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GRAY WHALE CALF PRODUCTION 1994–2000: ARE OBSERVED FLUCTUATIONS RELATED TO CHANGES IN SEASONAL ICE COVER?

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ABSTRACT

We conducted shore-based sighting surveys to estimate the number of northbound migrating gray whale calves passing Piedras Blancas, California, for seven consecutive years (1994–2000). In addition, we conducted aerial surveys to determine offshore distribution of the migration in 1994 and 1995, measured day/night migration rates with thermal sensors in 1994–1996, and maintained concurrent replicate watches near the peak of each migration to estimate the proportion of the cow/calf pairs missed by the standard watch team. During good weather, we counted 325, 194, 407, 501, 440, 141, and 96 calves during 1994–2000, respectively. Correcting these counts for periods not on watch and for calves missed, produced final estimates of 945 calves (SE = 68.21) for 1994, 619 calves (SE = 67.19) for 1995, 1,146 calves (SE = 70.67) for 1996, 1,431 calves (SE = 82.02) for 1997, 1,388 calves (SE = 91.84) for 1998, 427 calves (SE = 41.10) for 1999, and 279 calves (SE = 34.79) for 2000. Calf production indices (calf estimate/total population estimate) are 4.2%, 2.7%, 4.8%, 5.8%, 5.5%, 1.7%, and 1.1% for the years 1994–2000, respectively. Fluctuations in calf production over this time period were positively correlated with the length of time that primary feeding habitat was free of seasonal ice during the previous year.

Key words: gray whales, *Eschrichtius robustus,* reproduction, calf production, surveys, arctic ice.

During the spring of each year, gray whale (*Eschrichtius robustus*) cows and calves migrate northward from the nursery lagoons of Baja California, Mexico, to their feeding grounds in the Bering and Chukchi Seas. Along the central California coast and in some areas to the north, this migration passes very close to shore. In the late 1970s and early 1980s, counts of northbound cow/calf pairs were made from sites in Alaska, Oregon, and California to estimate

calf production for this stock (Hessing 1981, Herzing and Mate 1984, Poole 1984*a,b*). Hessing (1981) reported that calves represented 4.6% of the total count of gray whales migrating northward through Unimak Pass, Alaska. Herzing and Mate (1984) estimated that calves represented 4.6% of the population based on their 1980 survey of southbound and the northbound whales from Yaquina Head, Oregon. Poole (1984*a,b*) conducted the most intensive of these surveys in 1980 and 1981 from Pt. Piedras Blancas, California. From these surveys, Poole estimated calves passing this site comprised 4.7% to 5.2% of the population.

Since these surveys, the gray whale population has continued to increase at an estimated rate of about 2.5% per year reaching approximately 22,263 whales in 1995/1996 (Buckland and Breiwick, in press; Hobbs *et al.*, in press). During this same period, data collected from specimens taken in the Soviet aboriginal hunt suggested a steep decline in gray whale pregnancy rates (Zimushko and Ivashin 1980; Blokhin 1984, 1989, in press *a,b*). Reilly (1992) noted, however, that potential sampling biases in this hunt should be explored before conclusions were drawn from these data. In addition, benthic sampling in the Chirikov Basin from 1986 to 1988 revealed a 30% drop in biomass and a shift in the size structure of the amphipod community, which researchers suggested could indicate that gray whales were approaching the carrying capacity of this benthic resource (Highsmith and Coyle 1992; Coyle and Highsmith 1994; Stoker, in press).

In light of these studies, the National Marine Fisheries Service (NMFS) included a study of gray whale recruitment as part of the monitoring program associated with the removal of this stock from the List of Endangered and Threatened Wildlife and Plants (Rugh *et al.* 1999). In this paper we report the results of seven consecutive gray whale cow/calf surveys at Pt. Piedras Blancas between 1994 and 2000. Our primary objective was to determine whether the proportion of calves in the population (indexed here as the estimate of the number of calves passing Piedras Blancas divided by the population size estimated from surveys of southbound gray whales conducted by NMFS) had declined since the 1980 and 1981 calf surveys by Poole (1984*b*). We report estimates of the number of calves passing our research site during each survey year, the results of experiments conducted to estimate the proportion of calves missed by observers, and the results of day versus night migration rate experiments. We also explored the relationship between the duration of seasonal ice cover over primary feeding grounds and calf production for this population.

Methods

Survey Site

We conducted the surveys from Pt. Piedras Blancas, San Luis Obispo County, California (35°40′N, 121°17′W) (Fig. 1a, b). Pt. Piedras Blancas is approximately 160 km south of Monterey and 240 km north of Santa Barbara.

