Updated analysis of abundance and population structure of seasonal gray whales in the Pacific Northwest, 1998-2010

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Abstract

The existence of a small number of Eastern North Pacific gray whales that spend the spring, summer and fall feeding in coastal waters of the Pacific Northwest has been known for some time and localized short-term studies have examined aspects of the natural history of these animals. We report the results of a 13-year (1998-2010) collaborative study examining the abundance and the population structure of these animals conducted over a number of regions from Northern California to British Columbia using photographic identification. Some 14686 identifications representing 1031 unique gray whales were obtained. Gray whales seen after 1 June (after the northward migration) were more likely to be seen repeatedly and in multiple regions and years and therefore 1 June was used as the seasonal start date for the data included in the abundance estimates. Gray whales using the Pacific Northwest in summer and fall include two groups: 1) whales that return frequently and account for the majority of the sightings and 2) apparent stragglers from the migration seen in only one year, generally for shorter periods and in more limited areas. Abundance estimates for whales present in summer and fall using four different methods over different geographic scales revealed the abundance of animals to be at most a few hundred individuals. All of the estimators except those based on Lincoln-Petersen, which was likely biased by the violation of population closure, showed an increase in abundance in the late 1990s and early 2000s. This was during the period the eastern North Pacific gray whale population was experiencing a high mortality event and this created an apparent influx of animals into the area. While estimates during that period may have been altered by this event, the abundance since then has been very stable. Recent matches of photo-identified gray whales from the Pacific Northwest to other regions have provided new insights into the movement of some of these individuals including matches to Barrow, Alaska. The proportion of calves documented was generally low but varied dramatically among years and may have been biased downward by weaning of calves prior to entry in the study area or prior to much of the collaborative seasonal effort. Observations of calves returning to the Pacific Northwest in subsequent years documents one possible mechanism for recruitment. The results we present will be valuable in assessing the impacts of potential resumption of a gray whale hunt by the Makah Tribe.

1 Introduction

Although most gray whales in the Eastern North Pacific stock migrate each spring from calving lagoons in Baja Mexico to feeding grounds in the arctic, the existence of gray whales that spend the spring, summer and fall feeding in coastal waters of the Pacific Northwest has been known for some time. Starting in the 1970s, photographic identification demonstrated that some whales returned regularly to feed off the west coast of Vancouver Island (Darling 1984). The proximity of these whales to the traditional whale hunting grounds of the Makah Tribe coupled with the Tribe's interest in resuming gray whale hunts in the 1990s, made determination of the status and number of these whales of greater importance to management.

Beginning in 1996, a collaborative effort among a number of research groups was initiated to conduct a range-wide photographic identification study of gray whales in the Pacific Northwest (Calambokidis et al. 2000, 2002b). An initial publication of findings from 1998 demonstrated there was considerable movement of individual whales among sub-areas from northern California to southeastern Alaska (which we broadly refer to as the Pacific Northwest) and also provided initial estimates of the abundance of whales within that geographical area (Calambokidis et al. 2002a). The ability to look at movements and employ more sophisticated capture-recapture models, however, was restricted by the lack of multiple years of data with broad geographic coverage. A subsequent report by Calambokidis et al. (2004) characterized the group of whales feeding in these survey areas during the summer-fall period as a "Pacific Coast Feeding Aggregation" (PCFA). They proposed that a smaller area within the PCFA survey areas – from Oregon to Southern Vancouver Island (OR-SVI) – was the most appropriate area for abundance estimation for managing a Makah gray whale hunt (Calambokidis et al. 2004). Subsequently the IWC has adopted the term PCFG for Pacific Coast Feeding group so we will use PCFG in place of PCFA.

The collaborative effort to collect photographic identifications of gray whales from California to Alaska has continued since 1998 and these data now cover 13 years (1998-2010) and span fifteen survey regions along the coast from Southern California to Kodiak, Alaska (Figure 1). We provide estimates of abundance for the summer-fall seasons (1 June to 30 November) for survey regions comprising different combinations of subareas within this range.

2 Methods

Gray whales were photographed during small boat surveys conducted from California to Alaska by Cascadia Research, National Marine Mammal Laboratory and collaborating researchers between 1998 and 2010. Gray whale identifications were divided into the following regions (Figure 1): 1) SCA: Southern California, 2) CCA: Central California, 3) NCA: Northern California, 4) SOR: Southern Oregon, 5) OR: central Oregon, 6) GH+: Gray's Harbor and the surrounding coastal waters, 7) NWA: Northern Washington coast, 8) SJF: Strait of Juan de Fuca, 9) NPS: Northern Puget Sound, 10) PS: which includes southern Puget Sound, Hood Canal (HC), Boundary Bay (BB) and San Juan Islands (SJ), 11) SVI: Southern Vancouver Island, 12) WVI: West Vancouver Island, 13) NBC: Northern Vancouver Island and coastal areas of British Columbia, 14) SEAK: Southeast Alaska, and 15) KAK: Kodiak, Alaska. The NWA and SJF survey areas together make up the Makah Usual and Accustomed grounds (MUA). With some exceptions, research groups work primarily in one or two regions. Details of identifications obtained by the different research groups are are summarized in Tables 1-2.

Each year from 1998 to 2010, between 548 and 1500 identifications were obtained of gray whales totaling 14686 photos of 1031 unique gray whales for the entire period (Table 1). These were conducted from March through November with most effort from June to September. Surveys were most numerous in British Columbia, along the south and west coasts of Vancouver Island and just north of Vancouver Island (Table 2).

2.1 Photographic Identification Procedures

Procedures during surveys by different research groups varied somewhat but were similar to one another in identification procedures. When a gray whale was sighted, the time, position, number of animals, and behaviors were recorded. Whales were generally approached to within 40-100 m and followed through several dive sequences until suitable identification photographs and associated field notes could be obtained.

For photographic identification of gray whales, both left and right sides of the dorsal region around the dorsal hump were photographed when possible. Most identification photographs were obtained with 35mm cameras most often with large 300mm lenses. Researchers also photographed the ventral surface of the flukes for further identification when possible. The latter method was not as reliable since gray whales did not always raise their flukes out of the water. Markings used to distinguish whales included pigmentation of the skin, mottling, and scarring, which varied among individuals. These markings have provided a reliable means of identifying gray whales (Darling 1984). We also identified gray whales using the relative spacing between the knuckles along the ridge of the back behind the dorsal hump. The size and spacing of these bumps varies among whales and has not changed throughout the years these whales have been tracked, except with injury. Figure 2 shows typical photographs and features used in making gray whale identifications.

Comparisons of whale photographs were made in a series of steps. All photographs of gray whales were examined and the best photograph of the right and left sides of each whale (for each sighting) were selected and printed (7 x 2.5 inch). To determine the number of whales seen during the year, the prints were then compared to one another to identify whales seen multiple days. Finally a comparison was made to the CRC catalog of whales seen in past years. Whale photographs that were deemed of suitable quality but did not match our existing catalog (compared by two independent persons) were considered “unique” identifications and assigned a new identification number and added to the catalog.

2.2 Data Analysis

The abundance of gray whales was estimated with open and closed population models for four nested spatial scales consisting of contiguous survey regions (Figure 1; Table3) 1)

NCA-NBC: the survey regions from Northern California (NCA) through Northern Vancouver Island/British Columbia (NBC), 2) OR-NBC: survey regions from southern Oregon through NBC, 3) OR-SVI: survey regions from southern Oregon through Southern Vancouver Island (SVI), and 4) MUA-SVI: the survey regions from MUA which includes Northern Washington coast (NWA) and Strait of Juan de Fuca (SJF) and SVI . The proposed hunt by the Makah Tribe would be in NWA.

Gray whales photographed and identified anytime during the period between 1 June and 30 November (hereafter referred to as the "sampling period") within the defined region were considered to be "captured" or "recaptured". For each unique gray whale photographed, a capture history was constructed using 13 years of data from 1998-2010. For example, the capture history 0100100100000 could represent a gray whale photographed in 1999, 2002 and 2005 in the PCFG. The same gray whale may have had a capture history 0100100000000 for a smaller spatial scale such as OR-SVI or may not have been seen at all (0000000000000) and would not be used for the smaller spatial scale.

Multiple "detections" of a single whale within the sampling period were not treated differently than a single detection. A "1" in the capture history meant that it was detected on at least one day during the sampling period. However, multiple detections in the same year were used to construct an observed minimum tenure (MT) for each whale. MT was defined as the number of days between the earliest and latest date the whale was photographed with a minimum of one day for any whale seen.

2.2.1 Abundance using closed population models

Closed models for capture-recapture assume that the population is both geographically and demographically closed with no losses or gains. Closure would not be a reasonable assumption for the entire 13 year period but previous analysis has assumed closure for two consecutive years (e.g., Calambokidis et al. 2004). For those abundance estimates, a Lincoln-Petersen (LP) estimator (Seber 1982) was used in which each of the consecutive years (June-November) was a sampling occasion. Those estimates were based on the assumption that all whales that were available to be photographed in year y were also available to be photographed in year $y+1$ and vice versa. If new whales joined in $y+1$ or whales seen in year y did not return in $y+1$, the closure assumption would be violated. It is well known that the LP estimator is unbiased if there are only losses or only gains (Seber 1982) but not both (Kendall 1999). The only exception is a population with completely random movement into and out of the population but that is not plausible with gray whales because with approximately 20,000 whales there would be few if any matches between years if movement in and out of the PCFG was completely random.

The losses and gains each year are primarily from "transient" whales that are seen in one of the years and are never seen again in any other year. To remove this source of bias, we developed the following ad-hoc approach to remove the transients. For each pair of years in the computation of abundance with the LP estimator, we only used whales that were seen in one or more years other than the years being considered. For example, in computing an abundance estimate with 1999 and 2000 we only used whales that were also seen in 1998 or at least one year after 2000. This removed any transients that would have only been seen in either 1999 or 2000. It also removes those seen only in both years; while these are technically not single-year transients their removal was unavoidable using this approach. This was done for each year pairing and we have called this estimation method "Limited LP". We would expect these estimates to be biased low at the end of the time sequence because new whales at the end of the time sequence have had little or no opportunity to be sighted again and thus would not be included in the analysis. The bias will be apparent by comparing the estimates for 2007 and 2008 from Calambokidis et al. (2010) and the same estimates in this paper with the data extended through 2010.

2.2.2 Abundance using open population models

In addition to the closed models, we fitted open population models to the 13 year time series of capture history data for each spatial scale to estimate abundance and survival. Open models allow gains due to births/immigration and losses due to deaths/emigration. Using the RMark interface (Laake and Rexstad 2008) to program MARK (White and Burnham 1999), we fitted a range of models to the data using the POPAN model structure. The POPAN model structure (Schwarz and Arnason 1996) provides a robust parametrization of the Jolly-Seber (JS) model structure in terms of a super population size (N), probability of entry parameters (immigration), capture probability (p), and survival/permanent emigration (φ).

It is essential to consider the population structure and its dynamics to build adequate models. In particular, we know from previous analysis of a subset of these data (Calambokidis et al. 2004) that some whales were seen in only one year between 1 June and 30 November and were never seen again. Transient behavior is a well-known problem in capture-recapture models and it is often addressed using a robust design which involves coordinated multiple capture occasions within each year and typically assumes closure within the sampling period (June-November). Region-wide coordinated surveys may be possible but would be difficult with variation in weather conditions. Also, the closure assumption within the year would be suspect due to variable timing of whales arrivals and departures into the PCFG, so it would require nested open models. We know from prior analysis that whales newly seen in year (y) were less likely to return (i.e., seen at some year >y) than previously seen whales but also newly seen whales that stayed longer during their first year (i.e., longer MT) in the PCFG were more likely to return. Likewise, previously seen whales were more likely to be seen in the following year (y+1), if they had a longer MT in year y. Calambokidis et al. (2004) postulated that these observations were consistent with whale behavior that was determined by foraging success.

Transient behavior in which an animal is seen only once can be modeled by including a different "first year" survival (Pradel et al. 1997) for the newly seen animals. Survival in the time interval after being first seen is dominated by permanent emigration rather than true mortality. Survival in subsequent time intervals represents true survival under the assumption that animals do not permanently emigrate except in their first year. Pradel et al. (1997)were working with release-recapture data (Cormack-Jolly-Seber) where modeling this transient effect on survival is straightforward. For a Jolly-Seber type analysis where the first capture event is also modeled, the inclusion of a transient effect is less easily accommodated. We considered two approaches to accommodate the "transient" effect in these open models to remove the transients from the estimate of abundance. We will refer to these as JS1 and JS2.

Approach JS1 The first approach divided the whales into cohorts based on the year in which they were first seen ("newly seen"). In the models their first year survival could differ from subsequent annual survival as in Pradel et al. (1997). The first year survival was also allowed to vary as a function of MT. "Newly seen" is not a particularly useful concept for the first year of the study (1998), because all whales were being seen for the first time. Thus, we also considered a model that allowed for a different first year survival and effect of MT for 1998 than for years after 1998 and a model in which each cohort had a different first year survival to allow for different transient proportion in each year if this was not adequately modeled by MT. We also considered models that allowed a different first-year survival for whales identified as calves under the presumption that their true survival might be lower but that their probability of returning to the PCFG might be higher. Discussion at the 2012 intersessional AWMP meeting led to consideration of an additional covariate which split whales into 2 groups for estimation of post-first-year survival. Whales seen initially as calves and any whale newly seen in 1998 or was in the CRC catalog because it had been seen prior to 1998 were put in one group and the remaining whales newly seen in 1999 or later were put in another group. The expectation was that the first group would have higher post-first-year survival because many of the newly seen whales that entered after the stranding event in 1999/2000 might eventually emigrate. When this covariate was included it made such a large improvement that any model without it would have no support. Therefore, it was included in all 10 models for survival (Table 5).

In Calambokidis et al. (2010) we estimated a cohort-specific super-population size for each cohort using the median MT covariate value for unseen whales but during the April 2011 AWMP meeting it became apparent that this may lead to bias in estimating abundance. Therefore, we used the method outlined in the 2011 AWMP report which is similar to the method used by Calambokidis et al. (2004) in that we assume that all whales in the PCFG for the first year are seen so the super-population size for each cohort is the number seen and thus there are no unknown covariate values. We fixed capture probability (p) and probability of entry (pent) to 1 for each cohort in their entry year. We are not interested in the number of transient whales so we used an estimator of abundance for non-transient whales (2011 AWMP report) which is a modification of the Jolly-Seber estimator which for any year can be expressed as:

$$\hat{N} = n/\hat{p} = (u + m)/\hat{p}$$

where $n = u + m$, n is the number seen in a year being composed of new animals (u=unmarked) and previously seen animals (m=marked), and $\hat{p}$ is the capture probability estimate. For the PCFG we are assuming that any new whale is sighted ($p = 1$) and we are only interested in estimating the abundance of whales that will remain part of the PCFG which is portion of the new whales that do not permanently emigrate from the PCFG. We can modify the estimator for year j as follows:

$$\hat{N}_j = u_j\hat{\phi}_j + m_j/\hat{p}_j$$

where ϕ_j is the first year survival rate of "new" whales. When$\phi$and p contain whale specific covariates like minimum tenure (MT) the estimator becomes:

$$\hat{N}_j = \sum_{i=1}^{u_j} \hat{\phi}_{ij} + \sum_{i=1}^{m_j} 1/\hat{p}_{ij}.$$

To obtain an abundance estimate for 2010, we assumed that the parameter for first year survival intercept in that year was the same as in 2009. A variance-covariance matrix for the abundance estimates was constructed using the variance estimator in Borchers et al. (1998) for a Horvitz-Thompson type estimator with an adaptation for the first component of the abundance estimator for prediction of number of new whales that do not permanently emigrate. For the estimated capture probabilities (p) not fixed to 1, we fitted 3 models that varied by time (year) and/or varied by MT in the previous year (Table 5).

We used Test 2 and Test 3 results from the Cormack-Jolly-Seber structure (Lebreton et al. 1992) as a general goodness of fit for the global model and as a measure of possible over-dispersion creating the lack of fit. We fitted each combination of models for S (survival) and p (capture probability) and used AICc (Burnham and Anderson 2002) to select the most parsimonious model of the 30 fitted models. Model averaging was used for all models to compute estimates and unconditional standard errors and confidence intervals.

Approach JS2 The first approach will certainly underestimate the abundance in the initial years and particularly in the first year where the abundance estimate is less than or equal to the number seen in the first year because m=0 in the first year. As previously unseen non-transient whales are "discovered" the abundance estimator should approach the true abundance. However, that may distort any assessment of population trend and growth, so we devised the following alternative approach. If we assume that transient whales are those that are seen once and never seen again, then we can remove those from the data and use the remaining capture histories from whales seen in at least 2 years to estimate the abundance trend of non-transients with a standard POPAN model that estimates both p and pent and abundance through time. For this analysis we ignored covariates because they are not known for whales that enter but are not seen in the year they enter. Covariates for ϕ are less important because we are effectively assuming that transients have $\phi = 0$ and the non-transients have a common survival rate. We fitted a single model with time varying p and pent and a constant ϕ and used the derived estimates of abundance for the POPAN model of the data from NCA-NBC only. This is an admittedly ad-hoc approach and we expect that ϕ will be biased high because some of those seen only once will be non-transients that died before they were resighted. The abundance estimates at the end of the time series will be biased low because those newly seen in the 2010 and those seen in 2009 not resighted in 2010 are removed. Also, for the JS models it is not possible to estimate both a time-varying pent and p for for 1998 without constraints. We chose to set $p = 1$ for that year which will likely underestimate abundance.

A better approach would be a Jolly-Seber model that allowed for a mixture of entrants of transients with $\phi = 0$ and non-transients similar to the closed version of Conn et al. (2011) but we are unaware of any existing software that will fit that model. Current JS mixture models in MARK allow a mixture for p but it does not carry the mixture through to the remainder of the parameters like ϕ.

