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# Trends in the Abundance of Humpback Whales in the North Pacific Ocean from 1980 to 2006

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## Abstract

We examine long terms trends in abundance of humpback whales in the North Pacific overall and in specific regions based on data from SPLASH (a comprehensive collaborative study conducted 2004-06) and datasets from previous time periods incorporating several approaches to adjust for differences in sampling. The trends for the entire North Pacific Ocean were based on comparison of the overall abundance from two basin-wide studies conducted in 1990-93 and 2004-2006. These showed an increase from approximately 11,300, to 22,600 animals based on subsampling the more comprehensive 2004-2006 data to be similarly biased to the earlier study (5.5% per year over 13 years). A similar comparison but using all data and correcting for bias showed an increase from 9,500 to 21,063 in the same period or an increase of 6.3% per year. Trends for winter breeding regions in Hawaii and Mexico and feeding areas off the US West Coast (California and Oregon) and in SE Alaska were conducted with either inter-year or inter-regional mark-recapture estimates; these all showed rates of increase of 5 to 8% per year with the rates for US West Coast feeding areas and Mexico significantly higher than for Hawaii. Our results are consistent with a population that was reduced to low levels due to commercial whaling which occurred through 1966 and which has been recovering since then and, as of 2006, had not yet reached carrying capacity.

## Introduction

Since the end of commercial whaling, the abundance of North Pacific humpback whales has been estimated by a variety of methods and in different areas and time periods (Darling et al. 1983; Baker et al. 1986; Baker and Herman 1987; Calambokidis et al. 1990; Baker et al. 1992; Cerchio 1998; Urban et al. 1999; Mobley et al. 2001; Calambokidis and Barlow 2004; Calambokidis et al. 2004; Zerbini et al. 2006; Barlow

and Forney 2007; Straley et al. 2009; Barlow et al. 2011). It is clear from these studies that the abundance of humpback whales in the North Pacific has increased substantially since end of commercial whaling. Estimates of abundance for the entire North Pacific have increased from 850 in 1965-74 (Rice 1978) to about 21,000 whales in 2004-06 (Barlow et al. 2011). The reliability of early estimates of whale abundance has been questioned, but multiple lines of evidence indicate an increase. Because the previous studies have not used consistent methods, it is not possible to quantify population growth rates by comparing the published results of previous studies. It should, however, be possible to create subsets of more recent data that mimic the sampling used in earlier studies and thereby obtain comparable estimates of abundance. We use this approach to estimate rates of humpback whale population growth for the North Pacific.

Here we review the three photographic mark-recapture studies of humpback whale abundance that we use in estimating population growth rates:

1. Baker and Herman (1987) estimated the abundance of humpback whales in Hawaii (~1,400) using a weighted average of Petersen mark-recapture estimates from all combinations of paired years from 1980-83. Although their estimate was based only on whales photographed off Maui (C. S. Baker, pers. comm.), this is the earliest estimate that we could precisely duplicate using more recent data and is therefore important in documenting abundance trends in the 1980s.
2. A retrospective study was carried out based on photographs taken in 1990-93 over a much broader study area in the North Pacific that included both breeding regions and feeding areas (Calambokidis et al. 2001). Their estimate (~8,000 after correcting for sex-biased sampling in breeding areas; Calambokidis et al. 1997) was based on samples from breeding areas in Mexico, Hawaii, and Japan and from feeding areas from California to the eastern Aleutian Islands. Although this study was based on opportunistic photographs taken prior to the study without any sampling design, this is the earliest North Pacific estimates that are based on comparisons of feeding to breeding area (which helps correct for a bias caused by heterogeneity in capture probability).
3. The SPLASH project in 2004-2006 was the first study designed to estimate the abundance of humpback whales in the entire North Pacific. Photographic effort was allocated to obtain a representative sample all the known breeding and feeding areas (Barlow et al. 2011), adding Central America, the Philippines, the Bering Sea, and Russia to areas sampled in the 1990-93 study and greatly increasing the sampling effort in offshore waters in Alaska. The SPLASH abundance estimate (~21,000 in 2004-06) was based on a Petersen mark-recapture comparison of all breeding area samples to all feeding area samples corrected for various sources of sampling bias using a simulation approach.