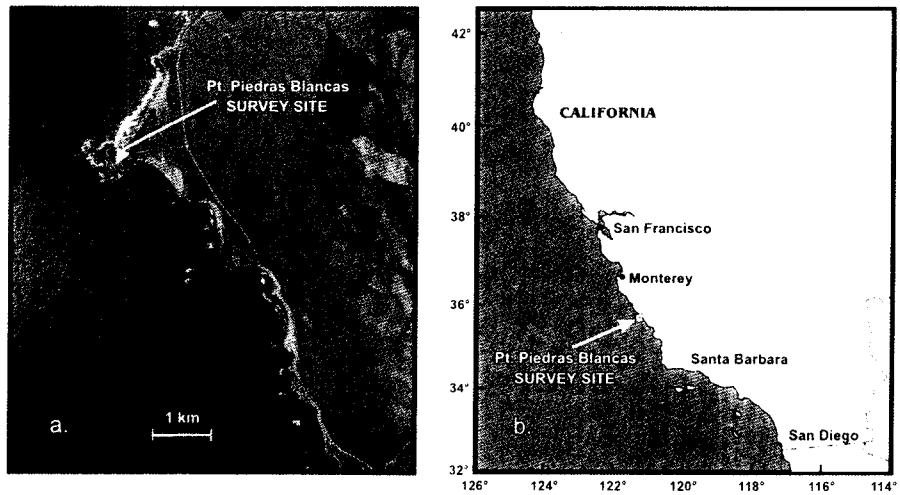

Figure 1. Aerial photograph of survey site at Pt. Piedras Blancas (a) and illustration showing location of site along the California coast (b).

Poole (1984*a,b*) selected this site for his 1980 and 1981 cow/calf surveys and noted it is the only point to intersect a straight-line course from Pt. Buchon to Pt. Sur along 160 km of the central California coast. A protected cove extends to the south and east of Pt. Piedras Blancas through which more than 90% of the cow/calf pairs passed during Poole's surveys.

Shore-based Surveys

We designed the surveys to encompass the entire duration of the northbound cow/calf phase of the migration as reported by Poole (1984*a*). The surveys began in March of each year and extended until late May or early June. Watches were maintained for 12 h/d, 6 d/wk. Two observers divided their effort between inshore and offshore watch areas (Fig. 2a). The offshore observer often assisted the inshore observer in determining the number of cow/calf pairs present and confirming their distance offshore as they rounded the point. Observers stood two, three-hour watches per day (3 h on watch followed by 3 h off watch), rotating from the offshore position to the inshore position after 1.5 h.

The primary searching technique was scans with the naked eye, but hand-held binoculars (7×) and tripod-mounted 25× binoculars were used for confirming the presence of a calf and for searching far offshore. The offshore observer used 25× binoculars mounted on an adjustable tripod to scan the distant offshore area for approximately five minutes every half hour. Offshore search effort with the 25× binoculars totaled two hours per day. As pods exited the viewing area, observers measured the distance offshore using the reticle scale in the 25× binoculars if the whales were beyond 400 m, the minimum distance measurable on the reticle scale. We used the formulae

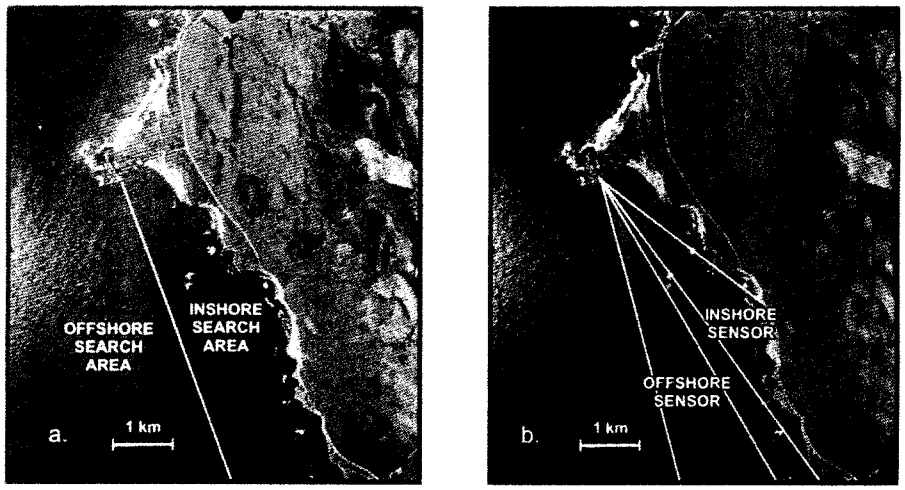

Figure 2. Approximate areas searched by inshore and offshore observers (a) and areas covered by two infrared sensors (b).

developed by Lerczak and Hobbs (1998) to determine offshore distance from reticle measurements. When cow/calf pairs passed too close to the shore to use the reticle scale, observers visually estimated the distance in meters. Observers recorded sea state (Beaufort scale) and visibility at the beginning of each watch and when conditions changed. We used the same visibility codes as Reilly *et al.* (1983), which range from a visibility code of 1 for excellent conditions to a code of 6 for unacceptable conditions. We chose, as did Poole (1984*b*), to exclude effort and sightings from periods when visibility conditions were poor (code 5, visibility <0.8 km).

