Abundance and population structure of seasonal gray whales in the Pacific Northwest, 1998-2008

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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 and short-term studies have examined aspects of the natural history of these animals. We report the results of an 11-year (1998-2008) 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 12,679 identifications representing 872 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 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 three different methods and different geographic scales revealed the abundance of animals to be at most a few hundred individuals. 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 much of the 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, currently proposed to target migrating whales by hunting prior to 1 June.

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 1998, 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, 002b). 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. 002a). 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).

The collaborative effort to collect photographic identifications of gray whales from California to Alaska has continued since 1998 and these data now cover 11 years (1998-2008) 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 2008. 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 briefly summarized below and are listed in Tables 1-2.

o National Marine Mammal Laboratory: NMML obtained identification photographs of 1159 gray whales representing 336 unique individuals sampling all years from 1998 to 2008 (except for 2004) from a variety of locations from northern California to Kodiak, Alaska. Identification photographs were mostly taken while conducting dedicated surveys for gray whales.

o Cascadia Research Collective: Cascadia obtained identifications photographs of gray whales on 1306 occasions representing 372 unique individuals. Surveys were conducted in all years using 5.3 m rigid hull inflatable boat at a wide range of locations from California to Southeast Alaska.

o Humboldt State University: HSU conducted surveys primarily off northern California from 1998 to 2002 and in 2008 and obtained 360 identifications of 156 unique whales.

o Brian Gisborne, Juan de Fuca Express: Brian Gisborne obtained identification photographs every year from 1998 to 2008 primarily along the West Coast trail of southern Vancouver Island during daily trips of this region. He obtained 5318 identifications of 297 unique whales.

o Jim Darling, West Coast Whale Research Foundation: Jim Darling provided identification photographs obtained during surveys along the west coast of Vancouver Island primarily from Clayoquot Sound to Barkley Sound in 1998, 2001, and 2002. These yielded 99 identifications of 59 unique whales.

o Coastal Ecosystems Research Foundation: CERF conducted regular surveys from 1998 to 2008 off British Columbia north of Vancouver Island primarily in the vicinity of Cape Caution. Identification photographs were obtained on 2289 occasions representing 107 unique individuals.

o University of Victoria: UVIC obtained identifications photographs from Clayoquot Sound north along the west side of Vancouver Island every year from 1998 to 2002 except 2001. Identification photographs were obtained on 760 occasions of 137 unique individuals.

o Volker Deecke, independent researcher: Obtained identification photographs of gray whales from 1998 to 2001 and 2006 off British Columbia and in Southeast Alaska including 170 photographs of 74 unique animals.

o Wendy Szanislo, independent researcher: Wendy Szanislo obtained identification photographs of gray whales from 2005 to 2008 along the west coast of Vancouver Island. She obtained 407 identification photographs of 101 unique whales.

o Makah: Makah tribal biologists conducted surveys along the coast of Northern Washington and into the Strait of Juan de Fuca from 2004 to 2008. They obtained 575 photos of 121 unique individuals.

o Other: Various independent researchers that have contributed photographs and related information.

Each year from 1998 to 2008, between 545 and 1490 identifications were obtained of gray whales totaling 12679 photos of 872 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 groups varied somewhat but were similar in identification procedures. When a gray whale was found, 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 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. We also photographed the ventral surface of the flukes for identification when possible. The latter method was not as reliable as the sides of the whale because the 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 does not change over the years we have tracked whales. 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-SEAK: the survey regions from Northern California (NCA) through Southeast Alaska (SEAK), 2) OR-NBC: survey regions from southern Oregon through Northern Vancouver Island/British Columbia (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 the eleven years of data from 1998-2008. For example, the capture history 01001001000 could represent a gray whale photographed in 1999, 2002 and 2005 in the PCFA. The same gray whale may have had a capture history 01001000000 for a smaller spatial scale such as OR-SVI or may not have been seen at all (00000000000) 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. Due to births/immigration and mortality/emigration, closure would not be a reasonable assumption for the 11 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. Thus, it was assumed that all whales that were available to be photographed from June-November, 1998 were also available to be photographed from June-November 1999 and vice versa. If new whales joined in 1999 or whales from 1998 did not return in 1999, the closure assumption would be violated. A sequence of abundance estimates can be constructed using each consecutive pair of years (e.g., 1998-1999,1999-2000, etc). It is well known that the LP estimator can be unbiased even if there are losses or gains (Seber 1982) but not both (Kendall 1999) except for a completely random movement model. A completely random movement model is unlikely in this case because with more than 20,000 whales there would be few if any matches between years if movement in and out of the area 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 for 1999-2000 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 transients their removal was unavoidable using this approach. This was done for each year pairing and we have called this estimation method “Limited LP”.

2.2.2 Abundance using open population models

In addition to the closed models, we fitted open population models to the 11 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 June-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 PCFA. We also 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 (i.e., longer MT) in the PCFA were more likely to return. Likewise, previously seen whales were more likely to be seen in the following year (y+1), if they stayed longer in year y. Calambokidis et al. (2004) postulated that these observations were consistent with whale behavior that was determined by foraging success/failure.

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. To accommodate the "transient" effect, the whales were divided into cohorts based on the year in which they were first seen. Each cohort's first year survival was allowed to vary from subsequent survivals. "Newly seen" is not a particularly useful concept for the first year of the study (1998), because all whales are 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 1999-2007 and another model in which each cohort had a different first year survival. 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 there probability of returning to the PCFA might be higher. In total we considered 8 models for survival (Table 5).

A cohort-specific super-population size was estimated for each cohort. These sizes were estimates of the number of whales that used the PCFA (or subset) during the sampling period for their first time. The estimated population size will be as large or larger than the number of whales newly seen during the year. This was a departure from Calambokidis et al. (2004) who assumed that all whales that were in the PCFA (or subset) were never missed and that capture probability reflected temporary emigration. In effect, Calambokidis et al. (2004) assumed each cohort super-population size was the number that were observed. The accidental discovery of a large number of whales in an area far offshore of Oregon in 2007 (Oleson et al. 2009; Calambokidis et al. 009b) made it particularly clear that this was a poor assumption. Thus, here we have not made this restrictive assumption and have chosen to use the standard assumption in JS models that newly seen whales have the same capture probability as previously seen whales. Lacking broad-scale data from a prior year, to estimate a cohort size for 1998 we had to assume that detection probability in 1998 was the same as in 1999 to make the former parameter estimable. We fitted 3 models for capture probability that varied by time (year) and/or varied by MT in the previous year (Table 5).

We used the individual covariate MT which was both whale and time-specific but we don't know those values for whales that were not caught. Thus, to fit these models we assumed that the covariate values for missed whales was the same as the average covariate value of captured whales. This was accommodated by centering the covariate values in each year such that the median was 0. Missed whales ("0" in the capture history) were assigned a value MT=0 and abundance estimation for each year was based on the median MT (centered 0 value).

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 18 fitted models. Model averaging was used for all 18 models to compute estimates and unconditional standard errors and confidence intervals.

3 Results

The database from all eleven years (1998-2008) contains 12679 records; however 1930 are replicate identifications of whales on the same day. The database contains photographs of 872 unique whales seen from Southern California to Kodiak, Alaska with an average of 12.3 sightings/whale (range: 1- 202) where a "sighting" is one or more photographs on a day. Only 51.9% 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 PCFA 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 872 unique whales, 204 whales were only seen before 1 June and 84.3% of those were only sighted once. In comparison, of the 668 whales sighted between June and November, 40% were only sighted once. If sightings in Alaska are excluded, then only 32.7% of the 566 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 the identifications are divided into subsets of survey regions (Figure 4). In particular, the difference across months is not as strong for regions such as the 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. The pattern across months is also weaker for Southern Vancouver Island

(SVI) which is in the main migration corridor; however, that is due to sampling efforts being focused on the spring herring spawn in Barkley Sound (effectively an inland waterway) and therefore undersampling 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. These observations are 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 will occur in NWA after 30 November and prior to 1 June. There have been 74 whale sightings in NWA prior to 1 June of which 20.3% (15) were of whales that were seen in the PCFA after 1 June at some time. All of those whales were sighted after 1 June in SVI and over 80% (12 whales) were seen in MUA (Figure 5). Of those 12 whales, 11 were seen in NWA, 9 were seen in SJF and only 1 whale was seen in SJF that was not seen in NWA. In comparison, 23 whale sightings were in SJF prior to 1 June of which 82.6% (19) were of whales that were seen in the PCFA 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 PCFA. Therefore, with a proposed hunt in the winter/spring in NWA, an assessment of impact on whales in the PCFA needs to consider a target population of whales contained in MUA and SVI after 1 June because all or most of the whales seen in the NWA before 1 June and seen after 1 June in the PCFA are likely to be found in the MUA and SVI.

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. 009b).

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 57-73% of the whales were seen at some point within MUA-SVI (Figure 6). However, whales seen in California or Alaska were much less likely to be seen in MUA-SVI.

If we look at latitudes of sightings of individual whales across the 11 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 40% of the whales (Figure 8) and it was more than 180 nautical miles for more than 15% 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 1998-2008 in the PCFA (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 PCFA 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 capture-recapture models for abundance estimation. For example, 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

While a relatively low proportion of calves have been sighted from the summer and fall sightings of gray whales, 33 different gray whales identified as PCFA whales were seen as definite or probable mothers with calves representing 41 likely births, six whales were seen with calves multiple seasons (two or three) (Table 11). Two individuals were sighted with calves in three years, the most we documented, however, in both cases one of these calves was documented outside the 1998 to 2008 primary study period. One individual (ID#81) was observed with a calf in 2001, 2003, and 2009 (not all data from 2009 has been analyzed) and the other individual (ID#67) was seen with a calf in 1995, 2002 and 2004.

Four of the 41 calves occurred outside our primary study period, three prior to 1998 and one known female who was known to have a calf in 2009, leaving 37 or just over three per year during our primary study period 1998-2008 (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 41 sightings. During this 4-year period an average of 7 calves were seen while an average of just over one calf per year was seen in the other seven years (9 calves in 7 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.

In 18 cases, a calf was seen associated with its mother early in the season and then either the mother or the calf was resighted later in the season apart, suggesting weaning had occurred. The latest a mother was 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 seven cases the weaning had occurred prior to a July sighting (and possibly earlier).

