2009), and the segregation of mother-calf pairs into shallow waters, apparently to avoid male harassment (Smultea, 1994; Cartwright et al. 2012; Craig et al., 2014). Work was also conducted on the relationships between the body size of individual humpback whales and their behavioral roles using underwater videogrammetry (Spitz et al., 2000). These studies showed that male size confers an advantage in competition, that larger females produce larger calves and attract greater numbers of escorts than do smaller females, that mature females prefer associating with the largest males in male-female dyads, that humpbacks exhibit size assortative pairing into dyads, and that both mature and immature (non-calf) males participate in singing (Spitz et al., 2002; Pack et al., 2009, 2012; Herman et al., 2013). Throughout this period of research productivity exploring the social matrix, ecology and behaviors of humpback whales in the Hawaiian breeding grounds, studies continued to document steady increases in their abundance (see below), as well as similar and changing trends in their distribution. These studies showed the four-island region and Penguin Bank continuing to house the largest concentration of whales and calves, a significant increase in the whales assuming residency in waters around Kauai, and an apparent re-population of the whales in the Northwestern Hawaiian Islands (Mobley et al., 1999; Johnston et al., 2007; Lammers et al., 2011). In addition, continuous annual efforts since the mid-1970s to photo-identify the tail flukes of individual humpbacks (see Katona et al., 1979), along with their pod membership and behavioral roles across the major periods of their residency in the Hawaiian breeding grounds produced extensive and rich archival catalogs of individual life histories many of which extended for decades providing key information on long-term site fidelity, sex ratios, calving rates, female demographics and the dynamics of behavioral roles of individuals (e.g. Herman et al., 2011).

### **Pre-SPLASH efforts to estimate abundance of humpback whales in Hawaiian waters**

The findings from several of the studies reviewed above bear directly on potential biases and challenges when considering making estimates of the humpback whale population abundance in Hawaiian waters. In theory, any factor that potentially modifies the “catch-ability” of some whales and creates heterogeneity of capture probabilities and recapture probabilities can affect abundance estimates. This includes heterogeneity in capture probabilities of groups of individuals based on sex, age class, residency differences, differences in migratory timing, geographic variations, trends in emigration and immigration, mortalities and recruitment. A common negative bias resulting in underestimates of a population is heterogeneity in the

probability of capture of groups of individuals. Examples of studies revealing heterogeneity in the probability of capture of groups of individuals in Hawaii include:

- ✓ A reported a male-biased sex ratio based on photo-identification of 1.86:1 (Craig & Herman, 1997; see also Herman et al., 2011).
- ✓ Differences in migratory timing into and out of Hawaii conditioned by reproductive state, age class and sex (Craig et al., 2003).
- ✓ Differences in the duration of residency as a function of age class, sex and reproductive condition (Craig et al., 2001).
- ✓ Geographic variation showing that individual females vary their habitat preferences depending on their reproductive condition: when with calf they favor Maui waters, when without calf they favor Hawaii Island waters (Craig & Herman, 2000).
- ✓ Heterogeneity in migratory movements within the islands and across different breeding grounds in different seasons apparently favoring males (Darling & McSweeney, 1985; Darling & Morowitz, 1986; Perry et al., 1990; Darling & Cerchio, 1993; Cerchio et al., 1998; Salden et al. 1999, Calambokidis et al. 2001).
- ✓ Geographic heterogeneity suggesting either that Kauai may be disproportionately composed of immature whales or like Hawaii Island may be favored by mature whales when without calf (Mobley et al., 1999).

Initial efforts to estimate the abundance of humpback whales in Hawaiian waters in the mid to late 1970s employed vessel-based surveys sometimes in combination with aerial-based surveys. These were followed by a variety of studies in the 1980s and 1990s using mark-recapture methods of photo-identified individuals. In parallel with these efforts in the 1990s, island-wide aerial survey methods were employed to estimate population abundance. Each of these efforts is presented below in chronological order, and key features are summarized in Table 1.

**A. Herman and Antinjoa (1977).** Herman and Antinjoa (1977) conducted both ship-based and aerial-based surveys of humpback whales in various sub-regions of the Hawaiian Islands from February 29-April 15, 1976. They estimated whale abundance by using a combination of ship-based surveys (to estimate pod density) and aerial surveys (to estimate mean number of whales per pod) on a single day during peak season (March 13) in Penguin Bank and portions of the four-island region (excluding the Auau channel), and then added data from March 14 from surveys in the Auau channel. They estimated an abundance of 200-250 humpbacks, based on estimates of 141-156 whales counted from their surveys bracketed by 50 whales at the lower end and 100 whales at the upper end to account for estimates of animals in outlying regions and islands. Herman and Antinjoa (1977) suggested that there was negative bias (i.e. bias downward towards underestimating the number of whales) due to several factors including: (a) heterogeneity of sampling (i.e. missing counts from other islands); (b) not taking into account any sex bias; (c) not taking into account early migrants that departed from Hawaii early and late migrants yet to arrive in the Hawaiian Islands.