In this report, we estimate population growth rates based on abundance estimates from these three studies. We use subsets of larger data collections and identical analytical methods in order to mimic the temporal and geographic coverage of previous studies and thereby obtain comparable abundance estimates. We use samples from Maui in 1990-93 and 2004-2006 to make estimates comparable to 1980-83 estimates of Baker and Herman (1987). We expand this to include samples from all the Hawaiian Islands to compare

1990-93 to 2004-06. We create comparable subsets of 1990-93 and 2004-06 data from Southeastern Alaska and Hawaii to compare estimates between a feeding area and a breeding area with strong migratory links. Finally, we exclude areas sampled exclusively in 2004-06 to create a subset comparable to the 1990-93 samples for a mark-recapture comparison of most breeding areas to most feeding areas.

## Methods

### *Population growth rates*

Annual rates of population growth ( $\lambda = e^r$ ) are estimated based on comparable population abundance estimates separated by at least 10 years. To ensure comparability, abundance estimates are computed using the same methods and with samples that are as geographically consistent as possible. Population growth rates are estimated from two abundance estimates ( $N_1$  and  $N_2$ ) as the  $n^{\text{th}}$ -root of the ratio of abundance in the two time periods:

$\lambda = [N_2 / N_1]^{1/t}$ , where  $t$  = the time period between samples,  $N_1$  = the abundance estimate for the first time period, and  $N_2$  = the abundance estimate for the second time period.

Growth rates are estimated based for the Pacific Basin as a whole and for specific regions (the breeding areas in Hawaii and Mexico and the feeding area off California and Oregon) in order to investigate possible regional differences in population growth rate. We tested whether estimates of population growth rates differed between time periods in one location and between geographic areas using a z-test based on estimated values of standard errors. The standard error in population growth rate is approximated assuming additive variances in the population estimates divided by the number of years,  $t$ , between estimates.

### *Pacific basin-wide abundance*

#### 1990-93 vs. 2004-06 Estimates based on comparable sampling

Because sampling effort was designed to representatively sample all regions and obtained large sample sizes, the 2004-06 SPLASH study produced a precise and relatively unbiased population estimate using mark-recapture methods (Barlow et al. 2011). Because the 1990-93 broad-scale photo-identification study (Calambokidis et al. 2001) was based retrospectively on photographs that had been collected opportunistically, sampling effort was not representative of the expected abundance in each area. Two feeding areas (Russia and northern Bering Sea) and two breeding regions (Central America and the Philippines) were not sampled at all, and only seven identification photographs were obtained from the Aleutian Island/Bering Sea feeding area. Population estimates from these two large-scale studies would not be directly comparable because non-representative geographic sampling would bias the 1990-93 estimates.

In this study, we sub-sample the 2004-06 SPLASH data to replicate the sampling that was achieved in the 1990-93 study in order to obtain an estimate of abundance that would be directly comparable to a mark-recapture based on those earlier data. Both the 1990-93 estimates and the sub-sampled 2004-06 estimates are expected to be biased by the non-representative geographic sampling, but the direction and magnitude of the biases are expected to be similar for both estimates. For these direct comparisons, we use the Stevick et al. (2001) modification of the Chapman-Petersen estimator, which corrects for the bias caused by missed matches (false negatives in the matching process). We used the estimated rates of missed matches from the studies in 1990-93 (3%, Calambokidis et al. 2001) and 2004-06 (8.6%, Barlow et al. 2011). The net bias-correction for all the factors examined by Barlow et al. (2011) was only 3.5%, and most of these biases would be expected to affect both samples equally. The Barlow et al. (2011) bias correction for non-representative geographic sampling would not be appropriate to apply to the extremely biased geographic coverage obtained in 1990-93 (see bias-corrected estimates below).

The actual 2004-06 SPLASH sample was sub-sampled by randomly selecting individuals from each year, season and region to match the sample sizes obtained in the comparable year, season and region in the 1990-93 study (Table 1). Samples from 1990 and 1991 were combined, as had been done in the earlier study (Calambokidis et al. 2001), since 1990 only consisted of photo-IDs from two areas in Mexico that had not been sampled adequately in 1991. SPLASH included three annual sampling periods (2004, 2005, 2006) and two feeding seasons (2004, 2005), so we similarly only used three wintering periods (1990-91, 1992, 1993) and two feeding seasons (1991, 1992) for the earlier data. Given this scheme, the 2004-06 samples were greater than comparable 1990-93 samples for all regions and seasons, except one. The 1992 summer sample in California and Oregon ( $n = 316$ ) was larger than the 2005 summer sample in the same region ( $n = 303$ ). In order to randomly sub-sample California and Oregon, the sub-sample size in summer 2005 was reduced by 16 to 300, and the sub-sample size in summer 2004 was increased by 16 to 206. Because each randomly selected sub-sample differed, the sub-sampling was repeated 100 times and the average was estimated from the resulting 100 mark-recapture estimates of population size.