Of the 33 likely mothers documented, 20 had been seen four or more years in the study area (13 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 including every years from 1999 to 2007. In only one of those years was she with a calf (2002). In 2008, however, she was seen on 19 April off Santa Barbara, Southern 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 Southeast 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 (Northern California to Southeast 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 other 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 39 calves or suspected calves identified with their mothers through 2008 in the study area. Just under half of these (18) had been seen only in the year they were calves and 21 (54%) had been resighted in years after they were calves. Using only the 30 calves seen through 2004 (to allow a 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, or 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 PCFA 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-SEAK. For those regions, we estimated over-dispersion values of $\widehat{c}$=2.11 and $\widehat{c}$=2.28 respectively, to adjust AICc and estimated standard errors. The lack of fit for OR-NBC and NCA-SEAK is probably related to the inclusion of NCA, WVI and NBC which are at the fringes of the PCFA. 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. For φ the best model depended on the spatial scale. For MUA-SVI and OR-SVI, model 7 was best with some support for model 8. For OR-NBC and NCA-SEAK, simpler models for φ with fewer parameters were supported due to the assumed over-dispersion. As shown in Calambokidis et al. (2004), the analysis demonstated 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. First year survival estimates were dominated by permanent emigration. For MUA-SVI, the estimates varied from 0.18 to 0.47 for non-calf whales with MT=1 in their first year and from 0.63 to 0.93 for MT>80 in their first year (Figure 11). For calves, they were more variable but generally higher presumably because they were more likely to return in a following year. Survival subsequent to the first year was assumed to be constant and represent true survival assuming there was little permanent emigration after the first year. Those estimates were 0.951 (se=0.0112), 0.95 (se=0.0098), 0.948 (se=0.0123) and 0.945 (se=0.0118)for MUA-SVI, OR-SVI, OR-NBC, NCA-SEAK respectively. For the analysis of MUA-SVI, there was large year to year variation in capture probability from 0.18 to 0.94 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.

3.5 Abundance and Recruitment

For MUA-SVI, OR-SVI, OR-NBC, and NCA-SEAK annual estimates of abundance were constructed with LP, Limited LP and model averaged values for the POPAN models (Figure 14, Tables 16-21). Estimates are only shown for 1999-2008 because with the closed models only 10 estimates can be constructed with the 11 years of data. In general, the estimates from the POPAN models are intermediate between the higher estimates from LP and lower estimates of Limited LP. This was expected because Limited LP estimates the abundance of whales excluding transient whales; whereas, LP attempts to estimate a total abundance which includes transient whales except that it is positively biased because there are losses and gains in each set of years. The POPAN models allow for gains and losses and the estimate of abundance each year includes the estimate of the new whales that entered that year and the number that have survived (i.e., lived and did not permanently emigrate) from whales seen in previous cohorts. The annual abundance estimate from the POPAN models includes some transient "new" whales that will permanently emigrate and thus should be higher than the Limited LP estimate which excludes transients. The abundance estimates from Limited LP for 2008 are biased low because new whales that enter that year have no chance to be re-sighted and thus they excluded even though some may return in the ensuing years. To a lesser degree, the estimates of 2007 and possibly 2006 are influenced in a similar manner because the whales may have been simply not seen yet even though they are returning.

Excluding the LP estimator which will be biased high and the Limited LP estimates for 2008 which will be biased low, the most recent N_{min}values range from 109 (Table 18) to 211 (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 ran calculations using the MMPA's Potential Biological Removal (PBR) formula (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 this group of whales would be 2.2 to 4.3. For the smallest region considered (MUA-SVI), the PBR would range from 2.2 to 2.5 whales for the 2007 limited LP (Table 18) and 2008 POPAN estimates (Table 20).

New whales have continually appeared annually and many of these new whales have subsequently returned and been re-sighted (Table 14). In MUA-SVI from 1999-2008, an average of 22.7 (range: 5.0, 56.0) new whales were seen each year. Of these new whales, on average 10.1 (range: 1.0, 19.0) whales returned and were seen in subsequent years. While these numbers vary annually there has been sufficient numbers of newly seen whales to replace a removal of at least 2 whales annually.

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. 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 or slightly less than the estimates from the Open models because the latter include stragglers that were present in each year. However, the Open models are not biased like the unadjusted Lincoln-Petersen because they include a first year "survival" that is lower for those whales because they are less likely to return. The Open models should provide a better estimate of the annual number of whales that are present.

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. (in prep.) have examined mtDNA differences in a larger sample of gray whales from Vancouver Island than tested by Steeves et al. (2001) and found significant differences in the haplotype frequencies between that sample and data reported for the breeding lagoons off Mexico. The Frasier et al. (in prep) study has had some limitations including samples taken from a single primary location off Vancouver Island, comparison to the breeding lagoons (where genetic differences in the lagoons have also been reported), and no verification by microsatelite analysis that whales have not been duplicated. However, Frasier et al. (in prep) provides 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. 009a). 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 non-migratory 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 few hundred animals depending on the estimating method and how broadly the region is defined geographically.

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Table 1: Contributions of numbers of photos and resulting number of uniquely identified whales by reseach group for 1998-2008. Totals for whales are unique whales across all research groups.

	Photos	Whales	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
B. Gisborne	5318	297	371	343	779	585	435	882	325	429	527	117	525
CERF	2289	107	101	145	243	456	290	173	779	11	42	11	38
CRC	1306	372	168	230	118	79	135	112	172	33	62	102	95
HSU	360	156	21	89	60	75	71	0	0	0	0	0	44
J. Darling	99	59	50	0	0	35	14	0	0	0	0	0	0
MAKAH	575	121	0	0	0	0	0	0	44	58	142	84	247
NMML	1159	336	132	194	133	128	88	76	0	133	93	39	143
Other	236	118	4	12	1	1	0	7	0	1	42	120	48
UVIC	760	137	351	159	128	0	121	0	0	0	0	1	0
V. Deecke	170	74	39	42	28	11	0	0	0	0	50	0	0
W. Szanislo	407	101	0	0	0	0	0	0	0	125	67	71	144
Photo Totals	12679	1878	1237	1214	1490	1370	1154	1250	1320	790	1025	545	1284
Whale Totals		872	156	248	176	198	253	178	195	205	185	157	222

Table 2: Regional distribution of numbers of photos and resulting number of uniquely identified whales by reseach group for 1998-2008. 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
B. Gisborne	0	0	0	0	0	0	0	1	0	5155	160	2	0	0
CERF	0	0	0	0	0	0	0	0	0	0	0	2289	0	0
CRC	19	85	185	138	201	86	23	66	343	33	0	120	7	0
HSU	0	323	0	37	0	0	0	0	0	0	0	0	0	0
J. Darling	0	0	0	0	0	0	0	0	0	6	93	0	0	0
MAKAH	0	0	0	0	0	153	422	0	0	0	0	0	0	0
NMML	0	4	34	0	0	267	275	0	22	196	177	13	0	171
Other	13	1	0	118	0	1	8	11	35	4	0	4	16	25
UVIC	0	0	0	0	0	0	0	0	0	1	759	0	0	0
V. Deecke	0	0	0	0	0	0	0	1	0	122	0	43	4	0
W. Szanislo	0	0	0	0	0	0	0	0	0	214	193	0	0	0
Photo Totals	32	413	219	293	201	507	728	79	400	5731	1382	2471	27	196
Whale Totals	24	159	79	92	91	170	110	32	43	294	209	114	21	108

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-SEAK	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	x			
(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. 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. MT is minimum tenure (centered so median is 0 each year) of a whale in its first year and 0 otherwise. $\beta_{Fy,1999}$ is for cohorts 1999-2007 and $\beta_{Fy,C}$ represents 9 cohort specific parameters for 1999-2007 (for the first year survival). β_{CF} is an adjustment for calf first year survival andβ_{CM} is an adjustment for calves to the slope of MT for survival. For the capture probability models, β_t has 9 levels for t=2000,...2008 and β_0 represents 1998 and 1999 value. Each POPAN model includes 11 parameters for the initial sizes of the 11 year cohorts.

Model	Parameter Logit Formula	Number of parameters
φ		
1	$\beta_0 + \beta_{Fy} Fy$	2
2	$\beta_0 + \beta_{Fy} Fy + \beta_M MT\, Fy$	3
3	$\beta_0 + \beta_{Fy,1998} Fy + \beta_{Fy,1999}(1 - Fc) Fy$	3
4	$\beta_0 + \beta_{Fy,1998} Fy + \beta_{Fy,1999}(1 - Fc) Fy + \beta_M MT\, Fy$	4
5	$\beta_0 + \beta_{Fy,1998}\, Fy + \beta_{Fy,1999}(1 - Fc)\, Fy + \beta_{M,1998} MT\, Fy + \beta_{M,1999}(1 - Fc)\, MT\, Fy$	5
6	$\beta_0 + \beta_{Fy,1998} Fy + \beta_{Fy,C} Fy\,(1 - Fc) + \beta_M MT\, Fy$	12
7	$\beta_0 + \beta_{Fy,1998} Fy + \beta_{Fy,C} Fy\,(1 - Fc) + \beta_M MT\, Fy + \beta_{CF} C\, F_y$	13
8	$\beta_0 + \beta_{Fy,1998} Fy + \beta_{Fy,C} Fy\,(1 - Fc) + \beta_M MT\, Fy + \beta_{CF} C\, F_y + \beta_{CM} C\, MT$	14
p		
1	$\beta_0 + \beta_t$	10
2	$\beta_0 + \beta_t + \beta_M MT$	11
3	$\beta_0 + \beta_M MT$	2

Table 6: Regional distribution of numbers of whales seen by month for 1998-2008.

	1	2	3	4	5	6	7	8	9	10	11	12
CA	0	0	0	7	4	0	6	6	1	0	0	0
NCA	0	0	0	0	2	38	83	31	13	56	15	0
SOR	0	0	0	2	0	0	22	22	48	25	0	0
OR	0	0	0	0	2	7	30	47	41	34	0	0
GH+	2	0	10	39	14	15	2	0	27	1	0	0
NWA	0	0	4	6	63	18	44	68	49	28	4	0
SJF	0	0	2	9	8	11	21	26	46	68	44	11
PS-HC-BB-SJ	0	1	3	15	6	6	5	2	1	1	2	0
NPS	0	0	15	23	28	10	0	0	0	0	0	0
SVI	1	0	50	24	70	164	198	152	115	34	3	2
WVI	0	1	1	5	0	38	133	125	85	15	0	0
NBC	0	0	0	0	2	24	75	100	80	0	0	0
SEAK	0	0	0	0	0	12	4	1	3	0	5	0
KAK	0	0	0	0	0	0	23	52	44	0	0	0

Table 7: Regional distribution of numbers of whales seen during June-November for 1998-2008.

