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ABUNDANCE OF BLUE AND HUMPBACK WHALES IN THE EASTERN NORTH PACIFIC ESTIMATED BY CAPTURE-RECAPTURE AND LINE-TRANSECT METHODS

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ABSTRACT

We estimated humpback and blue whale abundance from 1991 to 1997 off the west coast of the U.S. and Mexico comparing capture-recapture models based on photographically identified animals and line-transect methods from ship-based surveys. During photo-identification research we obtained 4,212 identifications of 824 humpback whales and 2,403 identifications of 908 blue whales primarily through non-systematic small-boat surveys along the coast of California, Oregon, and Washington. Line-transect surveys from NOAA ships in 1991, 1993, and 1996 covered approximately 39,000 km along the coast of Baja California, California, Oregon, and Washington out to 555 km from shore. The nearshore and clumped distribution of humpback whales allowed photographic identification from small boats to cost-effectively sample a substantial portion of the population, but made it difficult to obtain effective samples in the line-transect surveys covering broad areas. The humpback capture-recapture estimates indicated humpback whale abundance increased over the six years (from 569 to 837). The broader more offshore distribution of blue whales made it harder to obtain a representative sample of identification photographs, but was well suited to the line-transect estimates. The line-transect estimates, after correction for missed animals, indicated approximately 3,000 blue whales (CV = 0.14). Capture-recapture estimates of blue whales were lower than this: approximately 2,000 when using photographs obtained from the line-transect surveys as one of the samples. Comparison of the results from the two methods provides validation, as well as insight into potential biases associated with each method.

Key words: abundance, humpback whale, *Megaptera novaeangliae*, blue whale, *Balaenoptera musculus*, line transect, capture recapture, eastern North Pacific, assessment methods.

Humpback whales (*Megaptera novaeangliae*) and blue whales (*Balaenoptera musculus*) were depleted in the eastern North Pacific due to commercial exploitation that continued until 1966 (Rice 1978, Clapham *et al.* 1997). Rough estimates of post-whaling populations of humpback and blue whales in the North Pacific were 1,600 and 1,400 (Gambell 1976), respectively, although the methods used for these estimates are uncertain and their reliability questionable. More recently the abundance of humpback and blue whales in the eastern North Pacific has been estimated using both line-transect and capture-recapture methods (Calambokidis *et al.* 1990*a*; Wade and Gerrodette 1993; Barlow 1994, 1995; Barlow and Gerrodette 1996).

Eastern North Pacific humpback whales are seen in the spring, summer and fall along the coast of California, Oregon, and Washington and are part of a distinct feeding aggregation with little interchange with feeding areas in British Columbia or Alaska (Calambokidis *et al.* 1996). This site fidelity to specific feeding grounds appears to be the result of whales returning to their mother's feeding area on their first migration and has been detected through significant differences in the maternally inherited mtDNA among humpback whales in North Pacific feeding grounds (Baker *et al.* 1990, 1994). Humpback whales that feed off California, Oregon, and Washington migrate seasonally to wintering grounds off Baja California, mainland Mexico, and Central America (Steiger *et al.* 1991, Calambokidis *et al.* 2000, Urban *et al.* 2000).

Blue whales in the eastern North Pacific appear to be separate from populations in the central and western North Pacific based on differences in call types (Stafford and Fox 1996; Stafford *et al.* 1999, 2001). These blue whales feed off California from May through November (Calambokidis *et al.* 1990*b*) and migrate to waters off Mexico and as far south as 6°N (the Costa Rica Dome, Wyrtki 1964) in winter and spring (Calambokidis *et al.* 1990*b*, Stafford *et al.* 1999, Mate *et al.* 1999). Blue whales are found year-round on the upwelling-enriched Costa Rica Dome (Reilly and Thayer 1990), and it is not known whether there are non-migratory elements of this population.

Capture-recapture (or mark-recapture) techniques using photographically identified individuals have been used increasingly to estimate the population size of humpback and other large whales (Hammond 1986). These techniques rely on the ability to uniquely identify and track individuals based on photographs of their natural markings including the pigmentation, scars, and ridging on the underside of the flukes of humpback whales (Katona *et al.* 1979, Darling and Jurasz 1983) and the pigmentation and markings on the right and left sides of blue whales (Sears 1987, Calambokidis *et al.* 1990*b*, Sears *et al.* 1990). Capture-recapture techniques have been used to estimate abundance of humpback whales in a number of areas (*e.g.*, Darling and Morowitz 1986, Baker and Herman 1987, Hammond 1990, Katona and Beard 1990, Cerchio 1998, Smith *et al.* 1999, Urban *et al.* 1999) including those off California (Calambokidis *et al.* 1990*a*).

Ship line-transect methods (Buckland *et al.* 2001) have been used to estimate the abundance of whales in many studies, including minke whales in the Antarctic (Buckland 1987), fin whales in the North Atlantic (Buckland *et al.* 1992), and baleen whales in the North Pacific (Barlow 1995, Kishiro *et al.* 1997). Representative coverage is typically obtained using systematic transect lines that uniformly cover the study area. For marine mammals, diving can affect the probability of detecting trackline animals, and many of the recent developments in line-transect methodology have addressed the problem of trackline detection probability (*e.g.*, Garner *et al.* 1999). Previously, line-transect methods have been used to estimate blue and humpback whale abundance in two studies in the eastern Pacific: Wade and Gerrodette (1993) estimated 1,400 (CV = 0.24) blue whales in the eastern tropical Pacific (primarily off Baja California, on the Costa Rica Dome, and south west of the Galapagos) in summer/fall of 1986–1990, and Barlow (1995) estimated 2,250 (CV = 0.38) blue whales and 626 (CV = 0.41) humpback whales off the coast of California in summer/fall of 1991.

We use both photo-identification and ship line-transect data collected along the coasts of Baja California, California, Oregon, and Washington to provide the first estimate of the abundance of blue and humpback whales in the eastern North Pacific populations. Capture-recapture sampling has taken place continuously from 1986 to present and large-scale ship surveys took place in 1979, 1980, 1991, 1993, and 1996. For comparability, we limit both samples to a common time period: 1991–1997. We compare the resulting estimates and the strengths and weaknesses of both methods.