**B. Wolman and Jurasz (1977) and Rice and Wolman (1978,1979).** The National Marine Fisheries Service conducted vessel-based line-transect surveys around all of the main Hawaiian Islands in two-week periods in February or March from 1976-1979. Based on these surveys, the following estimates of population abundance were reported as cited in Darling and Morowitz

(1986): 373 individuals by Wolman & Jurasz (1977);  $500 \pm 90$  individuals by Rice and Wolman (1978) and 650 (550-790) individuals by Rice and Wolman (1979).

**C. Darling et al. (1983).** Darling et al. (1983) employed mark-recapture methods using photo-identified humpbacks in the four-island region to estimate whale abundance in the Hawaiian Islands. Darling et al. obtained 264 fluke identification photographs of humpback whales from 1977-1979. The high rate of newly identified whales in 1979 suggested to Darling et al. that their sample was but a small portion of the population visiting Hawaii. The data from 1978-1979 were used to derive an abundance estimate of 895 whales, 95% confidence limits = 592-1837 using a modified mark-recapture closed population Petersen test.

**D. Darling and Morowitz (1986).** Darling and Morowitz (1986) extended the fluke-identification dataset of Darling et al. (1983) in the four-island region by two years (i.e. 1977-1981) and excluding calves and yearlings employed mark-recapture methods to estimate whale abundance in the Hawaiian Islands. To arrive at their estimates, Darling and Morowitz (1986) employed three methods: (a) fitting the Bernoulli distribution to the observed sighting frequency of photo-identified humpbacks within seasons, (b) interpreting the rate of discovery of newly photo-identified humpbacks within and across breeding seasons, and projecting as to where the discovery curve might level off (i.e. saturate), (c) making direct counts of photo-identified whales within and across seasons. Direct counts of individually identified unique humpbacks yielded absolute minimum estimates of 521 whales in 1981 and 922 whales from 1977-1981. Darling and Morowitz (1986) estimated approximately 1000 humpbacks around the Hawaiian Islands in a single breeding season (based on data from 1981), and 2100 whales over five seasons (1977-1981). From the differences in abundance estimates based on a single season versus multiple seasons, Darling and Morowitz (1986) proposed that the collection of humpbacks assuming residency in the four-island region was different from year to year. Baker and Herman (1987) expressed skepticism of the estimates provided by Darling and Morowitz (1986) based on several criticisms of their analyses including that confidence limits were not reported for either within- or across-years abundance estimates, that distributions beyond Bernoulli were not tested (e.g., Poisson), and that the Bernoulli distribution was generally a poor fit to the observed data using goodness-of-fit tests and thus may not have yielded accurate estimates of within-year abundance, and that estimates based on rate of newly photo-identification of humpbacks across seasons are difficult to interpret without calculated confidence limits and information on recruitment. Additionally, two assumptions underlying the theory of the Bernoulli distribution are that the full population of humpbacks remains for the entire sighting season and that sightings are random. Data on the migratory timing and residency characteristics of humpbacks in Hawaiian waters (Craig et al., 2001, 2003) as well as on the heterogeneity of the resident population and geographic segregation and preferences (Craig & Herman, 1997; Craig et al., 2014) suggests that these assumptions may not have been met.

**E. Baker and Herman (1987).** Baker & Herman (1987) used data from sightings and resightings of photo-identified humpback whales in Hawaiian waters over four years from 1980-1983 to calculate three types of estimates of across-years whale abundance. These were: unbiased Petersen estimates for each pair-wise combination of years (i.e. the number of whales resighted between any pair of years); the weighted mean of the Peterson estimates of all four years (i.e. using the total number of individually –identified humpbacks sighted or resighted in