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
CA	0	1	0	5	0	0	4	0	3	0	0
NCA	15	38	27	32	37	15	3	0	0	1	47
SOR	0	0	0	2	46	24	13	1	0	23	15
OR	17	31	8	15	0	0	16	4	9	38	6
GH+	0	1	1	1	0	0	1	0	0	38	0
NWA	21	7	10	31	8	19	0	19	44	13	27
SJF	15	4	4	2	1	9	21	18	20	14	49
PS-HC-BB-SJ	3	8	4	0	0	0	0	1	0	0	0
NPS	0	0	10	0	0	0	0	0	0	0	0
SVI	60	45	52	102	66	90	86	91	70	34	77
WVI	57	66	53	29	85	9	0	54	40	13	23
NBC	23	26	23	40	44	51	91	12	21	5	21
SEAK	5	6	0	1	0	6	0	1	2	3	0
KAK	0	0	0	0	42	4	0	48	0	0	23

Table 8: Number of days in which whales were seen for each region and year from 1998-2008 from 1 June - 30 November.

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
CA	0	1	0	2	0	0	2	0	1	0	0
NCA	7	8	20	13	20	2	2	0	0	2	9
SOR	0	0	0	1	4	1	1	1	0	3	1
OR	6	9	5	7	0	0	1	1	7	38	1
GH+	0	1	1	1	0	0	1	0	0	3	0
NWA	22	10	7	11	4	9	0	12	13	7	11
SJF	15	9	8	4	1	15	5	14	17	25	34
PS-HC-BB-SJ	3	11	4	0	0	0	0	2	0	0	0
NPS	0	0	1	0	0	0	0	0	0	0	0
SVI	91	87	82	55	68	66	48	73	59	36	72
WVI	54	46	28	7	10	3	0	6	14	27	31
NBC	39	50	53	43	34	29	53	11	16	9	13
SEAK	2	3	0	1	0	3	0	1	2	2	0
KAK	0	0	0	0	4	2	0	7	0	0	5

Table 9: Interchange of whales across regions for all years (1998-2008) for June-November. The diagonal is the number of unique whales seen in that region over the 11 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	13												
NCA	0	158											
SOR	3	33	77										
OR	1	34	39	91									
GH+	1	7	7	10	40								
NWA	0	24	32	42	16	108							
SJF	0	9	8	19	13	44	99						
PS	0	0	0	0	0	1	1	24					
SVI	4	40	39	54	29	91	61	1	250				
WVI	2	29	28	45	23	68	52	1	140	203			
NBC	2	8	9	21	14	28	25	1	73	70	112		
SEAK	0	1	1	1	1	2	3	0	7	8	10	21	
KAK	0	4	1	3	0	1	0	0	7	6	6	1	108

Table 10: Number of photographs by month in all regions and years(1998-2008)for a sample of whale IDs.

	1	2	3	4	5	6	7	8	9	10	11	12
6	0	0	0	0	2	1	1	4	3	2	0	0
73	0	0	0	0	0	0	5	3	0	0	0	0
123	0	0	0	0	0	22	54	18	6	1	0	0
175	0	0	0	0	4	21	35	35	19	4	1	0
226	0	0	0	0	1	10	29	20	12	1	0	0
252	0	0	0	0	0	0	0	0	0	0	1	0
273	0	0	1	6	1	0	0	0	0	0	0	0
300	0	0	0	0	2	14	42	22	12	2	0	0
322	0	0	0	0	0	3	19	10	8	2	0	0
362	0	0	0	0	0	0	0	1	0	0	0	0
383	0	0	5	22	2	0	0	0	0	0	0	0
405	0	0	0	0	2	0	0	0	0	0	0	0
428	0	0	0	0	0	0	1	0	0	0	0	0
451	0	0	0	0	0	0	1	2	2	0	0	0
476	0	0	0	0	0	0	2	0	0	0	0	0
507	0	0	0	0	0	0	4	8	10	1	0	0
529	0	0	0	0	0	7	18	13	11	2	0	0
553	0	0	0	0	0	0	1	0	0	0	0	0
574	0	0	0	0	0	3	3	0	0	0	0	0
595	0	0	0	0	0	3	0	0	0	0	0	0
618	0	0	0	0	0	0	0	0	1	0	0	0
639	0	0	0	0	0	0	1	2	0	1	0	0
664	0	0	0	0	0	0	0	1	0	0	0	0
691	0	0	0	0	0	5	3	6	2	0	0	0
713	0	0	0	0	0	0	0	0	1	0	0	0
734	0	0	0	0	0	0	0	3	0	0	0	0
755	0	0	0	0	0	0	0	1	0	0	0	0
776	0	0	0	0	0	1	0	0	0	0	0	0
802	0	0	0	0	0	0	1	0	0	0	0	0
823	0	0	0	0	0	0	5	3	6	1	0	0
848	0	0	0	1	0	0	0	0	0	0	0	0
869	0	0	0	0	0	0	0	1	0	0	0	0
892	0	0	0	0	0	0	0	0	4	0	0	0
917	0	0	0	0	0	0	0	0	1	0	0	0
941	0	0	1	0	0	0	0	0	0	0	0	0
963	0	0	0	0	0	1	1	0	0	0	0	0
984	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
1029	0	0	0	0	0	0	1	0	0	0	0	0
1051	0	0	0	0	0	0	1	0	4	4	0	0
1072	0	0	0	0	0	0	1	0	0	2	0	0
1094	0	0	0	0	0	0	1	0	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 in bold with an asterisk. Total years seen includes 9 sightings of whales during 1984,1988, 1990-1992 that are not shown but no calves were seen in those few cases.

Mother ID	Calves	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	Years seen
43	2	21-Jul	**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	14-Jul	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	14-Jul		19-Aug		23-Sep	14-Jun	21-Jun	29-Jul	**20-Jun***	24-Jun	**28-Jul***	23-Jul	3-Jul	4-Jul	16-Jun		**NA***	13
91	1	1-Aug					23-Jun		22-Jul	15-Aug	**5-Jul***	17-Jun		23-Jun		11-Jul	18-Jun		9
92	1	1-Aug			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		14
93	1	1-Aug			17-Jul	23-Sep	14-Jun	22-Jun	12-Aug	21-Jun	16-Jul	2-Aug	**30-Jun***		4-Jul		18-Jun		13
94	1	31-Jul	4-Aug				27-Jun	6-Jul	24-Jul	7-Jul	15-Jul	23-Jul	5-Aug	13-Jul	18-Mar	**8-Jul***	8-Jul		13
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		17
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						3
143	1						27-Jun	29-Jun	1-May	6-Jul	**29-Jul***	17-Aug		5-Sep	12-Mar	24-Mar	22-Jun		10
144	1						11-Jul	13-Aug	6-Sep	6-Jul	**5-Jul***	30-Mar	19-Jun	26-May	4-Jul	31-Mar	25-May		11
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***		11
291	1						1-Oct	12-Jul	24-Aug	**8-Jun***	4-Aug	25-Jun	24-Jul	21-Jul	5-Jul		20-Oct		10
312	1						**12-Jun***			7-Jul									2
321	1						**25-Jun***												1
372	1							26-Jun	9-May		4-Aug	15-Jul	**25-Jun***	7-Jul	3-Jul	1-Sep			8
575	1									**5-Jun***									1
581	1									**5-Jun***					4-Jul	30-Jun			3
596	1									**26-Jun***	3-Jul								2
612	1								23-Jun	**1-Aug***	1-Jul	5-Jun	1-Jul	18-Jul	5-Nov				7
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***			1
993	1														1-May	**14-Aug***			2
Calves	41	0	2	1	0	0	2	0	0	9	9	5	5	3	0	3	1	1	

Table 12: Sighting histories of calves identified in the study area. First separate date represents sighting of either the calf or mother alone.

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	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
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
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

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	46.9987	16	1e-04
		Test 3	133.6637	17	0
		Total	180.6624	33	0
	Separate				
		Test 2	45.0847	36	0.1425
		Test 3	0	0	1
		Total	45.0847	36	0.1425
OR-SVI	Pooled				
		Test 2	55.7052	18	0
		Test 3	176.8239	17	0
		Total	232.5292	35	0
	Separate				
		Test 2	51.341	40	0.1079
		Test 3	0	0	1
		Total	51.341	40	0.1079
OR-NBC	Pooled				
		Test 2	84.9913	13	0
		Test 3	300.1332	17	0
		Total	385.1245	30	0
	Separate				
		Test 2	75.7837	36	1e-04
		Test 3	0	0	1
		Total	75.7837	36	1e-04
NCA-SEAK	Pooled				
		Test 2	97.2429	13	0
		Test 3	352.5911	17	0
		Total	449.834	30	0
	Separate				
		Test 2	79.777	35	0

Table 14: Number of whales seen each year, number that were new that year, and number that were new and were seen in a subsequent year for whales seen between June-November 1998-2008 in each region.

Region		1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
MUA-SVI	Seen	73	48	60	116	68	96	95	104	92	45	103
	Non-calf: New	73	13	23	56	22	31	25	21	12	5	19
	Non-calf: New and Re-sighted	53	8	15	18	9	19	9	8	4	1	0
	Calf: New	1	0	0	5	6	3	5	3	0	1	0
	Calf: New and Re-sighted	0	0	0	2	4	3	3	1	0	1	0
OR-SVI	Seen	84	71	67	129	103	110	114	109	99	113	119
	Non-calf: New	84	26	26	58	40	26	29	21	11	24	20
	Non-calf: New and Re-sighted	63	12	17	19	20	17	11	9	3	3	0
	Calf: New	1	0	0	6	7	3	5	3	0	2	0
	Calf: New and Re-sighted	0	0	0	3	5	3	3	1	0	1	0
OR-NBC	Seen	116	120	113	151	179	154	177	138	129	118	135
	Non-calf: New	116	50	37	54	51	26	35	22	8	25	22
	Non-calf: New and Re-sighted	92	16	21	19	26	16	11	9	1	2	0
	Calf: New	3	0	0	6	9	3	5	3	0	3	0
	Calf: New and Re-sighted	0	0	0	3	7	3	3	1	0	1	0
NCA-SEAK	Seen	135	157	137	175	205	161	179	138	131	121	172
	Non-calf: New	135	77	53	66	56	25	32	22	8	23	48
	Non-calf: New and Re-sighted	103	18	30	25	22	14	9	10	1	3	0
	Calf: New	3	0	0	6	9	3	5	3	0	3	0
	Calf: New and Re-sighted	1	0	0	3	7	3	3	1	0	1	0

Table 15: Delta AICc and QAICc (for OR-NBC and NCA-SEAK models) for 18 models fitted to each set of data.