Methods

Photographic Identification

Photographic identification studies of humpback and blue whales were conducted during both systematic line-transect surveys based from NOAA ships (see below) and during more coastal dedicated photographic identification surveys made with small boats (mostly 5.3-m inflatable boats) operating daily from shore. The coastal photographic identification effort was supplemented by some identifications made opportunistically from other platforms such as whale-watch boats. Geographic coverage of the dedicated coastal surveys was selected to maximize success in finding whales and to provide a broad sample from coastal areas.

Identification photographs of humpback and blue whales were taken with 35-mm cameras equipped with 300-mm telephoto lenses and high-speed black-and-white film. If possible, the pigmentation patterns on both the right and left sides of blue whales were photographed and, when shown, the ventral surface of the flukes. For humpback whales, photographs were taken showing both pigmentation and scarring on the ventral surface of the flukes and the ridging pattern along the trailing edge of the flukes.

The best identification photographs of each individual encountered in a sighting were printed (2 ½ × 3 ½ in. for humpback whales and 2 ½ × 7 in. for blue whales). Comparison of photographs were made by at least two matchers, and all matches were verified by a second person. Photographs were rated for quality. Humpback and blue whale identification photographs were first compared internally for each year and then compared to catalogs of all humpback and blue whales previously identified along California–Washington. These catalogs consisted of 965 different humpback whales and 1,070 different blue whales identified primarily since 1986 and extending through 1997. Individual whales identified in each year that did not match past years and that were of suitable quality were assigned new identification numbers and added to the catalogs.

Capture-recapture Estimates

Estimates of abundance were calculated using several capture-recapture models (Seber 1982, Hammond 1986). We used pairs of adjacent years taken from 1991 to 1997 for California, Oregon, and Washington to generate Petersen capture-recapture estimates. The Chapman modification of the Petersen estimate (Seber 1982) was used because it was appropriate for sampling without replacement (Hammond 1986). Abundance estimates were also obtained using the Jolly-Seber multiyear models and the annual samples from 1991 to 1997.

In addition to annual samples, we also calculated Petersen capture-recapture estimates using samples stratified by type of survey. To avoid heterogeneity of capture probability due to geographic sampling bias, we compiled identifications from two 3-yr periods (1991–1993 and 1995–1997) that were obtained during systematic SWFSC surveys that uniformly covered coastal and offshore waters of Baja California, California, Oregon, and Washington. These were the same SWFSC surveys used for the line-transect abundance estimates. Identifications from these surveys, although fewer in number, provided a sample that was not biased geographically. These systematic samples were paired with the larger, but more geographically-biased sample obtained during the more extensive coast-based surveys for the same 3-yr periods.

We employed a new, more conservative method for calculating the variance of Petersen capture-recapture estimates based on the jackknife procedure (Efron 1982). Traditional estimates of variance from capture-recapture estimates may be biased downward because identifications are not independent events. Geographical clumping of animals often resulted in a concentration of sampling effort in these regions. Other aggregations of animals may have not been seen and not sampled. Although humpback whales often range widely along the coast of California, Oregon, and Washington during the season, animals show a preference to return to similar areas each year. To incorporate the variance introduced by this geographic clumping of whales and sample effort, a jackknife estimate of variance was calculated using entire regions as samples. Each sample was divided into five to nine subsamples based on regions and time period. To obtain similar sample sizes, some adjacent regions were pooled together and some areas of high coverage divided into subsamples by season. For capture-recapture calculations that were based on multiyear samples taken from different platforms (SWFSC *vs.* other), each platform was divided into five roughly equal subsamples based on year of sample and broad regions. Pseudo-values for generating the jackknife variance were calculated by excluding each sample from the estimate. Because the Petersen estimate is based on two samples, between 10 and 16 pseudovalues were calculated for each estimate.

Variance was calculated as:

$$VAR = \frac{(n-1)}{n} \sum (P - P_i)^2$$

from Efron (1982), where n is the number of estimates, P_i is each of the abundance estimates calculated by excluding one set of samples, and P is the abundance estimate using all data.

Line-transect Field Methods

Surveys were conducted in 1991 (off California), in 1993 (off California and Baja California), and in 1996 (off California, Oregon, and Washington) using the same line-transect methods on two National Oceanographic and Atmospheric Administration (NOAA) research vessels: the 53-m *McArthur* (1991, 1993, and 1996) and the 52-m *David Starr Jordan* (1993 and 1996). Surveys were conducted between 17 July and 6 November, with dates varying slightly between years and vessels. Teams of three observers searched from the flying bridge deck of both vessels using line-transect methods (Hill and Barlow 1992, Mangels and Gerrodette 1994, Von

Saunder and Barlow 1999). Two observers searched through 25× pedestal-mounted binoculars while the third observer searched with unaided eyes and a 7× hand-held binocular; observation height at eye level was approximately 10 m above the water's surface for both vessels. The third observer was also responsible for recording all data on searching effort and sightings on a lap-top computer. Often a fourth "independent" observer also searched with unaided eyes and a 7× binocular to detect groups that were missed by the three primary observers. During daylight hours, the ships traveled at approximately 18 km/h (10 kn) along a grid of predetermined tracklines that uniformly covered the region between the coast and approximately 555 km (300 nmi) from shore (Fig. 1, 2). At night, the vessels either remained in an area (to begin the next morning where effort was terminated the previous evening) or transited to a new point along the trackline.

When a cetacean was sighted within 5.5 km (3 nmi) of the transect line, searching effort was typically discontinued, and the ship was directed toward the sighted individual or group to determine the species and to estimate group size. In this "closing mode," all observers aided in identifying species and made independent estimates of group size and the proportion of each species present in the group. Sometimes in closing mode, the ship did not end effort or divert from the trackline if observers believed that they could determine species present and obtain good estimates of group size without doing so. In a 1996 experiment approximately one third of the effort was conducted in "passing mode," during which time the vessel did not end effort or divert from its course when cetaceans were seen. The fraction of unidentified sightings was much higher in passing mode (Barlow 1997), and observers reported that they were less able to accurately estimate group size or species proportions. For analyses presented here, data from closing and passing mode were pooled.

Each observer team included at least one expert in species identification. Species were recorded only when positively identified. For groups that could not be identified to the species level, observers recorded the lowest classification level of which they could be certain (*e.g.*, "rorqual" or "large whale"). Observers were required to describe and draw all diagnostic features used to identify species.