Gray whale calves were identified by their small size, dark color, and lack of mature barnacle patches. Calves passed the survey site swimming in close association with an adult gray whale. We assumed that the large whale was the mother of the calf and refer to the two animals as a cow/calf pair. Our goal in these surveys was to count calves, but the presence of the cow with each calf greatly increased our probability of detecting the calves. Often the blow of a small calf was not visible to the observers even at a distance of 200 m, while the blows of adult gray whales were generally visible to the unaided eye beyond 4 km. Thus, we refer to cow/calf pairs when dealing with the topics related to detection of the passing calves and then to calves alone in sections concerning estimates of total calf numbers.

The probability of detection for a given cow/calf pair was not known in advance. To estimate the total number of whales that passed, we first needed to estimate these probabilities. For instance, whales that pass far offshore are less likely to be detected than those passing close to the survey team. In addition, no pairs which passed during off-watch hours (*e.g.*, at night or on Sundays) were recorded, and differing rates of passage during off-watch hours could bias estimates based on assumptions of equal rates. Finally, to account

for imperfect nearshore detection, we used a replicate watch scheme to estimate nearshore detection probability. Methods for addressing each of these sources of bias in our total calf estimate are discussed below.

Aerial Survey

To estimate the fraction of pairs that were unlikely to be detected because of their distance offshore, we conducted a series of aerial surveys (seven between 27 April and 8 May 1994 and eight between 20 April and 2 May 1995) of the area from Piedras Blancas to a point of land about 35 km to the southeast. Each survey consisted of seven parallel transects spaced 2 km apart with the final transect about 12.3 km offshore. The leg nearest the shore followed the contour of the coast about 30 m outside the surfline. We alternated the starting point of the surveys between southern end and the northern end of the nearshore leg to avoid visibility bias caused by glare on southbound legs. Survey speed was maintained at 185 km/h at an altitude of 305 m.

The surveys were flown in a twin-engine, high-wing Partenavia aircraft. The forward section of this aircraft is made of clear plexiglass, which provided excellent visibility below and ahead of the plane. Large bubble windows were installed in each side of the cabin. Three observers, one in the forward section and one at each bubble window, searched for gray whales along the trackline and out to a distance of about 1 km on each side of the trackline. Distances to whales were determined by measuring vertical angles with hand-held inclinometers. The observer in the nose of the aircraft also operated the data-acquisition system which automatically recorded time and aircraft position for each sighting.

Infrared Sensor Sampling

To determine if our calf estimate required correction for diel variation in migration rate, we collected data during the 1994–1996 surveys with two forward-looking infrared (FLIR) sensors developed by the U.S. Navy (model AN/KAS-1A). These sensors sample in the far infrared region of the spectrum (wavelengths 8–12 μm) and can detect differences in temperature of 0.1°C. Our previous experience with these sensors has indicated that they can detect the blow of a gray whale in a temperate environment up to 8 km away (Perryman *et al.* 1999). The instrument can be selected to operate in either a narrow (1.1° × 2.2°, magnification 9×) or wide (3.4° × 6.8°, magnification 3×) field of view. We sampled using only the wide field of view.

The instruments were mounted on tripods positioned on a knoll (about 20m above sea level) that was adjacent to the visual survey site. From this position, the infrared sensors captured roughly two-thirds of the area monitored by the survey team (Fig. 2b). Weather permitting (no fog or rain, light winds), we operated these sensors for four hours each day and night during the peak of the migration (mid-April to mid-May).

Output from these instruments is standard composite RS-170 video. We

recorded this output on 120-min VHS video tapes. Data titlers inserted between the instruments and the video recorders displayed time and date on the video record. We screened the tapes for blows at high speed and then reviewed sections with whales several times at normal speed. We identified cow/calf pairs by the relative sizes and frequencies of the blows and the relative position of the two whales. We used a paired *t*-test to test the null hypothesis of no difference in migration rates between our day (0700–1900) and night (1900–0700) strata. Counts from video tapes were paired for comparison with the most recent tape from the other stratum. Counts were not paired if the interval between day and night samples exceeded 24 h.