		φ Model							
Region	p model	1	2	3	4	5	6	7	8
MUA-SVI	1	72.8	41.1	62.6	33.1	41.5	33.2	31.7	33.8
	2	44.8	12.6	33.6	3.5	5.2	2.9	0.0	2.2
	3	132.8	97.0	125.0	92.1	93.7	89.2	87.3	89.4
OR-SVI	1	114.6	70.5	96.0	53.5	55.1	45.6	44.8	46.4
	2	72.4	27.0	52.4	8.4	10.2	1.8	0.0	1.6
	3	106.5	55.9	93.1	45.8	47.5	36.6	34.9	36.1
OR-NBC	1	76.9	60.5	27.2	35.1	35.9	32.0	33.9	35.8
	2	46.1	29.7	27.2	2.4	3.4	0.0	1.7	3.6
	3	69.6	51.8	53.1	28.8	30.3	27.2	28.9	30.7
NCA-SEAK	1	80.4	60.1	58.6	30.9	31.8	34.4	35.7	37.6
	2	52.2	31.4	28.8	0.0	1.1	4.7	5.7	7.6
	3	82.0	58.7	62.3	33.2	34.9	36.6	37.4	39.2

Table 16: Number of whales seen in each year and number seen in both years and abundance estimate ($\widehat{N}$), standard error and $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ for Lincoln-Petersen estimator applied to consecutive years from 1998-2008 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	92	61	156	7.4	150
	2007	92	45	30	136	11.6	127
	2008	45	103	33	139	10.1	130
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	99	64	167	7.9	161
	2007	99	113	59	188	10.7	179
	2008	113	119	69	194	9.3	186

Table 17: Number of whales seen in each year and number seen in both years and abundance estimate ($\widehat{N}$), standard error and $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ for Lincoln-Petersen estimator applied to consecutive years from 1998-2008 in OR-NBC and NCA-SEAK 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	129	92	193	6.1	187
	2007	129	118	74	205	9.4	197
	2008	118	135	73	217	10.5	208
NCA-SEAK	1999	135	157	80	264	13.1	253
	2000	157	137	74	289	16.5	275
	2001	137	175	93	257	10.2	248
	2002	175	205	121	295	9.5	287
	2003	205	161	126	261	6.7	255
	2004	161	179	118	243	6.7	238
	2005	179	138	97	254	9.4	246
	2006	138	131	94	191	5.9	186
	2007	131	121	74	213	10.1	204
	2008	121	172	76	272	14.1	260

Table 18: Number of whales seen in each year and number seen in both years and abundance estimate ($\widehat{N}$), standard error and $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ for limited Lincoln-Petersen estimator applied to consecutive years from 1998-2008 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	91	55	133	6.3	128
	2006	89	81	58	123	5.0	119
	2007	84	42	30	116	8.9	109
	2008	40	82	31	104	6.8	99
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	85	50	152	9.1	144
	2003	83	99	54	151	8.1	144
	2004	101	96	65	148	6.2	143
	2005	97	96	59	157	7.8	150
	2006	96	89	62	137	5.6	132
	2007	91	93	59	142	6.6	137
	2008	89	95	65	129	4.6	125

Table 19: Number of whales seen in each year and number seen in both years and abundance estimate ($\widehat{N}$), standard error and $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ for limited Lincoln-Petersen estimator applied to consecutive years from 1998-2008 in OR-NBC and NCA-SEAK 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	155	100	174	3.4	171
	2003	157	143	115	194	4.1	191
	2004	144	153	114	192	4.1	189
	2005	152	122	93	198	6.2	193
	2006	123	119	89	164	4.5	160
	2007	122	96	74	157	5.4	153
	2008	93	110	70	145	5.1	141
NCA-SEAK	1999	96	90	72	119	3.1	117
	2000	97	113	73	149	5.1	145
	2001	112	135	91	165	4.2	162
	2002	129	170	113	193	3.6	190
	2003	174	149	122	212	4.4	208
	2004	150	156	115	203	4.6	199
	2005	156	124	94	205	6.5	199
	2006	124	121	91	164	4.4	160
	2007	124	102	74	170	6.5	164
	2008	98	120	72	162	6.1	157

Table 20: Abundance estimate ($\widehat{N}$), standard error and $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ averaged over open population POPAN models using data from 1998-2008 in MUA-SVI and OR-SVI regions.

Region	Year	$\widehat{N}$	$se(\widehat{N})$	N_{min}
MUA-SVI	1998	78	2.9	75
	1999	64	5.0	60
	2000	81	5.8	76
	2001	130	7.5	124
	2002	113	8.9	106
	2003	121	8.3	114
	2004	143	10.2	135
	2005	136	9.5	128
	2006	129	10.3	121
	2007	125	12.1	115
	2008	136	12.7	125
OR-SVI	1998	88	2.7	86
	1999	88	5.5	83
	2000	99	7.2	93
	2001	144	7.8	138
	2002	143	9.3	136
	2003	134	8.6	127
	2004	167	10.7	158
	2005	157	10.5	148
	2006	146	11.0	136
	2007	164	12.8	153
	2008	153	13.2	142

Table 21: Abundance estimate ($\widehat{N}$), standard error and $N_{min} = \widehat{N}e^{-0.864\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ averaged over open population POPAN models using data from 1998-2008 in OR-NBC and NCA-SEAK regions.

Region	Year	$\widehat{N}$	$se(\widehat{N})$	N_{min}
OR-NBC	1998	118	1.8	116
	1999	151	5.3	146
	2000	145	6.0	140
	2001	184	8.3	177
	2002	181	7.5	175
	2003	178	8.6	170
	2004	206	9.8	197
	2005	197	11.3	188
	2006	175	11.2	166
	2007	207	15.4	194
	2008	185	14.2	174
NCA-SEAK	1998	138	2.2	136
	1999	191	6.6	185
	2000	174	7.2	168
	2001	216	9.5	208
	2002	209	8.7	201
	2003	192	9.8	184
	2004	209	10.8	200
	2005	200	12.0	190
	2006	178	11.8	168
	2007	202	14.6	190
	2008	225	16.4	211

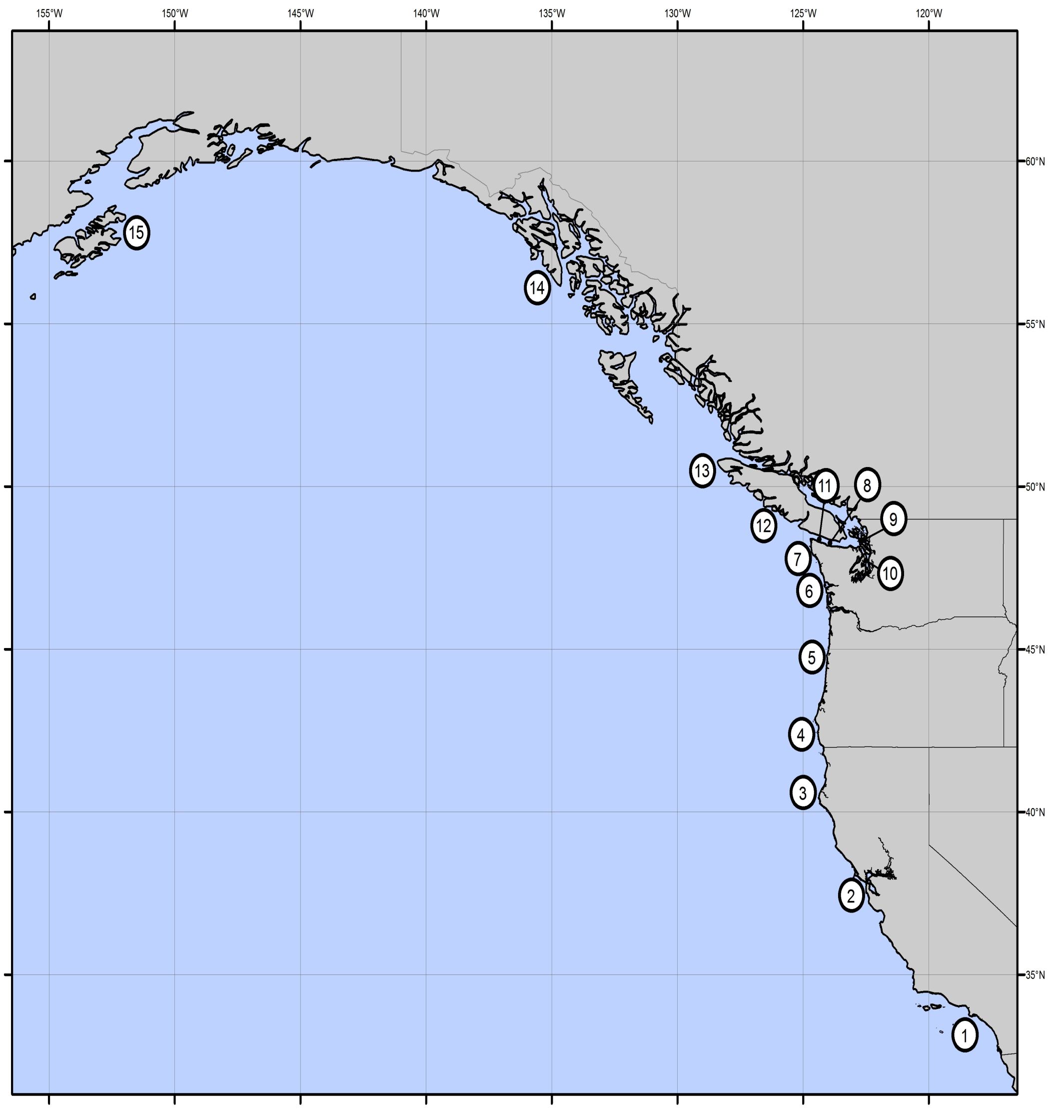

Figure 1: Locations for photo-identifications of gray whales. Numbers refer to values in Table 1.