Line-transect Estimates

Cetacean abundance was estimated using line-transect methods (Buckland *et al.* 2001). The study area was divided into four geographic strata (Fig. 1): inshore waters off California (264,300 km^2, corresponding to the aerial survey strata of Forney and Barlow 1998), offshore waters off California (550,600 km^2), waters off Oregon and Washington (324,000 km^2), and waters west of Baja California (953,221 km^2). The Baja California and Oregon/Washington strata were required because survey coverage differed greatly in those areas compared to California (Table 1, Fig. 1); the inshore California stratum was added to allow future comparison with results from nearshore aerial surveys.

Observations included 185 sightings of blue whales, 81 sightings of humpback whales, and 109 sightings of whales that could not be identified to species but which were classified as either "unidentified rorqual," "unidentified large whale," or "unidentified whale." The proportion of blue and humpback whales in this group was estimated by prorating the unidentified categories based on the relative proportions of identified whales. "Unidentified rorquals" were assumed to include blue, fin, sei, and Bryde's whales; "unidentified large whales" and "unidentified

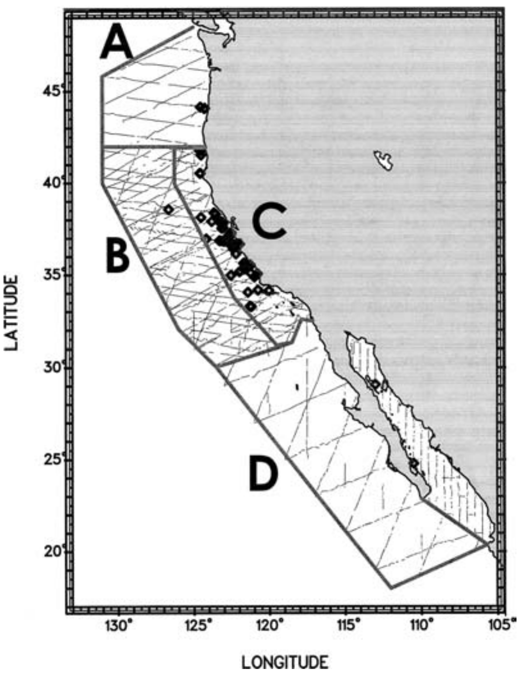

Figure 1. Line-transect survey lines and sightings of humpback whales, 1991–1996. Geographic strata include: (A) Oregon and Washington, (B) California Offshore, (C) California Inshore, and (D) Baja California.

whales" were assumed to include these species plus humpback, right, gray, and sperm whales. The number of unidentified whales estimated to be species j within geographic region a and group size category i is therefore estimated as:

$$u_{aij} = r_{ai} \cdot P_{raij} + w_{ai} \cdot P_{waij}$$

where r = number of unidentified whales classified as "unidentified rorqual," w = number of unidentified whales classified as "unidentified large whale" or "unidentified whale,"P_r = proportion of rorqual sightings in which species j was identified, and P_w = proportion of large whale sightings in which species j was identified.

Various pooling and stratification schemes for $f(0)$ were investigated including stratifications by group size, species, Beaufort sea state, and geographic region. A half-normal detection model was used to evaluate these approaches and, based on Akaike's Information Criterion (AIC), the best model was found to be stratification by estimated group size ($<$1.5 and $>$1.5), and pooling both species, all sea states (Beaufort 0–5), and all geographic regions. Therefore, the density, D_{aij}, for species j within geographic stratum a and group-size stratum i was estimated as

$$D_{aij} = \frac{(n_{aij} + u_{aij}) \cdot S_{aij} \cdot f_i(0)}{2 \cdot L_a \cdot g(0)}$$

where n = number of sightings identified as species j, u = prorated number of unidentified sightings estimated to belong to species j, S = mean group size, $f(0)$ = sighting probability density at zero perpendicular distance, L = length of transect

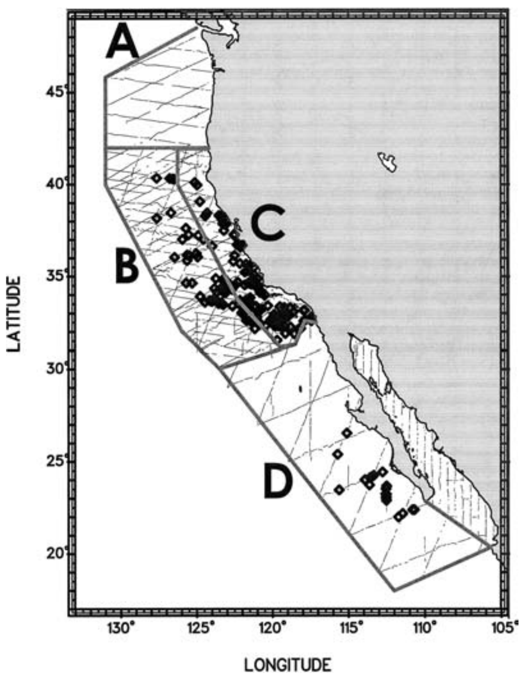

Figure 2. Line-transect survey lines and sightings of blue whales, 1991–1996. Geographic strata include: (A) Oregon and Washington, (B) California Offshore, (C) California Inshore, and (D) Baja California.

line completed, and $g(0)$ = probability of seeing a group directly on the trackline. We estimated $f(0)$ using options for hazard-rate and half-normal key functions, both with cosine adjustments, using the program DISTANCE 3.5 (Laake *et al.* 1994); based again on AIC, the best model was chosen to be a half-normal model with cosine adjustments. The distribution of perpendicular sighting distance for the various unidentified categories of whales was not significantly different from that of identified humpback and blue whales (K/S test, $P = 0.07$, $n = 111/266$, respectively), and these sightings were not used in estimation of $f(0)$ or mean group size. A truncation distance of 5.5 km (3.0 nmi) was used to eliminate the 5% of most distant sightings and to improve the fit of the detection function near the origin. Trackline detection probability [$g(0)$] for blue and humpback whales was estimated from independent observer data using the method of Barlow (1995). This method uses a conditionally independent observer who searches for whales that are missed by the primary observation team. Due to low number of sightings detected only by the independent observers ($n = 13$), the estimate of $g(0)$ was not stratified by group size.

The total abundance for species j in area a, (N_{aj}), was estimated as the sum of the densities in all s strata times the size of the study area, A_a,

$$N_{aj} = A_a \sum_{i=1}^{s} D_{aij}.$$

The coefficients of variation (CV) for abundance were estimated as the square root of the sum of the squared CVs of $f(0)$, $g(0)$, and the encounter rate ($n \cdot S/L$). The CV

Table 1. Area (A) and length of transect lines (L) in each of the geographic stratum. Proportional coverage is given as an index of survey effort in each stratum.