Replicate Watch Effort and Detection Probabilities

We conducted independent, concurrent replicate watches during part of each survey to estimate the fraction of calves passing near shore that are undetected by the primary observers (*e.g.,* Rugh *et al.* 1993). An experienced observer stood replicate watches at a site approximately 200 m from the primary observers. A small knoll located between the two locations prevented actions by observers at either location from cueing the other team to the presence of whales. Replicate observers stood watch for 6 h/d but the duration of each watch varied from two to three hours based on environmental conditions and personal preference.

To estimate the detection probabilities, we fit a heterogeneous mark-recapture model (Huggins 1989, Alho 1990, see also Appendix) to the paired standard/replicate watch data. This model is a "paired" logistic regression, and allows detection probability to depend on both environmental covariates (*e.g.,* sighting conditions) and sighting-specific covariates (*e.g.,* whale behavior), *via* a linear predictor and logistic link function. The model assumes independence in detections not only among different cow/calf pairs, but also between watch stations. No communication between watch teams is a necessary condition for between-station independence, but if detection probability varies among cow/calf pairs, it is not sufficient. Specifically, if one or more random factors that affect detection probability act on both watch stations simultaneously (*e.g.,* glare off the water), then detection will be correlated between watches unless these factors are included in the model through appropriate covariates. The correlation between stations can be either positive or negative, depending on the specific dependence on each random factor, but in either case it will create a bias in the estimated detection probabilities. Similarly, if random factors that affect detection probability are correlated among cow/calf pairs (*e.g.,* pod size), then detection will be correlated among cow/calf pairs unless these factors are included in the model, leading to overestimation of precision. Problems with non-independence are well-known in the context of mark-recapture models (*e.g.,* Seber 1982) and are not detectable in the data unless appropriate covariates are considered.

The detection probability covariates that we tested for significance were year (1994–2000), watch station (standard/replicate), pod size (1–4 pairs),

glare (present/absent), visibility code (1–4), number of other pairs being tracked (0–7), and migration path (inshore/offshore). We used conditional maximum likelihood (ML) (Huggins 1989, Alho 1990) to fit coefficients for these covariates and asymptotic normal approximations to estimate their covariance matrix. We selected covariates using approximate chi-squared tests for the difference in deviance between nested models, along with residual analysis using partial residual plots and simulated half-normal plots (*e.g.*, Collett 1991). Finally, we used a Taylor series approximation (*i.e.*, the delta method) to estimate the covariance matrix for the fitted detection probabilities themselves. Simulations indicated that the analytic approximations used to estimate precision were sufficiently accurate, particularly because the estimated probabilities were not the largest source of uncertainty in the final abundance estimates.

Conditional on the n cow/calf pairs that were sighted by one or both watch stations, the likelihood in the paired observer model is given by

$$l_c(\beta; y) = \prod_{i=1}^{n} \frac{p_{i,std}^{y_{i,skl}}(1 - p_{i,std})^{1-y_{i,skl}} p_{i,rep}^{y_{i,rep}}(1 - p_{i,rep})^{1-y_{i,rep}}}{1 - (1 - p_{i,std})(1 - p_{i,rep})}$$

where

$$p_{i,s} = e^{x_{i,s}'\beta}/(1 + e^{x_{i,s}'\beta})$$

is the unconditional probability of detection at watch station s for the ith sighting, $x_{i,s}$ is a vector of covariates for that station/sighting, β is the vector of coefficients to be estimated, and

$$y_{i,s} = \begin{cases} 1, & \text{if the } i^{\text{th}} \text{ sighting was detected at station } s \\ 0, & \text{otherwise} \end{cases}$$

are binary indicator variables for station-specific detections.

Given estimates of the detection probabilities, we could then estimate the number of whales that passed by undetected during watch periods. The usual method in a mark-recapture model would be to use counts from both watches to estimate the number of undetected animals. However, the replicate watch was only on station during part of the survey period. Therefore, we used a somewhat simpler (see Discussion) estimator which was similar to the "Horvitz-Thompson-like" estimators used by Huggins (1989) and Alho (1990), but used sighting counts only from the standard watch. With this, we estimated the total number of whales passing during each 3-h period that observers from the standard team were on watch:

$$\hat{N}_j = \sum_{i=1}^{n_j} \frac{1}{\hat{p}_{i,std}}$$

$$\hat{\sigma}_j^2 \equiv \widehat{\text{var}}\, \hat{N}_j = \sum_{i=1}^{n_j} \frac{1 - \hat{p}_{i,std}}{\hat{p}_{i,std}}\left(1 + \frac{\hat{\sigma}_i^2}{\hat{p}_{i,std}^2}\right) + \sum_{i=1}^{n_j} \sum_{i'=1}^{n_{j'}} \frac{\hat{\sigma}_{i,i'}^2}{\hat{p}_{i,std}\hat{p}_{i',std}}$$

