FINAL REPORT

GRAY WHALE PHOTOGRAPHIC IDENTIFICATION IN 1998-2003: COLLABORATIVE RESEARCH IN THE PACIFIC NORTHWEST

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TABLE OF CONTENTS

ABSTRACT

A collaborative effort to photographically identify of gray whales in the waters of the Pacific Northwest from California through Alaska from late spring through fall was conducted from 1998-2003. This report summarizes these results and provides new insights about the movements, abundance and survival of gray whales in the Pacific Northwest. Each year between 1,159 and 1,499 photographic identifications of gray whales were obtained. Surveys were most numerous along the south and west coasts of Vancouver Island and just north of Vancouver Island, British Columbia. Using all identification photographs, 600 unique whales were identified. We focused our analysis on 477 gray whales identified after 1 June to exclude whales that were seen during the course of the northward migration to the Bering Sea. Individual whales were commonly photographed in more than one region of the Pacific Northwest during the same year and between years including movements from the southernmost sampled areas of California and northernmost areas around Kodiak, Alaska. Gray whales were most likely to be re-sighted in adjacent regions indicating fidelity at a scale smaller than the entire Pacific Northwest but larger than a single region for most whales. Assessing the degree and scale of site fidelity is further complicated by its dynamic and temporal nature. Whales that were seen in more years were seen in more regions, so our ability to assess fidelity is limited by the timeframe of the observations.

Abundance of gray whales in the Pacific Northwest and sub-regions was estimated with closed and open population capture-recapture models. The well-known Petersen estimator for closed populations was used with adjacent years of photographs. The annual estimates for northern California to SE Alaska ranged from 261 to 298 and for Oregon to British Columbia (excluding Alaska and California), 197 to 256. Analysis of data collected from northern California to northern British Columbia (PCFA – Pacific Coast Feeding Aggregation) using open population models demonstrated a lack of geographic and demographic closure. Most whales seen for the first time were transients and were never seen again probably because they never returned (rather than mortality). Whales were more likely to return in a following year if they stayed for a longer time in their first year as measured by minimum residency tenure (MRT) (*i.e.*, time between first and last dates photographed within a year). MRT was also a useful predictor for the probability that a "returning(resident)" whale would be seen the following year. We propose that the mechanism for these relationships is related to foraging success or failure of whales. Whales visiting this feeding area during and following the migration may join the feeding aggregation depending on the success they have in locating food. The average annual survival rate of resident (returning) whales was 0.97 (SE=0.012). Annual abundance estimates of gray whales in the PCFA ranged from 200 to 225 during 2001-2003. An analysis of data from Oregon to southern Vancouver Island yielded lower estimates of abundance for this smaller region from 137 to 153 during 2001-2003.

INTRODUCTION

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 along the west coast of Vancouver Island there was a core group of individual animals returning each year (Darling 1984). The resumption of the aboriginal hunt of gray whales by the Makah Tribe in northern Washington in the 1990s made determination of the status and number of these individuals 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, 2002a, 2002b). Findings from 1998 demonstrated there was considerable movement of individual whales from northern California to southeastern Alaska and also provided initial estimates of abundance (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.

The collaborative effort to collect photographic identifications of gray whales from California through Alaska has continued since 1998 and these data now covers six years (1998-2003). This report summarizes this dataset and the new insights it provides about the movements, abundance and survival of these whales.

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 2003. Details of identifications obtained by the different groups are briefly summarized below and are listed in Tables 1-2. Principal study areas are shown in Figure 1.

- **National Marine Mammal Laboratory**: NMML obtained identification photographs of 754 gray whales representing 235 unique individuals sampling all years from 1998 to 2003 from a variety of locations from northern California to Kodiak, Alaska. Identification photographs were mostly taken while conducting dedicated surveys for gray whales.

- **Cascadia Research:** Cascadia obtained identification photographs of gray whales on 856 occasions representing 285 unique individuals. Surveys were conducted in all years using 5.3m RHIB at a wide range of locations from California to SE Alaska.

- **Humboldt State University**: HSU conducted surveys primarily off northern California from 1998 to 2002 and obtained 316 identifications of 127 unique whales.

- **Brian Gisborne, Juan de Fuca Express**: Brian Gisborne obtained identification photographs every year from 1998 to 2003 along the West Coast trail of southern Vancouver Island during daily trips of this region. He obtained 3,391 identifications of 199 unique whales during the trips from Port Renfrew to Bamfield.

- **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.

- **Coastal Ecosystems Research Foundation**: CERF conducted regular surveys from 1998 to 2003 off British Columbia north of Vancouver Island primarily in the vicinity of Cape Caution. Identification photographs were obtained on 1,442 occasions representing 77 unique individuals.

- **University of Victoria:** UVIC obtained identifications photographs from Clayoquot Sound north along the west side of Vancouver Island every year from 1998 to 2003 except 2001. Identification photographs were obtained on 759 occasions of 108 unique individuals.

- **Volker Deeke:** Volker Deeke obtained identification photographs of gray whales from 1998 to 2001 off British Columbia and in SE Alaska. He obtained 64 identification photographs of 39 unique animals.

Each year from 1998 to 2003, between 1,159 and 1,499 identifications were obtained of gray whales totaling 7,743 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).

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 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 taken with 35mm cameras and 200-300mm 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 whale 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 over the years we have tracked whales.

Comparisons of whale photographs were made in a series of steps. First, all negatives of gray whales were examined and the best shot 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 season, the prints were then compared to others to identify whales seen multiple days. Finally, a comparison was made to our 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 matchers) were assigned a new identification number and added to the catalog.

Data analysis

Interchange and tenure of whales

Initially gray whale identifications were grouped into 14 regions representing clusters of areas of effort (Tables1-2, Figure 1). To model some of the intra- and inter-year movements of gray whales, we grouped the range into 6 broader regions dropping some of the peripheral areas with infrequent sampling and low rates of interchange with the core area (Alaska and southern and central California, and some of the inland Washington waters). These six broader areas were: 1) northern California (NCA), 2) Oregon (OR), 3) northern Washington/Strait of Juan de Fuca (NWA), 4) southern Vancouver Island (SVI), 5) western Vancouver Island (WVI), and 6) northern Vancouver Island/British Columbia (NBC). The NWA region corresponds roughly with the Makah usual and accustomed tribal area. In particular, to address the issue of site fidelity and the abundance of gray whales at risk of potential harvest by the Makah, we were interested in the probability a whale would be observed in the NWA region given it was observed in one of the other regions. The interchange probability was estimated for each region within year, between years, and overall (either within or between). The dependent variable was 1/0 (seen/not seen in NWA) given that it was seen in a particular region/year. We used generalized linear modeling for a binomial random variable with a logit link in the R statistical software (R Development Core Team 2003).

For within-year interchange, in addition to region, we examined models with NWA survey effort or survey year, and the number of years a whale was seen as explanatory variables for the probability a whale was seen in NWA. For between-year interchange, we examined models with region, survey year and the number of years a whale was seen as explanatory variables. Survey year represented the year the whale was seen in one of the five other regions. For example, the model would estimate the probability that a whale seen in Oregon in 2000 would be seen at least once in 1998-1999 or 2001-2003. While we were primarily interested in regional differences in interchange, we thought they might also differ in time due to shifts in distribution. We also looked at overall (inter and intra-regional) interchange with NWA. For each whale seen at least once in a region during 1998-2003, we examined the probability it would also be seen at least once in NWA during 1998-2003. For overall interchange, we only considered region and number of years seen. We did not consider survey year because the analysis pooled the 6-year period. In each case, we used AIC (Burnham and Anderson 1998) to select the most parsimonious model. An overall goodness of fit was conducted for the best model using a chi-square test. The data were collapsed into categories as needed to achieve a sufficient expected value in most cells to yield a valid chi-square test.

Abundance/Survival using open population models

Population abundance and survival of gray whales was estimated with open population models for two spatial scales: 1) PCFA- the Pacific coast feeding aggregation from northern California (NCA) to northern Vancouver Island/British Columbia (NBC), and 2) ORSVI-Oregon to southern Vancouver Island. Gray whales photographed and identified anytime during the sampling period between 1 June and 30 November within the defined region were considered to be "captured" or "recaptured". For each unique gray whale photographed in the region, a capture history was constructed using the six years of data from 1998-2003. For example, the capture history 010010 represents a gray whale photographed in 1999 and 2002. The same gray whale may have had a capture history 010000 for the smaller spatial scale ORSVI or may not have been seen at all (000000) in ORSVI and would not be used.

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 within a region in the same year were used to construct an observed minimum residency time (MRT) for each whale. MRT 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. MRT for a whale seen on only one day was by definition 1 day and a whale not seen was assigned 0.

The capture history data for each region were fitted to a range of models using the POPAN model structure with the computer software MARK (White 2004). The POPAN model structure (Schwarz and Arnason 1996) provided a robust parameterization of the Jolly-Seber model structure in terms of a super population (N), the probability of entry (immigration), capture probability (p), and survival/permanent emigration (S). Models with constant and time-varying S were considered. We also considered models with different survivals for newly seen whales and previously seen whales allowing for the possibility of "transients" (Pradel et al. 1997) which are individuals that pass through (are seen once and then permanently emigrate) and do not return regularly. In addition, MRT for a newly seen whale was considered as a potential explanatory variable for permanent emigration (S) before the next sampling period.

The assumed parameter structure for capture probabilities (p) was important for estimation of abundance (N) particularly due to the limitations of the spatial scale. Clearly whales that typically returned to the PCFA or ORSVI could feed outside of these regions in some years. Thus, a whale may not have been photographed because it did not return to the region (temporary emigration) or it returned to the region at some time during the sampling period but was simply missed. Burnham (1993) has shown that abundance estimation is unbiased if the temporary emigration is random; however, we did not believe it was plausible to assume random temporary emigration for all whales. Instead we assumed that we photographed all whales that were within the defined region at sometime during the sampling period and whales were only missed because they did not return in that year. Thus, all newly seen whales (not seen in a previous year) were considered new immigrants to the "population" in that year and by assumption could not have immigrated in a previous year and been missed. While this assumption may not have been entirely true, it would result in an under-estimate of abundance that would be consistent with a risk-averse strategy in setting a harvest quota for the Makah. This approach was implemented within the POPAN model structure by creating a cohort/group for the newly seen whales in each of the six years. The probability of entry was fixed such that all of the whales in the cohort immigrated immediately prior to the sampling period in which they were seen and their capture probability (p) was fixed for the first occasion to be 1. Thus, the estimate of the initial size of the cohort was the number seen (*i.e.*, by assumption none were missed). Models with constant and time varying capture probabilities beyond the first occasion for each cohort were examined. In addition, we considered models in which the observed MRT for a whale on occasion t was used as a predictor variable for capture probability of the whale on occasion $t+1$. The abundance estimate for the population at time t was the number of newly seen whales at time t and the predicted number of surviving whales from previous cohorts. Surviving meant they were alive and did not permanently emigrate. Thus, the total abundance estimate at time t only includes possible transients from the newly seen cohort at time t. By excluding the size of the newly seen cohort, we constructed an estimate of abundance of non-transient whales from previous cohorts.

Our analysis could have also been done with the Cormack-Jolly-Seber (CJS) model structure in program MARK by treating each cohort of newly seen whales as a released cohort. However, MARK does not derive estimates of abundance for CJS because it is used primarily for survival estimation. However, we did use Test 2 + Test 3 results from the CJS 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 used AICc for our model selection criterion (Burnham and Anderson 1998) for selecting the most parsimonious model for estimation. Model averaging was used when two or more models were within a ΔAICc of 4.

RESULTS

Good quality identifications were obtained of gray whales totaling on 7,743 occasions for 1998-2003 and these yielded 600 unique animals (154-254 per year)(Tables 1-3). These included identifications from early in the season during the migration as well as peripheral areas (see following sections).

The proportion of gray whales identified that had been seen in more than one region or more than one year (in any region) varied dramatically by month with whales identified in March through May less likely to have been seen multiple years or in multiple regions than those seen June to November (Table 4). This was expected because the northbound migration of gray whales proceeds past Washington through May making it more likely that gray whales identified early in the season are whales still migrating north. Resighting rates of whales seen after 1 June remained high through November.