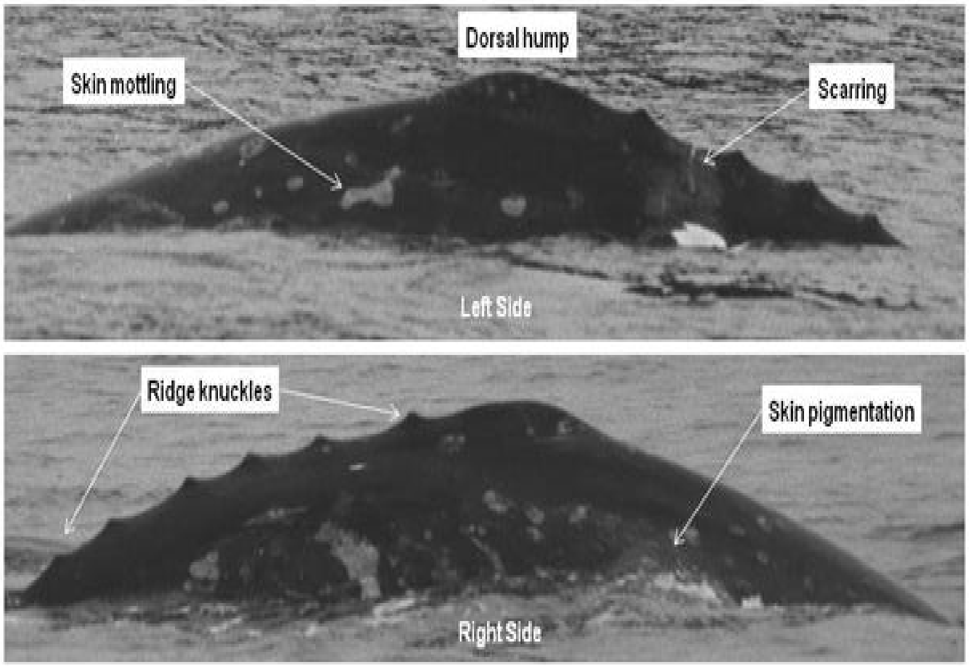

Figure 2: Characteristics used for gray whale photo-identification.

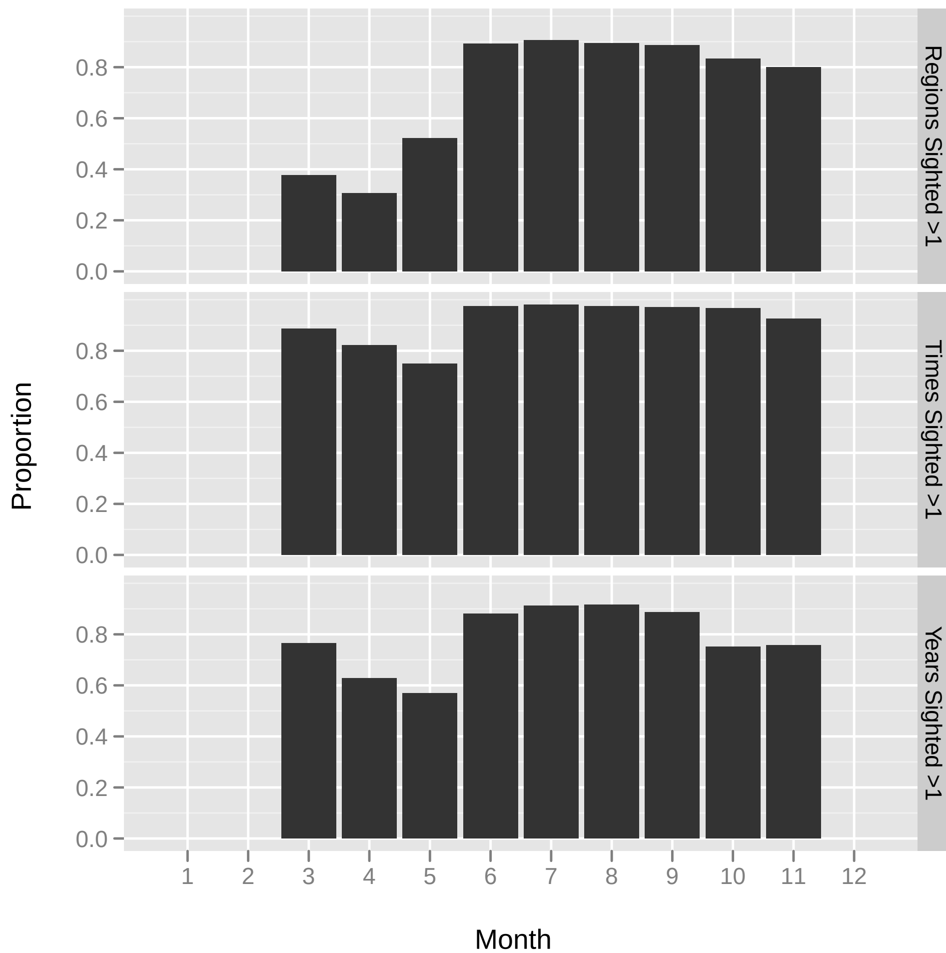

Figure 3: Monthly measures of proportion of whales that were seen in more than one region, seen on more than one day and seen in more than one year. The values include sightings from 1998-2008 in all regions from California to Alaska. Lower values imply whales were simply migrating through the area in 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.

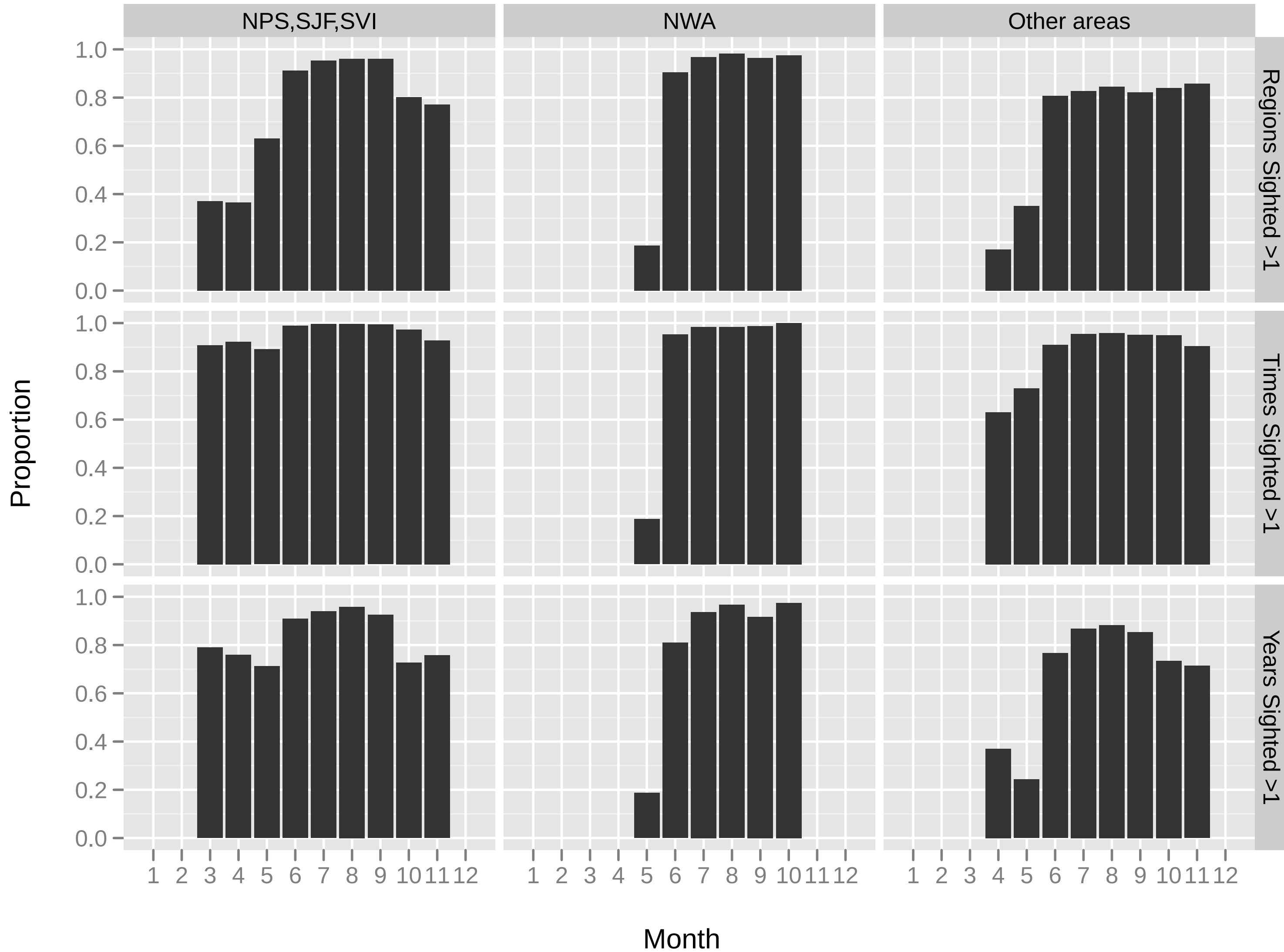

Figure 4: Region and monthly measures of proportion of whales that were seen in more than one region, seen on more than one day and seen in more than one year. The values include sightings from 1998-2008 in all regions from California to Alaska. Lower values imply whales were simply migrating through 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.