$$\hat{\sigma}_{j,j'}^2 \equiv \widehat{\text{cov}}(\hat{N}_j, \hat{N}_{j'}) = \sum_{i=1}^{n_j} \sum_{i'=1}^{n_{j'}} \frac{\hat{\sigma}_{i,i'}^2}{\hat{p}_{i,std}\hat{p}_{i',std}} \tag{1}$$

where j indexes three-hour periods, i indexes sightings within each period, n_j is the number of sightings during three-hour period j, and the quantities

$$\hat{p}_{i,std},\ \hat{\sigma}_i^2,\ \text{and}\ \hat{\sigma}_{i,i'}^2$$

are the conditional ML estimated probabilities and their estimated variances and covariances.

With the assumptions (1) that the number of whales that were completely undetectable because they passed too far offshore was negligible (see Results, Aerial Survey), and (2) that the estimated inverse detection probabilities ($1/\hat{p}_{i,std}$) were unbiased, these estimated three-hourly totals are unbiased. The assumption of no bias in the estimated inverse detection probabilities was based on simulations that indicated that their estimation bias was small with respect to their sampling variance, at least for the range of detection probabilities and sample sizes considered here.

To correct for periods when no observers were on watch, we embedded the above estimators in a finite population model. This model used 3-h periods as the sampling units, and we stratified by week to account for varying passage rates over time. The sample of observed hours was not taken at random: it comprised only daylight hours during acceptable observing conditions. However, with the assumption that whale passage rates did not depend on time of day or on weather (see Results, Infrared Sensor Sampling), the sample can be considered random with respect to the cow/calf pairs.

The actual number of whales passing during each 3-h period was not observed directly, but rather was estimated from the observed counts using the estimated detection probabilities. Thus, we used a finite population model that accounted for measurement errors (Cochran 1977) in the three-hourly totals. Specifically, from above, we assumed that the estimated three-hourly totals were unbiased and had uncertainty due both to random detection and from using estimated (*i.e.*, random) detection probabilities. Further, although individual detections were assumed independent, the estimated three-hourly totals were not independent because the estimated detection probabilities were used across all 3-h periods. With the assumption of no bias in the estimated three-hourly totals, the effect of correlated measurement errors is to inflate the true variance of the estimator of total abundance. Thus, we added appropriate terms to the usual finite population estimator of variance:

$$\hat{N} = \sum_k \frac{T_k}{t_k} \sum_j \hat{N}_j$$

$$\widehat{\text{var}}\ \hat{N} = \sum_k \frac{T_k}{t_k}\left(1 - \frac{t_k}{T_k}\right)s_k^2 + \sum_k T_k\hat{\sigma}_k^2(1 - \hat{\rho}_k) + \sum_k \sum_{k'} T_k T_{k'}\hat{\sigma}_k\hat{\sigma}_{k'}\hat{\rho}_{k,k'}$$

where k indexes weeks, T_k and t_k are the total number and the observed number of three-hour periods during week k, s_k^2 is the usual sample variance of estimated three-hour counts during week k, and the sums are over all weeks observed. The quantities

$$\hat{\sigma}_k^2 = \frac{1}{T_k} \sum_j \hat{\sigma}_j^2 \quad \text{and} \quad \hat{\rho}_{k,k'} = \begin{cases} \dfrac{1}{T_k T_{k'}} \displaystyle\sum_j \sum_{j'} \frac{\hat{\sigma}_{j,j'}^2}{\hat{\sigma}_k \hat{\sigma}_{k'}} & \text{when } k' \neq k \\ \dfrac{1}{T_k(T_k - 1)} \displaystyle\sum_j \sum_{j' \neq j} \frac{\hat{\sigma}_{j,j'}^2}{\hat{\sigma}_k^2} & \text{when } k' = k \end{cases}$$

are stratified versions of quantities defined by Cochran (1977), where j indexes three-hour periods within week, and the sums are over all watch periods in week k.

To develop indices of calf production from our surveys and those conducted by Poole (1984*b*) from the same site, we divided the calf estimate for each year by abundance estimates derived from an unweighted GLM model fit to point estimates from counts of southbound gray whales passing Granite Canyon, California (Buckland and Breiwick, in press). Annual estimates of abundance from this model for the years 1980, 1981, and 1994–2000 were 15,954, 16,360, 22,702, 23,281, 23,875, 24,484, 25,109, 25,750, and 26,407, respectively.[1] A Taylor series expansion (Seber 1982) was used to calculate the variance of the indices.