Similarly, whales identified at the geographic ends of the sampled range (central and southern California and Alaska) as well as those seen in greater Puget Sound were also less likely to have been seen in multiple years and regions (Table 4). In some of these regions, such as Puget Sound, many of these whales were seen in the spring and may represent migratory animals. Even with exclusion of these early season animals, only a low proportion of the whales seen in Washington inside waters and at the north and south end of our sampled range had been seen multiple years or in more than one region. Gray whales in northern Puget Sound had a higher inter-year resighting rate than those in other parts of Puget Sound, but these whales were seen primarily only in spring and then were generally not resighted, indicating they were moving on to some other area outside where we sampled.

We examined the rate of interchange among regions both within years and overall among years for the 1998-2003 period. Within-year interchange was extensive especially among the outer coast regions from northern California to British Columbia (Figure 2). The low rate of interchange and within-year movements between these areas and those in Puget Sound or at the north and south ranges of our sampling in areas California and Alaska can also be clearly seen (Figure 2). Interchange among specific regions regardless of year, shows that whales seen on one region are most likely to be resighted at regions close to there rather than farther away (Table 5, Figure 3). For each region examined there was a pattern of decreasing interchange with each jump farther to the north or south of that site (Figure 3).

Even though resightings in other regions were less common for the whales identified in the ore geographically peripheral areas like southern and central California and Alaska, some of these animals were resighted in other regions (Table 5). For example, two whales identified off Bodega Head in central California in August 2001 were both seen in 2003 off southern Vancouver Island. Similarly, 5 of 10 whales identified off southeastern Alaska and 8 of 46 whales identified off Kodiak, Alaska had been identified farther south. This includes one animal from each of these Alaska areas that was documented on feeding areas farther south in the same season as when it was identified in Alaska. Directions of movement were opposite, however, with one whale (ID#140) that moved from southeastern Alaska around September 1999 to northern California on 30 October 1999 and another whale (ID#691) seen off southern Vancouver Island from 9 June to 6 July 2003 and then off Kodiak on 9 and 11 August 2003. This latter movement would represent a minimum of 1,104 nmi (by most direct route) in no more than 34 days.

Because of the presence of large number of migrating whales in spring, we restricted our mark-recapture and other analyses to whales that had been identified after 1 June for 1998-2003 each year. This reduced the number of unique individuals identified from 1998 to 2003 from 600 to 477 (Table 3). Unless stated otherwise, all analyses through the rest of this report will only include identifications and effort after 1 June.

Relationships between interchange and tenure of whales

Some simple exploratory plots suggest some interesting relationships regarding tenure and movements of whales. Whales that were seen more frequently (more years) were seen in more regions (Figure 4). Also whales that were seen more frequently had longer minimum residency times in the first year they were seen (Figure 5). Whales with a minimum residency time of three weeks or more were twice as likely to be seen the following year as whales with a shorter minimum residency time (Figure 6).

The most parsimonious model of within year interchange of whales into NWA from the other regions was a function of region, the number of years a whale had been seen and the year (Table 6). The model fit the data reasonably well (χ^2 =94.9, df=78, p=0.09) with the number of years seen collapsed into three groups (1-2, 3-4, 5-6). The next best model replaced year with survey effort in NWA during that year. Observed interchange increased with increasing effort in NWA; thus, many whales may have passed through NWA but were not always seen. However, inclusion of year in the best model suggests that in addition to effort other annually varying factors (*e.g.*, annual variation in movements) influenced the interchange with NWA. As might be expected, regions closest to NWA (SVI, OR, and WVI) had the highest within year interchange with NWA and NCA and NBC on the fringes had much lower within year interchange (Figure 7). Whales seen more frequently were more likely to be seen in NWA and another region during the year (Figure 7) which was most likely associated with longer within-year tenures.

The most parsimonious model of between year interchange of whales into NWA from the other regions was a function of region, the number of years a whale had been seen and the year (Table 6). The model fit the data reasonably well (χ^2 =43.3, df=49, p=0.70) with the number of years seen collapsed into two groups (2-4, 5-6). Again whales seen in the closest regions were more likely to be seen in NWA (Figure 8). As expected, whales seen in more years were more likely to be seen in NWA (Figure 9), which was consistent with whales being seen in more regions (Figure 4).

For overall (within- and between-year) interchange with NWA, the most parsimonious model likewise included region and number of years seen (Table 6). The model fit the data reasonably well (χ^2 =26.3, df=24, p=0.34) using the number of years seen in the six separate groups. The overall interchange was greatest for OR and SVI which are the regions to the south and north of NWA. For whales seen in all 6 years, at least 30% would be expected to be seen in NWA from all regions in the PCFA and more than half were seen in NWA of those seen in SVI and OR.

Population estimates from closed models

Abundance estimates using a simple Petersen mark-recapture model with adjacent years gave fairly consistent estimates of abundance (Table 7). The five estimates from pairs of adjacent years ranged from 261 to 298 for northern California to SE Alaska. Using only sites from Oregon to British Columbia (excluding Alaska and California) lowered the estimates slightly to 197 to 256 (Table 7). These results are very similar to the past inter-year estimate conducted in this manner but using a more limited number of years and not as complete a sample as available for this analysis (Calambokidis *et al.* 2000, 2002a, 2002b). These estimates were consistent from year to year and had a high certainty (Coefficient of Variation of 0.03 to 0.06) reflecting the high recapture rates; estimates were based on up to 206 different individuals identified in a year and up 126 recaptures between years (Table 7).

PCFA open population models

From 1998-2003, 408 unique whales were photographed from 1 June to 30 November within the PCFA (NCA to NBC). Excluding the 24 newly seen whales in 2003, 49% of the whales were seen in only one year and 25% were seen in every year following their first encounter. The latter includes 49 whales that were seen in all 6 years. The minimum residency time in the first year seen was 1 week or less for 46% of the whales and greater than 2 months for 25% of the whales. Of 186 whales with a minimum tenure (MRT) of 1 week or less in their first year, 68% were seen during July-September, the middle of the survey period well outside the migration period.

The goodness of fit results for Test 2 + Test 3 (χ^2=251.6, 11 df, P<0.0001) demonstrated a strong lack of fit for a model with survival and capture probability varying by year but not cohort specific. The lack of fit was predominantly from test component 3.Sr (χ^2=212.0, 4 df, P<0.0001) due to differences between "newly seen" and "previously seen" animals as described by Burnham et al. (1987). We subsequently divided the whales into 3 groups for each survey period: 1) newly seen whales with their first MRT ≤ 3 weeks, 2) newly seen whales with their first MRT > 3 weeks, and 3) previously seen whales. The goodness of fit results for Test 2 + Test 3 (χ^2=28.9, 15 df, P=0.01) suggested some lack of fit for the model group-specific time varying survival and capture probabilities, although most of the lack of fit occurred in one component for occasion 5 (2002), 3.Sr5 (χ^2=13.4, 1 df, P=0.004), which most likely occurred because there was very little survey effort in WVI during 2003. We assumed the lack of fit was structural and there was little or no over-dispersion in the data.

Minimum residency time was an important predictor of "survival" for newly seen whales and capture probability of returning whales (Table 8). Survival of newly seen whales varied by year and was presumably dominated by permanent emigration. Survival of previously seen whales varied by year in the lowest AICc model but was constant in the next closest model (ΔAICc=1.8). In computing estimates we used model-averaging of models 1 and 2.

Estimates of first year survival and their standard errors (SE) were 0.85 (SE=0.04), 0.22 (SE=0.05), 0.57 (SE=0.07), 0.39(SE=0.07), and 0.54(SE=0.12) for cohorts of newly seen whales from 1998-2001 using the mean value of MRT for each year. This first year survival represents both mortality and permanent emigration. The predominance of permanent emigration in these estimates is demonstrated by a comparison of the 1998 cohort to the 1999-2002 cohorts. "Newly" seen whales in 1998 were different than those in other years because many whales first "seen" in 1998 may have regularly returned to the PCFA but were only "first seen" because that was the beginning of the dataset. This was evident in the mean MRT which was significantly greater for whales seen in 1998 (47.6 days, SE=3.7) than the average MRT for newly seen whales in 1999-2002 (24.6 days, SE=2.0) ($z=5.44$, $P<0.0001$). The "survival rate" for 1998 was higher because there was less permanent emigration from the 1998 cohort than 1999-2002. Excluding 1998, on average we could reasonably expect about 43% of newly seen whales will return in the following years. The odds of a whale remaining in the PCFA after being first seen nearly doubled (1.92 SE=0.40) for an increase of 30 days in their first MRT.

Annual survival of previously seen whales, presumably true survival, was estimated to be 0.97 (SE=0.012) in model 2. The model-averaged estimates of annual survival were 0.92 (SE=0.04), 0.99 (SE=0.02), 0.97 (SE=0.02), and 0.87 (SE=0.08) for 1999 to 2002.

Estimates of recapture probability were 0.79 (SE=0.04), 0.70(SE=0.05), 0.71(SE=0.04), 0.88(SE=0.03) and 0.74(SE=0.08) for 1999-2003 using the average MRT from the previous year (1998-2002) of whales seen through the previous year. If all whales present in the PCFA each year were observed (as we have assumed), then 12-30% of the regularly returning whales may have temporarily emigrated outside of the PCFA. The odds of a whale being seen in a year doubled (1.90 SE=0.35) for an increase of 30 days in MRT the previous year.

Estimated abundance increased from 129 in 1998 (count of new whales) to a peak of 225 in 2002 (SE=6.6) (Figure 10). By subtracting the newly seen whales, we obtained abundance estimates of returning whales that increased from 102 (SE= 5.7) in 1999 to a peak of 176 (SE=20.5) in 2003. The average annual increase of returning whales was 18.5 from 1999 to 2003.

ORSVI open population models

The patterns observed in this analysis were quite similar to the PCFA analysis because the data were a subset of the PCFA data; however, captures and measures of MRT were restricted to the ORSVI area. A whale newly seen in ORSVI may have been seen previously in the PCFA but not in ORSVI and it was treated as a newly seen whale. From 1998-2003, 260 unique whales were photographed from 1 June to 30 November within ORSVI. Excluding the 28 newly seen whales in 2003, 48% of the whales were seen in only one year and 19% were seen in every year following their first encounter. The latter includes 18 whales that were seen in all 6 years. The minimum residency time within ORSVI in the first year seen was 1 week or less for

41% of the whales and greater than 2 months for 26% of the whales. Of the 107 whales with a minimum tenure (MRT) of 1 week or less in their first year, 69% were seen during July-September, the middle of the survey period, well outside of the northward migration period.

The goodness of fit results for Test 2 + Test 3 (χ^2=106.4, 10 df, P<0.0001) demonstrated a strong lack of fit for the model with survival and capture probability varying by year but not cohort specific. As with the PCFA analysis, the lack of fit was predominantly from test component 3.Sr (χ^2=98.8, 4 df, P<0.0001). As with the PCFA data we divided the whales into 3 groups for each survey period: 1) newly seen whales with first MRT ≤ 3 weeks, 2) newly seen whales with first MRT > 3 weeks, and 3) previously seen whales. The goodness of fit results for Test 2 + Test 3 (χ^2=16.2, 12 df, P=0.18) suggested a reasonable fit for the model with group-specific time varying survival and capture probabilities.

Minimum residency time was an important predictor of "survival" for newly seen whales and capture probability of returning whales (Table 9). Survival of newly seen whales varied by year and was presumably dominated by permanent emigration. Survival of previously seen whales was constant in the lowest AICc model but varied by year in the next closest model ΔAICc=1.4). In computing estimates we used model averaging of models 1 and 2.

Estimates of survival and their standard errors (SE) were 0.82 (SE=0.05), 0.50 (SE=0.11), 0.69 (SE=0.10), 0.26(SE=0.07), and 0.64(SE=0.15) for cohorts of newly seen whales from 1998-2001 using the mean value of MRT for each year. This first year survival is presumably predominated by permanent emigration. This was evident in the mean MRT which was significantly greater for whales seen in 1998 (49.1 days, SE=5.0) than the average MRT for newly seen whales in 1999-2002 (27.5 days, SE=2.6) (z=3.86, P<0.0003). Thus there was less permanent emigration from the 1998 cohort than 1999-2002. Whales that are newly seen in ORSVI may not be new to the PCFA, thus we would expect that permanent emigration would be less as it was. On average we could reasonably expect about 53% of whales newly seen in ORSVI will return in the following years. The odds of a whale not permanently emigrating after being first seen, increased by 2.24 (SE=0.53) for an increase of 30 days in MRT.