2.3 Simulation

We performed a small-scale simulation study to investigate the properties of the various estimators of abundance that we have used. We considered 2 scenarios with constant ϕ=0.95 for non-transient whales, ϕ=0.0 for transient whales which are assumed to permanently emigrate and never return and for all whales a time constant p with values of 0.7 and 0.8 which cover the range of estimated probabilities for the gray whale data. In the first scenario, we simulated a population at equilibrium in which the number of new non-transients and transients matched the expected number of mortalities of non-transient whales ($N(1-\phi)$). In the second scenario, we used the observed number of transients (seen only in one year) and recruits to the non-transients from the PCFG gray whale data from NCA-NBC and a initial population size of 120 non-transients from previous years still alive in 1998. We constructed a single population entry structure for each scenario but then simulated 100 replicates of the survival and capture process. Even though p was constant in the simulated data, we fitted each open model with time varying p to make them similar to the real data analysis and to make the more similar to the closed estimators which estimate a separate p for each year. The biggest impact will be in the first abundance estimate in 1998 because it is necessary to assume p=1 which will result in an underestimate. For that reason we drop the first estimate which also makes the comparison to closed estimators consistent because we only get a single estimate for 1998-1999 which is assigned to 1999. We summarized the abundance time series for the 100 replicates for each estimator to examine bias in abundance and trend.

3 Results

The database from all thirteen years (1998-2010) contains 14686 records; however 2291 are replicate identifications of whales on the same day. The database contains photographs of 1031 unique whales seen from Southern California to Kodiak, Alaska with an average of 12 sightings/whale (range: 1- 240) where a “sighting” is one or more photographs on a day. Only 50.3% of the whales were seen on more than one day but many of these identifications are from early in the season during the migration as well as from peripheral areas such as Kodiak, Alaska (Table 6).

3.1 Seasonality

Whales have been photographed in every month of the year (Table 6) but with very few during December-February when most of the whales are in or migrating to Mexico and survey effort is reduced. Previous analysis of these data have always used 1 June - 30 November as the sampling period to describe the whales in the PCFG because whales seen prior to 1 June are more likely to be whales that are migrating through the region. The separation between May and June is clearly supported by the data. For example, of the 1031 unique whales, 286 whales were only seen before 1 June and 84.3% of those were only sighted once. In comparison, of the 745 whales sighted between June and November, 39.7% were only sighted once. If sightings in Alaska are excluded, then only 32.7% of the 630 were seen only once.

The break between May and June is apparent in various measures such as proportion of whales sighted more than once, sighted in more than one region, and sighted in more than one year (Figure 3). However, the break is more apparent if we separate out SJF, NPS and SVI from the other survey regions (Figure 4). The difference across months is not as strong for inland waters of Washington and British Columbia (NPS, SJF) because these are whales that have diverted from the migration and are either more likely to remain after 1 June or demonstrate high year-to-year fidelity during spring such as with NPS. Also, even though Southern Vancouver Island (SVI) is in the main migration corridor and not an inland water, the pattern across months is also weaker because the sampling has been focused on the spring herring spawn in Barkley Sound (effectively an inland waterway) and has purposefully undersampled passing migrant whales (Brian Gisborne, pers. comm.). The break between May and June is much more apparent for NWA and the other areas in the migration corridor which is consistent with the northbound migration of gray whales proceeding past Washington through May. Resighting rates of whales seen after 1 June remained high through November.

The proposed Makah gray whale hunt in the Makah Usual and Accustomed area (NWA and SJF) may occur in NWA after 30 November and prior to 1 June. A hunt conducted in spring (March-May) potentially could take whales from the PCFG although those chances are less in NWA than in SJF. There have been 118 whale sightings in NWA prior to 1 June of which 30% (35) were of whales that were seen in the PCFG after 1 June at some time. We tested whether this result was biased by the quality of photographs or the selection process by also looking at the resighting rate of only a subset of the animals with highest quality photographic identifications from that period. We found 17 of 48 (35%) were resighted after 1 June, fairly close to the 30% found with all whales. In comparison, 46 whale sightings were in SJF prior to 1 June of which 70% (32) were of whales that were seen in the PCFG after 1 June at sometime, emphasizing the importance of restricting a hunt to coastal waters of the MUA (i.e., the NWA) to limit the take of whales from the PCFG.

3.2 Regional Sighting Patterns

There is considerable variation in the annual regional distribution of numbers of whales photographed during the sampling period (Table 7) which is in part due to variation in effort. Although not a true measure of effort, the number of days whales were seen (Table 8) does reflect the amount of effort as well as abundance of whales. In particular, in comparison to other regions, the large number of sightings in SVI partly reflects large numbers of sampling days by Brian Gisborne who has routinely sampled SVI 2-3 days a week. On the other hand, the decline in sightings in SVI during 2007 was not due to reduced effort but to the distribution of whales with many of the whales having moved to waters off Oregon and Washington (Calambokidis et al. 2009b).

Whales were sighted across various survey regions and the interchange of whales (Table 9) between survey regions during 1 June - 30 November depends on proximity of the regions (Calambokidis et al. 2004). Of the whales sighted in regions from SOR to NBC, depending on the region, from 57.8% to 72.7% of the whales were seen at some point within MUA-SVI (Figure 6). However, whales seen in California or Alaska were less likely to be seen in MUA-SVI.

If we look at latitudes of sightings of individual whales across the 13 years using whales that have been sighted on at least 6 different days (Figure 7), we see that sightings of some whales are highly clustered; whereas, sightings of other whales are highly dispersed across several regions. We defined each whales primary range by the 75% inner quantile which is the middle of the range that includes 75% of the locations. The length of the 75% inner quantile in nautical miles exceeded 60 nautical miles (or 1 degree of latitude) for 41.2% of the whales (Figure 8) and it was more than 180 nautical miles for more than 17.9% of the whales. Thus, it makes little sense to compute an estimate of abundance for any region that spans less than a degree of latitude.

There was a large variation in the frequency of sightings for whales (Table 10). Most whales that were seen during June-November 1998-2010 in the PCFG (NCA to NBC) were only seen in one year and the whales that were seen in more years were sighted more often each year and therefore represented a large proportion of the sightings (Figure 9). Likewise, examination of MT in the first sighting year demonstrates that whales who stay longer in their first year were more likely to be seen in a following year (Figure 10). Whales “first” seen in 1998 includes some whales that were truly new to the PCFG in that year but many were only “new” because it was the first year of the study. This is evident (Figure 10) in the much higher proportions for 1998 than for the other years. These relationships are important in the capture-recapture models for abundance estimation. In a closed model, these transients can cause bias because there are both gains and losses. In an open population model, whales that do not return after their first year (a large percentage in this analysis) would appeared to have not survived because they have permanently emigrated (with a small fraction that died).

3.3 Mothers and calves

Mother and calf data were only available from some collaborators and much of the effort in the PCFG occurs during and after the period of weaning. Likely due to those a factors, a relatively low proportion of calves have been sighted from the summer and fall sightings of gray whales through 2010 (Table 11). Through 2010, 35 different gray whales identified as PCFA whales were seen as definite or probable mothers with calves representing 45 likely births, eight whales were seen with calves multiple seasons (two or three). Despite the many years of study, only two individuals were sighted with calves in three separate years, the most documented, however, in one of these cases one of the calves was documented prior to the 1998 start of regular effort. One individual (ID#81) was observed with a calf in 2001, 2003, and 2009 and the other individual (ID#67) was seen with a calf in 1995, 2002 and 2004.

Overall, 3 of the 45 occurred prior to 1998, leaving 42 or just over three per year during our primary study period 1998-2010 (Table 12). These likely represent a minimum estimate of the births occurring because: 1) collaborators did not always note the presence or absence of calves, 2) as described below, calves weaned from their mothers, making them unidentifiable as calves, as early as June and July. Both these factors would tend to result in underestimates of the presence of calves.

The number of mothers of calves seen varied dramatically by year from 0 to 9 and was concentrated in a four-year period (2001-2004) which accounted for 28 of the 45 sightings of known mothers with calves. During this 4-year period an average of 7 calves were seen while an average of 1.5 calves per year was seen in the other nine years (14 calves in 9 years). Even among these known or suspected mothers, the proportion of years they were seen where they had a calf average only 14% although it was 39% and 36% during the peak years of 2001 and 2002, which would be closer to what would be expected if females were getting pregnant almost every other year. The most recent year of data, 2010, also showed a higher number of calves from known PCFG whales with 4 documented mothers and calves out of 12 known mothers seen (33%). While these years with higher number of calves were likely higher birth years, it is also possible that longer weaning times those years may have contributed to a higher proportion of new calves still with their mothers being documented.

In 20 cases, a calf was seen associated with its mother early in the season and then the mother or the calf was resighted later in the season separately, suggesting weaning had occurred. The latest a mother was seen still seen associated with its calf was 6 September (CRC 67 with calf CRC 698 in 2002) and there were indications of separation of calves from their mothers as early as June. In two cases either the mother or calf was seen separated in June, however, in neither case was the calf resighted in the future year (although the mother was) suggesting these calves may not have survived. In at least eight cases the weaning had occurred prior to a July sighting (and possibly earlier).

Of the 35 likely mothers documented, 23 had been seen four or more years in the study area (12 had been seen only 1, 2, or 3 years). Even those animals with long sighting histories were seen with calves in only a small proportion of the years but as shown in Table 11, often the initial sighting of these animals was in late August or later, past the period when weaning may have occurred.

Some of these whales commonly seen in the Pacific Northwest were sighted with calves outside of this region and the somewhat atypical locations may suggest they may behave differently in years they have a calf. One mother (ID#281) was regularly sighted in the PCFA area every year from 1999 to 2007. In only one of those years was she with a calf (2002) and in 2008 she was seen on 19 April off Santa Barbara, S California apparently in the migration with a small calf but neither of them were seen that year in any of our effort farther north from Northern California to SE Alaska. Another case not included in our summary because the calf was never seen in the our study area and also there was uncertainty of who was the mother, was an apparent calf (ID 962) sighted off San Miguel Island on 27 July 2006 but which was accompanied by two adults (ID 359 and 718) both of whom were seen in most years from 2002 to 2008 in the Pacific Northwest (N California to SE Alaska), but not in 2006. Both the mothers and calves from these two sightings were not seen in the Pacific Northwest in their birth year (despite the mothers being seen most other years) and were only opportunistically sighted outside the region, suggesting there may be additional calves born to animals that use the Pacific Northwest that perhaps do not come into sampled areas (either within or outside the Pacific Northwest) in their birth year. This would negatively bias estimates of the number of calves born to these animals.

One important question in evaluating the population structure of the gray whales using the Pacific Northwest feeding areas is how animals are recruited to this group. We examined the sighting histories of the identified calves to determine if they tended to be seen in future years. Animals that were not seen in future years could reflect either mortality in the first year of life or animals that did not continue to feed in the Pacific Northwest in future years. There were 42 calves or suspected calves identified with their mothers through 2010 in the study area with 38 of these seen through 2009 and which had at least one subsequent year they would have had an opportunity to have been seen. Just over half of these (21 or 55%) had been seen in a year subsequent to the year they were calves. Using only the 30 calves seen through 2004 (to allow a longer follow up period to resight animals, 19 (63%) have been resighted in a later year. The 37% not seen in a following year could be the result of: 1) the calf dying, 2) the calf not returning to the area or not yet resighted during its return, 3) the calf not being recognized by photo-ID since calves can undergo changes in markings rapidly especially if not seen for several years. Given all these factors the resighting rate of calves does suggest a high proportion of surviving calves appear to become part of the small feeding aggregation that uses the Pacific Northwest.

3.4 Open Population Capture-Recapture Models

If the yearly cohorts were pooled, Test2+Test3 statistics indicated a significant lack of fit for the PCFG and subsets (Table 13) primarily resulting from Test 3. This was expected due to the different "survival" rates of previously seen whales (true survival) and newly seen whales of which many never returned (i.e., permanently emigrated) (Table 14) . By separating the cohorts, survival for each cohort was time-varying and thus each cohort has a separate first year survival. In this case, the goodness of fit test (Test 2 only) did not demonstrate a lack of fit except for OR-NBC and NCA-NBC. For those regions, we estimated over-dispersion values of $\widehat{c}$=1.79 and $\widehat{c}$=2.09 respectively, to adjust AICc and estimated standard errors. The lack of fit for those regions is probably related to the inclusion of NCA, WVI and NBC which are at the fringes of the PCFG. Effort in NCA and WVI has been less regular than the other survey regions and whales in NBC have a higher degree of interchange with Alaska.

The best fitted model (Table 15) was always model 2 for p with capture probability varying across years and higher when MT was greater in the previous year. For φ the best model was either model 4 or 5 with roughly equal support for each model. Both models included a separate first year survival which depends on MT. In both models the intercept for first year survival in 1998 differs from the other years and in model 5 the slope for MT differs for 1998. These results were consistent with Calambokidis et al. (2004) who demonstrated strong support for the effect of MT on first year survival (Figure 11-12) and capture probability (Figure 13) in the following year for all spatial scales. These results differ from Calambokidis et al. (2010) due to the use of MT directly rather than a median centered value. Use of MT with median centering was necessary to construct open model abundance estimates in the manner described in Calambokidis et al. (2010). However, that was not necessary for JS1 and JS2 and use of MT directly resulted in lower AICc values.

There was large year to year variation in capture probability. The values for MUA-SVI ranged from 0.23 to 0.97 depending on the year and value of MT (Figure 13). The lowest values were from 2007 which reflects the temporary emigration of whales from MUA and SVI to waters offshore of Oregon in that year.

First year survival estimates were dominated by permanent emigration. For MUA-SVI, the estimates varied from 0.42 to 0.51 for non-calf whales with MT=1 in their first year and from 0.80 to 0.94 for MT>80 in their first year (Figure 11). For calves, they were slightly higher but there was little support for a different first year calf survival. Survival subsequent to the first year was assumed to be constant but was less for non-calf whales that were newly seen in 1999 or later. Post-first-year suvival for calves and whales present in 1998 or earlier presumably represents true survival assuming there was little permanent emigration after the first year. Those estimates were 0.97 (se=0.0088), 0.972 (se=0.0078), 0.971 (se=0.0093) and 0.968 (se=0.0093) for MUA-SVI, OR-SVI, OR-NBC, NCA-NBC respectively. The post-first-year survival estimates for whales that entered in 1999 or later and not identified as a calf were 0.864 (se=0.0217), 0.878 (se=0.0183), 0.871 (se=0.0228) and 0.881 (se=0.0217) for MUA-SVI, OR-SVI, OR-NBC, NCA-NBC respectively.

3.5 Abundance and Recruitment

For MUA-SVI, OR-SVI, OR-NBC, and NCA-NBC annual estimates of abundance were constructed with LP, Limited LP and model averaged values for JS1 and JS2 (Figure 14, Tables 16-23). Estimates in Figure 14 are only shown for 1999-2010 because with the closed models only 12 estimates can be constructed with the 13 years of data and with the open models $p = 1$ for 1998 so it will be an underestimate. In general, the JS1 and JS2 estimates were similar to the Limited LP estimates because they are all removing the transients from the estimates. In contrast, LP attempts to estimate the total abundance which includes transient whales; however, as we show below with the simulation, it is positively biased because there are losses and gains in each set of years and even the trend is unreliable.

The Limited LP abundance estimates for 2010 are biased low because new whales that enter that year have no chance to be re-sighted and thus they were excluded even though some may return in the ensuing years. To a lesser degree, the estimate for 2009and possibly 2008 are influenced in a similar manner because the whales may have been simply not seen yet even though they are returning. The bias is evident by comparing the higher estimates for 2007 and 2008 in Tables 18- 19 to the same values given in Calambokidis et al. (2010) using data through 2008. This same problem occurs with JS2 because new whales that enter in 2010 are excluded because they are all presumed to be transients. Likewise, those that enter in 2009 and are non-transients but are not seen in 2010 are also excluded. This is not a problem for JS1 which includes those data and predicts the proportion of new whales that are non-transients based on the value of MT in their first year seen.

The JS1 sequence provides the best estimate for current N_{min} from 2010 because the LP estimator is biased high and the JS2 and Limited LP estimates for 2010 are biased low. The values of N_{min} range from 104 (Table 20) to 173 (Table 21) across the four spatial scales. To gain a sense for how these values might be relevant to estimating a possible level of removal (e.g., due to harvest) we computed the MMPA's Potential Biological Removal (PBR) (typically reserved for stock-level assessments). Using the PBR formula, with a default Rmax of 4% and a recovery factor of 1, the PBR for the smallest region considered (MUA-SVI), would be 2.1 and the PBR for the largest region (NCA-NBC) would be 3.5 .

New whales have continually appeared annually and many of these new (non-calf) whales have subsequently returned and been re-sighted (Table 14). In MUA-SVI from 1999-2010 , an average of 21.2 (range: 5.0, 56.0) new whales were seen each year. Of these new whales, on average 9.4 (range: 1.0, 19.0) whales returned and were seen in subsequent years. Currently recruitment appears to be offset by losses (either mortality or permanent emigration) as the abundance estimates have been fairly stable for the last 8 or 9 years. Presumably if there was a directed harvest recruitment would increase but if the take was 2-4 whales, it will take 5 to 10 years to see much change.

The AWMP implementation trials for the gray whale assessment is based on 1+ abundance. It is not possible to identify every calf when they entered and many were likely missed because much of the survey effort was conducted when calves could have been weaned. As an approximation to the 1+ abundance, we removed observed calves from the u_j in JS1. For NCA-NBC, there were 37 observed calves during the 13 years, but the total reduction in abundance across all years was approximately 20 because the JS1 estimator discounts newly seen whales based on their predicted survival probability. The reduction for OR-SVI is less because there were fewer calves observed in the smaller region. The sequence of estimates for NCA-NBC and OR-SVI are provided in Table . These estimates do not exclude whales first seen as calves in the abundance estimates when they were age 1 or older.

3.6 Abundance Simulation

The simulations clearly showed the positive bias that occurs with the LP estimator when a portion of the population are transients that are only in the population for one occasion (Figure 15). The LP estimates were greater than both total abundance and the abundance of the non-transients. When there was a decreasing trend in transients and an increase in non-transients as with the PCFG gray whales, the LP estimator produced a flat trend hiding the abundance increase. The bias in LP can be demonstrated algebraically. Assume that the population between 2 occasions is constant at N but only a proportion δ remains throughout both occasions and the remaining proportion $1-\delta$ are transient individuals which are only available in each occasion. The number of unique individuals in the population during the 2 occasions is $N\delta + 2N(1-\delta)$. The transient individuals at time 1 have no chance to be seen at time 2 and vice versa. The expected value of the LP estimator is $E(\hat{N}) = Np_1 * Np_2/(N\delta p_1 p_2) = N/\delta > N$. The proportional bias is $(1-\delta)/\delta$ for the annual abundance and $(\delta^2 - 2\delta + 1)/(2\delta - \delta^2)$ for the total unique number of individuals present at any time. Both are positive unless δ=1. For consecutive pairs of years, if δ changes so does the bias which can distort any trend.