Ice Conditions in the Northern Bering Sea

In a typical year, ice spreads rapidly southward through the Bering Straits in December, January, and February, driven by prevailing northerly winds. Ice continues to advance across the Bering Sea until late March and early April when melting and interactions with currents at the shelf edge stop its progress, and the ice slowly recedes. The temporal and spatial pattern of seasonal ice cover in the Bering Sea varies on both a seasonal and decadal scale. Several climatic features, including the position and intensity of the Aleutian Low, the sign and scale of the Pacific Decadal Oscillation (PDO), and El Niño-Southern Oscillation events probably all interact to drive the scale and timing of ice events (Cavalieri and Parkinson 1987, Francis and Hare 1994, Trenberth and Hurrell 1995, Maslanik *et al.* 1996, Mantua *et al.* 1997, Parkinson 2000). We selected sea ice as a factor to explore in our analysis of calf production because summer feeding in gray whales is restricted to specific shallow water areas that are ice-free only part of the year (Pike 1962, Moore and DeMaster 1997, Moore *et al.* 2000). Newly pregnant females are the first to return to these feeding grounds and they must store adequate fat to fast through the upcoming winter migration during which they give birth and lactate for a calf. Environmental effects that shorten the feeding season may affect the nutritive condition of these females and subsequently impact recruitment to the population.

We used a technique devised by Wyllie-Echeverria and Wooster (1998) to develop an ice index for comparison with our estimates of calf production. We obtained weekly ice charts for the Bering and Chukchi Seas from the National

[1] Personal communication from Jeff Breiwick, NMML, 7600 Sand Pt. Way, NE, Seattle, WA 98115, February 2001.

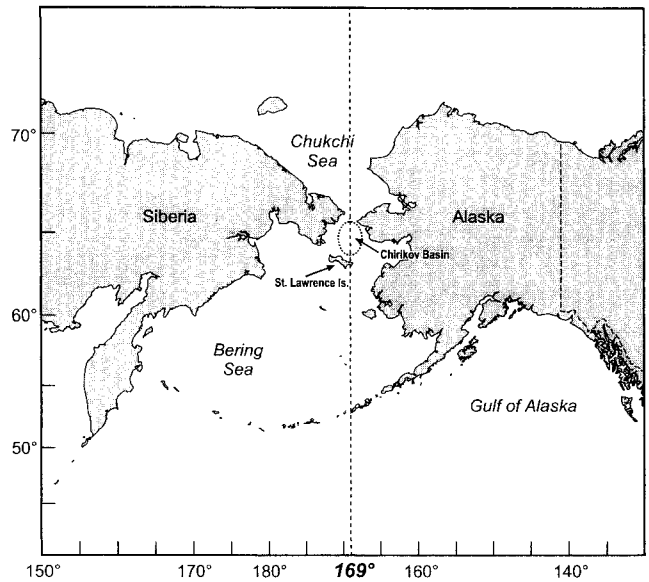

Figure 3. Location of 169°W longitude as it passes through the Bering Sea, across the Chirikov Basin feeding grounds and into the Chukchi Sea.

Snow and Ice Data Center (NSIDC) in Boulder, Colorado, for the years 1993–1999. From each chart, we determined the position of the ice edge along 169°W longitude. This meridian runs through St. Lawrence Island, across the primary gray whale feeding grounds of Chirikov Basin (Nerini 1984, Moore *et al.* 1986, Moore and DeMaster 1997), and then through the Bering Straits into the Chukchi Sea (Fig. 3). For each year, we developed a plot of the weekly locations of the ice edge along the selected meridian and then determined the length of time that a point near the center of the Chirikov feeding grounds (64°00′N, 169°00′W) was free of pack ice. We tested for correlations between the lengths of the feedings season (the ice-free periods) and our estimates of calf production for the following spring seasons. We also tested for such correlations with a one-year lag. If a reduction in feeding time impacts the probability that a pregnant female gray whale will carry a fetus to term, then a reduction in calf production should occur in the season immediately following the ice event. If a reduction in the feeding season impacts recruitment through suppression of ovulation or failure to conceive, there would be a one-year lag between the ice event and an observed reduction in the number of calves.

Results

Raw Survey Data

During the seven years of this study our observers spent over 4,679 h searching from the Piedras Blancas field station and sighted 2,106 gray whale calves (Table 1). Each year we began the survey in mid- to late March and

Table 1. A summary of effort and counts for gray whale cow/calf surveys conducted between 1994 and 2000 from Piedras Blancas, California.