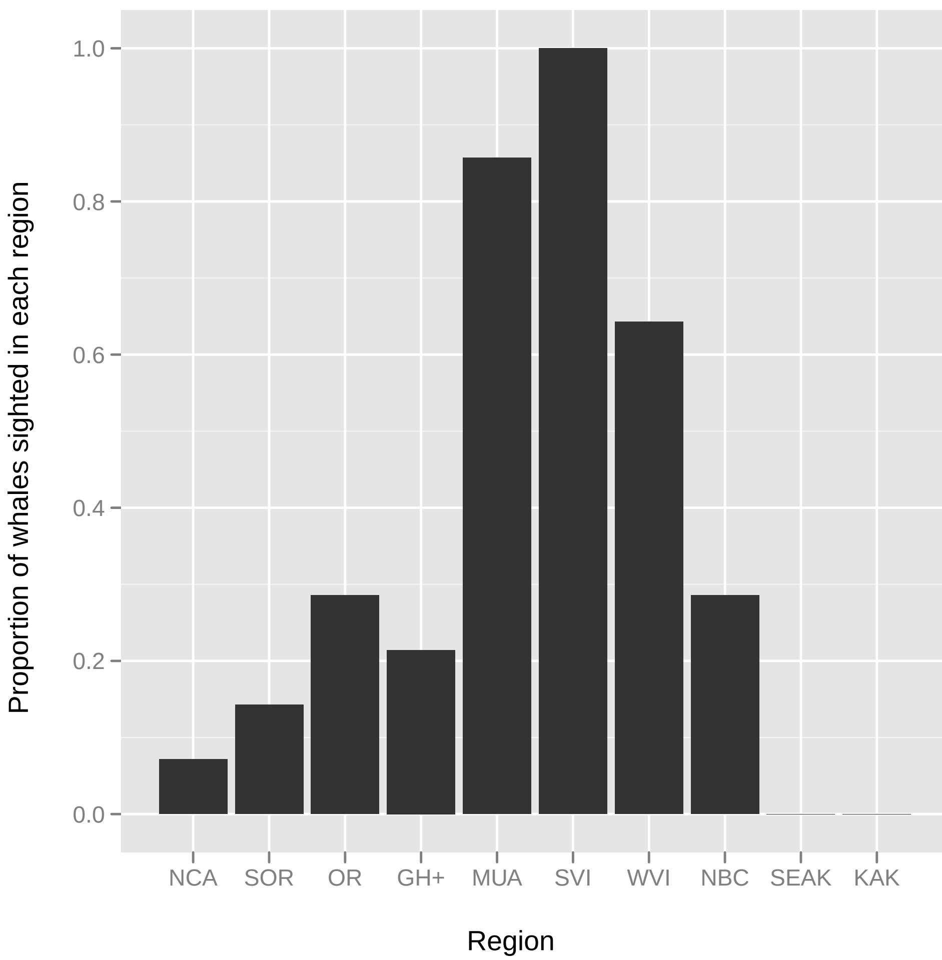

Figure 5: Proportion of the 14 whales seen in NWA during the spring and in the PCFA after 1 June that were seen in each PCFA sub-region after 1 June at least once from 1998-2008.

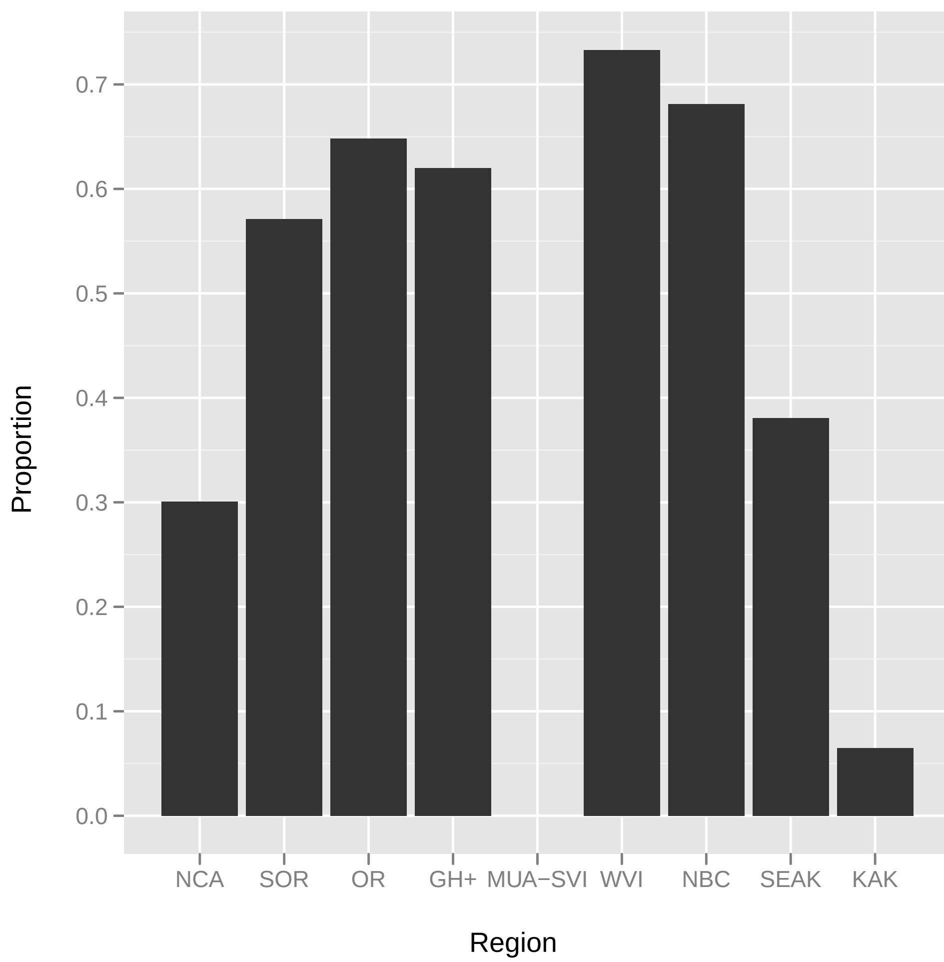

Figure 6: Proportion of whales in PCFA sub-regions that have been seen in the MUA-SVI using sightings after 1 June from 1998-2008.

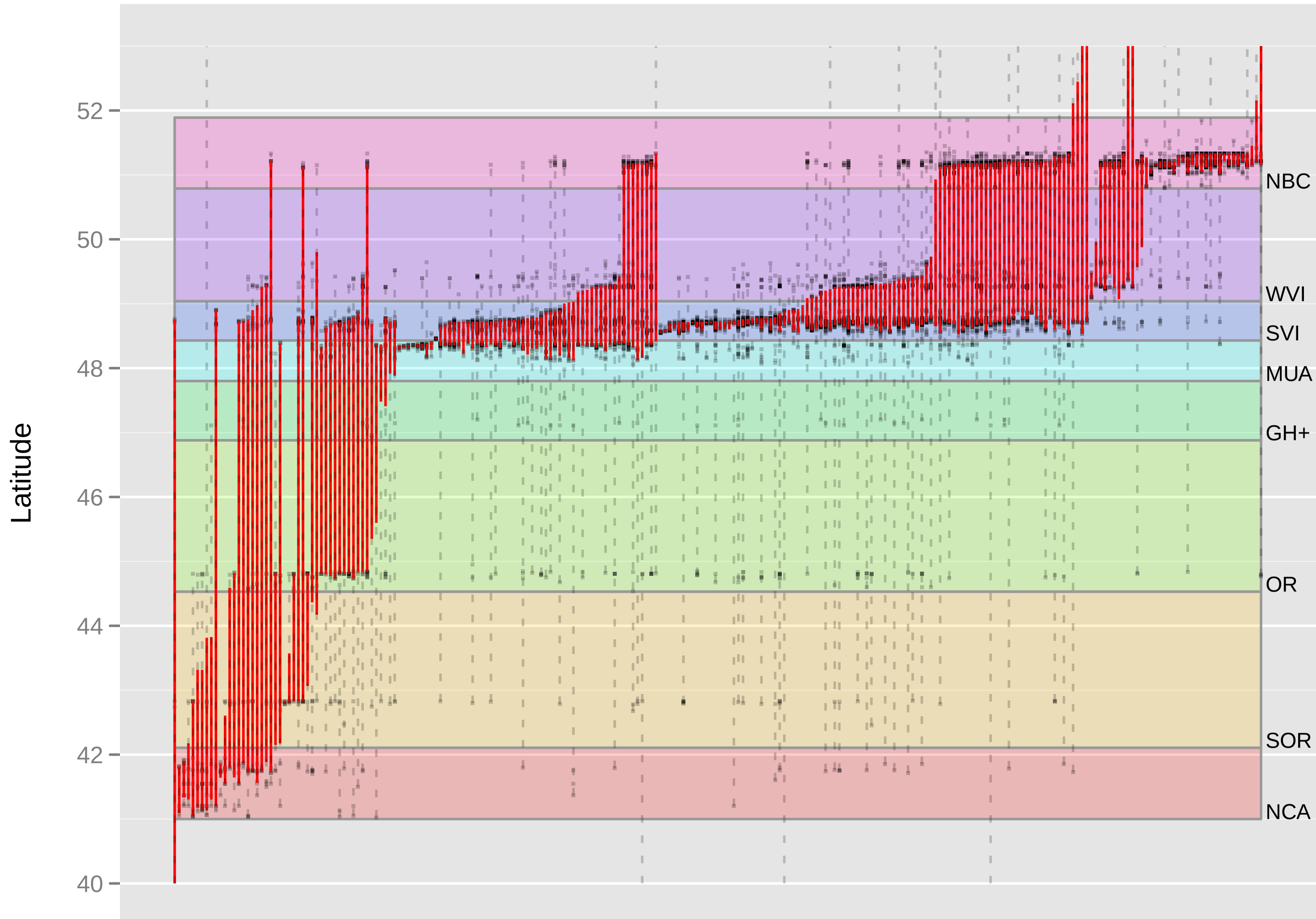

Figure 7: Distribution of latitudes of sightings (points) for whales with 6 or more sightings after 1 June from 1998-2008, the 75% inner quantile (solid thick line), and full range (light dashed line). Each position on the x axis represents an individual whale. Whales have been arranged on the plot by 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.