all earlier years combined); Jolly-Seber estimates (which assume an open population) for the middle two sampling years (i.e., 1981, 1982), using both the number of humpbacks sighted in only the most recent previous year as well as the total number of individually –identified humpbacks sighted or resighted in all earlier years combined. Baker and Herman (1987) suggested the weighted Petersen estimate as the most “robust” of the three types of estimates, based on its relatively narrow confidence limits and use of cumulative across-year data. This method estimates 1407 humpbacks (95% CI = 1113-1701) assuming temporary residence in Hawaiian waters from 1980-1983. This was slightly less than the abundance estimate of 1627 whales (95% CI = 1320-1924) derived using the weighted mean of the Petersen estimates by Baker et al. (1986) using photo-identification data from 1977-1983. Baker and Herman (1987) considered both potential positive and negative biases in their Petersen and Jolly-Seber estimates. Factors associated with positive bias were: (a) that the inability to account for births and deaths may have inflated weighted Petersen estimates up to 37%; (b) the unaccounted for degree of permanent emigration and immigration, as well as temporary emigration; and (c) failure to identify resightings of previously photo-identified individuals. A factor associated with negative bias was the extent of heterogeneity in photographic capture probabilities among different groups of individuals. For example, using photo-identification data from 1976-1991, Craig and Herman (1997), showed that the probability of an individual humpback being resighted in Hawaii across years favored males over females, a finding they suggested might be associated with not all females completing or even undertaking migration to Hawaii as well as the relatively short residency time of mature females without calf compared to mature males.

***F. Calambokidis et al. (1997).*** Ten years following the publication of Baker and Herman (1987), Calambokidis et al. (1997) calculated estimates of humpback whale abundance in Hawaii as well as two other wintering areas in the North Pacific (Mexico and Japan), based on photo-identification data and resightings of individuals in these wintering grounds as well as in feeding grounds stretching from California to the Aleutian Islands from 1991-1993 (as well as 1990 from Mexico). Photo-identification data from 16 independent research groups working in these areas were collated and matched for resightings. Because of the difficulty in reliably obtaining fluke photos of calves and because the pigmentation patterns on these flukes are more susceptible to change than those of non-calves, photographs of calves were excluded from the data set. Of 6414 contributed fluke ID photographs, 3650 were of acceptable quality and used for abundance estimates. Data from Hawaii were collected in waters off three islands, Maui (acceptable quality photos = 393, 368 Id's), Hawaii Island (acceptable quality photos = 433, 401 Id's) and Kauai (acceptable quality photos = 386, 375 Id's). Two separate teams independently matched all photographs resulting in the identification of 2712 unique whales. Abundance estimates were determined using several geographically stratified capture-recapture methods. The Darroch method (using data from pairs of years in winter areas only) yielded an average abundance estimate for Hawaii of 4,005 whales, SE = 381. The Hilborn method (based on data from winter areas only) yielded an average estimate of 3760 whales, SE = 439, based on estimates of 3,037, SE = 361 for 1992 and 4,483, SE = 548 in 1993. Corrections for male biased sampling in Hawaii (Craig & Herman, 1997) yielded 4,440 whales based on a 2:1 male bias and 5,000 whales based on a 3:1 male bias. Petersen mark-recapture estimates of abundance for Hawaii using marks from SE Alaska yielded an average estimate of 5151 whales, SE = 769. Aside from the negative sampling bias due to a skewed sex ratio towards males sampled on the wintering areas (Craig & Herman, 1997), other sources of bias due to heterogeneity of capture probabilities

were identified such as geographic sampling bias although this seemed to be less problematic for Hawaii compared to Mexico or Japan because those whales photographed off Hawaii demonstrated nearly random mixing among subareas between years. Because the Petersen method assumes that all humpbacks from SE Alaska migrate to Hawaii and all from California-Washington migrate to Mexico, Calambokidis et al. (1997) pointed out that abundance estimates based on this method using whales marked in SE Alaska and resighted in Hawaii were likely biased positively by the degree to which some of the marked SE Alaska whales may have moved to a wintering area aside from Hawaii and some that feed off California may have migrated to Hawaii.