	A (km^2)	L (km)	Proportional coverage L/A
CA inshore	261,730	9,212	0.035
CA offshore	557,100	17,814	0.032
OR/WA	323,734	4,362	0.013
Baja	953,221	7,527	0.008
Total	2,095,785	38,915	0.019

of the encounter rate was estimated empirically by breaking the transects into 300-km segments and calculating the standard error among segments (Buckland *et al.* 2001, p. 109). The CV of $f(0)$ was estimated by the program DISTANCE using an information matrix approach. The CV of $g(0)$ was estimated using an analytical formula (Barlow 1995).

Results

Capture-recapture Estimates for Humpback Whales

Most of the directed and systematic identification photographs of humpback whales were taken within 30 nmi of the coast (Fig. 3). Abundances of humpback whales based on the two-sample Petersen estimate ranged from 569 to 914 (Table 2). Estimates were generally very consistent and showed a steady increase from the lowest estimate based on the 1991 and 1992 samples to the highest estimates based on the samples through 1997. The two estimates utilizing the systematic and coastal samples pooled over three seasons provided estimates that were only slightly higher than the interyear comparisons for the same periods. Slightly higher estimates would be expected from the comparisons using the systematic samples because we pooled three seasons of data resulting in a larger violation of population closure (due to natality and mortality) than the interyear samples. The similarity of the two types of estimates indicates any additional downward bias to the inter-year samples from all vessels due to heterogeneity of capture probability (due to geographic sampling bias) must have been very small or non-existent.

Abundance results for humpback whales using the open population Jolly-Seber capture-recapture model using all seven annual samples from 1991 to 1997 (Table 3) yielded similar results to the Petersen estimates. The five abundance estimates (this procedure does not yield an estimate for the first and last year) ranged from 552 in 1992 to 795 in 1996. The model also estimated an average annual survival rate of 0.96 and an average estimated addition of 85 animals annually (from births or immigration).

Capture-recapture Estimates for Blue Whales

Most of the identification photographs of blue whales from the coast-based efforts were within 30 nmi of the coast, but photographic samples from the systematic surveys were more widely distributed both coastally and out to about 200 nmi offshore (Fig. 4). Blue whale abundances calculated using Petersen capture-recapture procedures were more sensitive to sample selection (Table 4) than were humpback abundances. Estimates based on pairs of adjacent years obtained from

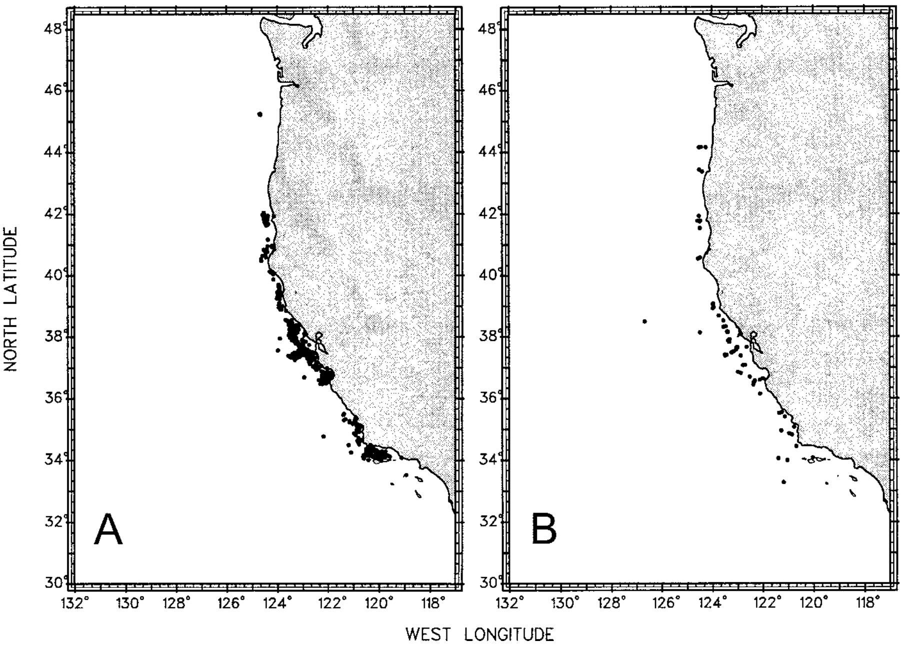

Figure 3. (A) Locations where humpback whales were identified photographically during opportunistic small boat surveys. (B) Locations where humpback whales were identified photographically during systematic surveys.

all platforms yielded highly variable abundances of from 658 to 1,502 (Table 4). Similarly, estimates using the Jolly-Seber model yielded highly variable abundances ranging from 525 to 1,244 (Table 5). These estimates appear unreasonably low since many are even below the 923 different individuals identified in the study from 1991 to 1997. Estimates based on pooled three-year periods with one sample from the systematic surveys that covered both coastal and offshore waters yielded more consistent and realistic estimates of abundance ranging from 1,167 to 2,357(Table 4).

Restriction of samples to only the better quality photographs (to reduce the chances of missed matches) did not dramatically change the estimates using pooled years although the smaller sample size resulted in a higher CV (Table 4). Restricting the sample from all to good quality photographs resulted only in two of the four estimates decreasing slightly and two others remaining virtually unchanged. Going from good to best quality photographs left only two unchanged and raised or lowered one each. The lack of a consistent decrease in estimates when restricted by quality suggests that missed matches is not a major source of bias in these estimates and elimination of this potential bias through restriction to higher-quality photographs is not worth the resulting higher variance to the estimates.

Line-transect Abundance Estimates

Surveys covered approximately 39,000 km in total, but were stratified with more concentrated effort in the California Inshore than the Offshore stratum (Table 1). The Baja stratum received the lowest level of coverage. Virtually all of the humpback

Table 2. Estimates of humpback whale abundance off California, Oregon, and Washington, using Petersen mark-recapture estimates with samples defined as either adjacent annual samples or types of surveys (systematic *vs.* coastal) during pooled years. For each sample we give the number of identification photographs, the number of unique identified whales (n), the number of subsamples used in the jackknife variance estimate, the number of matches found between samples (m), and the CV as measured by the conventional mark-recapture formula (CV1), and the CV from the jackknife procedure based on subsamples described in Methods (CV2).