Annual survival of previously seen whales was estimated to be 0.97 (SE=0.019) in model 2. The model-averaged estimates of annual survival were 0.95 (SE=0.04), 0.98 (SE=0.02), 0.98 (SE=0.02), and 0.94 (SE=0.09) for 1999 to 2002.

Estimates of recapture probability were 0.70 (SE=0.06), 0.55(SE=0.06), 0.80(SE=0.05, 0.58(SE=0.06) and 0.67(SE=0.10) for 1999-2003 using the average MRT from the previous year (1998-2002) of whales seen through the previous year. If all whales present in the ORSVI each year were observed, that would suggest that 20-45% of returning whales may temporarily emigrate outside of the ORSVI. These percentages were expectedly higher because whales may have returned to the PCFA but outside of ORSVI. The odds of a whale being seen in a year increased by more than 50% (1.56 SE=0.33) for an increase of 30 days in MRT the previous year.

Estimated abundance increased from 84 in 1998 (count of new whales) to a peak of 150 in 2003 (SE=20.5) (Figure 11). By subtracting the newly seen whales, we obtained abundance estimates of returning whales that increased from 61 (SE= 5.0) in 1999 to a peak of 122 (SE=20.5) in 2003. The average annual increase of returning whales was 15.2 from 1999 to 2003.

DISCUSSION

Gray whales annually migrate from their feeding grounds during summer/fall to the breeding grounds in Baja California during winter/spring. Most whales feed in the Bering Sea, but some whales regularly do not complete the migration north and remain in coastal waters along the Pacific coast and in the Gulf of Alaska during the summer/fall to feed. While all whales that migrate north to the Bering Sea pass through the region inhabited by the Pacific Coast Feeding Aggregation (PCFA), most northward migration occurs prior to 1 June.

The northward migration path along the Pacific coast provides a possible natural mechanism for recruitment to the PCFA. Northbound whales have traveled a long distance and may be in search of food to replenish fat stores that have been depleted during the migration. Whales that encounter adequate food along the Pacific coast may choose to remain there and not continue the migration northward. If they are successful in one year, they may continue this in future years. Other whales may not be successful in finding food and may stay a short while before proceeding northward or simply pass through. Whales that typically return regularly may choose to look elsewhere following a year in which they were less successful foraging in the PCFA.

This proposed mechanism for the dynamics of the PCFA whales is supported by the inclusion of minimum residency tenure (MRT) in the models for survival (emigration) and capture probability. It is important to recognize that the observed tenures are minimums and whales may have been within the PCFA longer and not seen because it was in a region that was not surveyed or sampled less frequently. Although whales with short tenures could have been seen as late spring migrants or early fall migrants on their way north or south, more than two-thirds of those with short tenures were seen from July- September.

Lower survival estimates for newly seen whales could reflect permanent emigration (whales passing through) or mortality. Mortality would be more likely in this group if whales in poor physical condition are more likely to stop along the Pacific Coast in search of food. The estimated annual average survival rate (0.97) of PCFA (returning) whales clearly includes very little to no permanent emigration and is consistent with natural survival for a long-lived species. The annual variability in survival of PCFA whales in model 1 may have resulted from some increased mortality in 1999 during the stranding event but also the lack of sampling in WVI during 2003 may have depressed the estimated survival rate for 2002. The evidence for annual variation in survival is equivocal as the model ordering flipped between the two analyses. The support for constant survival in the ORSVI analysis may be due to the smaller sample size, but it may also be a better approximation to reality because it would not have been affected by the lack of sampling in WVI during 2003.

Jolly-Seber capture-recapture models assume that the capture occasion is an instantaneous event. Although a 6 month-long sampling period violates this assumption, it is only practically important if there are losses or gains in the population during the sampling period. Any loss due to natural mortality (0.03) is unlikely to have any importance even if it occurs during the sampling period. And while there will be whales both entering and leaving the region during the sampling period, it should not affect our estimates of population size that conservatively assume that all whales in the region are seen and whales are only missed because they did not return.

We chose a very conservative approach to abundance estimation with the potential for under-estimating abundance. We did so to provide estimates that could be used to set harvest quotas that would be risk-averse. Also, our estimation approach for abundance is consistent with our proposed mechanism for the dynamics of the PCFA whales. We have assumed that whales are only missed because they are not in the PCFA during the year. Thus, the newly seen whales are all of the new immigrants of which some (50-60%) will never return. If they do not permanently emigrate, they may return some years but not others and this is assumed to be random based on the year and their MRT in the previous year as modeled by the capture probability. Thus the estimated abundance is the predicted number of returning whales (did not permanently emigrate) that have survived from each cohort of newly seen whales. This may under-estimate the number of immigrants but newly seen whales have shorter MRTs and thus would be less vulnerable to harvest. Returning whales have longer MRTs and are more vulnerable to harvest.

The abundance estimates from the open population models are lower than the Petersen estimates based on a closed model. There are two reasons for the difference. First, the Petersen estimator treats "newly" seen and "previously" seen the same with each having a capture probability of p. Whereas, we have assumed p=1 for newly seen and estimated p applies only to returning whales. Secondly, the Petersen estimate is only unbiased with an open population if there are only losses or only gains in the population. In this case, there are both and that can create a positive bias because some of the whales seen in year 1 do not return and some of those seen in year 2 were new immigrants that year. Both of these will underestimate p and overestimate abundance.

Selecting a region for estimation is a difficult problem because for any set of boundaries the population size is open to change due to shifts in geographic distribution. We know that even using the PCFA boundaries, some whales that typically return will go to southeastern Alaska or Kodiak or possibly the Bering Sea. There is also considerable interchange within the PCFA so regions within the PCFA will have substantial annual changes when whales shift their distribution in search for food. However, clearly there is some level of fidelity; otherwise the abundance estimates from ORSVI would have been the same as the estimate for the PCFA. We have shown that regions in close proximity have the highest interchange rate thus it is both logical and reasonable to use ORSVI as the region for abundance estimation in setting quotas for a harvest of whales from the NWA/SJF region.

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TABLES AND FIGURES

Tables

Figures

Table 1. Summary of identifications provided by contributing organizations by year and region.

		Unique	Year						Region													
Contr. Org.	**Records**	**IDs**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**CA**	**NCA**	**SOR**	**OR**	**GH+**	**NWA**	**SJF**	**PS-H(**	**NPS**	**SVI**	**WVI**	**NBC**	**SEAK**	**KAK**
Brian Gisborne	3391	199	373	343	779	586	435	875										3357	34			
Coastal Ecosystem Research Found. (CERF)	1442	77	100	150	251	466	295	180												1442		
Cascadia Research (CRC)	846	285	170	233	117	79	135	112	9	47	138	113	134	86	12	62	138	33		70	4	
Humpboldt State Univ. (HSU)	316	127	21	89	60	75	71			279		37										
Jim Darling	99	59	50			35	14											4	95			
National Marine Mammal Lab (NMML)	754	235	132	194	136	128	88	76		4	2			166	104		22	177	199	13		67
University of Victoria (UVIC)	759	108	351	159	128		121												759			
Volker Deeke	120	64	39	42	28	11										1		72		43	4	
Other *	16	13	3	12		1										8				4	4	
Grand Total	7727	1154	1236	1210	1499	1380	1159	1243	9	330	140	150	134	252	116	63	160	3643	1087	1568	8	67
Unique Ids		600	154	248	178	198	254	172	6	121	57	55	35	113	35	25	42	201	169	82	10	46

*Other includes IDs by G. Ellis and J Ford of DFO, SE AK ids compiled by Jan Straley

Table 2. Summary of effort and identifications by region.

	Days identifications obtained							Identifications of whales																
		Year						Total	Unique	Year						Month								
Region	Total	1998	1999	2000	2001	2002	2003	IDs	IDs	1998	1999	2000	2001	2002	2003	3	4	5	6	7	8	9	10	11
Central and S California	3	0	1	0	2	0	0	9	6		2		7							1	6	2		
N California	70	7	8	20	13	20	2	330	121	27	69	60	78	74	22			2	46	122	35	23	80	22
S Oregon	6	0	0	0	1	4	1	140	57				2	99	39					2	12	88	38	
Central Oregon	27	6	9	5	7	0	0	150	55	47	51	13	39						5	11	85	22	27	
Grays Harbor area	3	0	1	1	1	0	0	134	35	56	40	23	15			12	98	20	1	3				
N Washington coast	63	22	10	7	11	4	9	252	113	45	85	22	53	13	34			79	10	35	42	47	35	4
Str of Juan de Fuca	51	15	8	8	4	1	15	116	35	36	16	23	6	3	32	1	3	7	12	3	10	20	47	13
Other WA inside	17	3	11	3	0	0	0	71	25	9	53	9				3	15	23	21	4		1	1	3
N Puget Sound	1	0	0	1	0	0	0	160	42	27	47	53	13	4	16	34	70	44	12					
S Vancouver Is.	447	91	87	80	55	68	66	3643	201	487	398	833	643	441	841		5	145	709	1241	1035	468	40	
W Vancouver Is.	154	54	46	31	9	11	3	1087	169	401	262	195	57	138	34				95	422	422	131	17	
N British Columbia	248	39	50	53	43	34	29	1572	82	100	192	268	467	327	218				17	480	809	266		
SE Alaska	5	1	3	0	1	0	0	12	10	4	7		1						4		1	3		4
Kodiak, Alaska	6	0	0	0	0	4	2	67	46					60	7						67			
Sum	1101	238	234	209	147	146	127	7743	997	1239	1222	1499	1381	1159	1243	50	191	320	932	2324	2524	1071	285	46

Table 3. (5 pages). Sighting histories of identified gray whales. Only identifications after 1 June of 1998 to 2003 inlcuded.