#### 1990-93 vs. 2004-06 Estimates based on bias-correction

A simulation program, SimSPLASH, was used to estimate the bias corrections for the mark-recapture estimates for the 2004-06 SPLASH study (Barlow et al. 2011). The same approach is used here to estimate the biases associated with the 1990-93 study. The major differences in the biases between these two studies were that the geographic coverage was more complete and representative in the 2004-06 study and the estimated error rate due to missed matches was lower in the 1990-93 study (because photographs were independently matched twice). The simulation was initiated with 10,000 individuals and an equal sex ratio. We use the same six feeding areas, the same six breeding areas, and the same geographic structure (home feeding areas, feeding-to-breeding mixing matrix, and feeding-to-feeding mixing matrix) as were used by Barlow et al. (2011). We use the observed geographic distribution of sample sizes that was obtained from the

1990-93 study (Table 1). The simulation included births and deaths using the same parameters as Barlow et al. (2011): adult survival rate was 0.96, calf survival rate was 0.85, and the fraction of calves in the population was 11%. Calves were not sampled in the simulation. Missed matches were not simulated because abundance was estimated using the Stevick-Chapman-Petersen estimator that includes a correction for missed matches.

### ***Regional abundance estimates***

For examination of abundance and trends in more specific regional areas, we employed up to three approaches depending on the data available for that region:

- 1) Weighted Petersen abundance estimates for multi-year periods matching the approach used by Baker and Herman (1987) and allowing comparison of three time periods for Hawaii (see below).
- 2) Two multi-year closed mark-recapture models incorporating both time varying capture rates and heterogeneity (Darroch's  $M_{th}$  model and Chao's  $M_{th}$  model) generally compared for the most consistently sampled periods of the early 1990s (1990-93) and the SPLASH years (2004-06).
- 3) Petersen mark-recapture estimates for an area based on the initial capture sample from the feeding area (southeast Alaska) and the recapture from the wintering grounds (Hawaii). This approach was used as a way to avoid heterogeneity due to geographic sampling bias for an area where there was a high degree of confidence that the feeding area animals primarily migrated to one wintering area (see Calambokidis et al. 2001, 2008, Barlow et al. 2012).

We used all three approaches described above for estimating abundance in Hawaii:

- 1) Baker and Herman (1987) made mark-recapture estimates of humpback whale abundance in Hawaii based on photo-identification sampling in 1980-83, primarily off the lee sides of the islands of Hawaii and Maui (1980-81 were from both islands and other years off Maui only based on Herman et al., 2011). Because his best estimate was a weighted mean of between-year Petersen abundance estimates (with weights based on the inverse of the variances), we replicated their methods for two other time periods for which we have data: 1991-93 and 2004-06.
- 2) Estimates from the multi-year closed mark recapture models were compared between two time periods 1991-93 vs. 2004-06. For Hawaiian Island abundance estimates in the latter two time periods, we are not limited to using the Petersen estimator and are not limited to using data from just Hawaii and Maui. Here we use two multi-year closed mark-recapture models (Darroch's  $M_{th}$  model and Chao's  $M_{th}$  model) and expand our sampling to include Kauai. Oahu was sampled in latter time period, but not in the former, so we excluded Oahu samples to maintain comparability.
- 3) We conducted two Petersen mark-recapture estimates for 1990-93 and 2004-06 for Hawaii based on pooled year periods using identifications made in SE Alaska for as the first sample and those on the Hawaiian wintering grounds as the second sample. To avoid bias as a result of the more thorough geographic sampling

conducted in 2004-06 compared to 1991-93, the 2004-06 sample was constrained geographically to match the sample areas available for 1991-93. In SE Alaska, the 1991-93 sample came primarily from inside and near-shore waters of central and northern SE Alaska, so only identifications north of 56.6N and E of 136.75W were used for 2004-06 matching the scope of the earlier sample. For Hawaii the 1991-93 sample was from the Big Island, Maui, and Kauai areas with no samples from Oahu, so Oahu was dropped from the 2004-06 sample.