	Sample 1				Sample 2				Abundance			
Period	Type & year	Subsamples	Identifications	n	Type & year	Subsamples	Identifications	n	m	Estimate	CV1	CV2
Annual samples using all data												
1991–1992	All 1991	7	668	269	All 1992	8	1023	398	188	**569**	0.03	0.05
1992–1993	All 1992	8	1023	398	All 1993	6	512	254	173	**584**	0.03	0.06
1993–1994	All 1993	6	512	254	All 1994	6	402	244	108	**572**	0.05	0.15
1994–1995	All 1994	6	402	244	All 1995	9	661	331	100	**804**	0.06	0.17
1995–1996	All 1995	9	661	331	All 1996	7	564	331	144	**759**	0.05	0.08
1996–1997	All 1996	7	564	331	All 1997	7	382	264	104	**837**	0.06	0.16
Pooled years using survey type as samples												
1991–93	Systematic	6	87	68	Coastal	12	2116	523	57	**622**	0.05	0.07
1995–97	Systematic	8	91	75	Coastal	11	1516	601	49	**914**	0.08	0.13

Table 3. Humpback whale model parameters and population estimates from Jolly-Seber mark-recapture method using California, Oregon, and Washington (not including WA/BC border) for 1991–1997. Parameters are as described by Seber (1982).

Year	IDs	Prev. IDs	*r*	*z*	Survival rate	Births	Marked available	Population estimate	CV
1991	269	0	249	0	0.97				
1992	398	188	331	61	0.92	48	261	552	0.03
1993	254	198	209	194	0.98	84	434	556	0.03
1994	244	186	180	217	0.96	144	480	629	0.04
1995	331	228	195	169	0.98	63	514	746	0.05
1996	331	252	104	112			606	795	0.07
1997	264	216	0	0					
Mean	299	181	181	108	0.96	85	459	656	
SD	56	83	106	90	0.02	42	127	111	

whales were seen in the California Inshore stratum (Fig. 1); whereas blue whales were found in each of the three southern geographic strata (Fig. 2). The half-normal detection function with one cosine adjustment term was chosen as the best fit to groups of less than 1.5 individuals, and the half-normal detection function was chosen as the best fit to groups greater than 1.5 (Fig. 5). As expected, effective strip width [$1/f(0)$] was wider for sightings of multiple animals (3.20 km) than for sightings of singletons (2.18 km) and was narrower for sightings by the Independent Observers (1.9 km). Humpback whales were found in slightly larger groups, on average, but for both species, most groups included three or fewer whales. Accounting for missed trackline whales [$g(0)$] added approximately 10% to the uncorrected abundance estimates of each species. Prorating the unidentified whale sightings further increased the estimates by approximately 30% for blue whales and by approximately 9% for humpback whales. With both correction factors, humpback whale abundance in the study area in summer/fall is approximately 1,000 (CV = 0.20) (Table 6) and blue whale abundance is approximately 3,000 (CV = 0.14) (Table 7).

Discussion

Population Closure

Before comparing the above capture-recapture and line-transect abundance estimates, we first needed to consider whether they are measuring the same thing. The case for closed and comparable population estimates is clearest for humpback whales. During the line-transect surveys, only two humpback whales were seen south of California (both in the Gulf of California, Fig. 1). Although some humpback whales might be migrating southward before the end of the line-transect surveys (in early November), none were seen off Baja California in October or November. Photographic identification data show a clear separation between the humpback whales that feed from California to southern Washington and those that feed off British Columbia and Alaska (Calambokidis *et al.* 1996). Because our surveys covered this entire area from California to Washington, we conclude that the vast majority of humpback whales in this population would be expected to be within our study area.

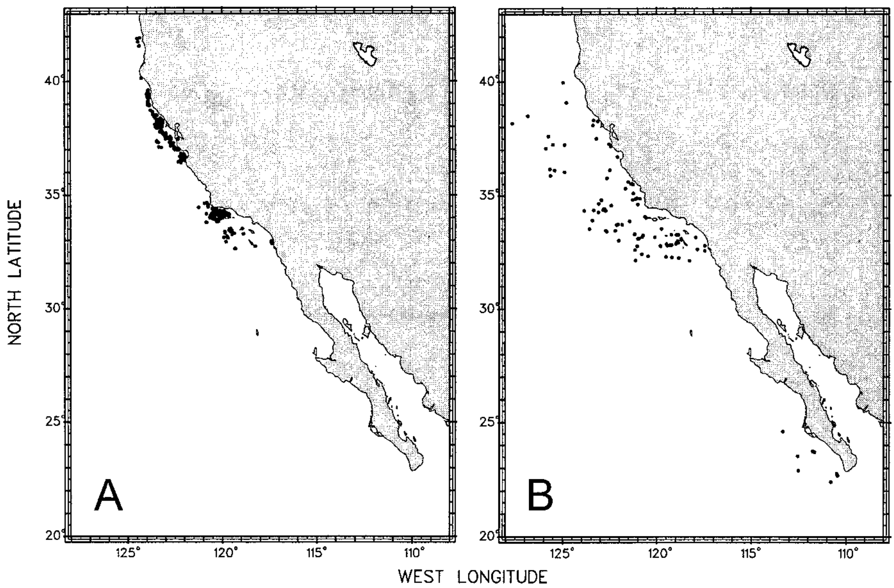

Figure 4. (A) Locations where blue whales were identified photographically during opportunistic small boat surveys. (B) Locations where blue whales were identified photographically during systematic surveys.

The case for a closed population estimate is less clear for blue whales. Although there is a northward hiatus in blue whale distribution (Fig. 2), to the south, blue whales are known to occupy the areas of the Eastern Tropical Pacific, particularly the Costa Rica Dome on a year-round basis (Reilly and Thayer 1990). While identified blue whales have been documented moving between California in summer/fall and the Costa Rica Dome in winter/spring, no matches have been found with those animals in the Eastern Tropical Pacific in summer (10 identifications, Southwest Fisheries Science Center and Cascadia Research, unpublished data). Vocalizations recorded on the Costa Rica Dome in summer/fall, however, link these animals to the eastern North Pacific population and showed an increase between August and November (Stafford *et al.* 1999). Two of eight blue whales that were satellite-tagged in southern California in late September or early October were located south of our line-transect study area by early November (Mate *et al.* 1999). With blue whales, the greatest unknown is whether their year-round residency on the Costa Rica Dome is indicative of a distinct, non-migratory population segment or whether some individuals may choose not to migrate every year. If the former is true, both of our methods would measure the abundance of the segment of the population that migrates to the waters off California and Mexico; if the latter is true, the capture-recapture method would measure the entire population, but the line-transect method would only measure the average number of individuals that migrate northward in a given year.