The limited LP had far less bias for the non-transient abundance although it tended to underestimate slightly at the beginning and end of the time series due to the way it was constructed. Excluding the initial 1998 estimate, there was also only a slight negative bias for JS1 and JS2, although the latter did better at the beginning of the time series and the former at the end of the time series which was expected due to the way they were constructed. For JS1 and JS2, the estimated population growth rates were generally slightly higher than the true rates (Table 25) except for the end of the series for JS2 due to the negative bias in abundance. Both JS1 and JS2 were less variable than the limited LP rates. If estimates from JS1 or JS were used to fit a generalized logistic growth model it would bias RMax, the maximum rate of increase, and z, the exponent that controls the location of the inflection point but it would not affect the conclusion that the population is above MNPL, maximum net productivity level, with the abundance pattern evident in the PCFG abundance. The sequences of JS1 and JS2 abundance estimates for the PCFG were quite similar so you would expect the same conclusion from either; however, given that JS1 does not suffer from bias at the end of the sequence, the JS1 abundance estimates from 1999-2010 would provide the best sequence for the population growth assessment.

3.7 Movements outside the PCFG area

Gray whale photographic identifications obtained since the analysis in Calambokidis et al. (2010) have revealed additional long distance matches of gray whales of potential significance to the status of whales in the Pacific Northwest. These are described below representing three specific insights that came from some of these specific comparisons.

3.7.1 Matches to western gray whales

A comparison of Cascadia's entire catalog of photo-identified whales regardless of location or time of year was made to gray whales identified in the western North Pacific off Sakhalin Island. No matches of known PCFG whales were found between these collections. As reported in Weller et al. (2011), six matches were found between these two collections but these six whales were known in the Cascadia catalog. As reported in Weller et al. (2011), the WNP/ENP catalog comparison resulted in six confirmed matches of individuals, including three known males and two known females. All six of the matches were from only two days of effort off southern Vancouver Island, with three whales identified on 2 May 2004 and three on 25 April 2008 by collaborators Brian Gisborne and Wendy Szaniszlo. While the above findings have major implications regarding western gray whales, one other implication relates to whales feeding in the PCFG. That this many (six) matches found to western gray whales was surprising even if most western gray whales did migrate through this area. The Cascadia ENP catalog focuses on gray whales seen in summer and fall and has a relatively small sample of a few hundred gray whales from the spring migration. Given the approximately 20,000 gray whales likely migrating in spring through the PCFG area, finding six matches to the small western gray whale population seems highly improbable. It suggests that western gray whales that come to the eastern wintering grounds may spend periods feeding in the spring in the PCFG area prior to making their longer migration to the west. This could account for their higher probability of having been photographed. Given that the sightings were from just two days, it also could have been more coincidental that these identifications were taken from a potentially associated group of gray whales going to feeding areas in the western North Pacific.

3.7.2 PCFG whales identified near Barrow, Alaska

Of greater significance to the potential status of PCFG whales, two matches were found to nine gray whales identified near Barrow, Alaska and provided by the North Slope Borough (thanks to Craig George and Lori Quakenbush). Five of these were identified in August 2006 and four in August and early September of 2010. Two of these were determined to be whales identified in other regions. Most surprisingly, one of the whales identified in 2010 off Barrow (CRC ID 850) had been seen in the PCFG area three years in the summer and fall. Sightings included a total of 10 resightings: two days in September and October 2004 and September and October 2006 in the Strait of Juan de Fuca and in June 2008 off west Vancouver Island. The 2nd whale identified off Barrow in August 2006 (CRC ID 1010), was resighted on a single day (24 March 2007) off southern Vancouver Island, consistent with an animal caught in migration. While a single whale out of nine identified off Barrow to be an animal intermittently seen as a part of the PCFG is more anecdotal, it does demonstrate that at least some of the whales seen in repeat years in the PCFG area do travel and feed to some of the farthest away feeding areas.

3.7.3 Photo-identification of satellite tagged migrating gray whales

Additional insights into some of the movements of PCFG whales were gained from recent photo-identification matches to satellite tagged gray whales. Movements of five gray whales were tracked by satellite tags as they migrated north from S Vancouver Island north through British Columbia (Ford et al. ress). Comparison of photographs of these whales to Cascadia's catalog revealed that thee of the five were whales previously identified:

- CRC ID 307 (tag 1 tagged 26 March 2009 in Ford et al. ress): This whale was identified twice in June 1998 and July 1998 off W Vancouver Island but not identified again until the photographed 26 March 2009 in the tagging effort. It transmitted 13 days moving 1,354 km to 58.1N at an average speed of 4.9 km/h (Ford et al. ress).
- CRC 178 (tag 2 in Ford et al. ress): This animal is another long history animal with 94 sightings starting in 1995 almost every year since in many regions including many in WA as well as BC. After being tagged on 24 March 2010, it transmitted 16 days moving 893 km to 55N at an average speed of 1.1 km/h (Ford et al. ress). Unlike the other two tags of matched whales Tag 2 hung around Hesquiat and looks like may have visited Cape Caution before heading north.
- CRC 135 (tag 3 in Ford et al. ress): After being tagged on 24 March 2010, it transmitted 8 days moving 1,141 km to 56.6 N at an average speed of 5.8 km/h (Ford et al. ress). This whale has been identified 168 times every year from 1998 to 2010 in many regions but mostly off S Vancouver Island. These identifications were from June on. These resightings included 29 on 2010 after it had been tagged and appeared to migrate north and were from 9 June to 14 September all at the south end of Vancouver Island near where the tagging had occurred.

There are a couple of important things these satellite tag data reveal. They suggest that some of the PCFG whales may migrate at least part way north and appear to be migrants prior to returning south to primary feeding areas in the PCFG. Only one of the three (ID 135) was actually documented feeding back south in the tag year and the other two either did not come back to the PCFG area that year or where there but did not happen to be photo-identified. The finding of a PCFG whale migrating north of the PCFG area in spring was also revealed by one of the gray whales tagged by OSU in fall 2009 that kept transmitting into spring 2010 (Mate et al. 2011). That animal after spending some time in the southern Vancouver Island area after migrating north from Baja, then continued north to Icy Bay in the Gulf of Alaska before the tag stopped transmitting. While that animal had been identified in the PCFG in 7 different years going back to 1985, most of these sightings were at the northern end of the PCFG (north of Vancouver Island) and was last identified in 2007 prior to being tagged in December 2009.

While at least two of these animals (Tags 1 and 3) appeared to be migrating animals, it is likely they were engaged in some type of behavior different than typical gray whales from the overall migration otherwise it seems highly improbable that three of the five tagged whales were known PCFG whales given how small a proportion of the overall gray whale migration would be PCFG whales.

4 Discussion

The population structure of gray whales using the Pacific Northwest in summer and fall is complicated and involves two elements. One group of whales return frequently and account for the majority of the sightings in the Pacific Northwest during summer and fall. This group is certainly not homogeneous and even within this group, there is some degree of preference for certain subareas. Despite widespread movement and interchange among areas, some of these gray whales are more likely to be seen returning to the same areas they were seen before. The second group of whales are apparent stragglers encountered in this region after the migration. These animals are seen in only one year, tend to be seen for shorter periods that year, and in more limited areas.

The existence of these two groups in the study area and their dynamics complicate estimating abundance. The various methods we used here for estimating abundance try to deal with this in different ways. The estimates from the unadjusted Lincoln Petersen incorporate whales from both of these groups and the inclusion of the stragglers violates the closure assumption and creates a positive bias. This explains the higher estimate obtained with this method. Even the trend can be distorted as we demonstrated in the simulations. The Limited Lincoln Petersen estimate specifically excludes the stragglers and only estimates the abundance of whales that return after the year of the initial sighting. It is useful except for the last year in which new whales that may return are excluded because they have not had a chance to return. The Limited Lincoln Petersen estimates were similar to the JS1 and JS2 estimates from the open models which also attempt to estimate the non-transient abundance. Excluding 1998, the JS1 sequence of abundance estimates provides the most reliable assessment of trend in the non-transient abundance and the best estimate of current abundance in 2010.

Despite extensive interchange among subregions in our study area, whales do not move randomly among areas. Abundance estimates were lower when using more limited geographic ranges but these more limited areas do not reflect closed populations. While the use of geographically stratified models can be useful in cases where populations have geographic strata they use (see for example Hilborn 1990), this would be difficult in our case because of the frequent sightings of animals in multiple regions within the same season and these models typically only allow an animal to be sighted in one strata per period. This could be dealt with by assigning animals to only a single region per season but this would be forcing the data into a somewhat inaccurate construct.

Several studies have considered the question of gray whale population structure. There is widespread agreement that at least two populations of gray whales in the North Pacific exist, a western North Pacific population (also called the Korean population) and an eastern North Pacific (ENP) population (sometimes called the California population) (Swartz et al. 2006; Angliss and Outlaw 2008; Rugh et al. 1999). The population structure of the gray whales feeding in the Pacific Northwest has remained in question and only a few studies have examined this. Steeves et al. (2001) did not find mtDNA differences in a preliminary comparison of gray whales from the summer off Vancouver Island and those from the larger ENP population. Ramakrishnan et al. (2001) did not find evidence that the Pacific Northwest whales represented a maternal genetic isolate, although even very low levels of recruitment from the larger overall population would prevent genetic drift. More recently, Frasier et al. (2011) generated mtDNA sequences from a larger sample of gray whales from Vancouver Island than tested by Steeves et al. (2001). They found significant differences in the haplotype frequencies between that sample and mtDNA sequence data reported for ENP gray whales, most of which were animals that stranded along the migratory route. The Frasier et al. (2011) samples were from a relatively small area; however,Lang et al. (2011) evaluated biopsy samples from California to southern Vancouver Island in the PCFG and ENP samples from whales sampled north of the Aleutians and also found significant mtDNA halpotype frequency differences. These two studies provide the strongest evidence to date that the Pacific Northwest whales might be sufficiently isolated to allow maternally inherited mtDNA to differ from the overall ENP population.

Population structure in other large whales has been the subject of recent inquiry and has revealed diverse results for different species. Clapham et al. (2008) examined 11 subpopulations of whales subjected to whaling that were extirpated possibly due to the loss of the cultural memory of that habitat and concluded subpopulations often exist on a smaller spatial scale than had been recognized. Studies of other baleen whales, particularly humpback whales, have shown evidence of maternally directed site fidelity to specific feeding grounds based on photographic identification studies (Calambokidis et al. 1996, 2001, 2008). This high degree of fidelity to specific feeding areas is often discernible genetically. In the North Pacific strong mtDNA differences were found among feeding areas even when there was evidence of low level of interchange from photo-ID (Baker et al. 2008). Similar findings were documented for humpback whales in the North Atlantic which feed in different areas but interbreed primarily on a single breeding ground (Palsboll et al. 1995) like ENP gray whales. In the North Pacific the differences for humpback whales were often dramatic. For example, humpback whales that feed off California have almost no overlap in mtDNA haplotypes with humpback whales feeding in Southeast Alaska (Baker et al. 1990, 1998, 2008). One difference between humpback and gray whales is the coastal migration route of gray whales which means gray whales going to arctic waters to feed would migrate right through the feeding areas to the south. Other species of large whales have not shown as strong site fidelity to specific feeding grounds. Blue whales have undergone an apparent shift in their feeding distribution in the North Pacific apparently due to shifting oceanographic conditions (Calambokidis et al. 2009a). Fin whales in the North Pacific have long migrations and while there do not appear to be multiple distinct feeding areas as was the case for humpback whales, there were some distinct and isolated apparently nonmigratory populations (Mizroch et al. 2009; Berube et al. 2004).

Even though the population structure of gray whales off the Pacific Northwest remains unresolved, there is a consistent group of animals that use this area and we provide several estimates of their abundance. Different abundance methods and geographic scopes yield varied results but all suggest the annual abundance of animals using the Pacific Northwest for feeding through the summer is at most a couple hundred animals depending on the estimating method and how broadly the region is defined geographically.

The apparent rapid increase in the abundance estimates derived from the limited LP and Jolly-Seber models in the first five years of this study appear incompatible with this being a relatively distinct group since it would require a high rate of external recruitment, however, the exact rate of this increase should be viewed with caution. This rapid increase at the start of our study occurred during a period the overall eastern North Pacific gray whale population was experiencing a high mortality event that included unusually high numbers of gray whales showing up in areas they were not common. The simulation did show that the initial estimates were negatively biased low and would over-estimate recruitment but reflected the general trend. We did expand the analysis to include the 1996 and 1997 data and the 1998 estimate did increase by about 7% but the sampling prior to 1998 was opportunistic and not broad scale, so it is possible that some of the "new" whales seen during 1999-2001 may have been present in the PCFG prior to 1998 in areas that were not sampled and included in the CRC database. The high rate of increase in the late 1990s and early 2000s should be verified with additional data such as compiling photographic identifications for this area from multiple sources to attempt to verify if the abundance of animals prior to the start of our study was as low as suggested by these trends. Even though the rate of increase may be too high, we believe the abundance did increase and now appears to be relatively stable since 2002.

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Table 1: Contributions of numbers of photos by reseach group for 1998-2010and resulting number of uniquely identified whales. Totals for whales are unique whales across all research groups.

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Whales
Brian Gisborne	373	343	779	585	435	883	325	429	527	117	525	368	633	358
Canada Fisheries/Oceans	0	0	0	0	0	0	0	0	0	0	0	0	12	11
Carrie Newell	0	0	0	0	0	0	0	0	13	73	0	20	2	46
CERF	101	150	251	466	295	180	781	11	42	11	38	4	7	107
CRC	170	231	118	79	135	112	182	33	62	102	95	56	76	388
Dawn Goley-HSU	21	89	60	75	71	0	0	0	0	0	44	19	88	183
Jan Straley-UASE	0	0	0	0	0	7	0	0	1	1	0	0	0	7
Jeff Jacobsen-HSU	0	0	0	0	0	0	0	0	0	1	0	6	129	57
Jim Darling	50	0	0	35	14	0	0	0	0	0	0	0	0	59
MAKAH	0	0	0	0	0	0	44	58	142	84	247	131	53	158
MAKAH-NMML	0	0	0	0	0	0	0	0	0	0	0	80	27	56
NMML	132	194	135	128	88	76	0	133	93	39	143	9	7	341
North Slope Borough	0	0	0	0	0	0	0	0	5	0	0	0	7	9
Opportunistic	4	12	1	1	0	0	0	1	29	48	23	64	49	95
OSU	0	0	0	0	0	0	0	0	0	0	0	20	0	18
UAF	0	0	0	0	0	0	0	0	0	0	25	0	23	40
UVIC	351	159	128	0	121	0	0	0	0	1	0	16	0	139
Volker Deecke	39	42	28	11	0	0	0	0	50	0	0	0	0	74
Wendy Szaniszlo	0	0	0	0	0	0	0	125	67	71	144	5	24	107
Photo Totals	1241	1220	1500	1380	1159	1258	1332	790	1031	548	1284	798	1137	
Whale Totals	156	248	176	198	253	178	195	205	191	158	221	222	218	1031

Table 2: Regional distribution of numbers of photos and resulting number of uniquely identified whales by reseach group for 1998-20102010. Totals for whales are unique whales across all research groups. NPS is northern Puget Sound and PS includes southern Puget Sound, San Juan Islands, Hood Canal and Boundary Bay.

	CA	NCA	SOR	OR	GH+	NWA	SJF	PS	NPS	SVI	WVI	NBC	SEAK	KAK
Brian Gisborne	0	0	0	0	0	0	0	1	0	6133	186	2	0	0
Canada Fisheries/Oceans	0	0	0	0	0	0	0	0	0	12	0	0	0	0
Carrie Newell	0	0	0	108	0	0	0	0	0	0	0	0	0	0
CERF	0	0	0	0	0	0	0	0	0	0	0	2337	0	0
CRC	29	101	185	140	211	90	23	68	444	33	0	120	7	0
Dawn Goley-HSU	0	430	0	37	0	0	0	0	0	0	0	0	0	0
Jan Straley-UASE	0	0	0	0	0	0	0	0	0	0	0	0	9	0
Jeff Jacobsen-HSU	0	105	28	3	0	0	0	0	0	0	0	0	0	0
Jim Darling	0	0	0	0	0	0	0	0	0	6	93	0	0	0
MAKAH	0	0	0	19	0	227	513	0	0	0	0	0	0	0
MAKAH-NMML	0	0	0	0	0	69	38	0	0	0	0	0	0	0
NMML	0	8	42	0	0	263	283	0	22	196	179	13	0	171
North Slope Borough	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opportunistic	24	2	0	35	0	1	27	34	77	9	1	11	7	0
OSU	0	20	0	0	0	0	0	0	0	0	0	0	0	0
UAF	0	0	0	0	0	0	0	0	0	0	0	0	0	48
UVIC	0	0	0	0	0	0	0	0	0	1	775	0	0	0
Volker Deecke	0	0	0	0	0	0	0	1	0	122	0	43	4	0
Wendy Szaniszlo	0	0	0	0	0	0	0	0	0	241	195	0	0	0
Photo Totals	53	666	255	342	211	650	884	104	543	6753	1429	2526	27	219
Whale Totals	36	205	85	105	97	216	129	42	51	352	214	116	21	121

Table 3: Survey regions and region subsets used for abundance estimation. Numbers refer to locations on the map in Figure 1.