**G. Cerchio (1998).** Cerchio (1998) explored the validity of providing abundance estimates of humpback whales in the Hawaiian islands based on capture-recapture methods of photo-identified individual humpbacks taken in waters off the island of Kauai from 1989-1993, using various modeling procedures. Cerchio's compiled identification photographs excluded calf photographs, non-calf photographs of only the left blade of the tail flukes (the least abundant and poorer quality of single blade captures), and photos of poorly rated quality overall. Cerchio then compared photos across days within and across breeding seasons for resightings. From the dataset of 988 observations (i.e., the photographic identification of a single identified whale on a given day), Cerchio identified 790 unique individuals. The probability of resighting an individual on more than one day within a breeding season was 14% or less and varied depending on year and effort. The probability of capturing an individual more than one time across seasons was also relatively low at 8%. To these data, Cerchio applied and compared six population models to generate abundance estimates that assume a closed population (Chapman's modified Petersen estimator for sampling *without replacement* [to avoid the possibility of introducing negative bias from sampling with replacement because of the non-independence of multiple captures within the same breeding season], weighted mean of the Petersen, Darroch's maximum likelihood estimator for capture probabilities that vary with time (Darroch  $M_t$ ), and Chao's model estimators for capture probabilities that vary with time, individual, and time in combination with individual: model  $M_h$  - which relaxes the assumption of equal probability of capture among individuals due to heterogeneity, model  $M_t$  - which relaxes the assumption of equal probability of capture among individuals due to variation among sampling occasions (i.e. capture probability varies with time), and model  $M_{th}$  - in which capture probability varies with time and individual. Cerchio (1998) also generated abundance estimates using one model (Fisher-Ford estimator) that assumes an open population. For the closed population model abundance estimator methods Cerchio (1998) reported that pair-wise comparisons using Chapman's modified Petersen estimator yielded abundance estimates ranging from 1489 individuals, 95% CI = 366-2612 (1989-1990 comparison) to 5042 individuals, 95% CI = 2434-7650 (1992-1993 comparison). These estimates had relatively poor precision (CVs ranged from 0.20-0.43) compared with those of the weighted mean of the Petersen for all years of data (N = 3880, 95% CI = 2958-4802, CV = 0.12). The remaining estimates based on the assumption of closed population estimates yielded a range of greater population estimates with confidence intervals overlapping a portion of the estimates based on the weighted Petersen to various degrees as follows: Darroch  $M_t$ , N = 3959 individuals, 95% CI = 3208-4941, CV = 0.11; Chao  $M_t$ , N = 4196 individuals, 95% CI = 3328-5362, CV = 0.12; Chao  $M_{th}$ , N = 4858 individuals, 95% CI = 3722-6434, CV = 0.14; and Chao  $M_h$ , N = 5346 individuals, 95% CI = 4181-6911, CV = 0.13. For the Fisher-Ford open population model abundance estimator, Cerchio (1998)



reported a 1993 estimate using all data of 3115 individuals. However, because the Fisher-Ford model does not provide a variance estimate, it was not possible for Cerchio (1998) to judge precision of estimates using this model. Among the problems associated with estimating abundance of the humpback population, Cerchio (1998) judged temporary emigration and non-random mixing of the population between sampling occasions as the greatest. After considering the various models and various biases, Cerchio (1998) proposed an abundance estimate for the Hawaiian Islands of 4,000 individuals with a likely range of between 3000 and 5000 individuals.

**H. Mobley et al. (2001).** Mobley et al. (2001) calculated abundance estimates of humpback whales in the Hawaiian Islands based on aerial surveys conducted around the main Hawaiian islands in four separate breeding seasons separated by 2-3 years from 1993-2000 overlapping the period of peak abundance (i.e. late February – early April). Distance sampling theory was used to derive estimates of abundance and findings were corrected for the probability of detecting whales at the surface by taking into account respiration data collected from shore-based observations. Abundance estimates corrected for probability of detecting whales at the surface were for 1993, 2754 humpbacks (95% CI = 2,044-3463); for 1995, 3776 humpbacks (95% CI = 2925-4627); for 1998, 4358 humpbacks (95% CI = 3261-5454); and for 2000, 4491 humpbacks (95% CI = 3146-5836). The annual rate of population increase was estimated at 7%. Identified potential sources of bias in abundance estimates included: omission of sightings directly below the plane due to downward visibility limitations, and whale residency rates which for some behavioral roles (e.g., newly pregnant females without calf, juveniles) may be relatively short leading to a downward bias in estimates of absolute abundance.

**Conclusions.** Mobley et al. (2001) noted that over the history of attempts to estimate abundance of humpback whales in Hawaiian waters using mark-recapture methods, there is a positive trend toward greater numbers of estimated whales over time (i.e., comparing estimates using photo-identification data from 1977-1983 versus 1989-1993). Likewise, increasing trends in abundance have been evidenced from aerial surveys conducting from 1993-2000. Key biases that needed to be taken into account when estimating abundance using mark-recapture methods were: a) male-biased sex ratio in photo-identification data; b) heterogeneity of probabilities of capture based on temporal and geographic factors; c) a population that is open to emigration and immigration; and d) estimates of mortality and recruitment. Because of its broader coverage in the Hawaiian Islands as well as Alaskan feeding areas than some of the earlier mark-recapture studies reviewed here, the SPLASH project (which used data from 2004-2006) attempted to mitigate some of the factors associated with heterogeneity of probabilities of capture. Whether using mark-recapture methods or aerial survey methods, future efforts to monitor trends in the abundance of humpback whales in Hawaiian waters should take into account those humpbacks that relatively recently have assumed residency in the NW Hawaiian Islands (Johnston et al., 2007; Lammers et al., 2011). Finally, in September 2016 NOAA removed humpback whales in Hawaii (Hawaii Distinct Population Segment or DPS) from being listed as endangered (see [http://www.fpir.noaa.gov/PRD/prd\\_humpback.html#hw-regs](http://www.fpir.noaa.gov/PRD/prd_humpback.html#hw-regs)). This year also marked the 10-year anniversary of the final season of the SPLASH research project. Thus, it has been a decade since the last abundance estimates were conducted on humpback whales in Hawaiian waters. It is recommended that research be devoted to developing updated estimates of humpback whale abundance in Hawaiian waters in order to closely monitor this DPS post delisting.