	Organization									Year						Month						Regions													
ID	BG	CERF	CRC	HSU	JD	NMML	OTH	UVIC	VD	###	###	###	###	###	###	6	7	8	9	10	11	CA	NCA	SOR	OR	GH+	NWA	SJF	PS-H	NPS	SVI	WVI	NBC	SEAI	KAK
6			6	2							1		4	3		1		4	1	2			2	1	5										
14			7		1	1						2	6	1			3	4		2				1	4	2	1					1			
15	44		1		1	7		1	1	20	12	2	7	14		4	32	18	1								1				50	4			
21						1						1				1														1					
22						2						2				2														2					
30	10	15	1			8		6		2	8	4	10	9	7	1	12	20	7									1			10	13	16		
32		34				2			3	2	16			18	3		3	24	12														39		
37	6		1		3	5		2		5	3	4	2	2	1	1	2	7	4	3							1				6	9	1		
41	42	33	3		2	8	1		1	9	7	22	29	14	9	15	35	23	15	1	1							2			47	4	37		
42	61	6	1		4	16		13	1	24	25	9	13	24	7	8	36	38	12	8								8			68	20	6		
43	63		4	2	1	5		1		3	19	18	3	23	10	8	43	14	7	4				1	5		2				66	2			
53						1						1				1														1					
67	2		8			1					5			6				2	3	5	1			5	3		1				2				
68			1						1	1	1					1					1													2	
71	1														1		1														1				
73	5							1				2	3	1			3	3													5	1			
76	16		4		1	3		1	1	7			2	8	9	5	12	5	2	1	1		2	2			2				18	2			
79	10	72	2			2		2	4	13	25	25	19	5	5	6	40	39	7								2				13	2	75		
80	120	11	3			8		8	3	36	13	42	30	8	24	26	55	52	19	1							3				131	8	11		
81	32	13	3		1	9	1	5	1	8	9	11	22	5	10	11	13	25	13	3							3				36	12	14		
83	3	47	9	1	1	5		12		10	9	8	30	13	8	4	27	29	12	6				3	2		6				3	16	48		
84	76		10	2		10		6	2	16	11	39	10	6	24	26	32	34	14					3	9						84	10			
85	11		1	1		3		3		11	8					7	10	1	1						2		2				12	3			
86		1	2			5		3	1	1	4	3		2	2		3	6	3													7	5		
87	75		2		2	9		17	3	24	12	36	18	10	8	26	20	40	19	3			1		1						82	24			
89	75		5		2	1		15	1	20	19	24	9	4	23	26	40	16	14	2	1		1	2	1						78	17			
91	7	31	5		2	2		4		10		15	11	10	5	6	16	17	10	2				5			2				7	6	31		
92	32					14		4	1	17	6	3	7	6	12	4	10	18	13	6							3				38	10			
93	37	7	3	2		8		1	4	10	9	18	13	8	4	19	16	11	13	3			1		1		2				47	3	8		
94	53		3	1		5		20		13	8	31	4	17	9	1	30	38	11	2				2	1						55	24			
98		3	3			1					1			4	2			7															7		
101	43				1	8		6	1	11	4	6	13	17	8	9	20	25	5									1			47	11			
105	16	18	4			3	1	12	3	13	5	7	25	5	2	11	17	25	4						1						20	12	24		
107	58		1	1		6			1	7		34	10	1	15	5	25	19	15	3					1		4				62				
120	8		2	1	1	1							4	9		4	6	2	1				1		2		1				9				
123	55			1		4		3		8	6	9	8	22	10	15	36	8	3	1			1								57	5			
126	6	4	2	1						10			3				4	3	5	1			3								6		4		
127	53		6	2		3				1	3	26	19	1	14	2	14	39	6	3			2	1	5		1				55				
130	30	5	2			7		2	2	13	1	16	6	2	10	4	13	13	17	1				2			2				34	4	5	1	
135	44	5			2	8		22	3	26	7	10	22	6	13	29	22	24	8	1											50	29	5		
136	24			1	2	4		14		9	1	9	7	2	17	8	19	16	1	1			1								24	20			
138	33	47	2		4	4		13	3	28	18	3	30	12	15	16	23	48	19												36	17	53		
140	29		1		2	4	1	8		4	2	17	8	2	12	1	13	11	18	2			1					1			30	12		1	
141	3	17	1		1	5		9	3	16	5		7	8	3	6	6	21	6								1				7	13	18		
143	11	3			1	7		5		8	7	4	4	3	1	3	6	8	10												12	12	3		
144	10	6	2		1	2		11		13	1	2	10	4	2		11	15	6												10	14	8		
145	4		2		5	1		43		37	6	6	6			14	30	8	2	1					2						4	49			
149		16	3		2	3		12		6	3	4	18	2	3	1	5	24	6													17	19		
150	7				1	2		12		21	1					2	3	13	4												9	13			
151								2			2							2														2			
152						3		3			5			1			1	4	1													5			1
153		29	1			1			1		5	14	11	2			11	15	6														32		
154	19				4			9		5		5	9	4	9	14	11	3	2	2											20	12			
164				2									1	1			1	1					2												
166	67		1			9		3	1	9	9	21	18	9	15	16	26	28	10	1							5				73	3			
169	8	1	6			3							3	5	10	2	6	4	3	3				5			3				8		2		
175	51		1		4	11		15	2	14	14	6	18	2	30	20	27	23	11	2	1		1				3				48	32			
177	46				1	8		9	5	17	52					11	17	28	12	1							2				57	10			
178		1				3		15		11	3	4			1	2	6	9	2													18	1		
185	63				2	6		15		6	18	20	14	2	26	19	32	19	13	3								4			58	24			
186	50		4	3		7		6	2	13	11	13	11	6	18	25	22	13	7	5			3		4						55	10			
187	95		2		1	19		1	4	14	21	50	6	4	27	14	41	43	18	5	1						11				107	4			
192	146		3			15		7	4	38	29	35	22	29	22	43	57	55	18	2				1	1		7				159	7			
193	2	1				1		14		11				6	1		8	5	5												2	15	1		
196	9		2			1						2		1	9	4	3	4	1					1	2						9				
202			1							1										1			1												
204	54		12	1		2		1		1	2	45	3	5	14	3	9	28	25	2	3		4	6	3		1				55	1			
205	1				2	14		1			6	1	3	3	5		5	6	5	1	1						14				1	3			
206			6	9		1				3	2	1	3	4	3	1	6	1	3	5			10	6											
209	4					1				5						3	2										1				4				
212	40		2		3	9		1		22	15		15	3		10	18	11	12	4											50	5			
215			4	2		4				1				5	4	2		4	3	1			2	3	1		1	3							
216	16	35				13		1	1	1	2	28	20	2	13	6	30	21	6	3							4	9			16	1	36		
219	100		3			12			3	24	20	33	14	16	11	16	39	34	26	3											116	2			
226	38		2			3			2	6	2	32	3	2		5	16	14	9	1			1	1			1				42				
227	69	3				5	1	5	2	10	2	19	8	31	15	7	39	37	2												72	8	3	2	
228						2				2											2							2							
229	8	26				4		2	1	5	6	3	11	12	4		7	16	18												8	6	27		
231	47		6			9			1	29	30			3	1	6	14	22	19	2				4							59				
232	10		1		1	4		1		6		1	2	2	6	2	10	5													13	2			2
233	4					2				6						1	5														6				
234	32		4			6		4	1	7	5	4	7	9	15	5	16	17	8	1				3							35	9			
236	17	6	2		1	3		2	1	26	6					3	5	22	2						1						20	3	8		
237	2	53	2	1	1			1	1	7	4	15	11	17	7		27	26	7	1					1						3	2	55		
238	23	18	1		1	4		2	5	11	19		16	1	7	10	23	18	3												27	3	24		
239						4				4										4								4							
242	44		3			19		1	2	8	24	12	18	7		18	13	19	10	6	3						3	14			51	1			
243	1					1				2							1		1												2				
244	18	10	2		2	6		6		10	6	9	10	8	1	1	15	12	14	2											21	12	11		
246						1		2		3							1	2													1	2			
247	2	1							1	3				1			4														3		1		
249			1			4				5										5								5							
250						1				1											1							1							
251						1				1							1										1								
252						1				1											1							1							
253						1				1										1								1							
254	10				1	6		13		9	5	12	1	3			9	6	15												12	18			
255						7				7										7								7							

Table 3. (5 pages). Sighting histories of identified gray whales. Only identifications after 1 June of 1998 to 2003 inlcuded.

	Organization									Year						Month						Regions													
ID	BG	CERF	CRC	HSU	JD	NMML	OTH	UVIC	VD	###	###	###	###	###	###	6	7	8	9	10	11	CA	NCA	SOR	OR	GH+	NWA	SJF	PS-H	NPS	SVI	WVI	NBC	SEAI	KAK
256			1							1											1													1	
257			1							1											1													1	
258			1							1										1									1						
259			2							2											2								2						
260			1							1											1								1						
261			1					1		1				1				1			1											1		1	
267			2							2										1	1							2							
268			2							2										1	1							2							
272						1				1								1									1								
274			1	1						1	1							1		1			2												
275			5	13						5		7	1	5		1	4	4	2	7			18												
276			1	1						1	1						1			1			2												
277			4			1				4		1						1		4			4									1			
278			3	4						1			2	2	2	3			2	2			5	2											
279			1							1										1			1												
280			7							3				3	1				2	4	1		4	3											
281	9	6	5	1		5		3	1		9	8	9	3	1	5	10	8	5	2				4	2						9	8	7		
284				6								5	1				3		1	2			6												
286	1		4	8	1			1		2		1	10	2			6	5		4			8		4						1	2			
289				6								1	4	1			1		3	2			6												
290				1						1							1						1												
291	6		5	9		2		2		2	2	1	3	6	10	7	4	2	2	8	1		10	1	3			2			6	2			
292				1						1								1					1												
293			1							1								1							1										
294				1						1										1			1												
295	2		5	1				3		7			1	1	2			8	1	1	1		2	1	3						2	3			
296	33		12	2		8		2		11	5	3	2	24	12		11	37	4	4	1		1		11		8				33	4			
297			7	2		1				2	2		4	1	1		1	5	1	3			1	1	7		1								
298				2						2								2							2										
300	40		2	1	2	4		19		22	4	39			3	7	28	20	12	1					2						43	23			
301	13		7	5		1		2		3	3	9	3	1	9	5	6	9	7	1			2	2	8						13	3			
302	14	2	4	5		1		1		4	4	1		4	14	2	7	15	3						9						14	2	2		
303	8		7	1				1		2	2		4	1	8			14	3						8						8	1			
304						3				3									2	1							3								
306	4	12			2	2		6	1	4	2	3	15	1	2	1	9	14	3												5	9	13		
307								2		2						1	1															2			
308		20	5		1	4		6	1	3	3	6	13	12			12	19	6													11	26		
309	3	1	1	1		1		2		1	2			5	1	3	3	2	1				1		1						3	3	1		
310				1				3		3	1					2	1	1					1									3			
311	8		2		1	3		19		10	2	4	3	3	11	1	11	16	1	2	2		3								8	22			
312	2				1			2		4			1			2	3														2	3			
314	1	52	2					5	1	9	14	12	9	15	2	2	17	36	6												1	5	55		
315	2	75			3	1		4	3	22	14	24	24	4		5	39	35	9												3	6	79		
316					2	2		5		7					2		4	5														7			2
317	22				2	1		63		33	25	5	12	2	11	17	42	26	2	1											22	66			
318								1		1								1														1			
319	8					7		5		2		2	13	2	1	2	9	6	2	1							5				10	5			
320	21	41	2		2	2		64		16	50	23	17	13	13	27	56	43	6												21	68	43		
321		1						5		6						2	2	1	1													5	1		
322	2	14						5		11		9		1			12	5	2	2											2	5	14		
323		25	2					1		12				4	12		14	14														1	27		
324		62							1	14	21	16		8	4	5	23	25	10														63		
325		36								9			13	10	4		13	15	8														36		
326		24					1		1	4	22						8	14	4														26		
327		14	3					4		1		6	11		3		4	15	2													4	17		
328		44	2			3		1		2	4	2	12	15	15		18	20	12													4	46		
329	3	13								1			14	1			5	11													3		13		
330		17								2				15			4	9	4														17		
351						2					2							2														2			
355						1					1						1											1							
356			1								1									1					1										
357			1								1						1												1						
358			1								1						1												1						
359			1								1					1													1						
360			4								4					4													4						
361				2							2						1	1					2												
362				1							1							1					1												
363			1	2							3							2		1			3												
364			6								1	2		3				3		3				3	3										
365			6	6							1	1	3	4	3	1	2		5	2	2		9	3											
366			3					1			1		1	2			1	1		2				1	2							1			
368	2		3								1		1	3		3	1	1						1		2					2				
372	18	3		2		7		1			21	4		1	5	1	17	7	1	5					2		3				22	1	3		
373				2							2						2								2										
374				2							2							2					1		1										
375				2							2						2						2												
376				1							1								1						1										
377				6							6						6						6												
378				2							2						2						2												
379				4							4						4						4												
380				3							3						3						3												
382						3		7			10					3	1	4	2													10			
384						2					2							2														2			
385						2					2							2														2			
392	2		1	5		5		6			10		5	1	3	3	10	6					5	1			1				2	10			
393						2					2							2														2			
396	33		1			12		2			1	4	17	4	22	10	13	19	4	2							8	1	1	1	35	2			
397			1								1					1													1						
399			10								10					10													10						
407				1							1						1						1												
408				1							1									1					1										
410			2								2								2			2													
411			1	15							1	3	8	4		3	4	1	3	5			16												
412				2							2						1	1					2												
419				1							1								1						1										
424						1					1							1														1			
427						1					1							1														1			
428				1							1						1						1												

Table 3. (5 pages). Sighting histories of identified gray whales. Only identifications after 1 June of 1998 to 2003 inlcuded.