Survey Region	Region Description	NCA-NBC	OR-NBC	OR-SVI	MUA-SVI
(1) SCA = Southern California					
(2) CCA = Central California					
(3) NCA = Northern California	Eureka to Oregon border; mostly from Patricks Pt. and Pt. St George	x			
(4) SOR = Southern Oregon		x	x	x	
(5) OR = Oregon Coast	Primarily central coast near Depoe Bay and Newport, OR	x	x	x	
(6) GH+ = Gray's Harbor	Waters inside Grays Harbor and coastal waters along the S Washington coast	x	x	x	
(7) NWA = Northern Washington	Northern outer coast waters with most effort from Cape Alava to Cape Flattery	x	x	x	x
(8) SJF = Strait of Juan de Fuca	US waters east of Cape Flattery extending to Admiralty Inlet (entrance to Puget Sound)	x	x	x	x
(9) NPS = Northern Puget Sound	Inside waters and embayments from Edmonds to the Canadian border				
(10) PS = Puget Sound	Central and southern Puget Sound (S of Edmonds), including Hood Canal, Boundary Bay, and the San Juan Islands				
(11) SVI = Southern Vancouver Island	Canadian waters of the Strait of Juan de Fuca along Vancouver Island from Victoria to Barkley Sound, along West Coast Trail	x	x	x	x
(12) WVI = West Vancouver Island		x	x		
(13) NBC = Northern British Columbia	British Columbia waters north of Vancouver Island, with principal effort around Cape Caution	x	x		
(14) SEAK = Southeast Alaska	Waters of southeastern Alaska with the only effort in the vicinity of Sitka				
(15) KAK = Kodiak, Alaska					

Table 5: Model specifications for survival (φ) and capture probability (p) parameters in POPAN models for gray whale photo-identification data. For survival models, β_0 is the baseline intercept for non-transient survival. Fy is 1 if it is year the whale was first seen and 0 otherwise. Fc is 1 for 1998 cohort and 0 otherwise. C is 1 if identified as a calf in its first year and 0 otherwise. R is 1 for calves or any whale seen in 1998 or was already in the catalog prior to 1998 and 0 otherwise. β_r is an adjustment to post-first-year survival. MT is minimum tenure value of a whale and β_M is the estimated slope parameter for φ or p. $\beta_{M,1998}$applies only to 1998 and $\beta_{M,1999}$ applies to 1999-2010. $\beta_{Fy,1999}$ is the first-year survival intercept adjustment for cohorts 1999-2009 and $\beta_{Fy,c}$ represents 11 cohort-specific first year survival parameters for 1999-2008. β_{CF} is an adjustment for calf first year survival and β_{CM} is an adjustment for calves to the slope of MT for survival. For the capture probability models, β_t has 11 levels for t=2000,...2010 and β_0 represents the 1999 value. For 1998 p=1.

Model	Parameter Logit Formula	Number of parameters
φ		
1	$\beta_0 + \beta_{Fy}Fy + \beta_r R(1 - Fy)$	2
2	$\beta_0 + \beta_{Fy}Fy + \beta_M MT\,Fy + \beta_r R(1 - Fy)$	3
3	$\beta_0 + \beta_{Fy,1998}Fy + \beta_{Fy,1999}(1 - Fc)Fy + \beta_r R(1 - Fy)$	3
4	$\beta_0 + \beta_{Fy,1998}Fy + \beta_{Fy,1999}(1 - Fc)Fy + \beta_M MT\,Fy + \beta_r R(1 - Fy)$	4
5	$\beta_0 + \beta_{Fy,1998}\,Fy + \beta_{Fy,1999}(1 - Fc)\,Fy + \beta_{M,1998}MT\,Fy + \beta_{M,1999}(1 - Fc)\,MT\,Fy + \beta_r R(1 - Fy)$	5
6	$\beta_0 + \beta_{Fy,1998}Fy + \beta_{Fy,c}Fy\,(1 - Fc) + \beta_M MT\,Fy + \beta_r R(1 - Fy)$	14
7	$\beta_0 + \beta_{Fy,1998}Fy + \beta_{Fy,c}Fy\,(1 - Fc) + \beta_M MT\,Fy + \beta_{CF}C\,F_y + \beta_r R(1 - Fy)$	15
8	$\beta_0 + \beta_{Fy,1998}Fy + \beta_{Fy,c}Fy\,(1 - Fc) + \beta_M MT\,Fy + \beta_{CF}C\,F_y + \beta_{CM}C\,MT + \beta_r R(1 - Fy)$	16
9	$\beta_0 + \beta_{Fy,1998}\,Fy + \beta_{Fy,1999}(1 - Fc)\,Fy + \beta_{M,1998}MT\,Fy + \beta_{M,1999}(1 - Fc)\,MT\,Fy + \beta_{CF}C\,F_y + \beta_r R(1 - Fy)$	6
10	$\beta_0 + \beta_{Fy,1998}\,Fy + \beta_{Fy,1999}(1 - Fc)\,Fy + \beta_{M,1998}MT\,Fy + \beta_{M,1999}(1 - Fc)\,MT\,Fy + \beta_{CF}C\,F_y + \beta_{CM}C\,MT + \beta_r R(1 - Fy)$	7
p		
1	$\beta_0 + \beta_t$	12
2	$\beta_0 + \beta_t + \beta_M MT$	13
3	$\beta_0 + \beta_M MT$	2

Table 6: Regional distribution of numbers of whales seen by month for 1998-2010.

	1	2	3	4	5	6	7	8	9	10	11	12
CA	0	1	3	7	5	2	6	6	6	1	0	1
NCA	0	0	0	0	9	44	93	52	28	74	40	16
SOR	0	0	0	2	0	0	24	22	52	32	0	0
OR	0	0	0	0	3	10	32	50	46	43	0	0
GH+	2	1	14	40	14	17	2	0	27	1	0	0
NWA	4	0	8	34	69	18	47	69	58	37	5	0
SJF	0	0	3	10	20	20	27	35	52	73	47	11
PS-HC-BB-SJ	0	1	6	21	8	9	5	2	1	1	3	1
NPS	0	2	16	28	30	12	1	0	0	0	0	0
SVI	1	1	63	55	79	175	208	164	128	51	14	7
WVI	0	1	2	5	2	44	135	127	87	15	0	0
NBC	1	0	0	0	2	24	76	101	82	0	0	0
SEAK	0	0	0	0	0	12	4	1	3	0	5	0
KAK	0	0	0	0	0	17	23	52	44	0	0	0

Table 7: Regional distribution of numbers of whales seen during June-November for 1998-2010.

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
CA	0	1	0	5	0	0	4	0	3	0	0	3	6
NCA	15	38	27	32	37	15	3	0	0	1	47	26	63
SOR	0	0	0	2	46	24	13	1	0	23	15	2	15
OR	17	31	8	15	0	0	16	4	9	38	6	12	18
GH+	0	1	1	1	0	0	1	0	0	38	0	2	0
NWA	21	7	9	31	7	19	0	19	44	13	27	25	22
SJF	17	4	5	2	1	9	21	18	21	14	49	34	4
PS-HC-BB-SJ	3	8	4	0	0	0	0	1	0	0	0	4	0
NPS	0	0	10	0	0	0	0	0	0	0	0	2	2
SVI	60	45	52	102	66	90	86	91	70	34	77	77	63
WVI	57	66	53	29	85	9	0	53	40	13	23	23	10
NBC	23	26	23	40	44	51	91	12	21	5	21	3	4
SEAK	5	6	0	1	0	6	0	1	2	3	0	0	0
KAK	0	0	0	0	42	4	0	48	0	0	23	0	17

Table 8: Number of days in which whales were seen for each region and year from 1998-2010from 1 June - 30 November.

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
CA	0	1	0	2	0	0	2	0	1	0	0	2	3
NCA	7	8	20	13	20	2	2	0	0	2	9	16	21
SOR	0	0	0	1	4	1	1	1	0	3	1	1	5
OR	6	9	5	7	0	0	1	1	7	38	1	11	4
GH+	0	1	1	1	0	0	1	0	0	3	0	1	0
NWA	22	10	7	11	3	9	0	12	13	6	8	5	14
SJF	16	9	9	4	2	15	5	14	18	26	34	25	4
PS-HC-BB-SJ	3	11	4	0	0	0	0	2	0	0	0	4	0
NPS	0	0	1	0	0	0	0	0	0	0	0	2	3
SVI	91	87	82	55	68	66	48	73	59	36	72	71	80
WVI	54	46	28	7	10	3	0	6	14	27	31	5	2
NBC	39	50	53	43	34	29	53	11	16	9	13	2	8
SEAK	2	3	0	1	0	3	0	1	2	2	0	0	0
KAK	0	0	0	0	4	2	0	7	0	0	5	0	2

Table 9: Interchange of whales across regions for all years (1998-2010) for June-November. The diagonal is the number of unique whales seen in that region over the13 year time span. Here PS includes NPS and CA represents SCA and CCA.

	CA	NCA	SOR	OR	GH+	NWA	SJF	PS	SVI	WVI	NBC	SEAK	KAK
CA	20												
NCA	4	197											
SOR	4	45	83										
OR	2	51	46	104									
GH+	1	12	8	14	42								
NWA	2	39	36	50	21	124							
SJF	1	17	12	25	14	54	112						
PS	0	0	0	0	0	1	2	31					
SVI	6	59	43	64	29	100	73	1	270				
WVI	2	40	29	51	24	74	57	1	141	206			
NBC	2	11	9	24	14	31	26	2	73	70	113		
SEAK	0	1	1	2	1	2	3	0	7	8	10	21	
KAK	0	4	1	3	0	1	0	0	8	6	6	1	121

Table 10: Number of photographs by month in all regions and years(1998-2010)for a sample of whale IDs.

	1	2	3	4	5	6	7	8	9	10	11	12
6	0	0	0	0	2	2	1	5	3	3	1	0
80	0	0	0	1	8	29	63	61	20	2	0	0
141	0	0	3	1	0	6	20	32	10	0	0	0
204	0	0	0	0	0	6	19	38	31	7	3	0
246	0	0	0	0	0	0	1	2	0	0	0	0
272	0	0	0	0	0	0	0	1	0	0	0	0
302	0	0	2	1	7	13	27	30	19	0	0	0
328	0	0	15	0	0	1	31	24	19	0	2	0
373	0	0	0	0	0	0	2	0	0	0	0	0
399	0	0	0	1	8	10	0	0	0	0	0	0
426	0	0	0	0	1	0	0	0	0	0	0	0
453	0	0	0	0	1	0	0	0	0	0	0	0
482	0	0	0	0	2	0	0	0	0	0	0	0
518	0	0	0	0	0	0	0	1	0	0	0	0
545	0	0	0	0	1	0	0	0	0	0	0	0
571	0	0	0	0	1	2	2	0	0	0	0	0
596	0	0	0	0	0	3	2	0	0	0	0	0
623	0	0	0	0	0	0	2	0	0	0	0	0
648	0	0	0	0	0	0	0	2	0	0	0	0
683	0	0	0	0	0	1	9	0	2	4	0	0
709	0	0	0	0	0	3	2	2	0	0	0	0
735	0	0	0	0	0	0	0	1	0	0	0	0
760	0	0	0	0	0	1	11	9	7	0	0	0
788	0	0	0	0	0	4	0	8	1	1	0	0
815	0	0	0	0	0	2	6	0	0	0	0	0
844	0	0	0	0	0	0	0	1	0	0	0	0
869	0	0	0	0	0	0	0	1	0	0	0	0
897	0	0	0	0	0	0	0	0	3	0	0	0
928	0	0	0	0	0	2	0	0	0	0	0	0
955	0	0	1	0	0	0	0	0	0	0	0	0
980	0	0	0	0	0	0	0	0	1	0	0	0
1007	0	0	1	0	0	0	0	0	0	0	0	0
1033	0	0	0	0	0	0	1	0	0	0	0	0
1059	0	0	0	0	0	1	0	2	0	7	0	0
1085	0	0	0	0	0	0	2	0	0	0	0	0
1110	0	0	0	0	0	0	0	0	0	3	0	0
1135	0	0	0	1	0	0	0	0	0	0	0	0
1160	0	0	0	0	0	2	0	0	0	0	0	0
1185	0	0	0	2	0	0	0	0	0	0	0	0
1211	0	0	0	0	3	1	0	0	0	0	0	0
1236	0	0	0	0	0	0	0	2	0	1	0	0
1261	0	0	0	0	0	0	0	1	0	0	0	0

Table 11: History of mothers seen with calves during study. Each year a whale was seen, the first confirmed sighting date is shown for that year. Years where a calf was documented are shown with an asterisk. Total years seen includes 16 sightings of whales during 1984,1988, 1990-1993 that are not shown but no calves were seen in those few cases.

Mother ID	Calves	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Years seen
43	2	9-Jul*	22-Jul	15-Jul	9-Aug	11-Jul	16-Jul	19-Jun	18-Jul*	12-Jul	24-Jun	4-Jul		7-Jul					16
67	3		19-Jul*	2-Jul	6-Jul		10-Aug			7-Aug*		4-Jun*	3-Aug	4-May					9
80	2	25-Aug	23-Jun	8-Aug		8-Jun	27-Jun	3-Jul	7-May	22-May*	27-Apr	25-Jun	18-Jun*						12
81	3		19-Aug		23-Sep	14-Jun	21-Jun	29-Jul	20-Jun*	24-Jun	28-Jul*	23-Jul	3-Jul	4-Jul	16-Jun		16-Jul*		14
91	1					23-Jun		22-Jul	15-Aug	5-Jul*	17-Jun		23-Jun		11-Jul	18-Jun			9
92	2			27-Jul	9-Aug	4-May	30-Jun	29-Jul	9-Jul	4-Aug	27-Jul	11-Jul	27-Jun*	18-Jun	8-Jun	22-May	4-Apr	5-Jun*	16
93	1			17-Jul	23-Sep	14-Jun	22-Jun	12-Aug	21-Jun	16-Jul	2-Aug	30-Jun*		4-Jul		18-Jun	8-Jun		14
94	1	4-Aug				27-Jun	6-Jul	24-Jul	7-Jul	15-Jul	23-Jul	5-Aug	13-Jul	18-Mar	8-Jul*	8-Jul	2-Jun	31-Mar	15
101	1	22-Jun	6-Sep	5-Sep		11-Jun	8-Jul	29-Jul	8-Jun	9-Jul	9-Aug	15-Jun*	1-Aug	7-Jun	8-Jun	28-Jun	24-Apr	15-Jun	19
105	1	9-Jul*				17-Jun	9-Jun	20-Jul	22-Jun	3-Jul	2-Aug	23-Jul	24-Jul	28-Jul	22-Jun				11
120	1								13-Jun*	11-Jun		2-Jun						6-Jul	4
143	1					27-Jun	29-Jun	1-May	6-Jul	29-Jul*	17-Aug		5-Sep	12-Mar	24-Mar	22-Jun	14-Aug	10-Mar	12
144	1					11-Jul	13-Aug	6-Sep	6-Jul	5-Jul*	30-Mar	19-Jun	26-May	4-Jul	31-Mar	25-May	4-Apr	26-Mar	13
175	1		22-Jul	13-Jun	27-Jun	26-May	9-Jun	29-May	15-Jun	3-Jul	12-May*	30-Jun	21-Jul	4-Jul	15-Jul				13
216	1				27-Jun	23-Aug	30-Jul	29-Jun	15-Jun	15-Jul	26-Jul*	4-Jun	9-Jun						9
232	2					6-Jul		30-Jul	5-Jul*	15-Aug	9-Jun*								5
237	1					23-Jul	25-Jul	4-Jul	5-Jul	1-Jul	29-Apr*	19-Jul							7
281	2						20-Jul	15-Jul	21-Jun	17-Aug*	5-Sep	19-Jul	13-Aug	7-Jul	14-Sep	19-Apr*	14-Aug		12
291	1					1-Oct	12-Jul	24-Aug	8-Jun*	4-Aug	25-Jun	24-Jul	21-Jul	5-Jul		20-Oct	14-Nov	6-Aug	12
312	2					12-Jun*			7-Jul									22-Jun*	3
321	1					25-Jun*													1
372	1						26-Jun	9-May		4-Aug	15-Jul	25-Jun*	7-Jul	3-Jul	1-Sep		10-Jul	5-Aug	10
566	1							6-Jul		17-Aug		14-Aug	2-Sep					22-Jun*	5
575	1								5-Jun*										1
581	1								5-Jun*					4-Jul	30-Jun				3
596	1								26-Jun*	3-Jul									2

Table 11: continued

Mother ID	Calves	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Years seen
612	1							23-Jun	1-Aug*	1-Jul	5-Jun	1-Jul	18-Jul	5-Nov					7
668	1									6-Sep		22-Sep			19-Aug			9-May*	4
683	1									25-Jul*		27-Oct	18-Jun						3
684	1									4-Jul*	11-Aug								2
717	1									3-Jul*									1
801	1										7-Jul	2-Aug	3-May*						3
815	1											19-Jun*				14-Jul			2
973	1														14-Sep*			6-Aug	2
993	1													1-May	14-Aug*				2
Calves	45	2	1	0	0	2	0	0	9	9	5	5	3	0	3	1	1	4	

Table 12: Sighting histories of calves identified in the study area. First separate date represents sighting of either the calf or mother alone. An asterisk by the calf ID implies it is suspected to be a calf; others are all known to be calves.

Calf ID	Mother ID	First date w/ mother	Last date w/ mother	First separate date	1994	1995	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Yrs
104	105	9-Jul-94	9-Jul-94		1																1
107	43	9-Jul-94	4-Aug-94		2	1	2	7	1	34	10	1	15	11	9	10	3	12			14
169*	67	19-Jul-95	23-Jul-95			4					3	5	10	5	3	7	2	5			9
246*		11-Aug-98	17-Aug-98					3													1
307	312	28-Jun-98	9-Jul-98					2													1
310	321	25-Jun-98	4-Jul-98	6-Jul-98				3	1												2
583	581	5-Jun-01	4-Oct-01								5	1	6		6	2	12	13			7
584	81	20-Jun-01	18-Jul-01	22-Jul-01							3	1		27	3	4	2				6
595	596	26-Jun-01	29-Jun-01								3										1
611	43	18-Jul-01	31-Jul-01	28-Oct-01							4						1				2
620	232	5-Jul-01	31-Jul-01								2										1
626	291	8-Jun-01	8-Jun-01	15-Jun-01							2										1
657	281	17-Aug-02	6-Sep-02									2	1		1	1	3	2			6
682	80	22-May-02	29-Jul-02	18-Aug-02								6	23	2	7	10	3	13			7
685	684	4-Jul-02	4-Aug-02									5									1

Table 12: continued

Calf ID	Mother ID	First date w/ mother	Last date w/ mother	First separate date	1994	1995	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Yrs
686	717	3-Jul-02	3-Jul-02									3									1
687	683	25-Jul-02	29-Jul-02									2				7	1	3			4
688	91	5-Jul-02	15-Jul-02	6-Sep-02								6	5	4	10	11	2	4			7
698*	67	7-Aug-02	6-Sep-02	14-Oct-02								4	8	1	12	9	1	10			7
714	144	5-Jul-02	4-Aug-02									1				6		16			3
720	143	29-Jul-02	3-Sep-02	30-Sep-02								1	10	7	6	5	6	18			7
786	232	9-Jun-03	3-Jul-03	15-Jul-03									11	6	2	16	5	11			6
797	81	28-Jul-03	28-Jul-03	30-Jul-03									1	2	7	18	12	11			6
798*	175	12-May-03	12-May-03	16-Jun-03									1								1
860*	216	26-Jul-03	28-Jul-03	26-Aug-03									3	4	4	9	2	1			6
811	815	19-Jun-04	17-Jul-04											5							1
814	372	25-Jun-04	30-Jun-04											2							1
818	101	17-Jul-04	17-Jul-04	20-Aug-04										2	2	5	2				4
819	67	4-Jun-04	27-Aug-04	22-Sep-04										8	6	20	20	14			5

Table 12: continued

Calf ID	Mother ID	First date w/ mother	Last date w/ mother	First separate date	1994	1995	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Yrs
824	93	30-Jun-04	11-Jul-04	14-Aug-04										4	8			9			3
862*	801	3-May-05	3-May-05	21-Jul-05											5						1
863	92	27-Jun-05	24-Jul-05	4-Aug-05											10						1
882	80	18-Jun-05	19-Jun-05	4-Jul-05											3	10	13	14			4
976*	973	14-Sep-07	14-Sep-07														1				1
990	94	8-Jul-07	5-Aug-07														4	7			2
994	993	5-Aug-07	14-Aug-07														1				1
1066	281	19-Apr-08	19-Apr-08															1			1
1173	81	16-Jul-09	18-Jul-09																2		1
1212	668	9-May-10	9-May-10																	1	1
1234	566	22-Jun-10	1-Jul-10																	2	1
1237	312	22-Jun-10	1-Jul-10	6-Aug-10																4	1
1254	92	5-Jun-10	7-Jul-10	18-Jul-10																20	1

Table 13: RELEASE goodness of fit results for 3 regions using pooled and separate cohorts. When cohorts are separated as groups, Test 3 is always 0 because there are no sub-cohorts.