For Mexico, we were only able to use the multi-year closed population models to compare 1987-90 vs. 2003-2006. Martinez-Aguilar (2011) estimated abundance for all of the Mexico breeding areas using the Darroch and Chao  $M(th)$  methods applied to identification photographs from two time periods: 1987-90 and 2003-06 and including the four main geographic areas: Baja California, coastal mainland, and the Revillagigedo Archipelago. We reproduce his abundance estimates in our tables and estimate population growth rate using our method.

For estimating abundance on the feeding area off California and Oregon we used the multi-year closed population models to compare 1991-94 vs. 2003-06 using all available identifications. This is an area that is sampled annually using primarily small boat surveys that cover the entire range of this feeding area (Calambokidis and Barlow 2004). Despite the availability of annual samples starting in 1991 that sampled this region, we conducted our trend analysis with two 4-year periods that were similar to the time periods used in other regions; 1991-94 and 2003-06.

## **Results**

### ***Pacific Basin abundance estimates and trends***

#### **1990-93 vs. 2004-06 Pacific Basin Abundance Comparison**

Using samples that are biased but comparable, humpback whale abundance estimates for the entire North Pacific basin doubled between the 1990-93 and 2004-06 study periods (Table 2). The abundance of humpback whales in 1990-93 is approximately 11,300, based on the mark-recapture comparison of feeding areas to breeding areas for all sampling seasons combined. The comparable mean estimate for the 2004-06 study is approximately 22,600 based on subsets of the 2004-06 data with the same sample size and same geographic distribution of samples as the 1990-93 data. Both estimates are likely to be biased by the lack of systematic geographic coverage in that earlier study. These estimates imply a population growth of approximately 5.5% per year over this 13-year period.

#### **Bias-corrected Estimates of Humpback Whale Abundance in 1990-93**

A similar, approximate doubling in population estimates from 1990-93 to 2004-07 is seen when a simulation approach to correct biases from non-systematic geographic sampling, births, deaths, exclusion of calves, and missed matches (Table 2). The

simulation showed a positive multiplicative bias of 1.18 in the simple mark-recapture estimate for the 1990-93 period. Correcting for this bias reduces the estimate of abundance to approximately 9,500 (Table 2). The bias-corrected estimate for the 2004-07 period is based on the actual sampling in those years, which had much broader and more systematic geographic coverage. The overall positive bias for 2004-07 was estimated to be a multiplicative factor of 1.035, and the bias-corrected estimate was approximately 21,063 (Table 2). These estimates imply a population growth of approximately 6.3% per year.

### ***Regional abundance estimates and trends***

#### 1980-83 vs. 1991-93 vs. 2004-06 Abundance Comparison for Hawaii and Maui

Petersen estimates of population size for the Hawaiian Islands of Hawaii and Maui increased between our three time periods (Table 3). The rates of increase were 1.075 (CV = 0.15) per year from an early 1980-83 study (Baker and Herman 1987) to our 1991-93 study and 1.057 (CV = 0.13) per year from our 1991-93 study to our 2004-06 study. These two growth rates, separated in time by a decade, are not statistically significantly different (z-test,  $p = 0.17$ ). Analyses of trends in Hawaiian humpback whale populations in 1991 and later years are not limited to the Petersen mark-recapture method to maintain comparability with earlier methods, and the growth rates estimated using the Darroch and Chao *Mth* methods for 1991-93 vs 2004-06 bracket the rate estimated using the Petersen method (Table 3). Population estimates are, however, appreciably larger using the Chao *Mth* method, likely because this method corrects for a negative bias caused by heterogeneity in capture probability.

#### 1991-93 vs. 2004-06 Abundance Comparison for overall Hawaiian Islands

Analyses of trends in Hawaiian humpback whale populations since 1991 are not limited to studies off Hawaii and Maui to maintain comparability with earlier methods and could include data from Kauai. Using this larger regional dataset, the Darroch and Chao *Mth* methods show very similar estimates of the 1991-1993 to 2004-06 population growth rate (1.051 & 1.052, respectively) (Table 3). Abundance estimates are again larger with the addition of data from Kauai, likely because more of the Hawaiian population was sampled and because the larger sample helps reduce heterogeneity in capture probability.