	Organization									Year						Month						Regions													
ID	BG	CERF	CRC	HSU	JD	NMML	OTH	UVIC	VD	###	###	###	###	###	###	6	7	8	9	10	11	CA	NCA	SOR	OR	GH+	NWA	SJF	PS-H	NPS	SVI	WVI	NBC	SEAI	KAK
429				4							4							3		1			3		1										
432				1							1						1						1												
433						1					1							1														1			
434						1					1							1														1			
438			4								4					4													4						
439				2							2						2						2												
440				2							2						2						2												
444				3							3						3						3												
448				5							5						5						5												
449				2							2						2						2												
450				1							1							1					1												
451						3		2			1	4					1	2	2													5			
460				1							1								1						1										
464				8								2		6		1	2	3		2			8												
468				2							2							2					2												
470				1							1							1					1												
471				1							1						1						1												
474				1							1						1						1												
476				2							2						2						2												
477						1					1							1														1			
478				1							1						1						1												
480						1					1								1													1			
483						1					1							1														1			
485						2					2							2														2			
489				2							2							1		1			1		1										
490						1					1							1														1			
492								1				1						1														1			
496								2				2					1	1														2			
501						1						1				1														1					
502						2						2							2													2			
503			1									1							1						1										
505						1						1				1														1					
506						1		1				2						1	1													2			
507	19		1			2			1			17	6				4	8	10	1							2				21				
508			2			4						6						1	1	4					1			5							
509						1						1				1														1					
510	9		6			5						2	1	11	6		1	11	6	2				6			5				9				
511	1					1		2				4					2	2													1	3			
514						1						1						1														1			
515	29					3		2				28	4	2		2	9	14	9								2	1			29	2			
516			1			3						4					1			3								4							
518						1						1						1														1			
519			1									1				1															1				
525	1				1	2						1	2	1			1		2	1											1	3			
527			1									1						1													1				
528						1						1						1														1			
529	40		1		2	3		5			5	35	11			8	17	13	11	2											43	8			
532	23				1	2		1				20	1	4	2		5	15	6	1							2				23	2			
536						1						1							1													1			
537			1	2								2			1				1	1	1		2	1											
538		7	4									4	3	4				8	3						4								7		
539						2						2				2														2					
542						2						1		1					2								1					1			
543						1						1				1														1					
546			1			1						2				1	1												1	1					
548			1									1					1												1						
551			2	1								1		2			1			2			1	2											
552				4								3		1			3		1				4												
553				1								1					1						1												
554			4	5								3	2	2	2	1	1			4	3		7	2											
555			5	7		1						6		4	3	1	5	3	1	1	2		9	4											
556				2								2					2						2												
557				3								3					1	2					3												
558				1								1					1						1												
559				2								2				2							2												
560				1								1				1							1												
561	11			2				3				2	2	3	9	2	7	5	2				2								11	3			
562			1	5								2		4		1	1	1	3				6												
563				1								1				1							1												
564				1								1					1						1												
565			2	1								1		2					2		1		1	2											
566				3		1						3		1			3	1					3												1
567	31		1			1		1					7	15	12	2	21	9		2							2				31	1			
569	13												13			4	4	5													13				
570	5					2							7			3	4														7				
571	4												4			2	2														4				
572	20				1	1		1				7	10	1	5	5	8	7	3												19	4			
573	4												4			3	1														4				
574	5					1							6			3	3														6				
575	1												1			1															1				
576	6					1							7			3	3		1								1				6				
577	22					1							14	9		7	5	11													23				
578	2												2			2															2				
580	1												1				1														1				
581	3												3			2	1														3				
582	1												1			1															1				
583	10				1			1					5	1	6	2	3		6	1											4	8			
584	3							1					3	1		2	2														3	1			
586	28												6	22		10	11	7													28				
587	6					2		3					8	3		3	6	1	1												8	3			
588	1												1			1															1				
589	1												1				1														1				
590	6												6			2	4														6				
591	2												2			1	1														2				
592	4					1							5			3	1		1								1				4				
593	3					1							4			1	3														4				
594	6	27	1						1		5	9	13	7	1	3	10	15	7												6		29		
595	1					2							3			3											2				1				

Table 3. (5 pages). Sighting histories of identified gray whales. Only identifications after 1 June of 1998 to 2003 inlcuded.

	Organization									Year						Month						Regions													
ID	BG	CERF	CRC	HSU	JD	NMML	OTH	UVIC	VD	###	###	###	###	###	###	6	7	8	9	10	11	CA	NCA	SOR	OR	GH+	NWA	SJF	PS-H	NPS	SVI	WVI	NBC	SEAI	KAK
596	1					2		2					3	2		3	2										1				2	2			
597	2	34	2					1	1			18	20	1	1		12	22	6												2	1	37		
598	1					1							2				2														1	1			
599	2												2				1		1												2				
600	1												1				1														1				
601	2	4	1			1						1	2		5		4	3	1												2	1	5		
602						1							1			1											1								
603						2							2			1	1										2								
604	18					1							1		18	5	12	2									1				18				
605	11				1	10		2					11	11	2	1	5	11	3	2	2						7	3			11	3			
606					1	1							2				2															2			
607			1	1		2							2	2			1	2		1			1				3								
608						1							1						1								1								
610						3							3							1	2							3							
611	2			1	1								4				3			1			1								2	1			
612	2	47						6	2			22	18	7	10	2	24	25	6												2	6	49		
613	5							2					2	2	3		4	2	1												5	2			
614	1												1					1													1				
615	1			1									1	1					1	1			1								1				
617	1			2									3				2		1				2								1				
618	1												1						1												1				
619				3									3				1		1	1			3												
620	1				1								2				2														1	1			
621			1	6									7			1	6						7												
622				1									1							1			1												
623				2									2				2						2												
624			9										2	4	3	1			6	2				8	1										
625			4					2					4	2				4	1	1					4							2			
626			2										2			1		1							2										
628		31	3				1		1		1	14	16	3	2		10	20	6														35	1	
629		20	1										11	9	1		3	14	4														21		
634			1										1					1				1													
635	22		1										1		22	3	4	13	3			1									22				
637	1		2										2		1			3				2									1				
638			3	2									3		2	1	1	1	2				2	2	1										
639				1		2							1	2				2		1			1												2
640				2									2			1	1						2												
641	12			6		1							3	3	13	2	2	10	5				6				1				12				
642			1	3									3	1			1	1	1	1			3	1											
643			1	1		1		1					1	2	1				2	1	1		2									2			
644				3									2	1						3			3												
645				3									3				3						3												
646				1										1		1							1												
647			1										1				1					1													
648			2										2					2				2													
649					2								2						1	1												2			
651		46	1						3			21	24		5	1	13	30	6														50		
652		3											3				3																3		
653	9	9			1								3	8	8		6	6	7												9	1	9		
654			1											1						1				1											
655	9		1											1	9		4		5	1				1							9				
656			2											1	1				1	1				2											
657			3											2	1			1	2					3											
658			2											2					2					2											
659			2											2					2					2											
660			1											1						1				1											
661			1											1				1						1											
664			1											1				1					1												
665			3											1	2				3					3											
668			5											5					3	2				5											
669			5											3	2			1	2	2				5											
670			1	1										2		1				1			1	1											
671		25	1											9	17		17	5	4														26		
673			1												1			1															1		
674		2	6											5	3		4	4															8		
675		15	2											8	9	1	9	7															17		
676			3											3			2	1															3		
681	2							1						3			3														2	1			
682	25							1						4	22	5	6	10	5												22	4			
683	1							1						2			2														1	1			
684	4					1		1						5	1		4	2													4	1			1
685	4							1						5			4	1													4	1			
686	1							2						3			1	2													1	2			
687	1							1						2			2														1	1			
688	9		1					1						6	5		6	3	2					1							8	2			
689	1													1		1															1				
691	6					3								2	7	3	3	3													6				3
692	12					1								1	12	2	7	4										1			12				
694	4	19	3						2			12		12	4	2	6	14	6												4		24		
695	1													1				1													1				
696	9					10								3	16	2	5	2	8	2							3	7			9				
697	19													19		3	4	8	4												19				
698	10		2											4	8		6	3	3					2							10				
699	2			1										1	2	1	1	1					1								2				
700				1										1		1							1												
701				1										1				1					1												
702				3										3		2	1						3												
703				2										2				1	1				2												
704				1										1		1							1												
705				1										1		1							1												
706				2										2		2							2												
707				1										1		1							1												
708				1										1		1							1												
709	5			2										2	5	3	2	2					2								5				
710				5		1								6		3			2	1			6												
711				2										2		2							2												
712	7				1			1						2	7		1		7	1												9			
713								1						1					1													1			

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	Organization									Year						Month						Regions													
ID	BG	CERF	CRC	HSU	JD	NMML	OTH	UVIC	VD	###	###	###	###	###	###	6	7	8	9	10	11	CA	NCA	SOR	OR	GH+	NWA	SJF	PS-H	NPS	SVI	WVI	NBC	SEAI	KAK
714								1						1			1															1			
715								1						1					1													1			
716								1	1			1		1			1	1														1	1		
717								1						1			1															1			
718	10	1						2					1	2	10	2	4	5	2												10	2	1		
719	10							1						1	10			9	2												10	1			
720	7					3		1						1	10		2	6	3									3			7	1			
721						1								1				1																	1
722						1								1				1																	1
723						3								3				3																	3
724						2								2				2																	2
725						1								1				1																	1
726						1								1				1																	1
727						1								1				1																	1
728						1								1				1																	1
729						3								3				3																	3
730						1								1				1																	1
731						2								2				2																	2
732						1								1				1																	1
733						1								1				1																	1
734						3								3				3																	3
735						1								1				1																	1
736						1								1				1																	1
737						1								1				1																	1
738						1								1				1																	1
739						1								1				1																	1
740						1								1				1																	1
741						2								2				2																	2
742						1								1				1																	1
743						2								2				2																	2
744						1								1				1																	1
745						1								1				1																	1
746						1								1				1																	1
747						2								2				2																	2
748						1								1				1																	1
749						1								1				1																	1
750						2								2				2																	2
751						1								1				1																	1
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756						2								2				2																	2
757						2								2				2																	2
758						2								2				2																	2
759		24												15	9		8	10	6														24		
760		15	1											7	9		7	5	4														16		
761		19	1											12	8		7	8	5														20		
762		13	1						1		3			9	3		2	6	7														15		
763		11							2			12			1			12	1														13		
764		13										13						7	6														13		
766									1			1							1										1						
767	1										1								1												1				
768	21										21					1	8	11	1												21				
769									1		1							1															1		
772									1		1					1																		1	
773	4										4						1	2	1												4				
776	1											1				1															1				
777	2											2				2															2				
781			1												1				1					1											
782						8									8		2	5		1							3	5							
783						3									3		3										3								
784						1									1			1																	1
785	2					2									4	1		1	2								1	1			2				
786	11														11	1	2	3	5												11				
787	6														6	1	2	3													6				
788	11					1									12	2		8	1	1							1				11				
789	6														6	1	2	2	1												6				
790	11														11	1	2	7	1												11				
791	7														7			2	5												5	2			
792	11														11		5	4	2												11				
793	2														2	2															2				
794	2														2			2													2				
795	5														5	1	3	1													5				
796	3														3		2	1													3				
797	1														1		1														1				
800		7													7	1	5	1															7		
801		8													8		8																8		
802		1													1		1																1		
803		1													1			1															1		
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805								1			1						1															1			
806								1			1						1															1			
807								1			1					1																1			
808								1			1							1														1			

Table 4. Gray whales seen in more than one region or year by month and region.

	1998-2003 all seasons			1998-2003 after 1 June		
	IDs	**Seen >1yr**	**Seen >1 region**	**IDs**	**Seen >1yr**	**Seen >1 region**
Month						
March	22	14 (64%)	7 (32%)			
April	67	26 (39%)	17 (25%)			
May	142	43 (30%)	41 (29%)			
June	191	124 (65%)	123 (64%)	191	120 (63%)	119 (62%)
July	274	176 (64%)	169 (62%)	274	176 (64%)	165 (60%)
August	294	180 (61%)	169 (57%)	294	179 (61%)	164 (56%)
September	206	163 (79%)	147 (71%)	206	163 (79%)	145 (70%)
October	130	101 (78%)	97 (75%)	130	100 (77%)	96 (74%)
November	33	23 (70%)	22 (67%)	33	23 (70%)	22 (67%)
Region						
Central and S California	6	2 (33%)	2 (33%)	6	2 (33%)	2 (33%)
N California	121	58 (48%)	54 (45%)	120	58 (48%)	53 (44%)
S Oregon	57	49 (86%)	46 (81%)	57	49 (86%)	46 (81%)
Central Oregon	55	42 (76%)	46 (84%)	55	41 (75%)	45 (82%)
Grays Harbor area	35	11 (31%)	6 (17%)	2	2 (100%)	2 (100%)
N Washington coast	113	53 (47%)	60 (53%)	63	49 (78%)	56 (89%)
Str of Juan de Fuca	35	18 (51%)	22 (63%)	31	16 (52%)	19 (61%)
Other WA inside	25	3 (12%)	6 (24%)	14	1 (7%)	2 (14%)
N Puget Sound	42	11 (26%)	8 (19%)	10	1 (10%)	2 (20%)
S Vancouver Is.	201	132 (66%)	149 (74%)	192	132 (69%)	148 (77%)
W Vancouver Is.	169	122 (72%)	133 (79%)	169	122 (72%)	132 (78%)
N British Columbia	82	72 (88%)	57 (70%)	82	72 (88%)	56 (68%)
SE Alaska	10	6 (60%)	5 (50%)	10	6 (60%)	5 (50%)
Kodiak, Alaska	46	8 (17%)	8 (17%)	46	7 (15%)	7 (15%)

Table 5. Sumnary of inter-regional matches of whales among regions. Matrix shows number of different whales that have been identified in both regions sometime between 1998 and 2003.