Capture-recapture Abundance Estimates

A key assumption of most capture-recapture procedures is that all animals have an equal probability of being captured. Photographic identification of cetaceans

Table 4. Summary of Petersen mark-recapture estimates for blue whales off California and west coast of Baja California, Mexico, with samples defined as either adjacent years or types of surveys (systematic *vs.* coastal) in pooled years. For each sample, the number of unique identified whales in each sample (n1 and n2) and the number of matches or recaptures (m) are indicated. Coefficients of variation (CV1 and CV2) are based on analytical formulae and jackknife (respectively). Number of subsamples in jackknife was 17 for pooled years and 12–14 for the combination of annual samples.

	Left sides						Right sides						Left/Right
Samples used	n1	n2	m	Pop. est.	CV1	CV2	n1	n2	m	Pop. est.	CV1	CV2	mean
Pooled years using survey type as samples													
1991–1993 all qualities	61	293	8	**2,024**	0.29	0.40	74	289	10	**1,976**	0.26	0.32	**2,000**
1991–1993 good quality	54	277	7	**1,910**	0.30	0.47	66	272	8	**2,031**	0.29	0.47	**1,971**
1991–1993 best quality	54	180	4	**1,990**	0.38	0.69	66	175	4	**2,357**	0.39	0.49	**2,174**
1995–1997 all qualities	43	350	7	**1,930**	0.30	0.37	34	361	7	**1,583**	0.29	0.30	**1,756**
1995–1997 good quality	36	329	6	**1,743**	0.32	0.47	31	344	6	**1,576**	0.31	0.38	**1,660**
1995–1997 best quality	36	193	3	**1,794**	0.42	0.58	31	218	5	**1,167**	0.34	0.37	**1,480**
Annual samples using all types (all quality)													
1991–1992	57	241	19	**701**	0.17	0.44	70	242	22	**749**	0.16	0.36	**725**
1992–1993	241	108	39	**658**	0.11	0.28	242	98	29	**801**	0.14	0.58	**730**
1993–1994	108	169	17	**1,028**	0.20	0.70	98	166	10	**1,502**	0.26	0.70	**1,265**
1994–1995	169	174	26	**1,101**	0.16	0.20	166	180	27	**1,079**	0.16	0.17	**1,090**
1995–1996	174	135	24	**951**	0.16	0.18	180	124	16	**1,330**	0.21	0.50	**1,140**
1996–1997	135	146	22	**868**	0.17	0.34	124	149	26	**693**	0.15	0.29	**781**

Table 5. Model parameters and population estimates from Jolly-Seber mark-recapture method using California and west coast Baja blue whales for 1991–1997. Estimates based on either right or left side and using all suitable quality photographs. Parameters are as described by Seber (1982).

Year	IDs	Prev. IDs	*r*	*z*	Survival rate	Births	Marked available	Pop. estimate	CV
Left sides only									
1991	57	0	30	0	0.76				
1992	241	19	108	11	0.97	192	43	525	0.21
1993	108	39	39	80	0.81	297	257	700	0.18
1994	169	51	53	68	0.81	361	265	867	0.16
1995	174	50	47	71	0.92	−101	309	1060	0.17
1996	135	61	22	57			398	873	0.21
1997	146	79	0	0					
Mean	147	43	43	41	085	187	227	805	
SD	57	26	34	36	0.09	204	134	202	
Right sides only									
1991	57	0	31	0	0.82				
1992	241	19	103	12	1.14	272	47	568	0.21
1993	98	32	29	83	0.67	289	306	918	0.21
1994	166	45	54	67	0.99	355	248	902	0.17
1995	180	52	39	69	0.65	−24	364	1244	0.19
1996	124	50	26	58			319	781	0.20
1997	149	84	0	0					
Mean	145	40	40	41	0.85	223	257	883	
SD	60	27	32	36	0.21	169	124	246	

may violate this assumption a number of ways including geographic sampling bias, difference among individuals in how often they present portions of their body for photographing (*i.e.*, flukes), and differences in the distinctiveness of their markings. The degree to which these and other factors contribute to these biases has been considered by several studies (Whitehead 1982, Hammond 1986, Calambokidis *et al.* 1990*a*, Friday *et al.* 2000). A potential cause of heterogeneity of capture probabilities apparent in our study was that created by geographic sampling bias. If the geographic coverage was not systematic or representative and individual whales did not mix randomly between samples, then some individuals would be more likely to be captured and recaptured than others, resulting in a downward bias to the estimate. This is apparent in the dramatically lower estimates of humpback whale abundance obtained in earlier more geographically limited samples from this population (Calambokidis *et al.* 1990*a*). The non-random mixing and clumped geographic distribution of many whales on their feeding grounds can make the magnitude of the bias due to heterogeneity of capture probabilities created by geographic sampling bias very large. This would have biased many past estimates of abundance in other studies based on capture-recapture of photographically identified whales because samples have often been obtained from limited geographic areas. While capture-recapture can prove to be an extremely valuable and accurate method to estimate cetacean abundance, limited and uneven geographic sampling can be a major bias causing serious underestimation. Estimates of humpback whales in the North Atlantic and North Pacific based on