Region	Cohort	Test	χ^2	df	P
MUA-SVI	Pooled				
		Test 2	53.6	19	0
		Test 3	165.2626	21	0
		Total	218.8626	40	0
	Separate				
		Test 2	56.5057	47	0.1613
OR-SVI	Pooled				
		Test 2	85.9075	25	0
		Test 3	211.3463	21	0
		Total	297.2538	46	0
	Separate				
		Test 2	65.0763	53	0.1235
OR-NBC	Pooled				
		Test 2	126.9031	18	0
		Test 3	333.0608	21	0
		Total	459.964	39	0
	Separate				
		Test 2	89.7225	50	5e-04
NCA-NBC	Pooled				
		Test 2	143.1829	19	0
		Test 3	432.4828	21	0
		Total	575.6657	40	0
	Separate				
		Test 2	102.5383	49	0

Table 14: Number of whales seen each year, number that were new that year in that region, and number that were new and were seen in a subsequent year for whales seen between June-November 1998-2010 in each region. The year a whale was seen as new can vary across regions and if it differs will be later in the smaller region.

Region		1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
MUA-SVI	Seen	73	48	60	116	68	96	95	104	93	45	103	97	72
	Non-calf: New	73	13	23	56	22	31	25	21	13	5	17	20	8
	Non-calf: New/Resighted	53	8	15	18	9	19	9	9	5	1	6	4	0
	Calf: New	1	0	0	5	6	3	5	3	0	1	1	1	1
	Calf: New/Resighted	0	0	0	2	4	3	3	1	0	1	0	0	0
OR-SVI	Seen	84	71	67	129	103	110	114	109	100	113	119	107	94
	Non-calf: New	84	26	26	58	40	26	29	21	12	24	18	19	11
	Non-calf: New/Resighted	63	12	17	19	21	17	11	11	4	5	7	5	0
	Calf: New	1	0	0	6	7	3	5	3	0	2	1	1	1
	Calf: New/Resighted	0	0	0	3	5	3	3	1	0	1	0	0	0
OR-NBC	Seen	116	120	113	151	179	154	177	138	130	118	134	113	104
	Non-calf: New	116	50	37	54	51	26	35	22	9	25	20	19	13
	Non-calf: New/Resighted	92	16	21	19	27	16	11	10	2	5	6	5	0
	Calf: New	3	0	0	6	9	3	5	3	0	3	1	1	1
	Calf: New/Resighted	0	0	0	3	7	3	3	1	0	1	0	0	0
NCA-NBC	Seen	130	152	137	174	205	157	179	138	130	119	171	128	147
	Non-calf: New	130	75	54	65	57	21	32	22	9	22	46	25	21
	Non-calf: New/Resighted	101	17	31	25	23	13	10	10	2	7	12	9	0
	Calf: New	3	0	0	6	9	3	5	3	0	3	1	1	3
	Calf: New/Resighted	1	0	0	3	7	3	3	1	0	1	0	0	0

Table 15: Delta AICc and QAICc (for OR-NBC and NCA-NBC models) for 30 models fitted to each set of data.

		φ Model									
Region	p model	1	2	3	4	5	6	7	8	9	10
MUA-SVI	1	120.7	82.5	113.8	81.4	83.1	86.4	88.4	90.3	90.3	86.7
	2	30.6	1.1	25.2	0.0	1.2	7.2	9.2	11.3	3.1	5.1
	3	100.0	69.1	94.3	67.8	69.1	72.7	74.7	76.7	70.9	72.8
OR-SVI	1	170.4	122.6	159.1	120.1	121.4	118.6	120.7	121.9	123.3	124.5
	2	39.6	2.6	30.5	0.0	0.6	0.3	2.4	3.9	2.6	4.2
	3	48.8	12.3	39.7	9.6	10.1	8.7	10.8	12.3	12.0	13.6
OR-NBC	1	137.6	95.3	24.6	89.7	89.6	95.1	96.9	97.3	91.7	92.1
	2	40.4	6.5	24.6	0.7	0.0	7.2	9.0	9.7	2.0	2.7
	3	54.4	20.5	38.4	14.4	13.7	19.3	21.0	21.7	15.7	16.3
NCA-NBC	1	127.0	87.2	105.4	77.0	77.2	83.0	85.1	86.0	79.0	80.0
	2	42.9	10.6	23.8	0.3	0.0	7.4	9.4	10.7	1.8	3.0
	3	57.9	25.3	38.9	15.3	14.9	21.2	23.2	24.4	16.7	17.9

Table 16: Number of whales seen in each year and number seen in both years and abundance estimate ($\widehat{N}$), standard error and minimum population estimate $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ for Lincoln-Petersen estimator applied to consecutive years from 1998-2010 in MUA-SVI and OR-SVI regions.

Region	Year (y)	Seen in year y-1	Seen in year y	Seen in both years	$\widehat{N}$	$se(\widehat{N})$	N_{min}
MUA-SVI	1999	73	48	35	99	6.1	94
	2000	48	60	29	98	8.1	91
	2001	60	116	46	150	8.1	143
	2002	116	68	42	186	14.0	174
	2003	68	96	40	162	12.4	151
	2004	96	95	56	162	8.8	154
	2005	95	104	56	175	10.1	167
	2006	104	93	61	157	7.5	151
	2007	93	45	30	138	11.8	128
	2008	45	103	33	139	10.1	130
	2009	103	97	68	146	5.6	141
	2010	97	72	50	138	7.4	132
OR-SVI	1999	84	71	45	131	8.0	125
	2000	71	67	34	138	11.9	128
	2001	67	129	50	171	9.4	163
	2002	129	103	53	249	18.2	234
	2003	103	110	59	191	11.0	182
	2004	110	114	68	183	8.6	176
	2005	114	109	61	202	11.6	193
	2006	109	100	64	169	8.1	162
	2007	100	113	59	190	10.9	181
	2008	113	119	69	194	9.3	186
	2009	119	107	78	162	5.5	158
	2010	107	94	60	166	8.5	159

Table 17: Number of whales seen in each year and number seen in both years and abundance estimate ($\widehat{N}$), standard error and minimum population estimate $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ for Lincoln-Petersen estimator applied to consecutive years from 1998-2010 in OR-NBC and NCA-NBC regions.

Region	Year (y)	Seen in year y-1	Seen in year y	Seen in both years	$\widehat{N}$	$se(\widehat{N})$	N_{min}
OR-NBC	1999	116	120	70	198	9.5	190
	2000	120	113	66	204	10.8	195
	2001	113	151	84	202	7.4	196
	2002	151	179	106	254	8.5	247
	2003	179	154	119	231	5.8	226
	2004	154	177	117	232	6.1	227
	2005	177	138	97	251	9.3	243
	2006	138	130	92	194	6.2	189
	2007	130	118	74	206	9.5	198
	2008	118	134	73	215	10.4	207
	2009	134	134	84	179	6.0	174
	2010	113	113	68	172	7.6	165
NCA-NBC	1999	130	152	77	255	13.0	244
	2000	152	137	71	292	17.5	277
	2001	137	174	93	255	10.2	247
	2002	174	205	121	294	9.4	286
	2003	205	157	126	254	6.2	249
	2004	157	179	118	237	6.3	232
	2005	179	138	97	254	9.4	246
	2006	138	130	92	194	6.2	189
	2007	130	119	74	208	9.7	200
	2008	119	171	76	266	13.6	255
	2009	171	128	92	237	8.8	229
	2010	128	147	86	218	8.6	210

Table 18: Number of whales seen in each year and number seen in both years and abundance estimate ($\widehat{N}$), standard error and minimum population estimate $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ for limited Lincoln-Petersen estimator applied to consecutive years from 1998-2010 in MUA-SVI and OR-SVI regions.

Region	Year (y)	Seen in year y-1	Seen in year y	Seen in both years	$\widehat{N}$	$se(\widehat{N})$	N_{min}
MUA-SVI	1999	51	41	33	62	2.7	60
	2000	43	52	29	76	5.2	72
	2001	49	77	43	87	2.9	84
	2002	77	56	39	109	6.7	104
	2003	58	86	39	127	8.4	119
	2004	83	78	52	123	5.9	118
	2005	81	92	55	134	6.4	129
	2006	90	82	58	126	5.3	122
	2007	85	42	30	117	9.0	110
	2008	42	92	33	116	7.2	109
	2009	89	78	65	106	2.7	104
	2010	77	60	46	99	4.4	96
OR-SVI	1999	60	54	42	76	2.9	74
	2000	57	58	34	96	6.6	91
	2001	55	90	47	104	3.9	101
	2002	90	86	50	154	9.3	146
	2003	84	99	54	153	8.3	146
	2004	101	96	65	148	6.2	143
	2005	97	98	59	160	8.1	153
	2006	98	90	62	141	6.0	136
	2007	92	95	59	147	7.0	141
	2008	94	107	68	147	5.6	142
	2009	105	90	75	125	3.1	123
	2010	88	78	55	124	5.5	119

Table 19: Number of whales seen in each year and number seen in both years and abundance estimate ($\widehat{N}$), standard error and minimum population estimate $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ for limited Lincoln-Petersen estimator applied to consecutive years from 1998-2010 in OR-NBC and NCA-NBC regions.

Region	Year (y)	Seen in year y-1	Seen in year y	Seen in both years	$\widehat{N}$	$se(\widehat{N})$	N_{min}
OR-NBC	1999	88	82	66	109	2.9	106
	2000	85	96	65	125	4.2	121
	2001	96	118	83	136	2.9	133
	2002	113	156	100	175	3.5	172
	2003	158	143	115	196	4.2	192
	2004	144	153	114	192	4.1	189
	2005	152	123	93	200	6.3	195
	2006	125	121	90	167	4.7	163
	2007	123	99	74	164	5.9	158
	2008	98	119	72	161	6.1	156
	2009	117	96	81	138	3.3	135
	2010	94	86	63	127	4.7	123
NCA-NBC	1999	95	87	70	117	3.1	115
	2000	93	113	70	149	5.4	145
	2001	112	135	91	165	4.2	162
	2002	129	170	113	193	3.6	190
	2003	174	148	122	210	4.3	207
	2004	149	157	115	203	4.6	199
	2005	157	124	94	206	6.6	201
	2006	125	121	90	167	4.7	163
	2007	123	105	74	173	6.8	168
	2008	104	136	75	187	7.6	181
	2009	135	110	90	164	4.2	161
	2010	103	117	77	156	5.1	151

Table 20: JS1 abundance estimates ($\widehat{N}$), standard errors and minimum population estimate $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ using data from 1998-2010 in MUA-SVI and OR-SVI regions.

Region	Year	$\widehat{N}$	$se(\widehat{N})$	N_{min}
MUA-SVI	1998	53	4.2	49
	1999	60	7.9	53
	2000	74	9.5	66
	2001	105	6.9	99
	2002	106	15.4	93
	2003	124	11.7	114
	2004	132	13.8	121
	2005	137	11.8	127
	2006	128	12.2	118
	2007	125	24.4	106
	2008	122	9.2	114
	2009	121	11.6	111
	2010	117	15.9	104
OR-SVI	1998	63	4.2	60
	1999	78	8.4	71
	2000	89	11.9	79
	2001	120	9.2	113
	2002	137	15.2	124
	2003	153	13.8	142
	2004	161	15.5	148
	2005	164	15.7	151
	2006	154	15.3	142
	2007	153	14.5	141
	2008	150	12.5	140
	2009	147	14.9	134
	2010	144	16.8	131

Table 21: JS1 abundance estimates ($\widehat{N}$), standard errors and minimum population estimate $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ using data from 1998-2010 in OR-NBC and NCA-NBC regions.

Region	Year	$\widehat{N}$	$se(\widehat{N})$	N_{min}
OR-NBC	1998	93	5.7	88
	1999	117	10.5	108
	2000	124	11.8	115
	2001	153	10.7	144
	2002	169	8.2	162
	2003	187	13.6	175
	2004	198	12.6	188
	2005	200	20.2	183
	2006	180	16.2	167
	2007	175	21.4	158
	2008	169	15.8	156
	2009	163	20.3	146
	2010	161	21.4	144
NCA-NBC	1998	103	6.4	98
	1999	135	12.0	125
	2000	141	13.2	130
	2001	175	12.6	165
	2002	193	9.3	185
	2003	202	16.5	188
	2004	209	14.9	197
	2005	208	22.6	189
	2006	190	18.8	175
	2007	184	23.1	165
	2008	192	16.1	179
	2009	185	23.2	166
	2010	188	18.7	173

Table 22: JS2 abundance estimates ($\widehat{N}$), standard errors and minimum population estimate $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ using data from 1998-2010 in MUA-SVI and OR-SVI regions.

Region	Year	$\widehat{N}$	$se(\widehat{N})$	N_{min}
MUA-SVI	1998	53	6.1	48
	1999	62	6.7	57
	2000	79	7.6	73
	2001	91	6.6	85
	2002	107	8.0	100
	2003	123	7.2	117
	2004	125	6.4	119
	2005	125	5.8	120
	2006	121	5.8	116
	2007	118	6.7	112
	2008	115	6.4	110
	2009	112	6.7	106
	2010	106	7.1	100
OR-SVI	1998	63	6.7	58
	1999	76	7.4	70
	2000	98	8.9	91
	2001	108	7.4	102
	2002	141	9.1	134
	2003	147	7.4	141
	2004	153	7.1	147
	2005	155	6.0	150
	2006	147	6.5	141
	2007	145	7.0	139
	2008	144	7.2	138
	2009	140	7.5	133
	2010	132	8.0	126

Table 23: JS2 abundance estimates ($\widehat{N}$), standard errors and minimum population estimate $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ using data from 1998-2010 in OR-NBC and NCA-NBC regions.

Region	Year	$\widehat{N}$	$se(\widehat{N})$	N_{min}
OR-NBC	1998	92	10.2	84
	1999	107	10.7	99
	2000	125	11.0	116
	2001	138	10.3	130
	2002	162	9.3	154
	2003	174	9.2	166
	2004	175	8.7	168
	2005	175	8.6	168
	2006	165	9.3	157
	2007	163	10.3	155
	2008	157	10.5	149
	2009	152	10.9	143
	2010	143	11.5	133
NCA-NBC	1998	102	11.7	92
	1999	119	12.3	109
	2000	149	13.1	138
	2001	166	12.0	156
	2002	182	10.6	174
	2003	191	10.6	182
	2004	191	10.3	182
	2005	192	10.2	183
	2006	181	10.9	172
	2007	183	12.1	172
	2008	182	12.1	172
	2009	178	12.3	168
	2010	168	13.1	157

Table 24: JS1 abundance estimates ($\widehat{N}$) and standard errors in OR-SVI and NCA-NBC after exclusion of known calves from the year in which they were identified as calves.

Region	Year	$\widehat{N}$	$se(\widehat{N})$
OR-SVI	1998	63	4.1
	1999	78	8.4
	2000	89	11.9
	2001	117	8.9
	2002	133	15.0
	2003	151	13.7
	2004	157	15.5
	2005	162	15.7
	2006	154	15.3
	2007	152	14.5
	2008	150	12.5
	2009	146	14.9
	2010	143	16.8
NCA-NBC	1998	101	6.2
	1999	135	12.0
	2000	141	13.2
	2001	172	12.6
	2002	189	9.2
	2003	200	16.4
	2004	206	14.9
	2005	206	22.6
	2006	190	18.8
	2007	183	23.1
	2008	191	16.1
	2009	185	23.2
	2010	186	18.7

Table 25: Simulation assessment of bias for in population trend for limitedLP, JS1 and JS2 estimators with p=0.7 and 0.8 with an increasing trend in non-transients and decreasing trend in transients and no trend (lower 2 plots). Value is $(\hat{N}_{t+1} - \hat{N}_t)/\hat{N}_t - (N_{t+1} - N_t)/N_t$ using average estimated abundance and true abundance for each time. Estimate from 1998 was excluded because it is not available for limitedLP and for JS1 and JS2 it was assumed that $p = 1$ for 1998 which will create bias.