Survey year	Begin date	End date	Hours searched	Total calf count	Median migration date
1994	17 March	4 June	671	325	26 April
1995	20 March	26 May	610	194	20 April
1996	20 March	31 May	694	407	27 April
1997	10 March	28 May	709	501	29 April
1998	23 March	22 May	554	440	18 April
1999	22 March	10 June	737	141	11 May
2000	13 March	2 June	704	96	15 April

continued until sightings of gray whale cows and calves dwindled to insignificant numbers in late May or early June (Fig. 4). Because the timing of the northbound migration proved to be less predictable than the southbound gray whale migration, we adjusted timing and duration of our surveys to adapt to the passage rates of the northbound whales. The median migration dates ranged from 15 April to 11 May, and there was no statistical correlation between median date and total calf count ($r = 0.403$, $P = 0.460$). There was a 5.2-fold difference between our low count of 96 calves in 2000 and the high count of 501 calves in 1997.

Most of the northbound cows and calves (87.4% of pods) passed the survey site at a distance offshore that was too close to measure with the reticulated 25× binoculars (<400 m), so these distances were estimated by the survey team (Fig. 5). The two most distant detections were of two pairs that passed the point just over 1 km offshore, a distance at which gray whales can still be easily detected with the unaided eye.

Cows and calves generally remained close together, swimming side by side, as they approached and passed the survey site. On a few occasions, the calf was seen turning back into the protected cove when its mother rounded the point heading northward. On all these occasions, the mother turned back into the cove and retrieved the calf. Associations between cow/calf pairs and other northbound cows with calves or the occasional adult or juvenile were very ephemeral in nature, and most sightings (86%) were of single pairs. The largest aggregation of cows with calves that we recorded consisted of three pairs.

Aerial Surveys

In 1994 we flew nine complete replicates of the seven track lines extending from Pt. Estero to Pt. Piedras Blancas. Of the 34 cow/calf pairs sighted during the aerial surveys, all except two were found during flights along the most inshore tracking (Fig. 6a). Both of the offshore pairs were swimming toward the shore rather than parallel to the survey track lines. During the 1995 survey, we completed eight replicates of the same seven transects. All of the 41 cow/

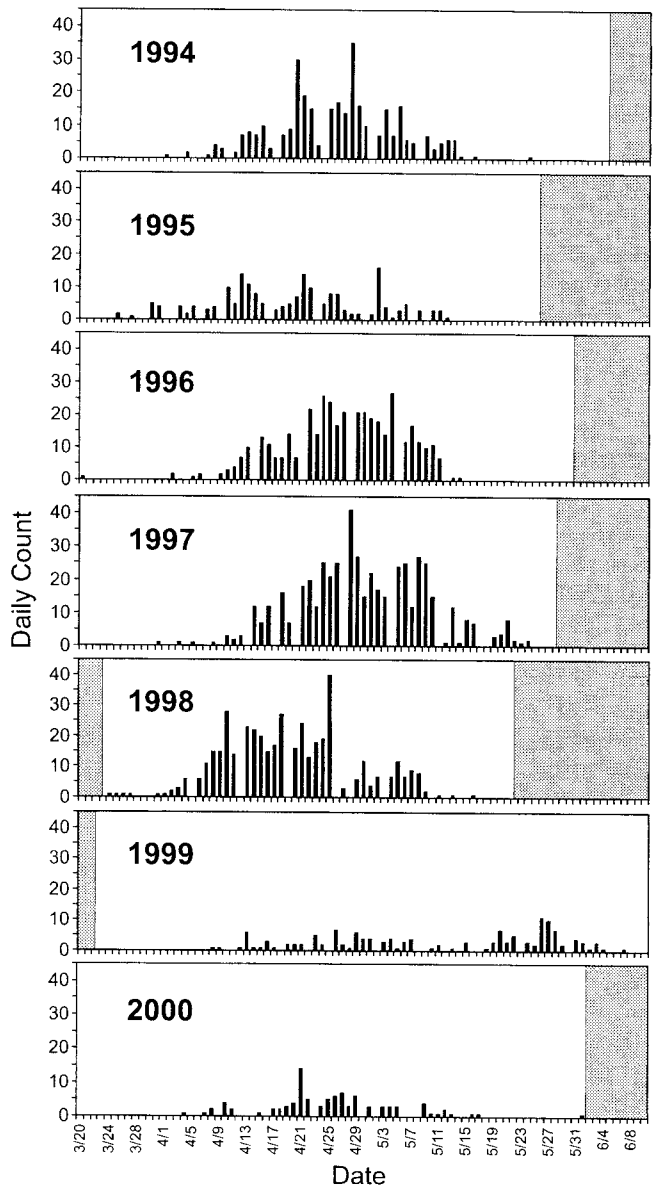

Figure 4. Daily counts of northbound gray whale calves from surveys conducted from Piedras Blancas, California. Shaded areas indicate days before and after survey period for that year.