Region	IDs	CA	NCA	SOR	OR	GH+	NWA	SJF	PS-H(	NPS	SVI	WVI	NBC	SEAK	KAK
All seasons															
Central and S California	6														
N California	121	0													
S Oregon	57	0	24												
Central Oregon	55	0	20	22											
Grays Harbor area	35	0	2	3	2										
N Washington coast	113	0	13	16	17	1									
Str of Juan de Fuca	35	0	3	2	3	0	9								
Other WA inside	25	0	0	0	0	0	1	1							
N Puget Sound	42	0	0	0	1	1	1	1	6						
S Vancouver Is.	201	2	29	27	31	1	53	18	1	1					
W Vancouver Is.	169	0	23	19	29	1	39	14	2	2	113				
N British Columbia	82	0	3	5	10	0	14	5	0	0	48	43			
SE Alaska	10	0	1	1	0	0	1	1	0	0	4	4	3		
Kodiak, Alaska	47	0	2	0	0	1	0	0	0	0	4	4	0	0	
Only identifications taken after 1 June of each year															
Central and S California	6														
N California	120	0													
S Oregon	57	0	24												
Central Oregon	55	0	20	22											
Grays Harbor area	2	0	0	2	1										
N Washington coast	63	0	13	16	15	1									
Str of Juan de Fuca	31	0	3	2	3	0	9								
Other WA inside	14	0	0	0	0	0	1	1							
N Puget Sound	10	0	0	0	0	0	1	1	2						
S Vancouver Is.	192	2	29	27	31	1	50	16	1	1					
W Vancouver Is.	169	0	23	19	29	1	35	13	1	1	113				
N British Columbia	82	0	3	5	9	0	12	4	0	0	48	43			
SE Alaska	10	0	1	1	0	0	1	1	0	0	4	4	3		
Kodiak, Alaska	47	0	2	0	0	0	0	0	0	0	4	4	0	0	

Table 6. Model selection results of analysis of within year, between year and overall interchange between NWA and the other 5 regions.

Analysis	Model	# of parameters	AIC
Within-year interchange	Region + Year + #Years seen	11	705.7
	Region + Effort + #Years seen	7	706.7
	Region + Effort	6	707.5
	Region + Year	10	707.6
	Region*Year + #Years seen	31	718.2
	Region	5	730.4
Between-year interchange	Region + Year + #Years seen	11	1179.1
	Region + #Years seen	6	1187.0
	Region*Year + #Years seen	31	1205.5
	Region	5	1248.6
	Year	6	1275.0
Overall interchange	Region + Year + #Years seen	11	1179.1
	Region + #Years seen	6	1187.0
	Region*Year + #Years seen	31	1205.5
	Region	5	1248.6
	Year	6	1275.0

Table 7. Petersen capture-recapture abundance estimates for seasonal res
gray whales. Excludes identifications made before 1 June and those from
Sound area.

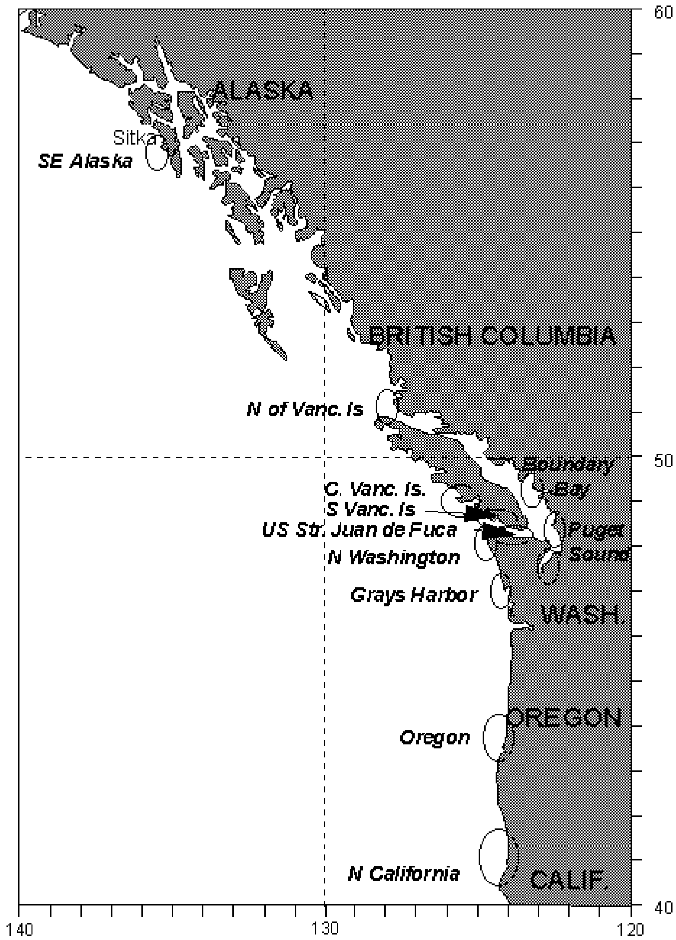
Sample 1		Sample 2				
Year	**n**	**Year**	**n**	**Match**	**Est.**	**CV**
Identifications from N California to SE Alaska						
1998	133	1999	157	80	**260**	0.05
1999	157	2000	140	74	**296**	0.06
2000	140	2001	175	92	**266**	0.04
2001	175	2002	206	121	**298**	0.03
2002	206	2003	160	126	**261**	0.03
Identifications from Oregon to Northern British Columbia only						
1998	115	1999	120	70	**197**	0.05
1999	120	2000	115	66	**208**	0.05
2000	115	2001	151	83	**209**	0.04
2001	151	2002	180	106	**256**	0.03
2002	180	2003	157	119	**237**	0.03

Table 8. Model selection results for open population models fitted to PCFA (N. CA to N. British Columbia) capture history data. Survival for newly seen whales represents survival (and permanent emigration) for the year immediately following their first encounter. It varied by year (t) for all models while some models also included MRT. Survival for previously seen whales was either constant or varied by year (t). Capture probability models with variation by year and MRT in the previous year were considered.

	Survival		Capture Probability	# par	ΔAICc
	Newly seen	Previously seen			
1	t + MRT	T	t + MRT	16	0
2	t + MRT	Constant	t + MRT	13	1.8
3	t + MRT	T	MRT	12	8.5
4	t + MRT	Constant	MRT	9	16.5
5	MRT	Constant	t + MRT	9	43.9
6	t + MRT	Constant	t	12	66.7
7	t	Constant	t+MRT	12	107.3
8	t	Constant	t	11	133.8

Table 9. Model selection results for open population models fitted to ORSVI capture history data. Model numbers in correspond to ordering of models in PCFA analysis (Table 8). The same models were considered in both analyses.

	Survival		Capture Probability	# par	ΔAICc
	Newly seen	Previously seen			
2	t + MRT	Constant	t + MRT	13	0
1	t + MRT	T	t + MRT	16	1.4
3	t + MRT	T	MRT	12	8.6
4	t + MRT	Constant	MRT	9	11.9
5	MRT	Constant	t + MRT	9	14.0
6	t + MRT	Constant	t	12	19.2
7	t	Constant	t+MRT	12	45.3
8	t	Constant	t	11	57.7



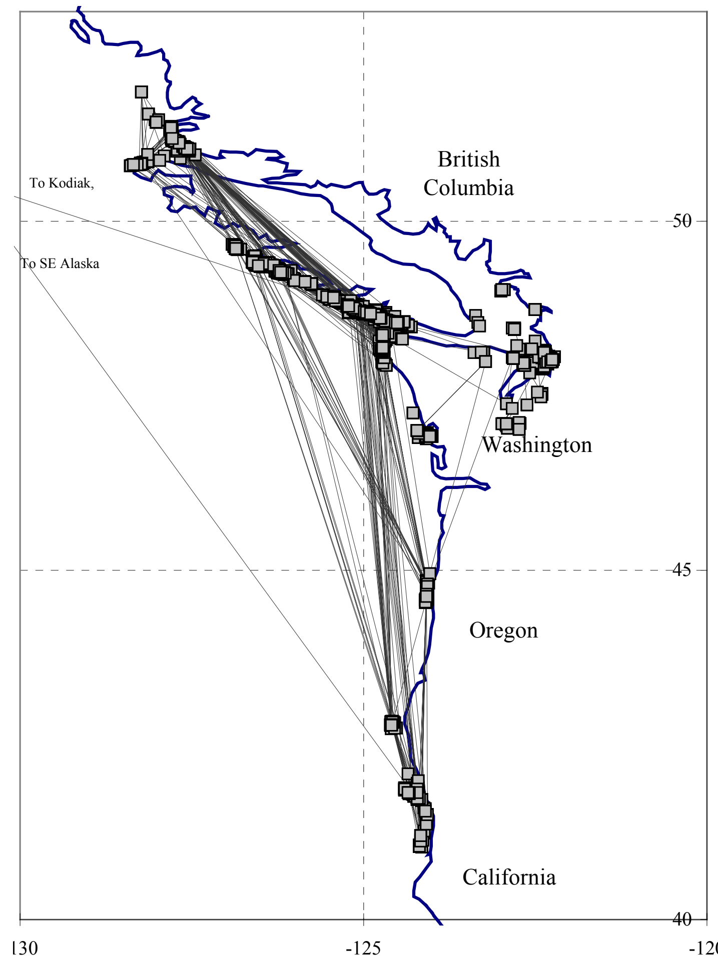


Figure 1. Study areas with principal areas of effort shown by circles.

Figure 2. Locations whales were identified in the central study area. Lines connect re-sightings of whales within a year.