	JS1		JS2		Limited LP	
	p=0.7	p=0.8	p=0.7	p=0.8	p=0.7	p=0.8
Trend						
1999	1.9	0.5	1.5	1.3	13.4	13.3
2000	3.8	1.8	0.9	0.5	-3.1	-4.0
2001	0.8	-0.2	1.6	0.3	-0.3	-0.5
2002	2.2	1.7	0.6	0.7	-7.0	-7.2
2003	1.7	1.2	0.5	0.8	-1.1	-0.7
2004	0.5	0.4	0.4	0.7	-0.7	-0.9
2005	1.7	1.3	1.3	1.0	-3.8	-3.8
2006	-0.4	-0.4	0.6	0.9	2.3	3.2
2007	0.0	-0.0	0.3	0.4	1.6	1.0
2008	-0.1	-0.1	-1.7	-1.2	-4.0	-2.8
2009	-0.9	-1.1	-4.0	-4.3	-8.3	-8.0
No Trend						
1999	11.3	8.0	1.3	0.8	7.0	8.2
2000	3.0	1.6	0.8	1.1	1.2	1.7
2001	0.7	0.4	1.0	0.7	1.1	-0.5
2002	0.6	-0.1	1.4	0.5	0.5	0.9
2003	0.4	-0.0	1.2	1.0	0.3	-0.1
2004	-0.4	0.1	0.3	0.7	-0.7	-0.5
2005	0.1	-0.1	0.8	0.6	-1.2	0.1
2006	-0.4	0.0	-0.0	0.4	0.2	-0.3
2007	0.4	0.0	0.7	0.1	-0.6	-0.7
2008	0.2	-0.3	-2.3	-1.5	-2.7	-1.4
2009	0.6	0.4	-4.2	-4.3	-8.7	-9.6

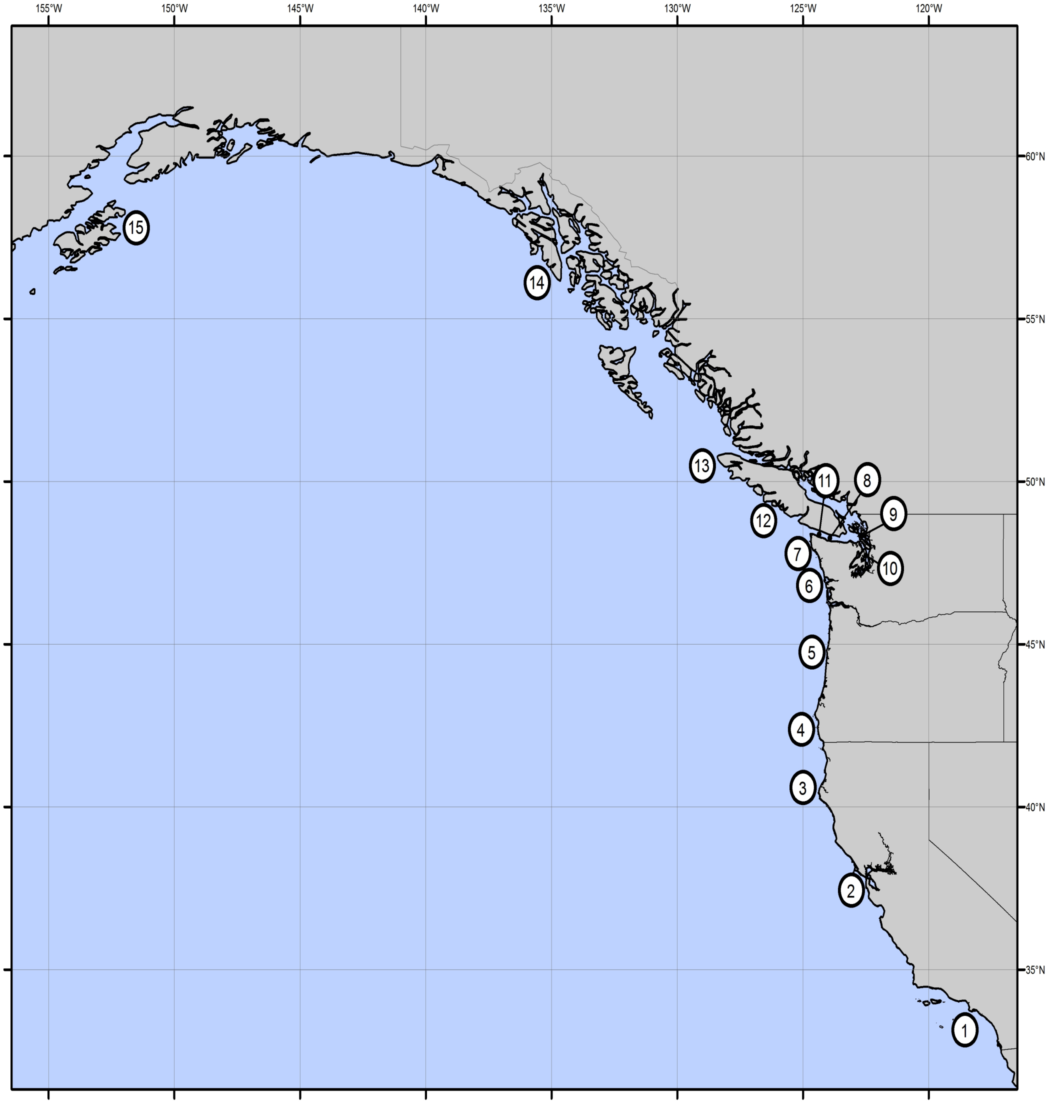

Figure 1: Locations for photo-identifications of gray whales. Numbers refer to values in Table 1.

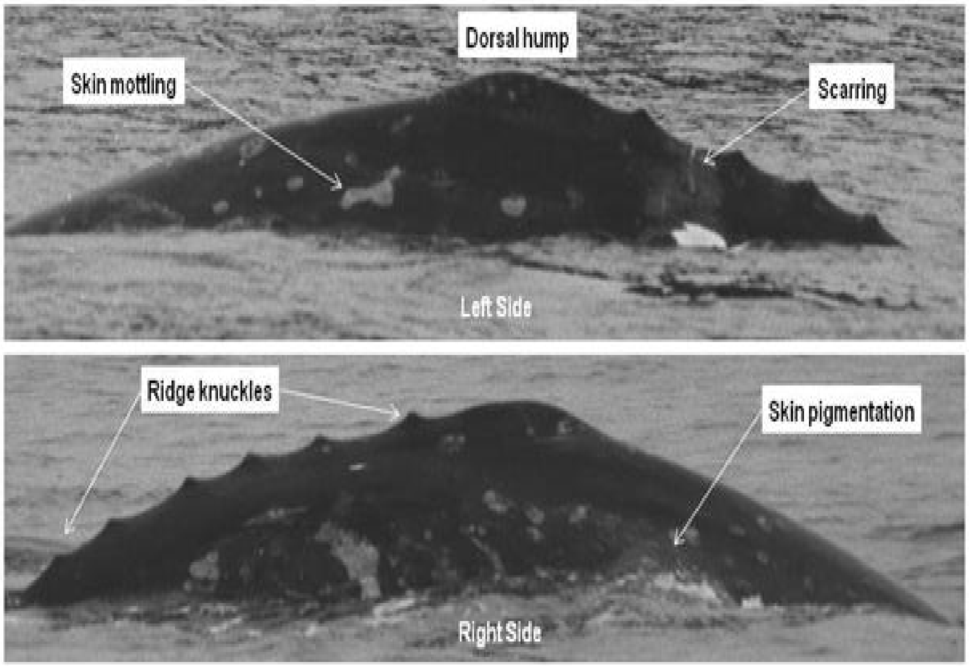

Figure 2: Characteristics used for gray whale photo-identification.

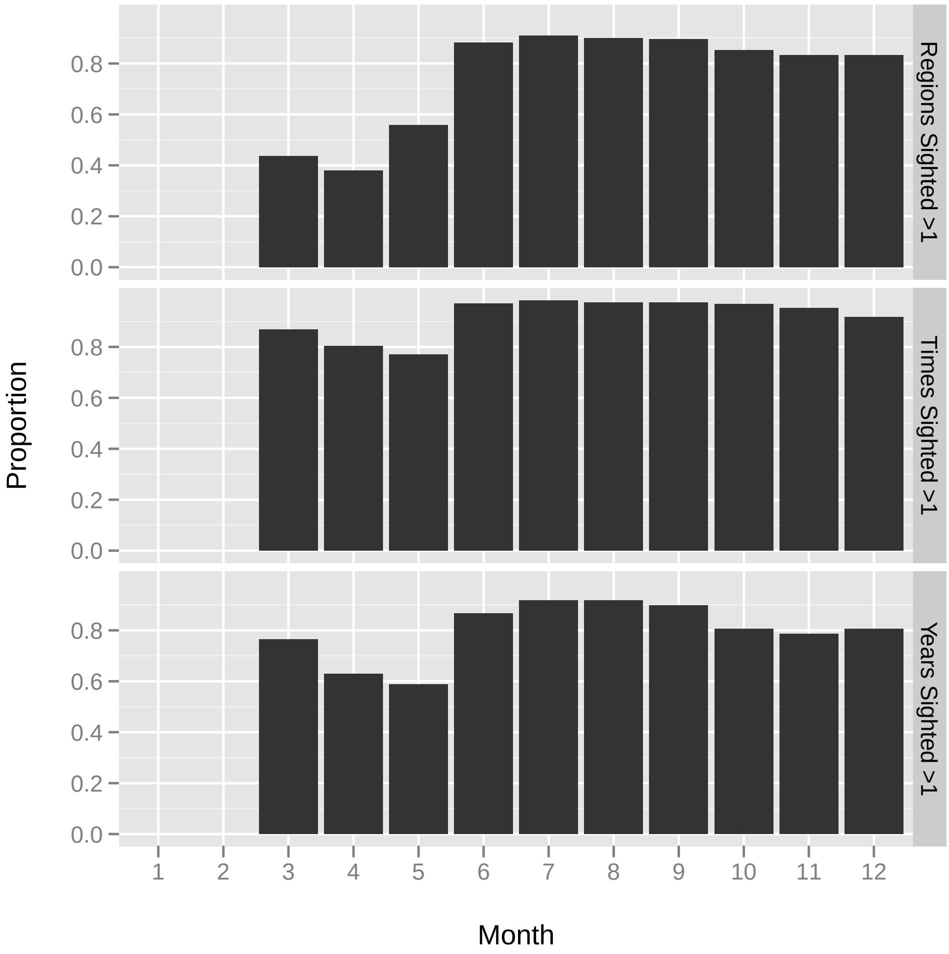

Figure 3: Monthly measures of proportion of whales that were seen in more than one region, seen on more than one day and seen in more than one year. The values include sightings from 1998-2010 in all regions from California to Alaska. Lower values imply whales were simply migrating through the area in a short time frame and were thus less likely to be seen at other times and in other regions. Values are not shown for months with fewer than 20 sightings.

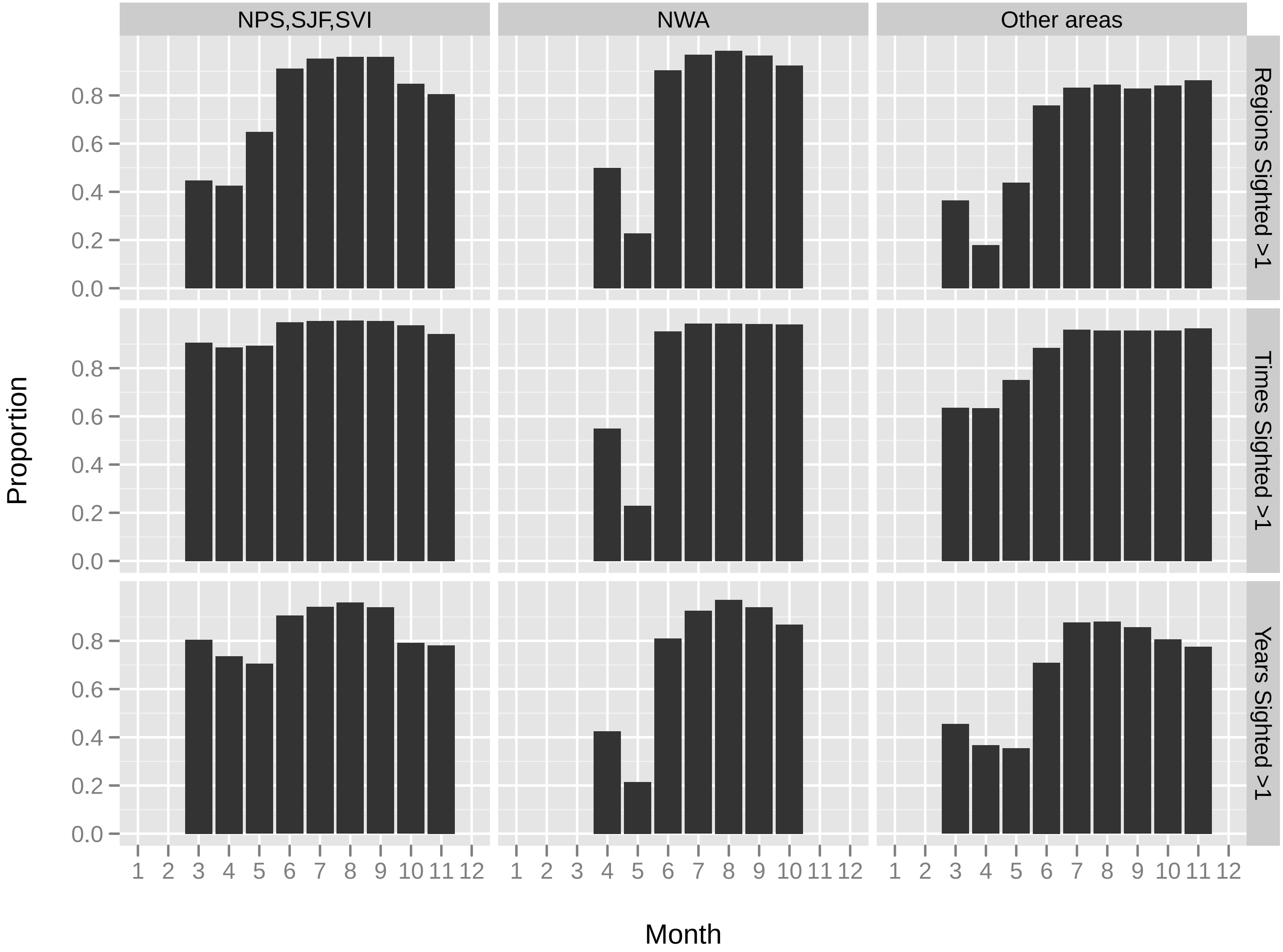

Figure 4: Region and monthly measures of proportion of whales that were seen in more than one region, seen on more than one day and seen in more than one year. The values include sightings from 1998-2010 in all regions from California to Alaska. Lower values imply whales were simply migrating through the area in a short time frame and were thus less likely to be seen at other times and in other regions. Values are not shown for months with fewer than 20 sightings.

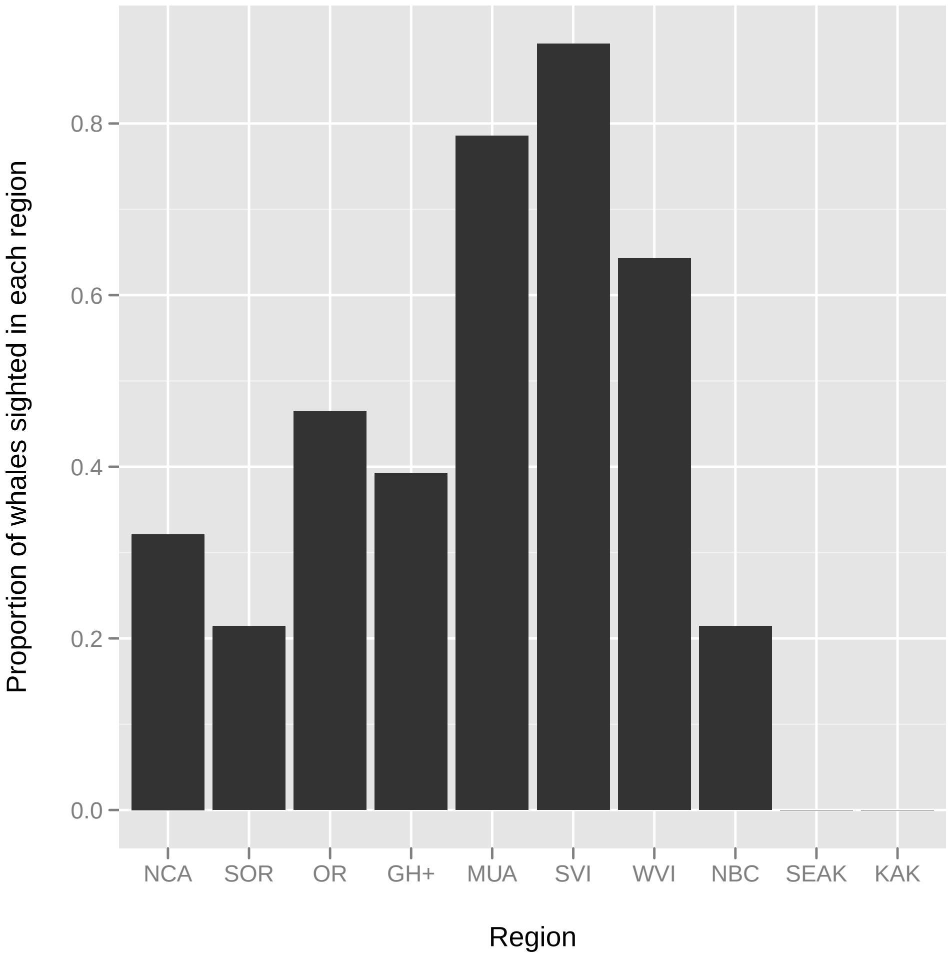

Figure 5: Proportion of the 14 whales seen in NWA during the spring and in the PCFG after 1 June that were seen in each PCFG sub-region after 1 June at least once from 1998-2010.