Table 1. Summary of studies estimating abundance of humpback whales in Hawaiian waters (pre-SPLASH). (adapted from Mobley et al. 2001 with expansion)

Source	Method	Period of data collection (locations)	Abundance estimate(s)
Herman & Antinaja (1977)	Combination ship-based survey and aerial survey	March 13 (Penguin Bank and portions of Maui Nui region excluding Auau channel) March 14 (Auau channel)	200-250
Rice and Wolman (1979)	Line transect vessel surveys	1976-1979 (around main Hawaiian Islands)	650 (550-790)
Baker et al. (1986)	Tail fluke photo-identification (mark-recapture)	1977-1983 (four-island region)	Petersen (weighted mean): 1627 (SE = 157)
Darling & Morowitz (1986)	Tail fluke photo-identification (mark-recapture)	1977-1981 (four-island region)	Bernoulli distribution: 1,000 (single season) 2100 (five seasons) (no SE or CI reported)
Baker & Herman (1987)	Tail fluke photo-identification (mark-recapture)	1980-1983 (four-island region)	Peterson weighted (all years combined): 1407, SE = 150 (95% CI = 1113-1701)
Cerchio (1998)	Tail fluke photo-identification (mark-recapture)	1989-1993 (Kauai)	Model: Peterson: 3880, SE = 471 Chao $M_h$ : 5346, SE = 690 Darroch $M_t$ : 3959, SE = 439 Chao $M_g$ : 4196, SE = 514 Chao $M_{th}$ : 4858, SE = 685
Calambokidis et al. (1997)	Tail fluke photo-identification (mark-recapture)	1991-1993 (Maui, Big Island, Kauai as well as Mexico, Japan, SE Alaska and other feeding areas from CA to Aleutian Islands)	Model: Darroch: 4005, SE = 381 Hilborn: 3760, SE = 439 Petersen: 5151, SE = 769
Mobley et al. (2001)	Aerial surveys (distance sampling)	1993, 1995, 1998, 2000 (all main Hawaiian islands)	1993: 2754, SE = 362 1995: 3776, SE = 434 1998: 4358, SE = 559 2000: 4491, SE = 686

## Literature Cited

- Au, W. W. L., Mobley, J. Jr., Burgess, W. C., Lammers, M. O. & Nachtigall, P. E. (2000). Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. *Marine Mammal Science* 16, 530–544.
- Au, W. W. L., Pack, A. A., Lammers, M. O., Herman, L. M., Deakos, M. H., Andrews, K. (2006). Acoustic properties of humpback whale songs. *Journal of the Acoustical Society of America*, 120, 1103-1110.
- Baker, C. S. 1985. The population structure and social organization of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. Doctoral dissertation, University of Hawaii, Honolulu, HI. 306 pp.
- Baker, C. S. and Herman, L. M. (1981). Migration and local movement of humpback whales (*Megaptera novaeangliae*) through Hawaiian waters, *Canadian Journal of Zoology* 59: 460-469
- Baker, C.S. and Herman, L. M. (1984). Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Canadian Journal of Zoology*, 62, 1922-1937.
- Baker, C.S. and Herman, L.H. (1987). Alternative population estimates of humpback whales (*Megaptera novaeangliae*) in Hawaiian waters. *Canadian Journal of Zoology*, 65, 2818-2821.
- 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. *Marine Ecology Progress Series*, 31, 105-119.
- Baker, C. S., Perry, A., & Herman, L. M. (1987). Reproductive histories of female humpback whales *Megaptera novaeangliae* in the North Pacific. *Marine Ecology Progress Series*, 41, 103-114.
- Calambokidis, J., Steiger, G.H., Straley, J.M., Quinn II, T.J., Herman, L.M., Cerchio, S., Salden, D.R., Yamaguchi, M., Sato, F., Urban, J., Jacobsen, J., von Ziegesar, O., Balcomb, K.C., Gabriele, C.M., Dahlheim, M.E., Higashi, N., Uchida, S., Ford, J.K.B., Miyamura, Y., de Guevara, P.L., Mizroch, S.A., Schlender, L. and Rasmussen, K. (1997). Abundance and population structure of humpback whales in the N. Pacific Basin. Final Report to the Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038.
- Calambokidis, J., Steiger, G. H., Straley, J. M., Herman, L. M., Cerchio, S., Salden, D. R., Urban, R. J., Jacobsen, J. K., Von Ziegesar, O., Balcomb, K. C., Gabriele, C. M. & Dahlheim, M. E. (2001). Movements and population structure of humpback whales in the North Pacific. *Marine Mammal Science* 17, 769 – 794.
- Calambokidis, J., Falcone, E. A., Quinn, T. J., Burdin, A. M., Clapham, P. J., Ford, J. K. B., Gabriele, C. M., LeDuc, R., Mattila, D., Rojas-Bracho, L., Straley, J. M., Taylor, B. L., Urban, J., Weller, D., Witteveen, B. H., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggins, J., & Maloney, N. (2008). *SPLASH: Structure of Populations, Levels of Abundance and Status of Humpback Whales In the North Pacific*. Final report for Contract AB133F-03-RP-0078 for U.S. Department of Commerce. Cascadia Research. 57p.