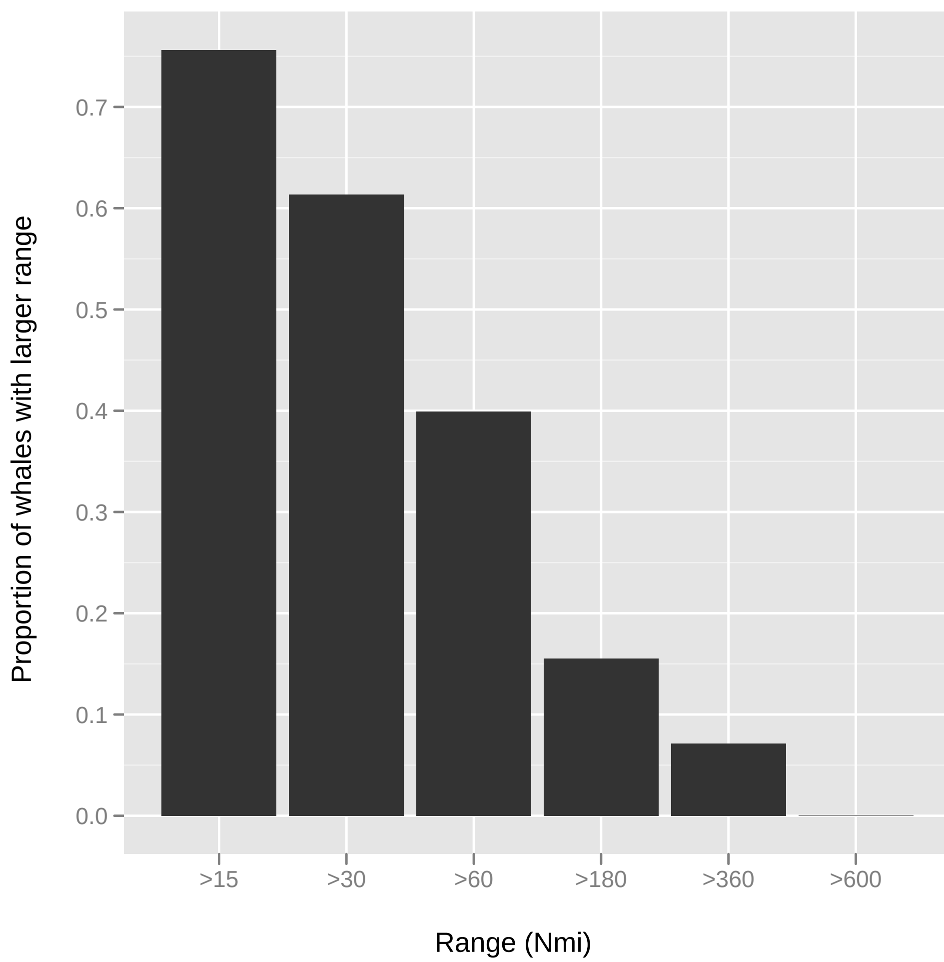

Figure 8: Distribution of ranges of 75% inner quantiles of latitudes expressed in nautical miles for whales sighted on 6 or more days during 1998-2008.

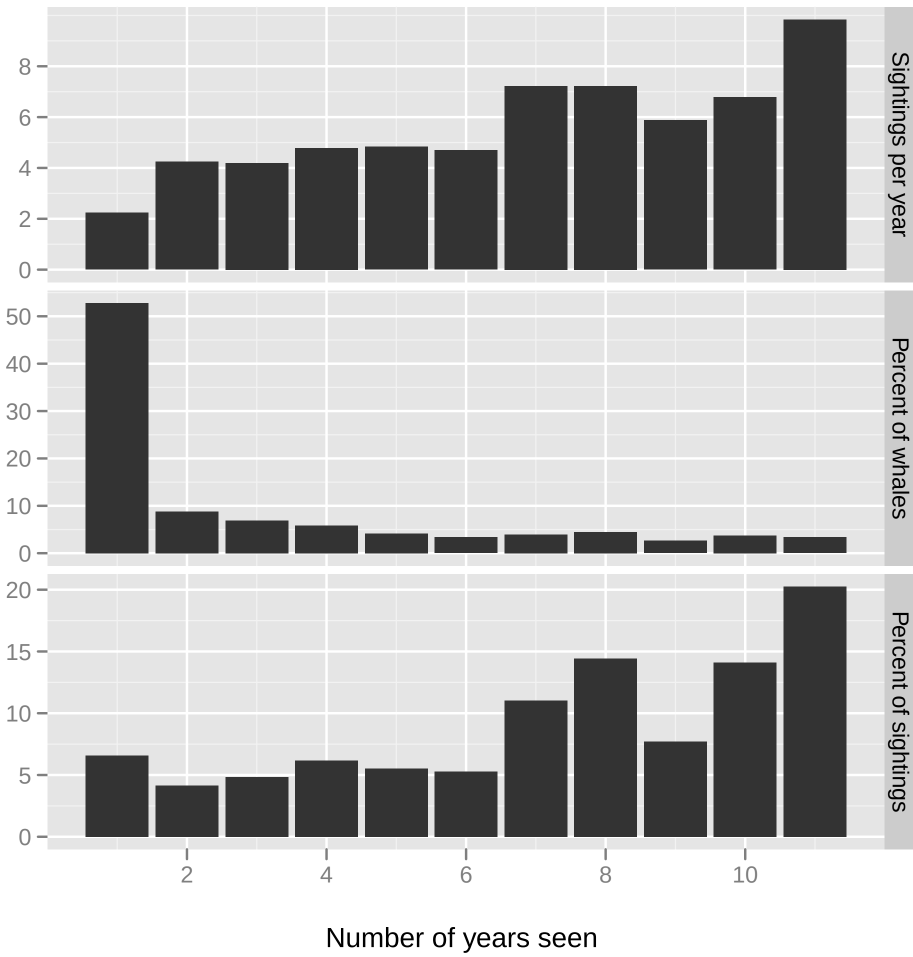

Figure 9: Average number of sightings per year and distribution of whales and numbers of sightings based on numbers of years a whale was seen in NCA-NBC between June-November during 1998-2008.

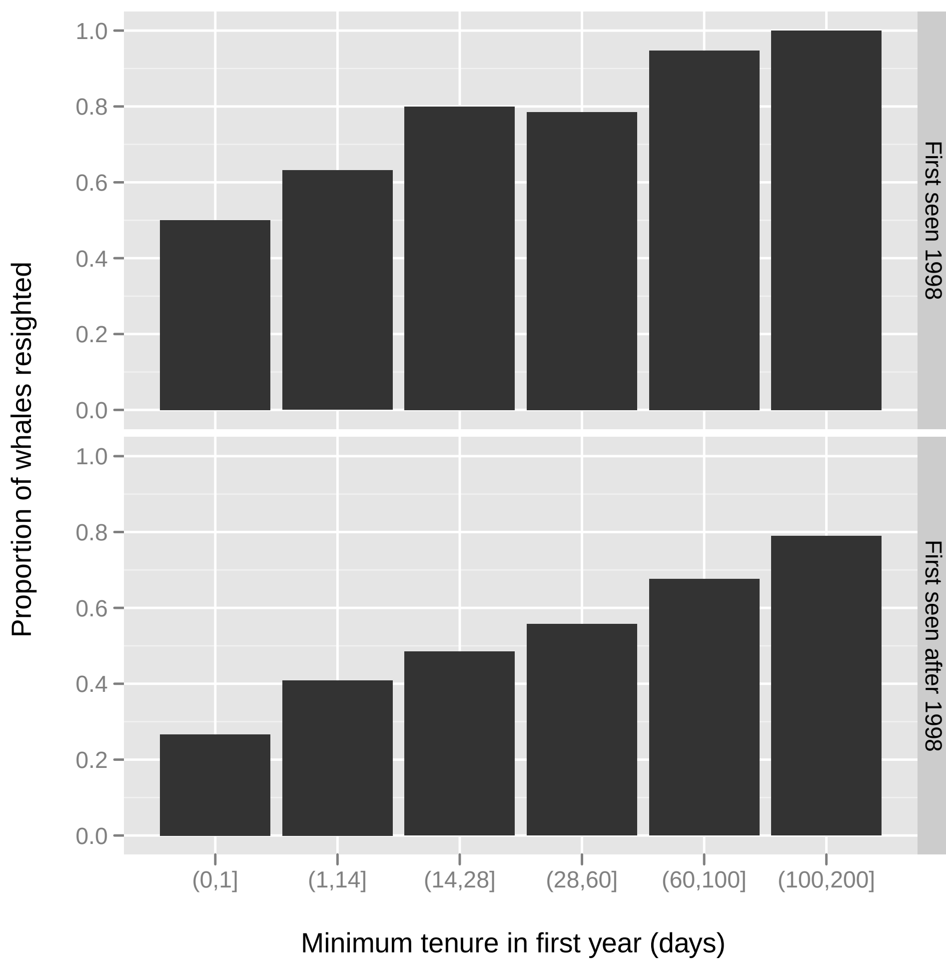

Figure 10: Influence of minimum tenure (MT) in the first year the whale was photographed on the probability it will be re-sighted in one or more following years for whales seen in NCA-NBC for June-November 1998-2008. The bar graphs are divided for 1998 and >1998 because 1998 is the start of the study and it may not be the first year for many of those whales. Re-sightings for 2008 are used but initial sightings for 2008 are excluded because there are no data beyond to evaluate re-sighting probability.

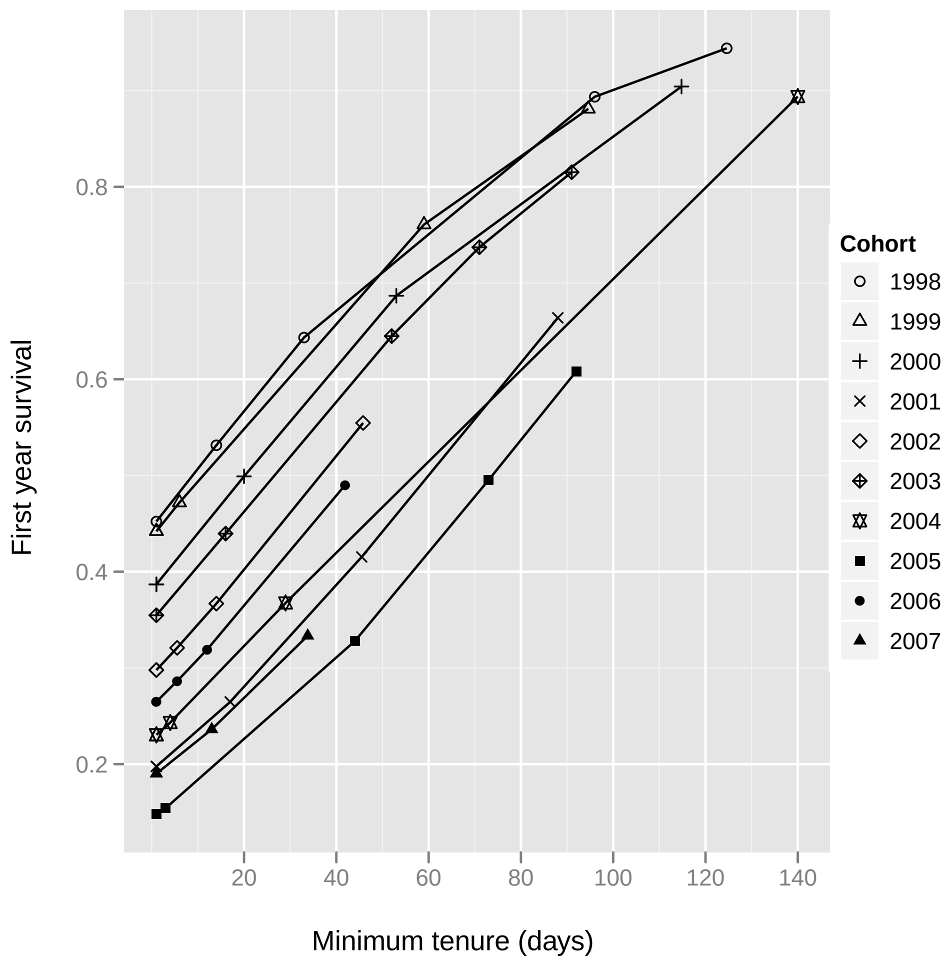

Figure 11: For MUA-SVI analysis of 1998-2008 data, model-averaged estimates of first year survival of non-calves for each cohort at 5%, 25%, 50%, 75%, and 95% quantiles of minimum tenure values for that cohort.