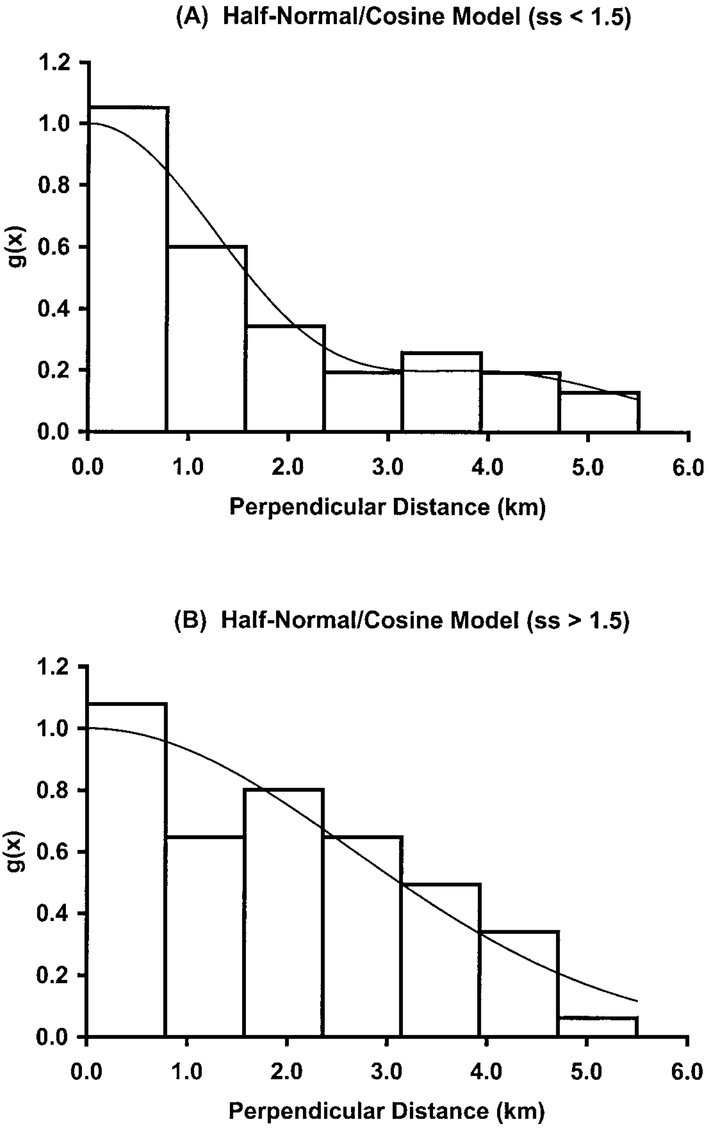

Figure 5. Best line-transect models (smoothed curves) fit to distributions of blue and humpback whale perpendicular distances (histograms), pooled over geographic regions and stratified by group size (ss).

broader more geographically representative samples have yielded higher estimates of abundance than previous estimates based on samples from more geographically limited coverage (Smith *et al.* 1999, Calambokidis *et al.* 1997).

The Petersen and Jolly-Seber models provided very similar estimates of abundance for humpback whales. Additionally, the Jolly-Seber model provided reasonable estimates of both survival and natality for humpback whales. Survival estimates across years were fairly consistent (0.92–0.98) and the average survival rate calculated (0.96)

Table 6. Humpback whale density (*D*) and abundance (*N*) in the eastern North Pacific based on line-transect surveys off California, Oregon, Washington, U.S. and, off Baja California, Mexico, stratified by geographic area and group size. Estimates were based on the number of identified humpback whale sightings (n1) plus a prorated number of unidentified whale sightings (n2). Expected group size, S, was based only on identified groups of humpback whales. Effective strip widths (ESW) were pooled over all geographic strata and both species. The probability of seeing a trackline group (g(0)) was pooled over geographic and group size strata. Survey effort and areas of geographic strata are given in Table 1.

Geographic strata	Group size strata	n1	n2	S	ESW $1/f(0)$ (km)	$g(0)$	D (km^{-2})	N	CV(N)
CA Inshore	<1.5	35	5.2	1.02	2.18	0.902	0.00113	297	0.34
	>1.5	43	2.9	2.73	3.20	0.902	0.00236	617	0.27
	Subtotal	78	8.0				0.00349	913	0.21
CA Offshore	<1.5	0	0.0	0.00	2.18	0.902	0.00000	0	0.38
	>1.5	1	0.0	2.52	3.20	0.902	0.00002	14	0.37
	Subtotal	1	0.0				0.00002	14	0.37
OR/WA	<1.5	2	0.4	1.00	2.18	0.902	0.00014	45	0.72
	>1.5	0	0.0	0.00	3.20	0.902	0.00000	0	0
	Subtotal	2	0.4				0.00014	45	0.72
Baja	<1.5	0	0.0	0.00	2.18	0.902	0.00000	0	
	>1.5	0	0.0	0.00	3.20	0.902	0.00000	0	
	Subtotal	0	0.0				0.00000	0	0.00
Sum of geographic strata								**973**	**0.20**

was virtually identical to the 0.95 estimated for Gulf of Maine humpback whales for 1976–1985 (Buckland 1990) or the 0.96 rate for 1979–91 (Barlow and Clapham 1997) and 0.95 rate for 1992–2000 (Clapham *et al.* 2003) for female non-calves in the Gulf of Maine. Annual natality/immigration rate estimates from the Jolly-Seber models for humpback whales were also fairly consistent (48–144 per year). This is higher than the 5% crude birth rate from visual observation of mothers and calves (Steiger and Calambokidis 2000), but this was known to be biased downward.

In contrast to humpback whales, the Jolly-Seber model results for blue whales did not yield realistic estimates of abundance or other demographic parameters. Not only were abundances underestimated compared to the Petersen estimates using the systematic identifications as one of the samples, but estimated survival rates (0.81–0.97) and births (−101–361) were highly variable year to year and did not yield realistic averages. These are likely the result of the problem of heterogeneity of capture probabilities due to geographic sampling bias (lack of coverage of the offshore component of the population).

Line-transect Abundance Estimates

Our new line transect estimates for blue and humpback whales are greater than previous estimates for these species that were based, in part, on the same data (Barlow 1995, 1997). For blue whales, the increase was largely due to the addition of the Baja stratum (which was excluded in previous analyses) and due to the prorating of unidentified whales. For humpback whales, estimates increased over those presented by Barlow (1995), which included only 1991 survey results, but are roughly comparable to estimates presented by Barlow (1997), which included the 1996 surveys during which the encounter rate for humpback whales increased substantially.

Line-transect abundance estimates can be biased by failure to meet a variety of assumptions (Hammond and Laake 1983). The greatest likelihood for bias in the line-transect abundance estimates would be the exclusion of individuals in the populations that were outside the study area. As discussed above, this is more likely to be a problem for blue whales because they appear to begin their southward migration at an earlier date and because they may have non-migratory components to their population. Another bias will occur as some whales will be diving and will be missed by the primary observation team. Our estimation of $g(0)$ compensates for missed whales if all whales are available to be seen at some point, but underestimates the fraction of whales missed if some never surface within visible range. Abundance estimates based on "closing mode" could be biased downwards if these off-effort segments occur in areas with higher than usual whale density or could be biased upwards if the vessel is drawn into areas of higher density. Passing mode estimates may be biased downward because some individuals in a group are not seen and not counted. Every effort was made to measure bearing angles and sighting distances accurately to avoid biases associated with errors in these measurements.