- Cartwright, R. and Sullivan, M. (2009). Behavioral ontogeny in humpback whale (*Megaptera novaeangliae*) calves during their residence in Hawaiian waters. *Marine Mammal Science*, 25(3), 659-680.
- Cartwright, R., Gillespie, B., LaBonte, K., Mangold, T., Venema, A., Eden, K. & Sullivan, M. (2012). Between a rock and a hard place: habitat selection in female-calf humpback whale (*Megaptera novaeangliae*) pairs on the Hawaiian breeding grounds. *PLoS ONE* 7(5): e38004. doi:10.1371/journal.pone.0038004.
- Cerchio, S. (1998). Estimates of humpback whale abundance off Kauai, 1989 to 1993: Evaluating biases associated with sampling the Hawaiian Islands breeding assemblage. *Marine Ecology Progress Series*, 175, 23-34.
- Cerchio, S., Gabriele, C. M., Norris, T. F., & Herman, L. M. (1998). Movements of humpback whales between Kauai and Hawaii: Implications for population structure and abundance estimation in the Hawaiian Islands. *Marine Ecology Progress Series*, 175, 13-22.
- Clapham, P. J. (1996). The social and reproductive biology of humpback whales: an ecological perspective. *Mammal Review*, 26, 27-49.
- Craig, A. S. and Herman, L. M. (1997). Sex differences in site fidelity and migration of humpback whales (*Megaptera novaeangliae*) to the Hawaiian Islands. *Canadian Journal of Zoology*, 75, 1923-1933.
- Craig, A. S. and Herman, L. M. (2000). Habitat preferences of female humpback whales *Megaptera novaeangliae* are associated with reproductive status. *Marine Ecology Progress Series* 193: 209-216.
- Craig, A. S., Herman, L. M., & Pack, A. A. (2001). *Estimating residence times of humpback whales in Hawaii*. Report to the Hawaiian Islands Humpback Whale National Marine Sanctuary Off of National Marine Sanctuaries, National Oceanic and Atmospheric Administration, U.S. Department of Commerce and Department of Land and Natural Resources, State of Hawaii.
- Craig, A. S., Herman, L. M., & Pack, A. A. (2002). Male mate choice and male-male competition coexist in the humpback whale (*Megaptera novaeangliae*). *Canadian Journal of Zoology*, 80, 745-755.
- Craig, A. S., Herman, L. M. Gabriele, C. M. & Pack, A. A. (2003). Migratory timing of humpback whales (*Megaptera novaeangliae*) in the central North Pacific
- Craig, A. S., Herman, L. M., Pack, A. A., & Waterman, J. O. (2014). Habitat segregation by female humpback whales in Hawaiian waters: avoidance of males? *Behaviour*, 151, 613-631.
- Darling, J. D., & Berube, M. (2001). Interactions of singing humpback whales with other males. *Marine Mammal Science*, 17, 570
- Darling, J. D. and Cerchio, S. (1993). Movement of a humpback whale (*Megaptera novaeangliae*) between Japan and Hawaii. *Marine Mammal Science*, 9, 84-89.
- Darling, J. D., Gibson, K. M. & Silber, G. K. (1983). Observations on the abundance and behavior of humpback whales (*Megaptera novaeangliae*) off west Maui, Hawaii. 1977-79. In R. S. Payne (Ed.), *Communication and behavior of whales* (pp. 201-222). Boulder, CO: Westview Press.
- Darling, J. D., Jones, M. E., & Nicklin, C. P. (2006). Humpback whale songs: Do they organize males during the breeding season? *Behaviour*, 143, 1051-1101.