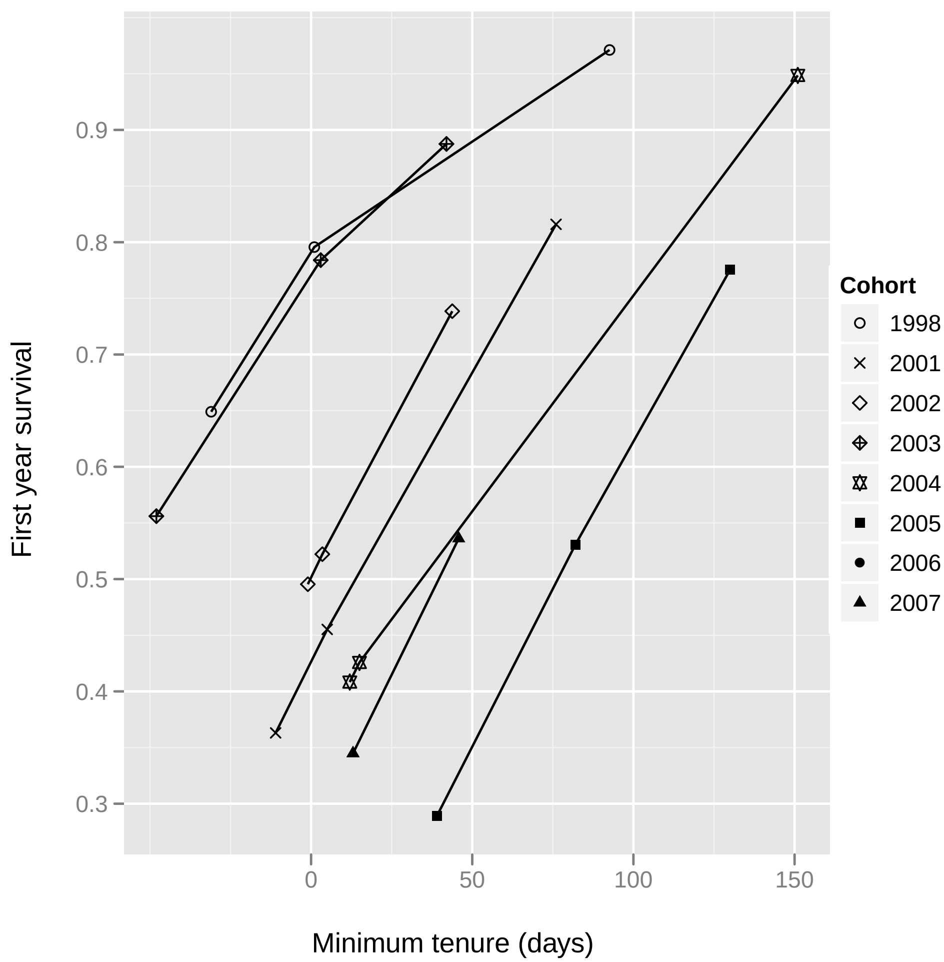

Figure 12: For MUA-SVI analysis of 1998-2008 data, model-averaged estimates of first year survival of calves for each cohort at 5%, 50%, and 95% quantiles of minimum tenure values for that cohort of calves. Cohorts 1999 and 2000 are not shown because no calves were identified in those years.

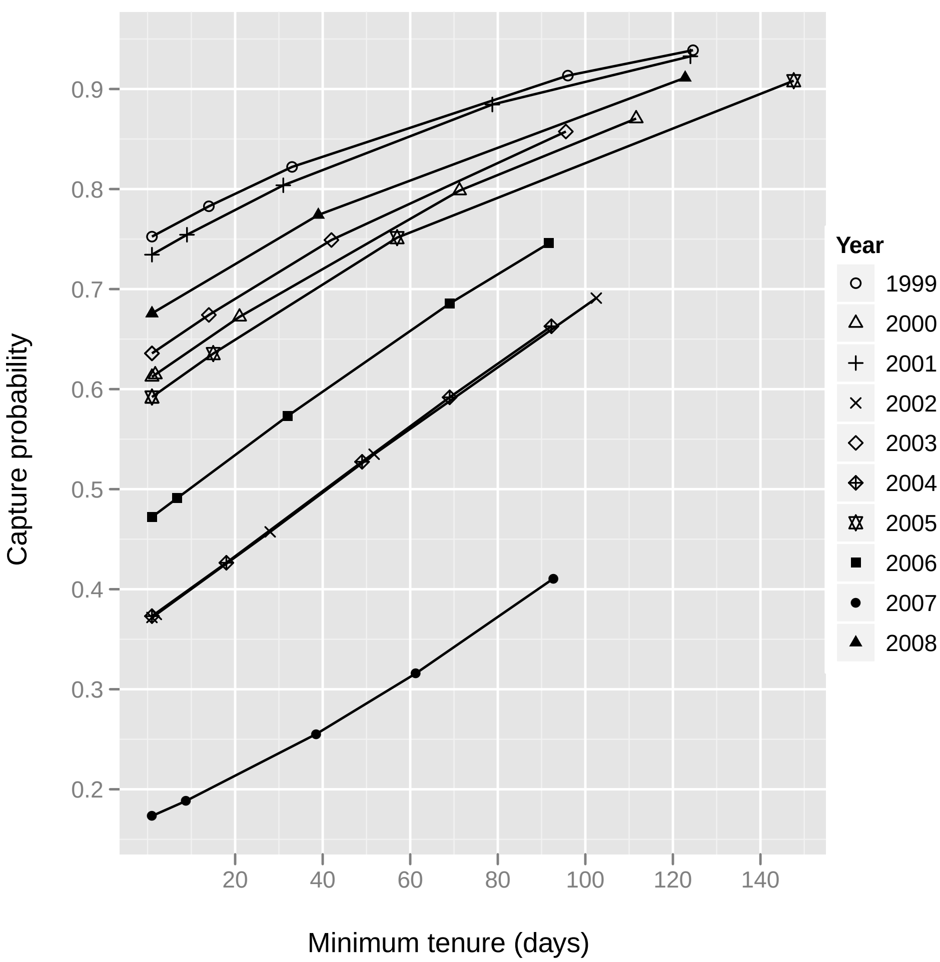

Figure 13: For MUA-SVI analysis of 1998-2008 data, model-averaged estimates of capture probability for each year at 5%, 25%, 50%, 75%, and 95% quantiles of minimum tenure values for whales in the previous year.

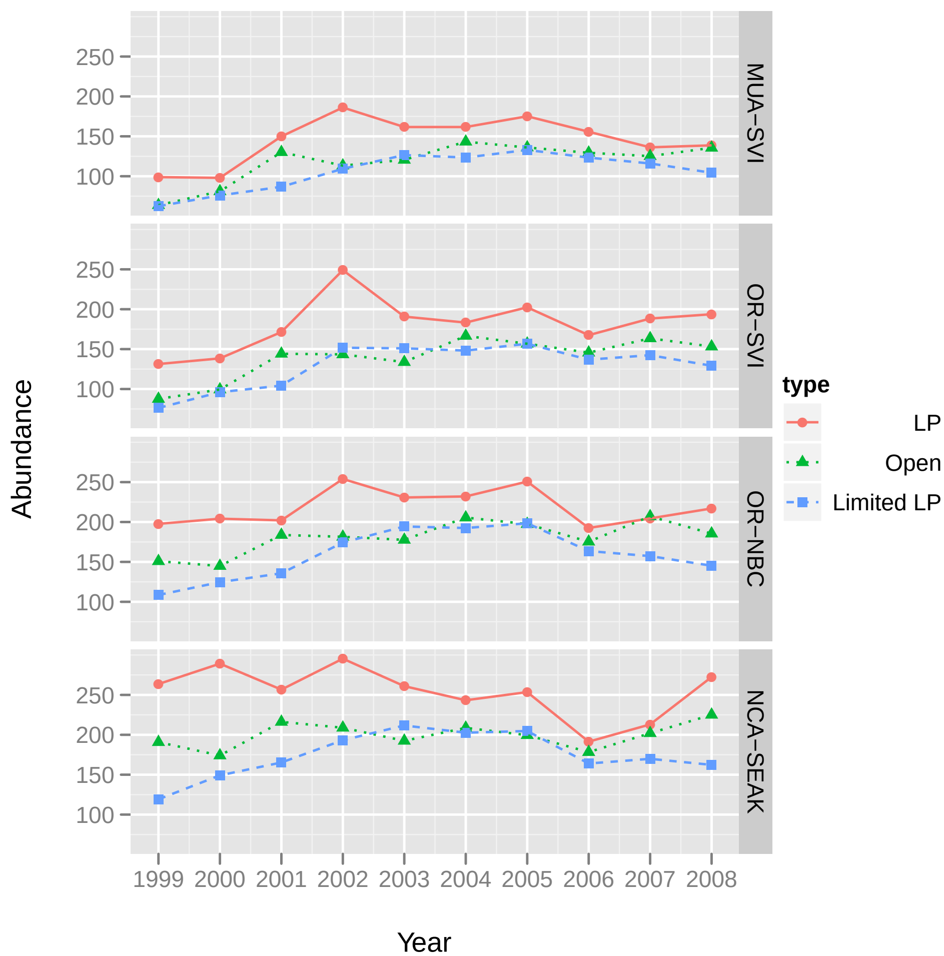

Figure 14: Annual abundance estimates for 1999-2008 in three sub-regions using closed population models, Lincoln-Petersen (LP) and Limited LP and the model averaged estimates for the open POPAN (Jolly-Seber) models.