#### 1991-93 vs. 2004-06 Abundance Comparison for the Hawaiian Islands and Southeast Alaska

The Petersen method is used to estimate population size for two time periods by including all the pooled samples from one feeding area (Southeast Alaska) to pooled samples from its breeding area (the Hawaiian Islands). Population estimates using this method are higher than estimates for Hawaii based on samples only from Hawaii, Maui and Kauai (Table 3). The population growth rate estimate from 1991-93 to 2004-06 is 1.068 (CV = 0.13).



### 1987-90 vs. 2003-06 Abundance Comparison for Mexico

Martinez-Aguilar (2011) estimated population sizes for Mexico for two time periods (1987-90 and 2003-2006) using the Darroch and Chao *Mth* methods and estimated population growth rates between these two time periods. Their abundance estimates are repeated in Table (3), but our slightly different methods resulted in slightly different population growth rates (Table 3) than estimated by Martinez-Aguilar (2011). Population growth rates for the Darroch and Chao *Mth* methods are 1.073 (CV = 0.07) and 1.093 (CV= 0.10), respectively. Abundance estimates using Chao's *Mth* method are larger than estimates based on Darroch's method.

### 1991-94 vs. 2003-06 Abundance comparison for California and Oregon

Abundance was estimated for 4-year periods of mark-recapture effort for the California-Oregon feeding population using both the Darroch and Chao *Mth* methods (Table 3). Once again, estimates based on Chao's *Mth* method (1.082) are larger than estimates based on Darroch's method (1.077), likely because the former corrects for a negative bias caused by heterogeneity in capture probabilities but the population growth rates from 1991-94 to 2003-06 are very similar for the two methods (Table 3).

### ***Geographic and Temporal Differences in Population Growth Rates***

We tested to see whether the observed differences in our measures of population growth rate are statistically significant. The temporal comparison with the greatest time span is the comparison of weighted Petersen estimates for the islands of Hawaii and Maui from an early time period (1980-83 to 1991-93) to a later time period (1991-93 to 2004-06). This comparison is complicated because they share the same mid-points, which results in a lack of independence (a negative correlation) in growth rate estimates. This negative correlation could lead to a spurious rejection of the null hypothesis of no difference. However, the early estimate is not significantly different from the later estimate (Table 4,  $p = 0.17$ ), and negatively correlated estimates would make this even less significant.

We tested geographic difference in population growth rates within the time period of 1991 to 2006 (actually starting in 1987 for Mexico). The growth rates in Mexico were not significantly different from the growth rates in California/Oregon using either the Darroch or Chao *Mth* estimators (Table 4). This result is not surprising given that most of the humpback whales in California/Oregon migrate to Mexico to breed and given birth. However, we found that population growth rates did differ significantly between the Hawaiian Island and both Mexico and California/Oregon (again, using either the Darroch or Chao *Mth* estimators) (Table 4).

## Discussion

While we use a variety of approaches to address the data available from different spatial and temporal scales, these different approaches generally yielded very consistent rates of growth. Abundance estimates we calculated for Hawaii for 2004-2006 varied widely from just over 6,000 using Petersen mark-recapture to inter-year samples to over 11,000 from the feeding to wintering areas samples, yet both methods resulted in very similar growth estimates when compared to estimates calculated the same way from the early 1990s. There are many sources of bias in mark-recapture estimates (Hammond 1986), but these may still provide accurate estimates of trends. We demonstrate a number of approaches that were available to allow such comparisons over extended time periods in the North Pacific through selection of models, down-sampling of data, and bias correction.

Our results on recovery rate of humpback whales in the North Pacific are consistent with previous estimates from specific subareas. Long term trends of humpback whales off the US West Coast based on mark-recapture and, to a more limited degree, from line-transect have show similar increases (Calambokidis and Barlow 2004). A regional study of trends in humpback whale abundance was conducted for Mexico based on estimates of abundance for two time periods separated by 16 years (1987-90 and 2003-06) estimated population growth rates of 7.0% per year using the Darroch estimator and 8.9% per year using the Chao  $M_{th}$  model by (Martínez-Aguilar 2011). They also present estimates for four sub-areas within Mexico, which range from 5.8% per year to 11.2% per year for the Darroch estimator (Martínez-Aguilar 2011).