Abundance Comparisons

Among the estimates we generate from the two separate survey methodologies, we can identify those that most accurately estimate the abundance for each species. For humpback whales, our best estimates of abundance are the paired between-year Petersen estimates (Table 2); these estimates are more precise than the paired systematic/coastal estimates and do not show bias due to geographic heterogeneity. The average abundance of humpback in 1991–1997 would therefore be the average of the six year-pairs, or 687 (CV = 0.05). This estimate is within the normal 95% confidence interval of, and is not significantly different from, our line-transect estimate of humpback whale abundance (973, CV = 0.20). The capture-recapture estimate is considerably more precise than the line-transect estimate for humpback whales. For blue whales, our best estimates are from the line-transect surveys (Table 7); these estimates are more precise than those from capture-recapture and do not have potential biases caused by the offshore component of the population. For all regions the total abundance of blue whales from the line transects was 2,997 (CV = 0.14).

The relative merits of the two different survey methods are exemplified by the two species we examined. Humpback whales had a distribution that was highly clumped near the edge of the continental shelf and relatively accessible from shore-based small boats. This resulted in small-boat based photographic identification conducted broadly along the coast, successfully providing unbiased samples of these animals while they were on their feeding areas. The proportion of the humpback whale population sampled was very high, generally, close to 50% in each sample period, resulting in high capture probabilities which improved the accuracy of the mark-recapture abundance estimates and allowed the Jolly-Seber models to provide realistic estimates of survival and natality. Line-transect surveys covering a broad habitat area, however, had difficulty obtaining a suitable sample to estimate density, and density estimates were highly variable due to the clumped distribution

Table 7. Blue whale density (D) and abundance (N) in the eastern North Pacific based on line-transect surveys off California, Oregon, Washington, U.S., and off Baja California, Mexico, stratified by geographic area and group size. Estimates were based on the number of identified blue whale sightings (n1) plus a prorated number of unidentified whale sightings (n2). Expected group size, S, was based only on identified groups of blue whales. Effective strip widths (ESW) were pooled over all geographic strata. The probability of seeing a trackline group ($g(0)$) was pooled over geographic and group size strata. Survey effort and areas of geographic strata are given in Table 1.

Geographic strata	Group size strata	n1	n2	S	ESW $1/f(0)$ (km)	$g(0)$	D (km^{-2})	N	CV(N)
CA Inshore	<1.5	54	24.0	1.04	2.18	0.902	0.00224	587	0.18
	>1.5	55	9.4	2.23	3.20	0.902	0.00270	707	0.19
	Subtotal	109	33.4				0.00494	1,294	0.13
CA Offshore	<1.5	22	11.1	1.01	2.18	0.902	0.00048	266	0.38
	>1.5	33	4.9	2.05	3.20	0.902	0.00076	421	0.37
	Subtotal	55	16.0				0.00123	687	0.27
OR/WA	<1.5	0	0.0	0.00	2.18	0.902	0.00000	0	
	>1.5	0	0.0	0.00	3.20	0.902	0.00000	0	
	Subtotal	0	0.0				0.00000	0	
Baja	<1.5	16	6.3	1.01	2.18	0.902	0.00076	726	0.42
	>1.5	5	1.4	2.03	3.20	0.902	0.00030	286	0.43
	Subtotal	21	7.7				0.00106	1,012	0.33
Sum of geographic strata								**2,994**	**0.14**

of whales. Blue whales were distributed over a broader offshore region, making the offshore component of the population harder to sample for photographic identification from small boats. The lack of either random mixing or complete separation between offshore and inshore components of the population made it difficult to obtain an unbiased photographic identification sample using shore-based small-boat surveys. Additionally, the proportion of the population sampled with blue whales was much lower than for humpback whales resulting in lower recapture probabilities. Line-transect methods using a larger ship, however, were able to obtain adequate samples to accurately estimate density and abundance. Accurate capture-recapture estimates with photographically identified blue whales were obtained only when the larger coastal samples were paired with identifications obtained during the systematic line-transect surveys.

Use of two methods to estimate abundance has a number of advantages. It has allowed us to evaluate the relative merits and limitations of the two methods and to select the estimates most suitable to the distribution of that species. Agreement and disagreement between the different estimates allowed better determination of their accuracy and potential biases. Additionally, the two methods measure slightly different things. The line transect method provided estimates of the density and abundance of animals present at a given moment in time within a prescribed area. Capture-recapture estimates provide an estimate of the overall population of animals whether or not they are all present within the study area at a particular moment in time. Agreement between the estimates obtained by these two methods can therefore be used to evaluate what portion of the population was present in a given area. The higher estimates of blue whale abundance from line-transect surveys suggest all or at least most of the blue whales in this population were present in the Mexico to California region during the summer/fall surveys. The higher line-transect estimates could be the result of a consistent portion of the population tending to stay in Mexican waters where there was line-transect survey effort but no photographic identification effort.

Implications of New Abundance Estimates

The overall abundance of humpback and blue whales we determined is considerably higher than other postwhaling estimates, but may still be below prewhaling levels. Sighting rates of both humpback and blue whales off California increased from 1979/1980 to 1991 (Barlow 1994). Our data show a clear increasing trend for humpback whales from 1991 to 1997. Despite the increasing abundance estimates for humpback whales we report here, it is clear these populations remain below prewhaling levels. Takes of humpback whales from three whaling stations from northern California to southern Washington from 1919 to 1926 alone totaled 2,473 indicating that the preexploitation stock was considerably larger than our estimates (Clapham *et al.* 1997). Humpback whales also feed extensively in other areas of the North Pacific including off British Columbia, in Alaskan waters, and in the western North Pacific (Calambokidis *et al.* 2001) with a total abundance of 6,000–8,000 estimated for the early 1990s (Calambokidis *et al.* 1997). The estimates we report, supported by two types of survey methods, confirm that the number of humpback and blue whales inhabiting the waters off the west coast of the U.S. and Mexico are larger than previously documented since commercial whaling. This area represents an important feeding ground for the overall North Pacific populations of both species.

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