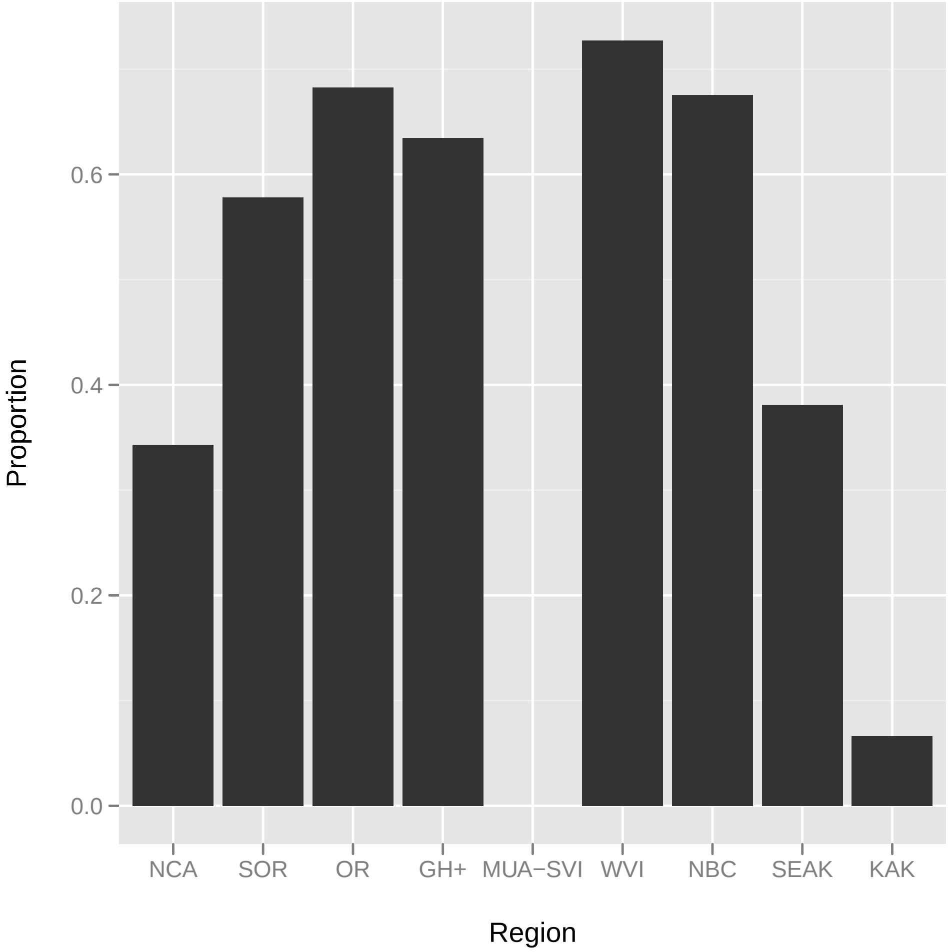

Figure 6: Proportion of whales in PCFG sub-regions that have been seen in the MUA-SVI using sightings after 1 June from 1998-2010.

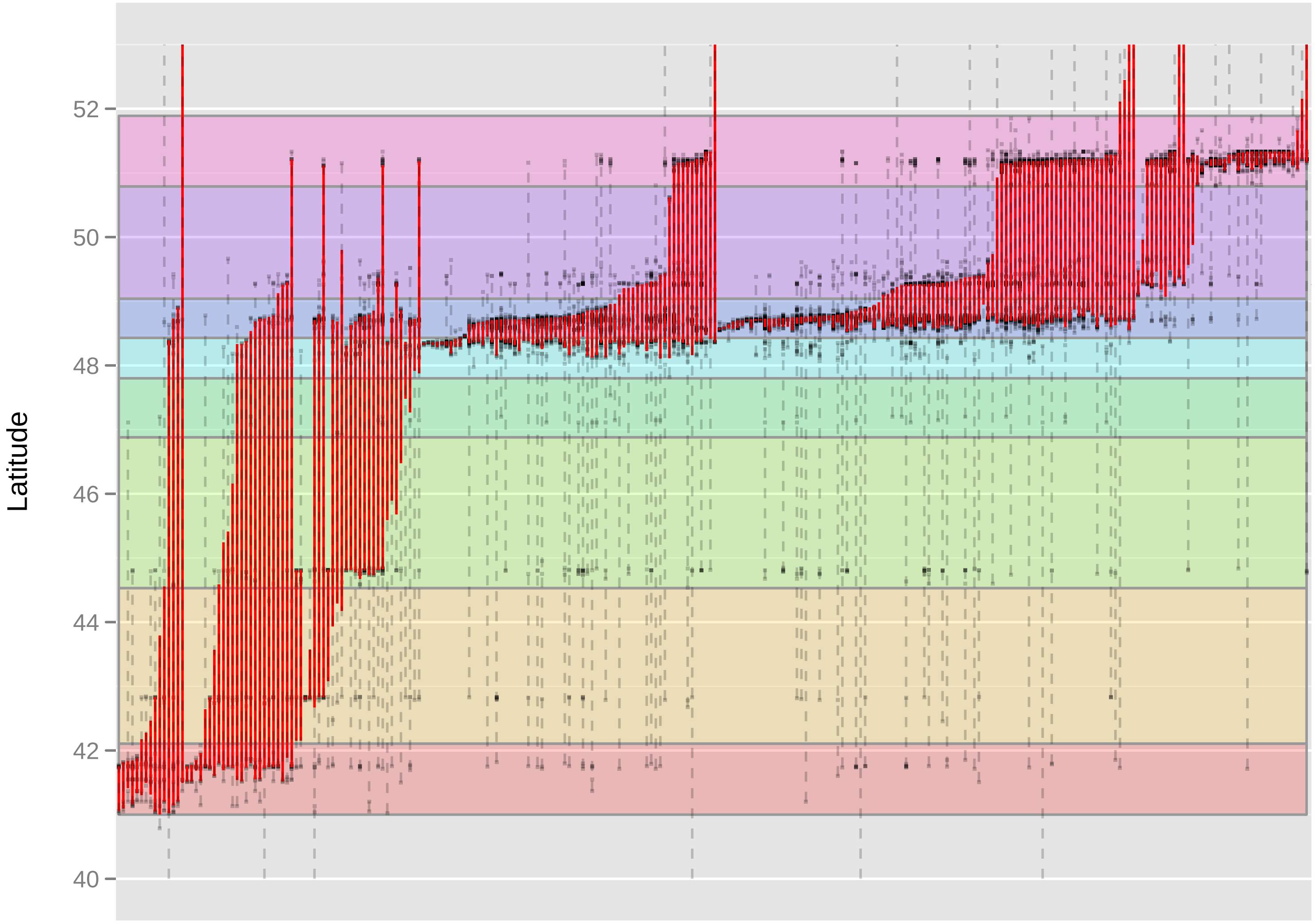

Figure 7: Distribution of latitudes of sightings (points) for whales with 6 or more sightings after 1 June from 1998-2010, the 75% inner quantile (solid thick line), and full range (light dashed line). Each position on the x axis represents an individual whale. Whales have been arranged on the plot by sorting first on the lower bound of the inner quantile (to a half-degree) and then the upper bound of the quantile. This has the effect of sorting from south to north and clusters whales with smaller quantile ranges followed by whales with larger ranges.

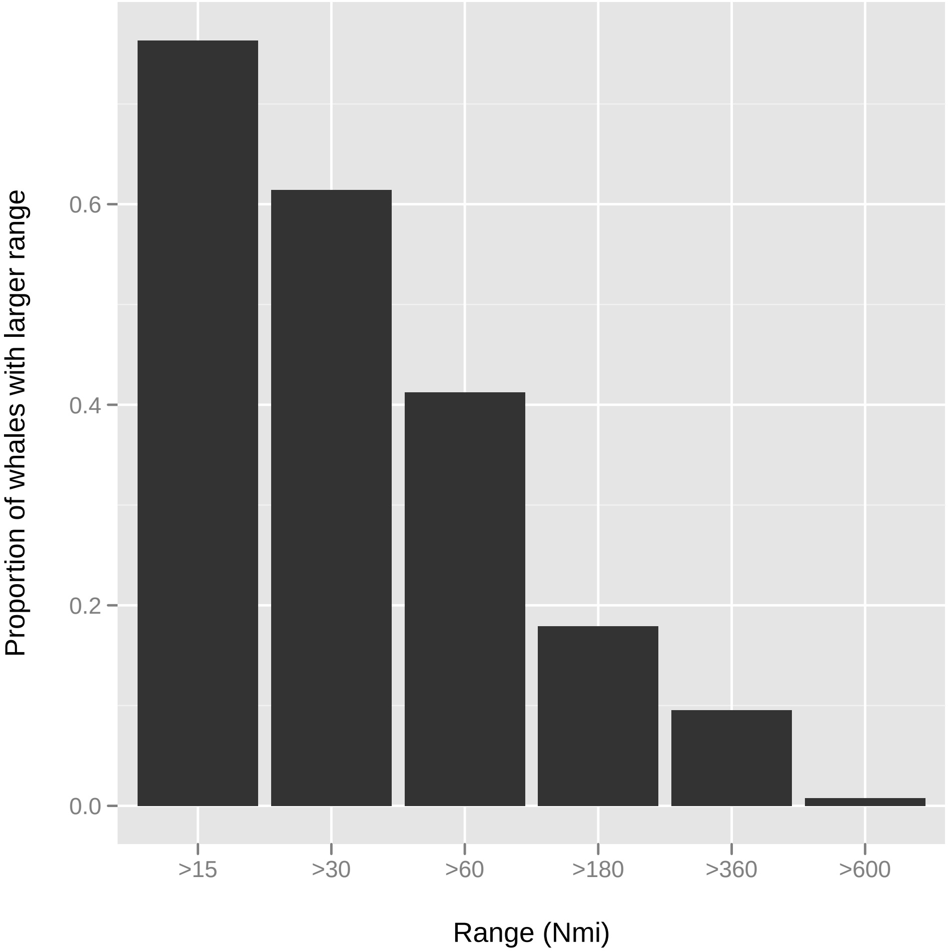

Figure 8: Distribution of ranges of 75% inner quantiles of latitudes expressed in nautical miles for whales sighted on 6 or more days during 1998-2010.

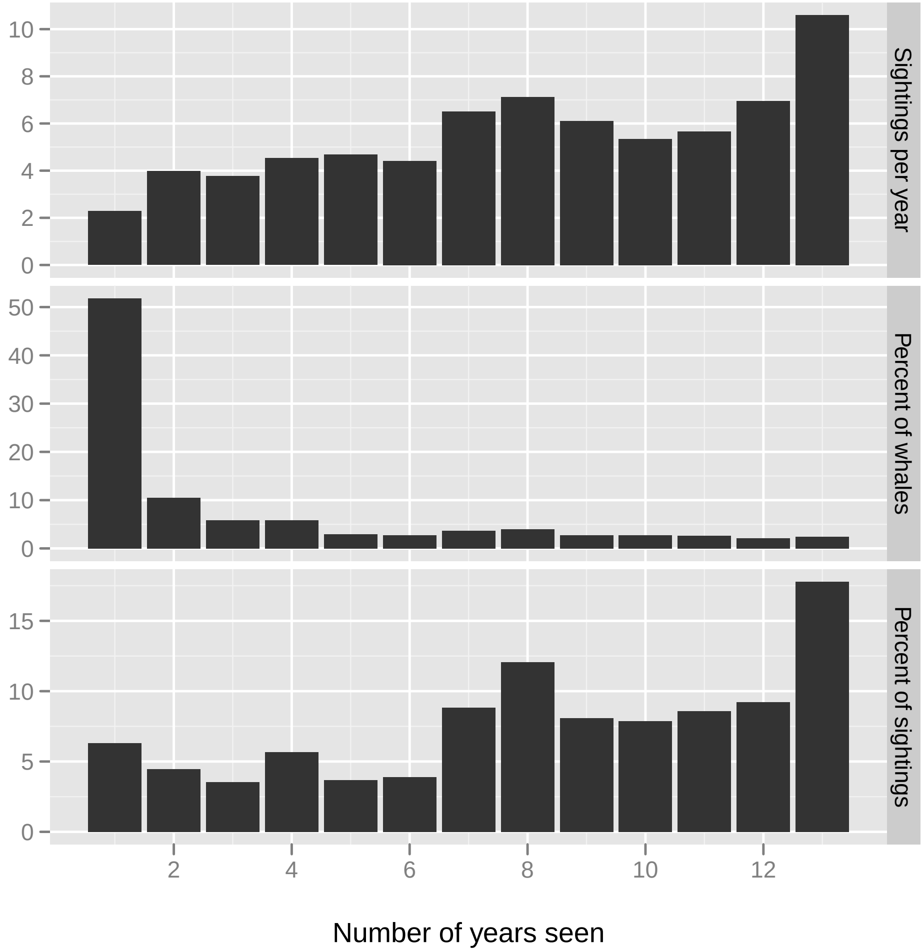

Figure 9: Average number of sightings per year and distribution of whales and numbers of sightings based on numbers of years a whale was seen in NCA-NBC between June-November during 1998-2010.

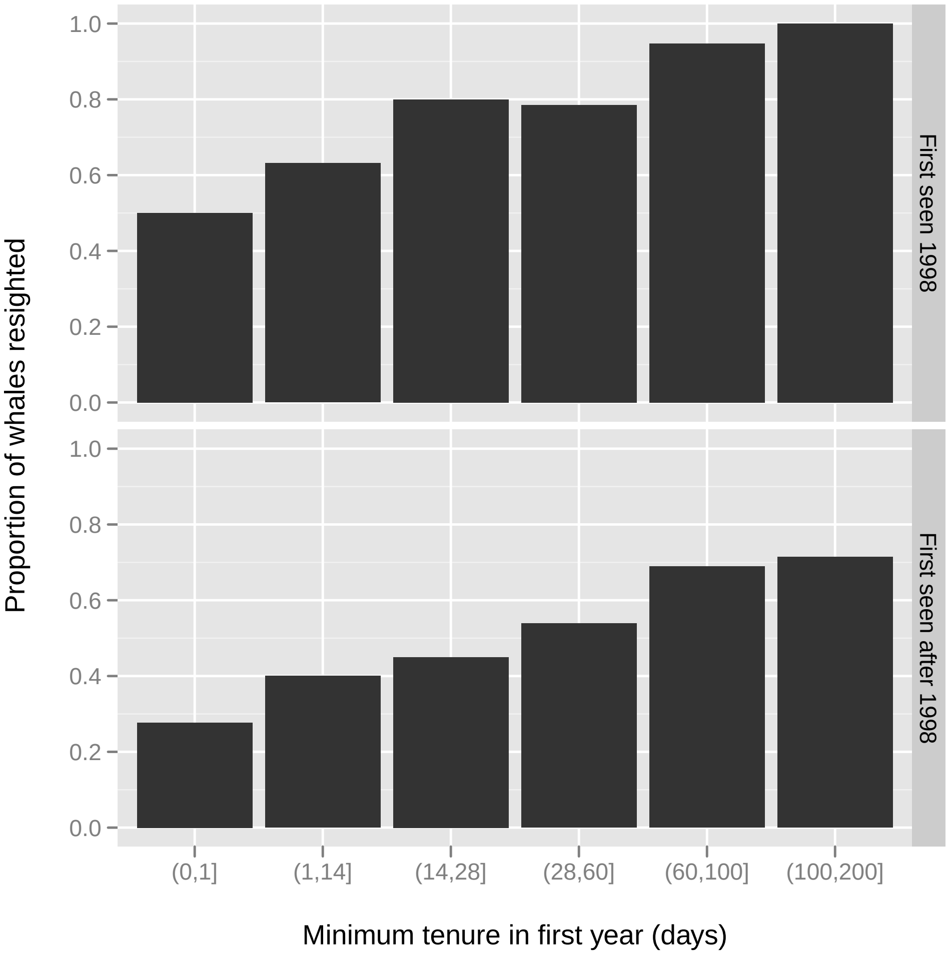

Figure 10: Influence of minimum tenure (MT) in the first year the whale was photographed on the probability it will be re-sighted in one or more following years for whales seen in NCA-NBC for June-November 1998-2010. The bar graphs are divided for 1998 and >1998 because 1998 is the start of the study and it may not be the first year for many of those whales. Re-sightings for 2010 are used but initial sightings for 2010 are excluded because there are no data beyond to evaluate re-sighting probability.

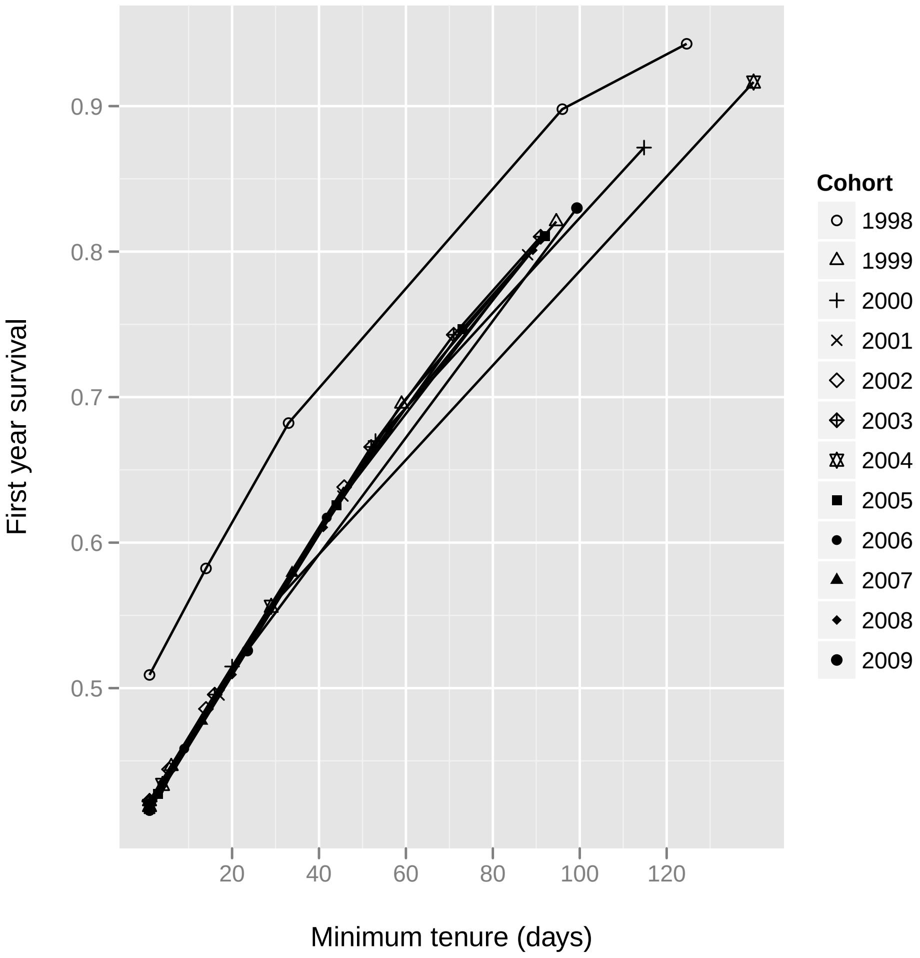

Figure 11: For MUA-SVI analysis of 1998-2010 data, model-averaged estimates of first year survival of non-calves for each cohort at 5%, 25%, 50%, 75%, and 95% quantiles of minimum tenure values for that cohort.