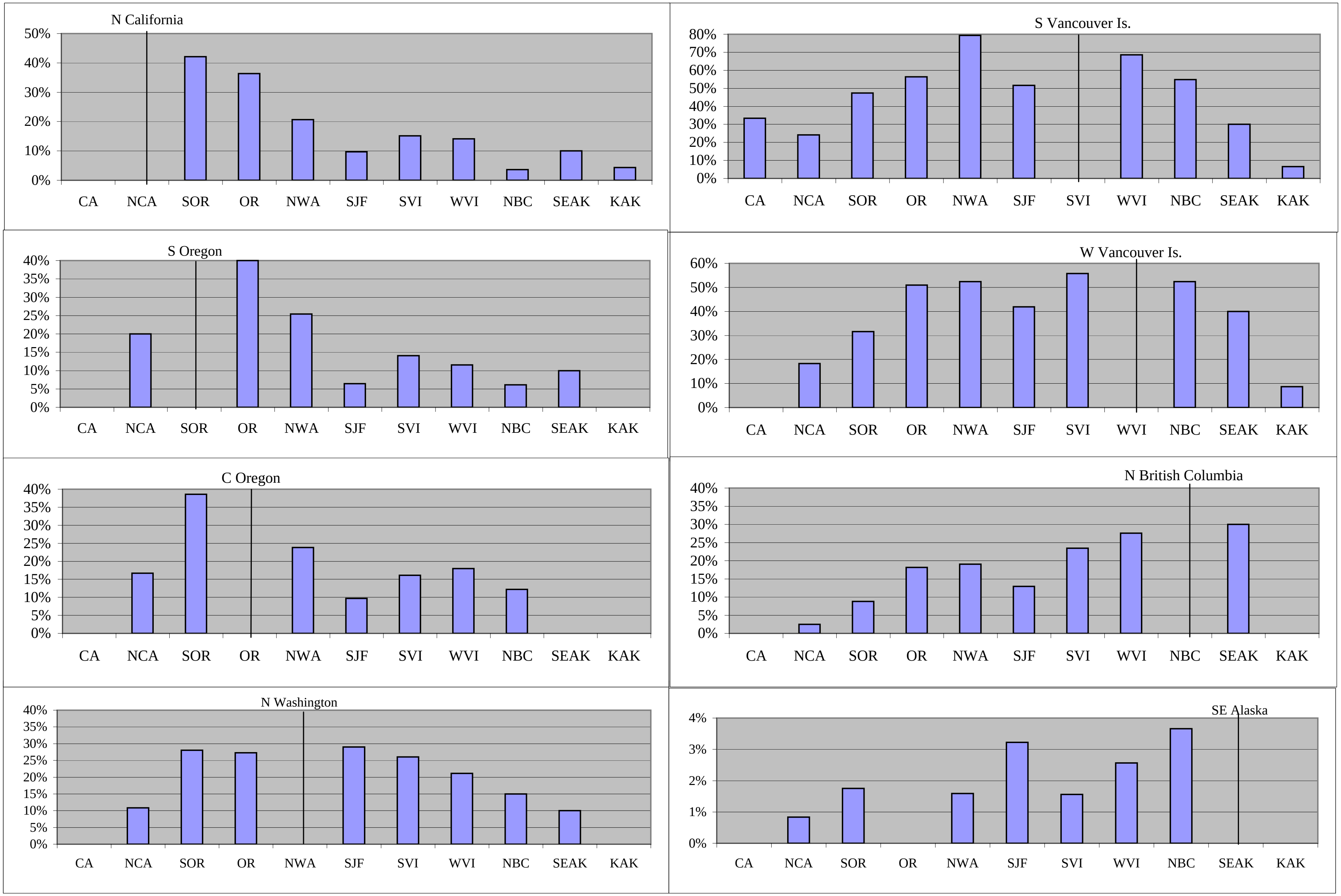


Figure 3. Percent of identified gray whales seen in different regions that match area marked for 1998 to 2003.

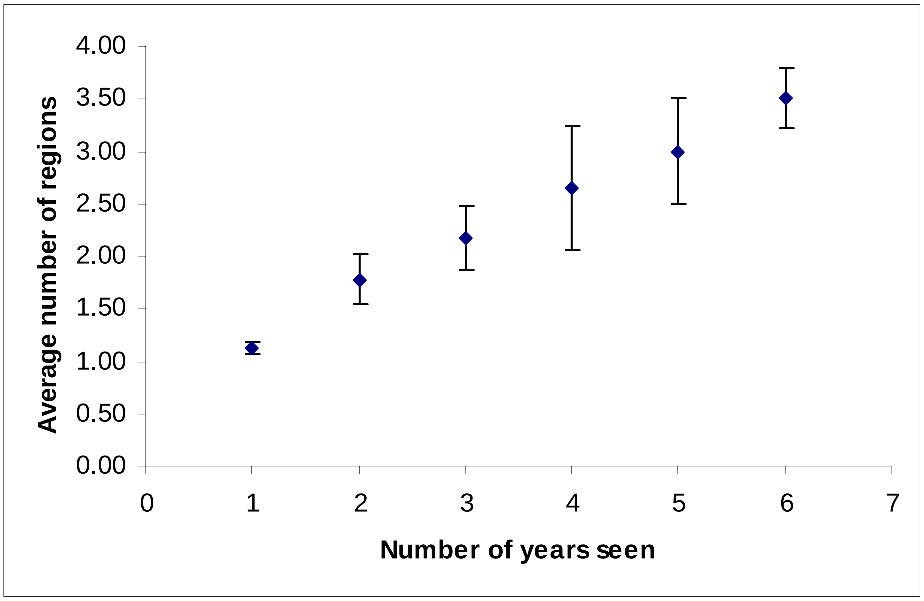


Figure 4. The average number of regions (among the six) in which a whale was seen increases for each year it was seen. Error bars are 95% confidence intervals for means.

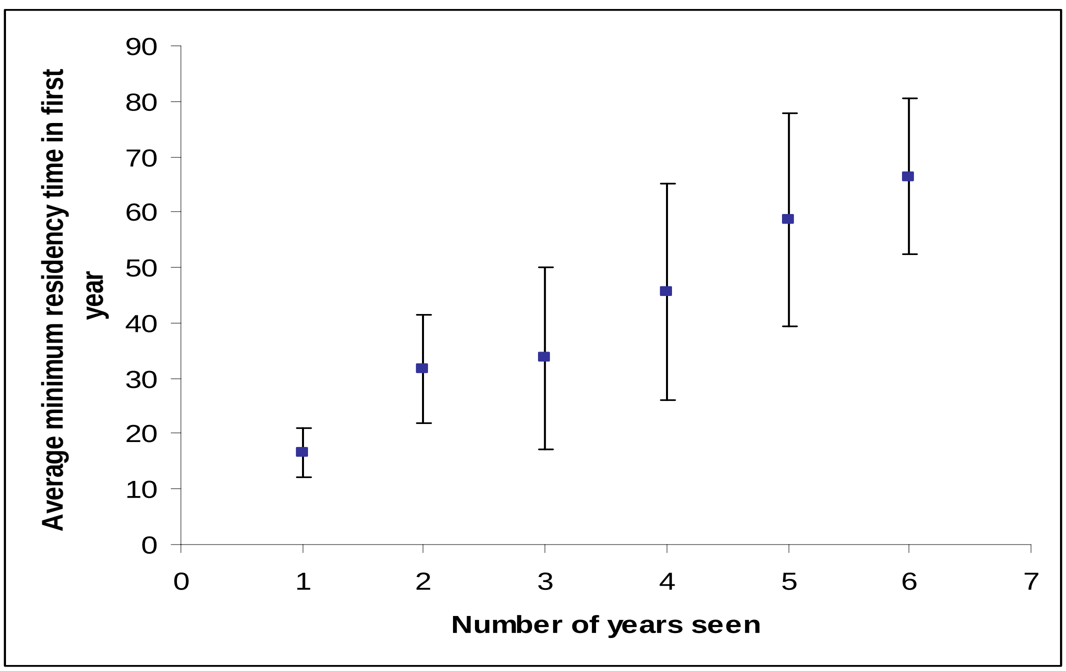


Figure 5. Relationship between number of years seen and the minimum residency time in the first year the whale was seen. Error bars are 95% confidence intervals for means.

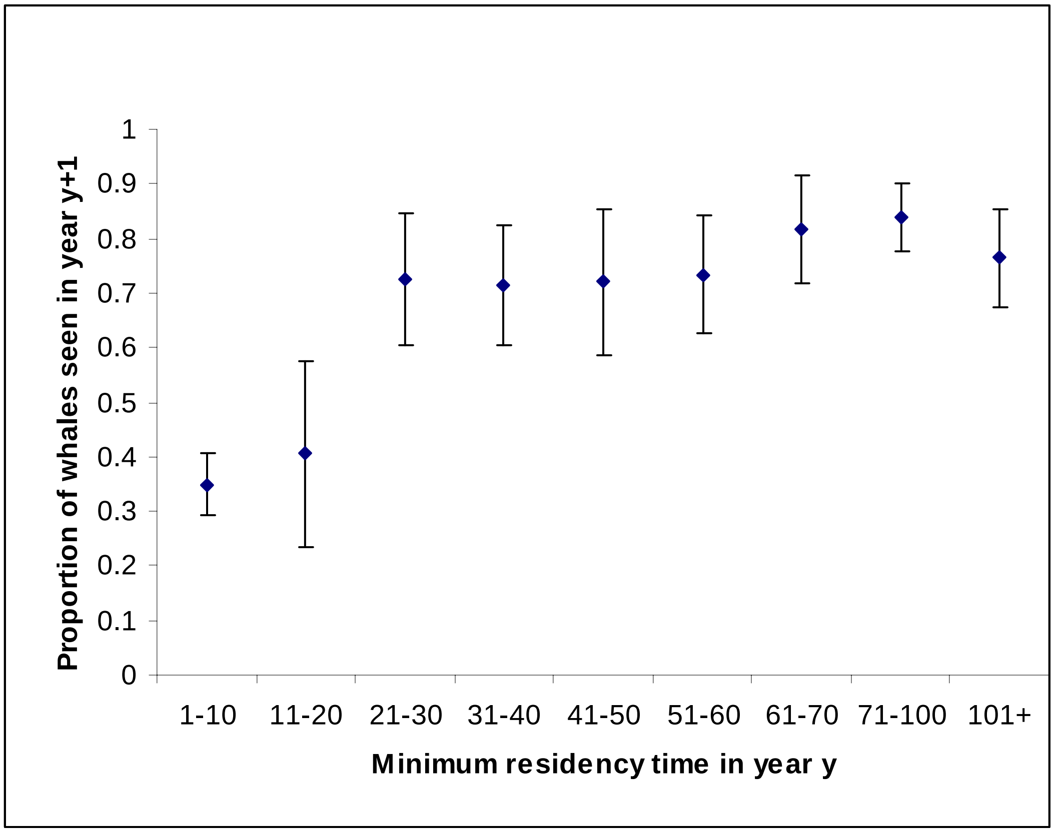


Figure 6. Relationship between minimum residency time in year *y* and the proportion of whales seen in year *y* +1. Error bars are 95% confidence interval based on normal approximation to binomial.

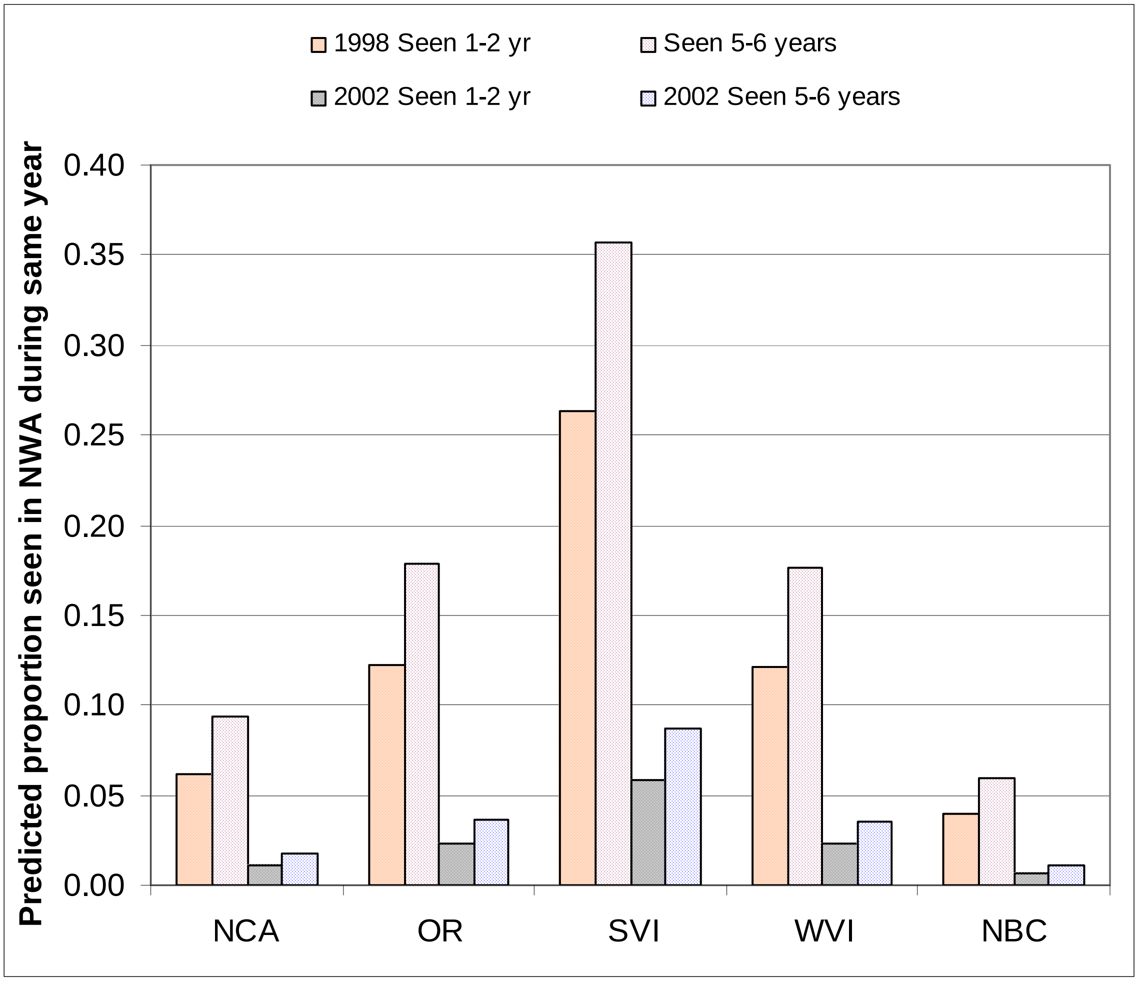


Figure 7. Predicted proportions of within-year interchange with NWA for the highest (1998 - most effort) and lowest (2002 - least effort) years and for whales seen 1-2 years and 5-6 years.