- Darling, J. D., Jones, M. E., Nicklin, C. P. (2012). Humpback whale (*Megaptera novaeangliae*) singers in Hawaii are attracted to playback of similar song (L). *Journal of the Acoustical Society of America*, 132, 2955-2958.
- Darling, J. D. & McSweeney, D. J. (1985). Observations of the migrations of North Pacific humpback whales (*Megaptera novaeangliae*). *Canadian Journal of Zoology*, 63, 308-314.
- Darling, J. D. and Morowitz, H. (1986). Census of 'Hawaiian' humpback whales (*Megaptera novaeangliae*) by individual identification. *Canadian Journal of Zoology*, 64:105- 111.
- 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. *Canadian Journal of Zoology*, 73, 1134-1146.
- Gabriele, C. M., Straley, J. M., Mizroch, S. A., Baker, C. S., Craig, A. S., Herman, L. M., Glockner-Ferrari, D., Ferrari, M. J., Cerchio, S., von Ziegesar, O., Darling, J., McSweeney, D., Quinn II, T. J., & Jacobsen, J. K. (2001). Estimating the mortality rate of humpback whale calves in the central North Pacific Ocean. *Canadian Journal of Zoology*, 79, 589-600.
- Gambell, R. (1976). World whale stocks. *Mammal Review*, 6, 41-53.
- Glockner, D. A. (1983). Determining the sex of humpback whales *Megaptera novaeangliae* in their natural environment. In R. S. Payne (Ed.), *Communication and behavior of whales* (pp. 447-464). Boulder, CO: Westview Press.
- Helweg, D. A. and Herman, L. M. (1994). Diurnal patterns of behaviour and group membership of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Ethology* 98: 298-311.
- Herman, L. M. (1979). Humpback whales in Hawaiian waters: A study in historical ecology. *Pacific Science* 33: 1-15.
- Herman, L. M. (2016). The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: Review, evaluation, and synthesis. *Biological Reviews*. doi: 10.1111/brv.12309
- Herman, L. M. and Antinaja, R. C. (1977). Humpback whales in the Hawaiian breeding waters: Population and pod characteristics. *Scientific Reports of the Whales Research Institute (Tokyo)* 29: 59-85.
- Herman, L.M., Forestell, P. H. & Antinaja, R. C. (1980). Study of the 1976/77 migration of humpback whales into Hawaiian waters: Composite description. *Final Report to the U.S. Marine Mammal Commission*. (Report No. MMC-77/19). United States National Technical Information Services, Arlington, VA.
- Herman, L. M., Pack, A. A., Rose, K., Craig, A., Herman, E. Y. K., Hakala, S., & Milette, A. (2011). Resightings of humpback whales in Hawaiian waters over spans of ten to 32 years: site fidelity, sex ratios, calving rates, female demographics, and the dynamics of social and behavioural roles of individuals. *Marine Mammal Science*, 27, 736-768.
- Herman, L. M., Pack, A. A., Spitz, S. S., Herman, E. Y. K., Rose, K., Hakala, S. & Deakos, M. H. (2013). Humpback whale song: Who sings? *Behavioural Ecology and Sociobiology*, 67, 1653-1663.