While all areas tested showed increases in abundance of 5-8%, the significant differences in rate of increase may reflect some differences in status among regions. That both California-Oregon and Mexico had similarly high rates of increase would be expected given this represents the primary feeding and wintering area for the same population (Calambokidis et al. 2000, 2001, Urban et al. 2000). Commercial whaling for humpback whales occurred in some of these areas, including two whaling stations off central California through 1966 (Rice 1963, 1974). Humpback whales that feed in Southeastern Alaska and winter in Hawaii were not recently hunted as extensively and also have a longer migration route possibly reducing feeding time or causing higher calf mortality.

Our estimated rates of population growth demonstrate that humpback whales were capable of relatively rapid recovery from depletion once they were protected. Rates of increase we report here are under the maximum plausible rate (11.8%) and close to the estimated rates of 7.3% and 8.6% (depending on juvenile survival rate) from available life history data (Zerbini et al. 2010). Humpback whales, despite being hunted through the mid 20<sup>th</sup> century, appear to be showing encouraging signs of recovery in many parts of their range.

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Table 1. Sample sizes of distinct individuals sampled in each of six feeding areas (summer sampling) and six breeding areas (winter sampling) during two periods: 1990-93 and 2004-06. For the 1990-93 time period, winters of 1990 and 1991 were combined as Winter 1 for the Mexico wintering area (other areas sampling was only in 1991).

| Area                         | 1990-93 Study Period |            |            | 2004-06 Study Period |             |             |
|------------------------------|----------------------|------------|------------|----------------------|-------------|-------------|
|                              | Winter 1             | Winter 2   | Winter 3   | Winter 1             | Winter 2    | Winter 3    |
| Central America              | 0                    | 0          | 0          | 18                   | 45          | 45          |
| Mainland Mexico              | 135                  | 4          | 0          | 210                  | 252         | 317         |
| Baja California, Mexico      | 90                   | 100        | 56         | 175                  | 149         | 82          |
| Revilagigedo Islands, Mexico | 158                  | 10         | 0          | 308                  | 694         | 183         |
| Hawaiian Islands             | 393                  | 325        | 494        | 694                  | 838         | 1016        |
| Western Pacific              | 140                  | 159        | 149        | 183                  | 209         | 287         |
| <b>TOTAL</b>                 | <b>916</b>           | <b>598</b> | <b>699</b> | <b>1588</b>          | <b>2187</b> | <b>1930</b> |

  

| Area                                | 1990-93 Study Period |            | 2004-06 Study Period |             |
|-------------------------------------|----------------------|------------|----------------------|-------------|
|                                     | Summer 1             | Summer 2   | Summer 1             | Summer 2    |
| California & Oregon                 | 190                  | 316        | 248                  | 303         |
| Northern Washington & Southern B.C. | 11                   | 0          | 72                   | 136         |
| Northern B.C. and Southeast Alaska  | 150                  | 181        | 1167                 | 690         |
| Gulf of Alaska                      | 46                   | 111        | 923                  | 528         |
| Aleutian Islands and Bering Sea     | 0                    | 7          | 289                  | 326         |
| Russia                              | 0                    | 0          | 25                   | 38          |
| <b>TOTAL</b>                        | <b>397</b>           | <b>615</b> | <b>2724</b>          | <b>2021</b> |

Table 2. Estimates of humpback whale abundance in the entire North Pacific and implied annual rates of population growth using photo-identification data collected in 1990-93 and 2004-06. The geographically biased estimates for both periods were based on mark-recapture methods using the actual geographic distribution of 1990-93 samples and are therefore biased by the non-systematic sampling of that opportunistic study. The bias-corrected estimates are corrected for biases from non-systematic sampling and other factors (see text) using a simulation approach. The bias-corrected estimates for 2004-06 are from Barlow et al. (2011).

| Study Period        | Geographically Biased Estimates |       | Bias-Corrected Estimates |       |
|---------------------|---------------------------------|-------|--------------------------|-------|
|                     | N                               | CV(N) | N                        | CV(N) |
| 1990-1993           | 11,297                          | 0.068 | 9,512                    | 0.081 |
| 2004-2007           | 22,612                          | 0.098 | 21,063                   | 0.027 |
| Implied Growth Rate | 1.055                           |       | 1.063                    |       |