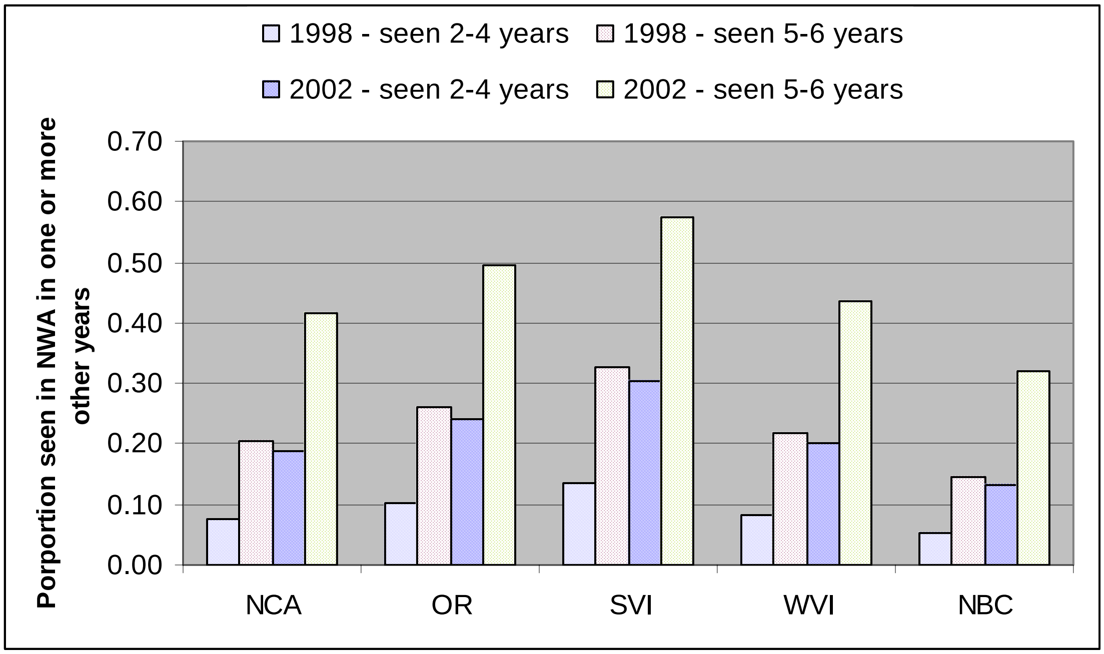


Figure 8. Predicted proportions of between-year interchange with NWA for the highest (2002) and lowest (1998) years and for whales seen 2-4 years and 5-6 years.

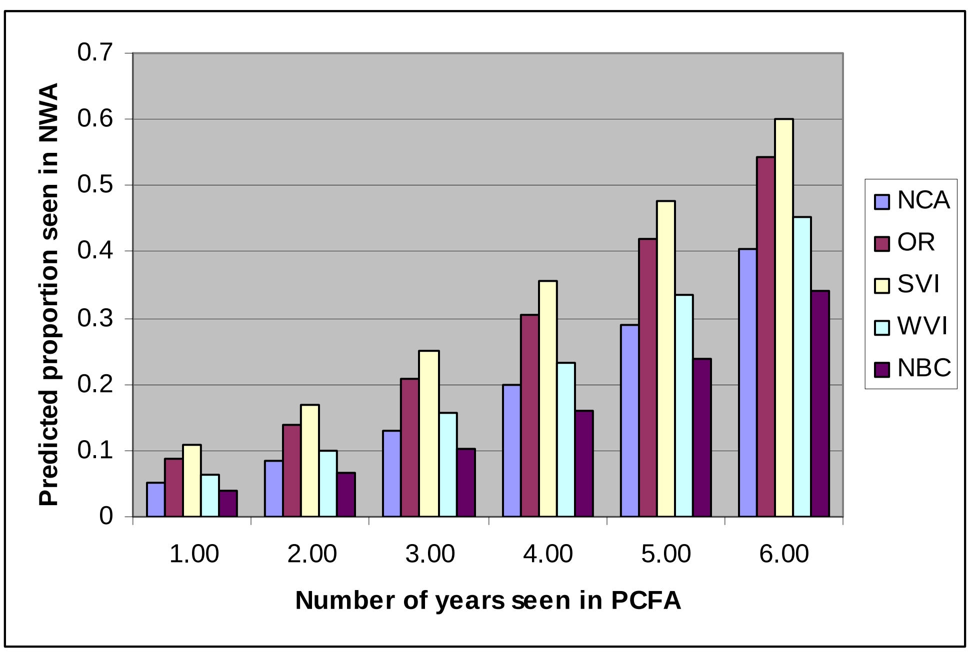


Figure 9. Predicted proportions of overall interchange with NWA for each region and number of years seen.

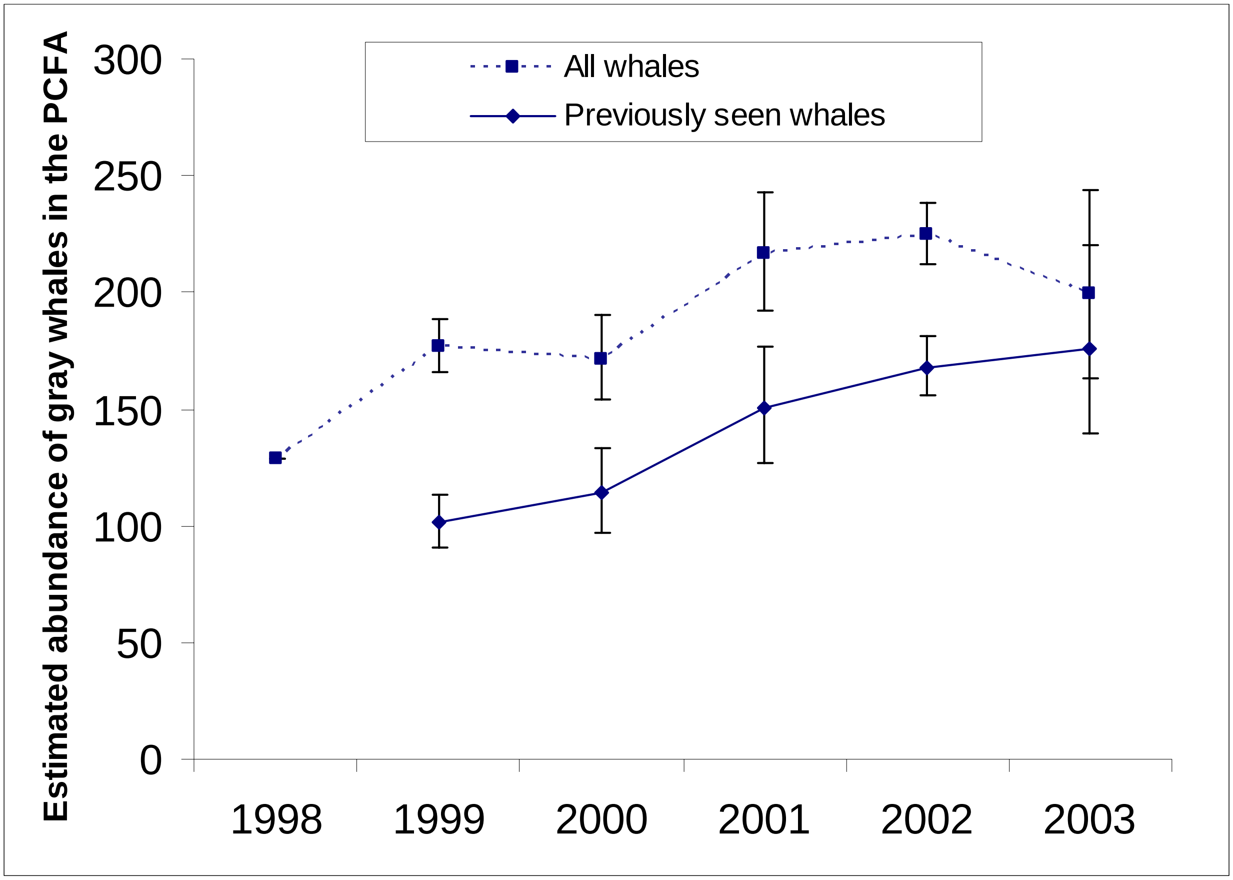


Figure 10. Estimated annual abundance of all whales in the PCFA and returning whales in the PCFA (log-normal 95% confidence intervals shown).

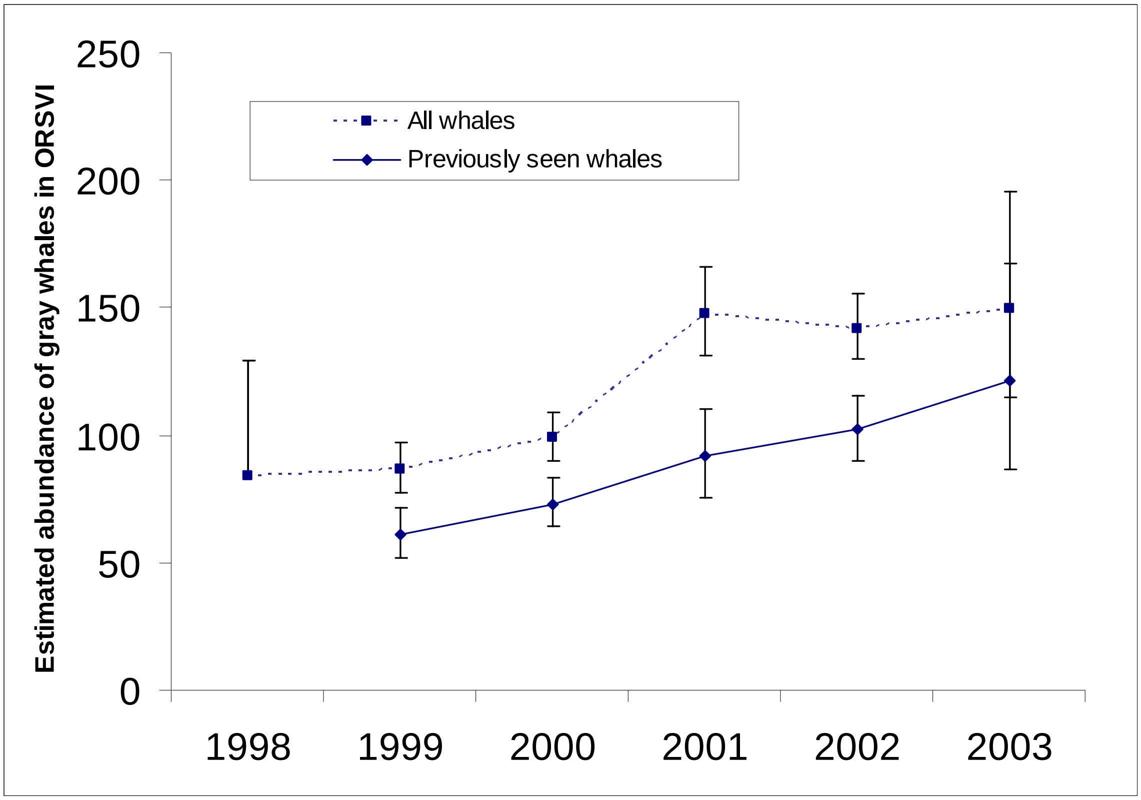


Figure 11. Estimated annual abundance of all whales in ORSVI and returning whales in ORSVI (log-normal 95% confidence intervals shown).