- Herman, L. M. & Tavolga, W. N. (1980). The communication systems of cetaceans. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 149-209). New York: Wiley Interscience.
- Johnson, J.H. and Wolman, A.A. (1985). The humpback whale, *Megaptera novaeangliae*. *Marine Fisheries Review* 46: 30-37.
- Johnston D. W., Chapla M. E., Williams L.E., Mattila D.K. (2007) Identification of humpback whale *Megaptera novaeangliae* wintering habitat in the Northwestern Hawaiian Islands using spatial habitat modeling. *Endangered Species Research*, 3, 249–257
- Katona, S., Baxter, B., Brazer, O., Kraus, S., Perkins, J., & Whitehead, H. (1979). Identification of humpback whales by fluke photographs. In H. E. Winn & B. L. Olla (Eds.), *Behavior of marine animals. Vol. 3: Cetaceans* (pp. 33-44). New York: Plenum Press.
- Lammers, M. O., Fisher-Pool, P. I, Au, W. W. L, Meyer, C. G., Wong, K. B., & Brainard, R. E. (2011). Humpback whale *Megaptera novaeangliae* song reveals wintering activity in the Northwestern Hawaiian Islands. *Marine Ecology Progress Series*, 423, 261-268.
- Mizroch, S. A., Herman, L. M., Straley, J. M., Glockner-Ferrari, D. A., Jurasz, C., Darling, J., Cerchio, S., Gabriele, C. M., Salden, D. R., & von Ziegeler, O. (2004). Estimating the adult survival rate of central north Pacific humpback whales (*Megaptera novaeangliae*). *Journal of Mammalogy*, 85, 963-972.
- Mobley, J. R. Jr., Bauer, G. B. & Herman, L. M. (1999). Changes over a ten-year interval in the distribution and relative abundance of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Aquatic Mammals* 25: 63-72.
- Mobley, J.R. & Herman, L.M. (1985). Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. *Canadian Journal of Zoology*, 63, 763-772.
- Mobley, J.R., Herman, L.M., & Frankel, A.S. (1988). Responses of wintering humpback whales (*Megaptera novaeangliae*) to playback of recordings of winter and summer vocalizations and of synthetic sound. *Behavioural Ecology and Sociobiology*, 23, 211-223.
- Mobley, J. R., Jr., Spitz, S., Grotefendt, R., Forestell, P., Frankel, A., and Bauer, G. (2001). Abundance of humpback whales in Hawaiian waters: Results of 1993 – 2000 aerial surveys. *Report to Hawaiian Islands Humpback Whale National Marine Sanctuary*.
- Pack, A. A., Herman, L. M., Spitz, S. S., Craig, A. S., Hakala, S., Deakos, M. H., Herman, E. Y. K., Milette, A. J., Carroll, E., Levitt, S. Lowe, C. (2012). Size assortative pairing and discrimination of potential mates by humpback whales in the Hawaiian breeding grounds. *Animal Behaviour*, 84, 983-993.
- Pack, A. A., Herman, L. M., Spitz, S. S., Hakala, S., Deakos, M. H., & Herman, E. Y. K. (2009). Male humpback whales in the Hawaiian winter grounds preferentially associate with larger females. *Animal Behaviour*, 77, 653-662.
- Perry, A., C. S. Baker and L. M. Herman. 1990. Population characteristics of individually identified humpback whales in the central and eastern North Pacific: A summary and critique. Report of the International Whaling Commission (Special Issue 12):307–317.
- Rice, D. W. (1978) The humpback whale in the North Pacific: distribution, exploitation, and numbers. In: K. S. Norris and 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.*
- Rice, D. W. and Wolman, A. A. (1978). Humpback whales census in Hawaiian waters – February 1977. In: K. S. Norris & R. R. Reeves (Eds.). Report on a Workshop on ‘Problems Related to Humpback Whales (*Megaptera novaeangliae*) in Hawaii (pp. 45-53). U.S. Department of Commerce, NTIS PB280 794.
- Rice, D. W. and Wolman, A. A. (1979). Census of humpback whales wintering around the Hawaiian Islands. 1976-1979. International Whaling Commission. Doc. IWC SC/31/Doc.38.
- Salden, D. R., Herman, L.,M., Yamaguchi, M., & Sato, F. (1999). Multiple visits of individual humpback whales (*Megaptera novaeangliae*) between the Hawaiian and Japanese winter grounds, *Canadian Journal of Zoology*, 77, 504-508.
- Silber, G. K. (1986). The relationship of social vocalization to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). *Canadian Journal of Zoology*, 64, 2075-2080.
- Smultea, M. A. (1994). Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. *Canadian Journal of Zoology*, 72, 805-811.
- Spitz, S. S., Herman, L. M. & Pack, A. A. (2000). Measuring sizes of humpback whales (*Megaptera novaeangliae*) through underwater videogrammetry. *Marine Mammal Science*, 16, 664-676.
- Spitz, S. S., Herman, L. M., Pack, A. A. & Deakos, M. H. (2002). The relation of body size of male humpback whales to their social roles on the Hawaiian winter grounds. *Canadian Journal of Zoology*, 80, 1938-1947.
- Tyack, P. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology*, 8, 105-116.
- Tyack, P. L. (1983). Differential responses of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds. *Behavioral Ecology and Sociobiology*, 13, 49-55.
- Wolman, A. A. and Jurasz, C. M. (1977). Humpback whales in Hawaii: vessel census 1976. *Marine Fisheries Review*, 39, 1-5.
- Zoidis, A. M., Smultea, M. A., Frankel, A. S., Hopkins, J. L., Day, A., & McFarland, A. S. (2008). Vocalizations produced by humpback whale (*Megaptera novaeangliae*) calves recorded in Hawaii. *Journal of the Acoustical Society of America*, 123, 1737-1746.

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