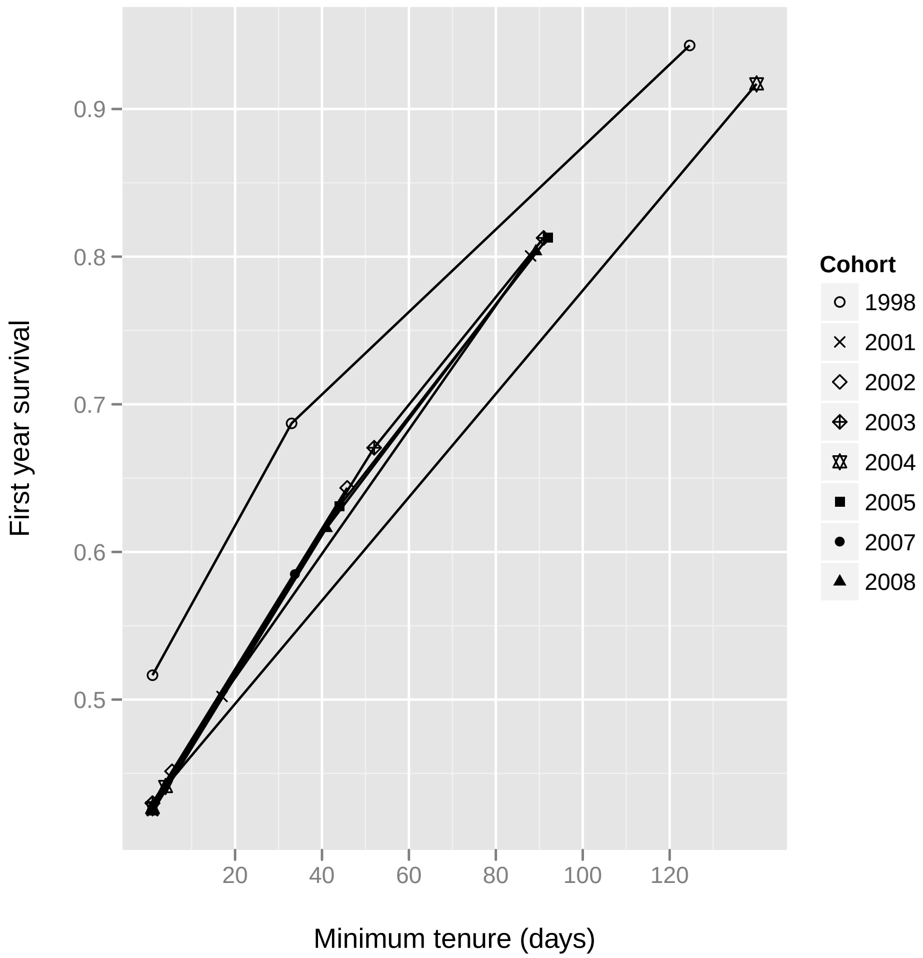

Figure 12: For MUA-SVI analysis of 1998-2010 data, model-averaged estimates of first year survival of calves for each cohort at 5%, 50%, and 95% quantiles of minimum tenure values for that cohort of calves. Cohorts 1999 and 2000 are not shown because no calves were identified in those years.

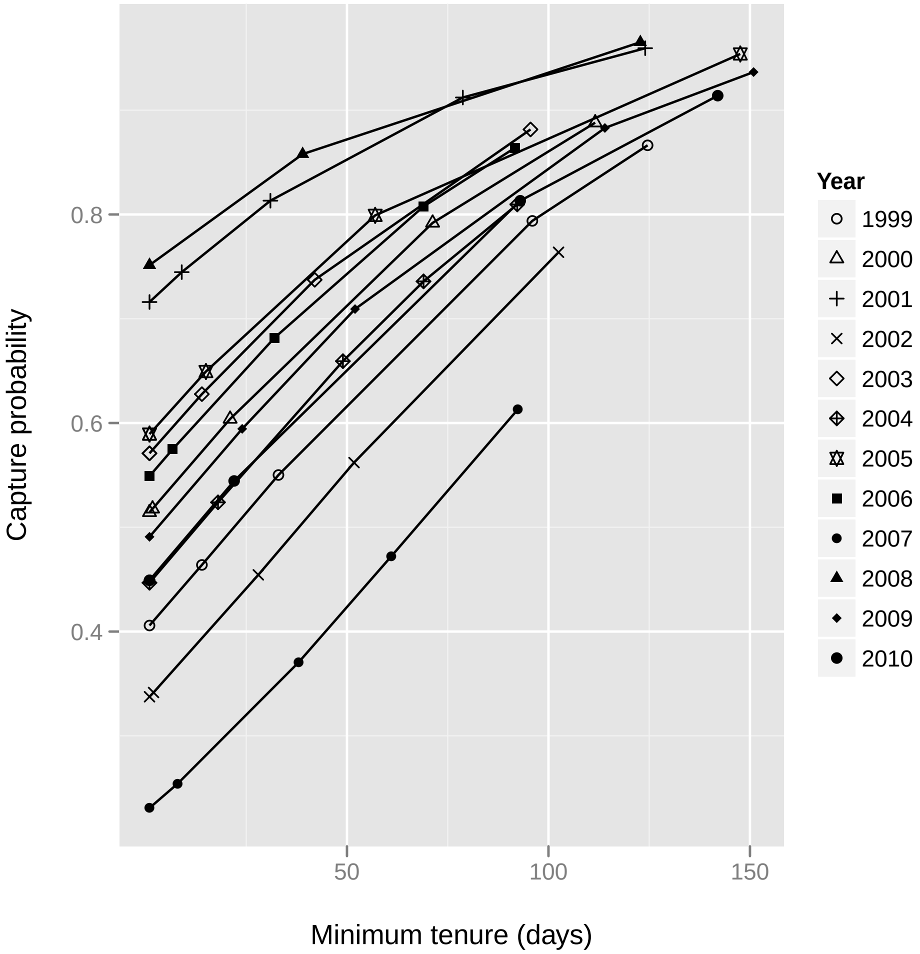

Figure 13: For MUA-SVI analysis of 1998-2010 data, model-averaged estimates of capture probability for each year at 5%, 25%, 50%, 75%, and 95% quantiles of minimum tenure values for whales in the previous year.

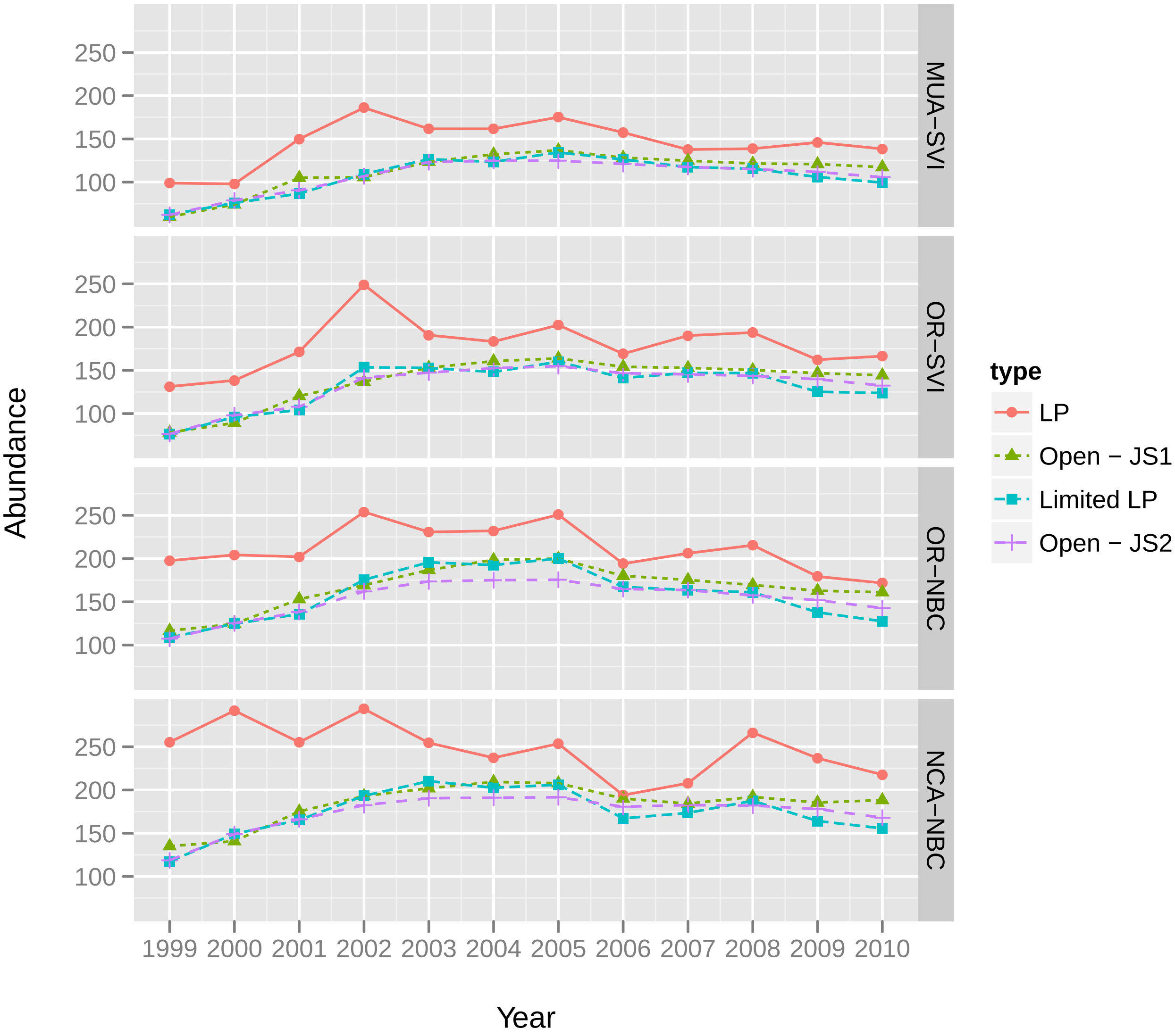

Figure 14: Annual abundance estimates for 1999-2010 in four sub-regions using closed population models, Lincoln-Petersen (LP) and Limited LP and the open (Jolly-Seber; POPAN parametrization) population models using the 2 alternative approaches JS1 and JS2.

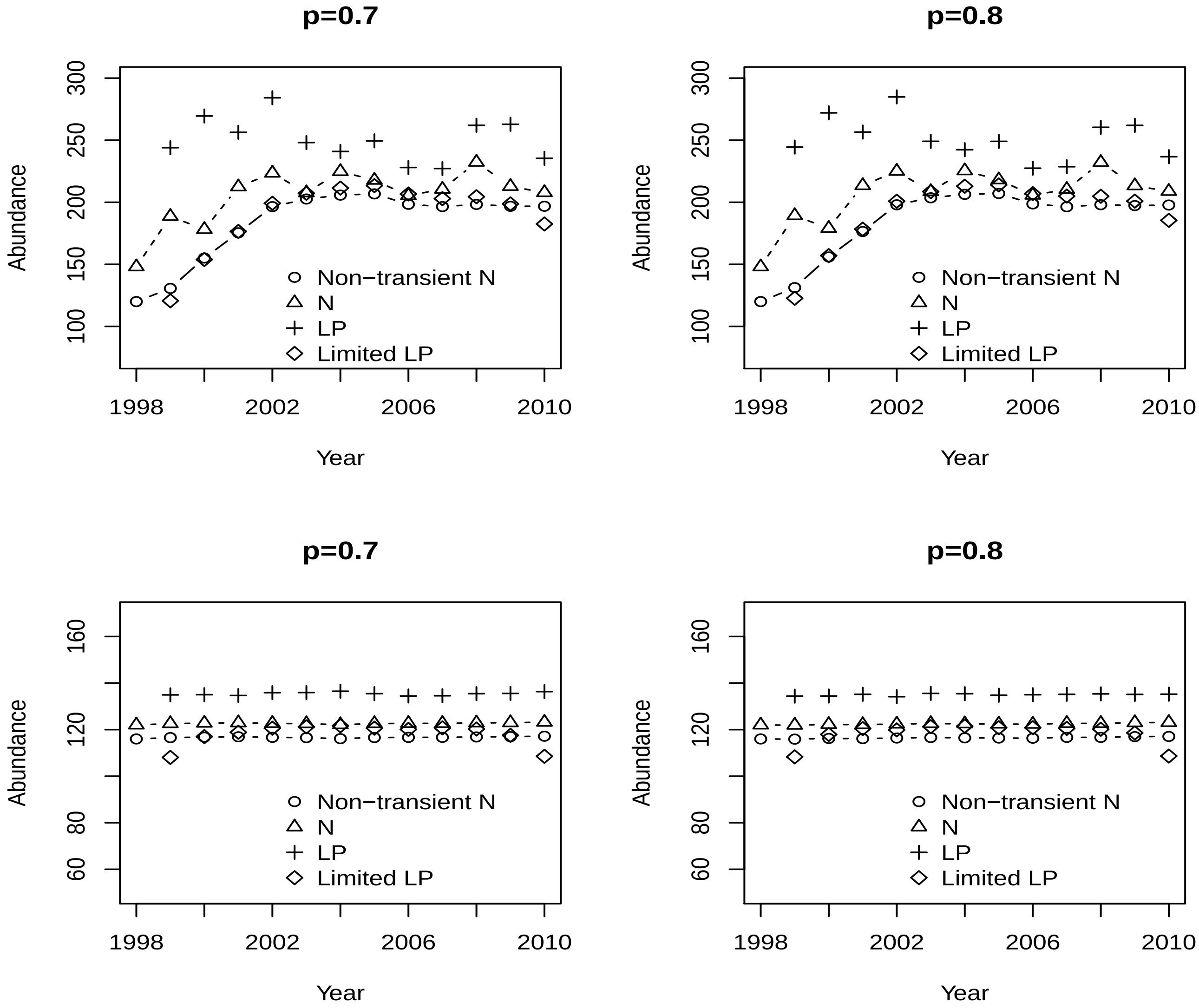

Figure 15: Simulation results for closed estimators with p=0.7 and 0.8 with an increasing trend in non-transients and decreasing trend in transients (upper 2 plots) and no trend (lower 2 plots). The true average simulated non-transient N and total N are shown with lines and the average estimates for LP and limited LP are shown with symbols.

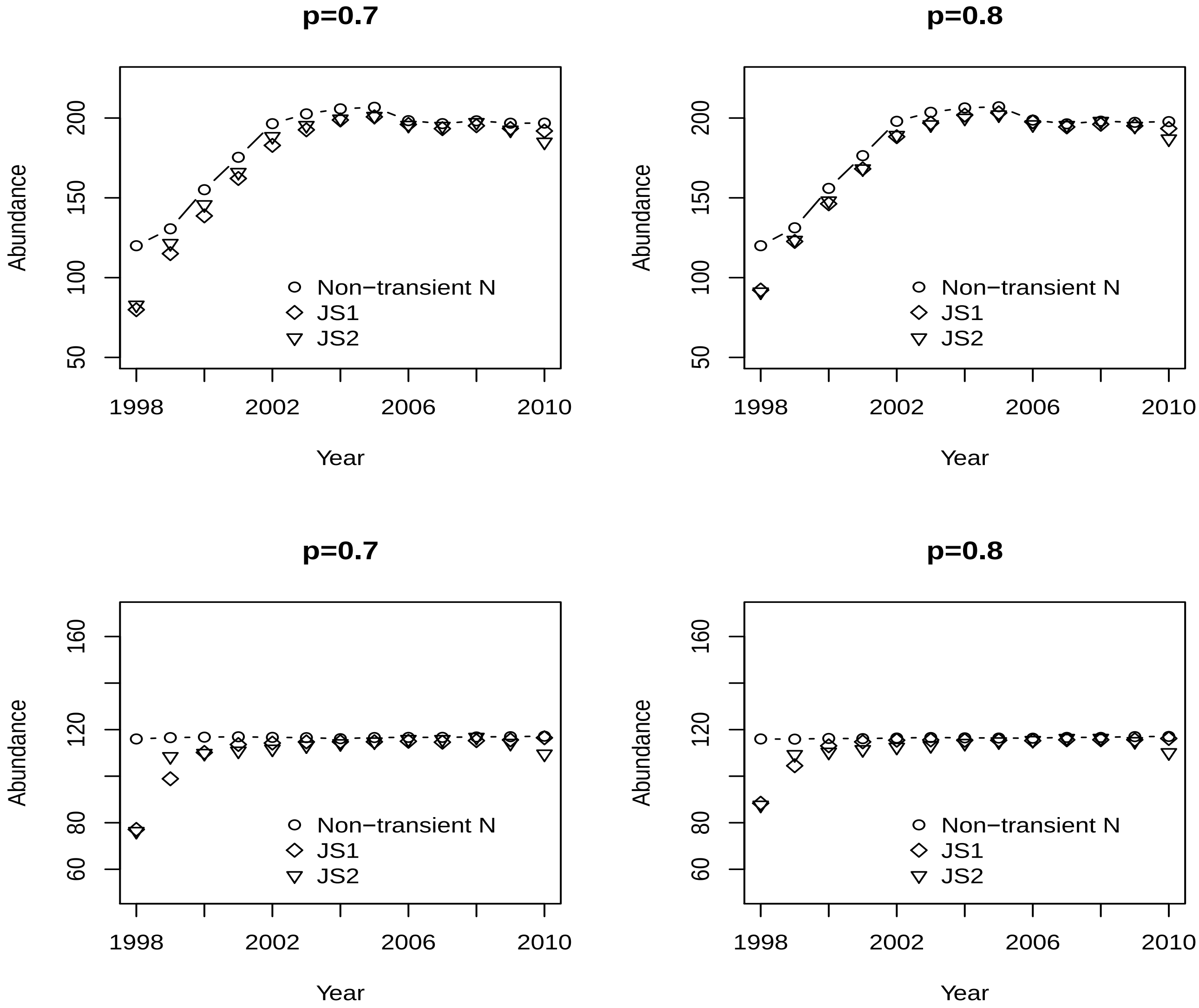

Figure 16: Simulation results for JS estimators with p=0.7 and 0.8 with an increasing trend in non-transients and decreasing trend in transients (upper 2 plots) and no trend (lower 2 plots). The true average simulated non-transient N is shown with the line and the average estimates for JS1 and JS2 are shown with symbols.