Table 3. Regional estimates of abundance in two time periods and population growth rates based on these changes in estimated abundance. Methods include a weighted mean of between-year Petersen estimates (weighted by the inverse of the variance), Darroch's multi-year mark-recapture method with time-varying capture probability, and Chao's model with both time-varying capture probability and individual heterogeneity in capture probability. Coefficients of variation (CV) are also given for abundance and growth rate estimates.

| Locations                               | Method   | Earlier Years |      |       | Later Years |        |       | Growth Rate |       |      |
|---|----------|---------------|------|-------|-------------|--------|-------|-------------|-------|------|
|   |          | Period        | N    | CV(N) | Period      | N      | CV(N) | Years       | Rate  | CV   |
| Hawaii+Maui                             | Petersen | 1980-1983     | 1407 | 0.10  | 1991-1993   | 3015   | 0.11  | 10.5        | 1.075 | 0.15 |
| Hawaii+Maui                             | Petersen | 1991-1993     | 3015 | 0.11  | 2004-2006   | 6192   | 0.06  | 13          | 1.057 | 0.13 |
| Hawaii+Maui                             | Darroch  | 1991-1993     | 3330 | 0.12  | 2004-2006   | 7015   | 0.06  | 13          | 1.059 | 0.13 |
|   | Chao Mth | 1991-1993     | 4371 | 0.19  | 2004-2006   | 7825   | 0.09  | 13          | 1.046 | 0.21 |
| Hawaii+Maui+Kauai                       | Darroch  | 1991-1993     | 4000 | 0.08  | 2004-2006   | 7658   | 0.06  | 13          | 1.051 | 0.10 |
|   | Chao Mth | 1991-1993     | 4629 | 0.13  | 2004-2006   | 8965   | 0.09  | 13          | 1.052 | 0.16 |
| Southeast Alaska vs<br>Hawaiian Islands | Petersen | 1991-1993     | 4756 | 0.11  | 2004-2006   | 11,124 | 0.07  | 13          | 1.068 | 0.13 |
| Mexico (all) <sup>1</sup>               | Darroch  | 1987-1990     | 1628 | 0.06  | 2003-2006   | 5007   | 0.03  | 16          | 1.073 | 0.07 |
|   | Chao Mth | 1987-1990     | 1964 | 0.09  | 2003-2006   | 8168   | 0.05  | 16          | 1.093 | 0.10 |
| California+Oregon                       | Darroch  | 1991-1994     | 639  | 0.01  | 2003-2006   | 1554   | 0.04  | 12          | 1.077 | 0.04 |
|   | Chao Mth | 1991-1994     | 797  | 0.04  | 2003-2006   | 2045   | 0.07  | 12          | 1.082 | 0.08 |

<sup>1</sup>from Martinez-Aguilar (2011)

Table 4. Statistical comparisons of population growth rates between different time periods (Hawaii & Maui only) and between different geographic locations. Probabilities (Prob.) are based on a z-test of the differences in the growth rates. Standard errors of the differences are estimated as the square root of the average variance.

| Comparison   | Method   | Growth Rate Difference | SE Difference | Prob.  |
|--|----------|------------------------|---------------|--------|
| Hawaii+Maui Early (1980-1991) vs. Late (1991-2006)             | Petersen | 0.018                  | 0.013         | 0.1728 |
| Hawaiian Islands (1991-2006) vs. Mexico (1987-2006)            | Darroch  | 0.022                  | 0.007         | 0.0012 |
| Hawaiian Islands (1991-2006) vs. Mexico (1987-2006)            | Chao Mth | 0.041                  | 0.010         | 0.0001 |
| Hawaiian Islands (1991-2006) vs. California+Oregon (1991-2006) | Darroch  | 0.026                  | 0.006         | 0.0000 |
| Hawaiian Islands (1991-2006) vs. California+Oregon (1991-2006) | Chao Mth | 0.030                  | 0.010         | 0.0046 |
| Mexico (1987-2006) vs. California+Oregon (1991-2006)           | Darroch  | 0.004                  | 0.004         | 0.2986 |
| Mexico (1987-2006) vs. California+Oregon (1991-2006)           | Chao Mth | 0.011                  | 0.007         | 0.1028 |