calf pairs sighted were on the leg closest to shore (Fig. 6b). Our surveys indicated that most cow/calf pairs were found very close to shore and that the few found offshore were heading inshore. These results were consistent with the seven years of survey effort which indicated that cow/calf pairs are occasionally sighted offshore, south of Pt. Piedras Blancas, but that these pairs

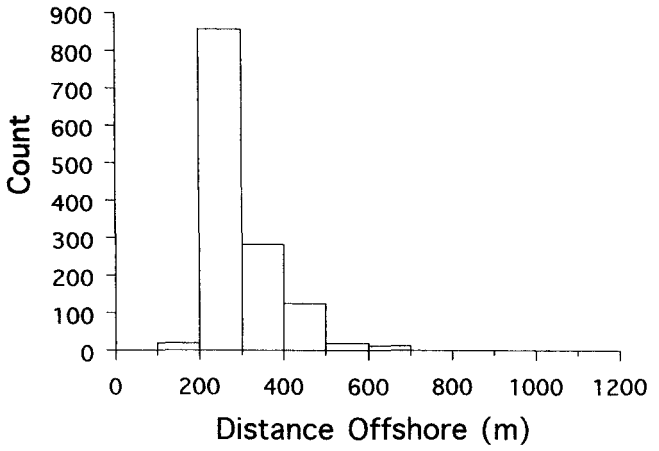

Figure 5. Distribution of offshore distances for gray whale calves passing Piedras Blancas during the surveys. Distances <400 m were estimated and those >400 m were calculated from measurements using 25× binoculars.

consistently pass the point <1 km offshore. Based on these results we did not adjust our estimates for calves passing far offshore.

Infrared Sensor Sampling

We compared day and night migration rates for northbound cow/calf pairs with data collected simultaneously by the two FLIR sensors (paired *t*-test) and found no evidence of diel differences in migration rates (Table 2). To increase the power of this test, we lumped the data from all three years and again tested for differences in counts between the day and night strata. This test also supported the hypothesis of no difference in day-night migration rates for

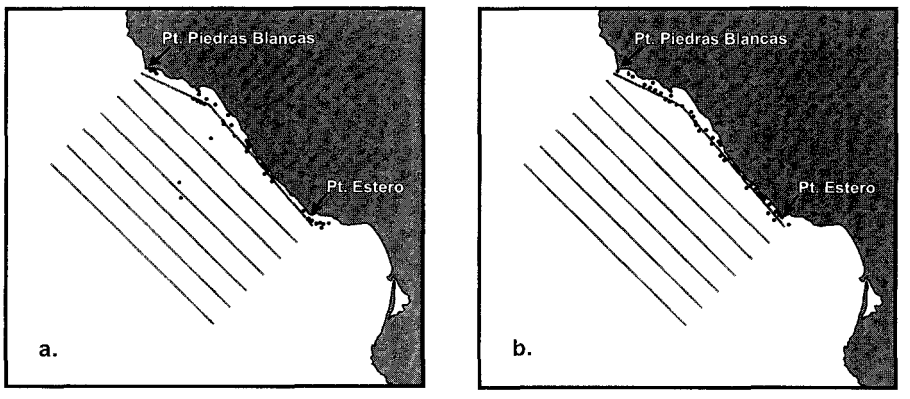

Figure 6. Aerial survey transects and gray whale calf sightings for 1994 (a) and 1995 (b). In 1994, nine surveys were flown and 34 calves were sighted. During eight surveys flown in 1995, 41 calves were sighted.

Table 2. Results of analysis of paired day and night counts of northbound gray whale calves on 2-h video tapes recorded from thermal sensors. Mean differences are absolute values for differences between all pairs of 2-h tapes in that test, and tapes averaged about 2 cow/pairs each.

Survey year	Paired samples	Mean differences	Paired t	P
1994	26	0.0	0.33	0.74
1995	32	0	0	1
1996	30	0.3	0.57	0.57
All years	88	0.2	0.19	0.85

cow/calf pairs passing the survey site (paired t-test, $P = 0.847$, df = 87). Given these results, we made no adjustment to our final calf estimate for diel differences in migration rate.

Replicate Watch

Of the covariates considered (year, watch station, pod size, glare, visibility code, number of other pairs being tracked, and migration path), only the main effects for year, pod size, and glare were significant at the 5% level (Table 3a). The significance of a yearly effect was due to the difference between a relatively large estimated detection probability for 1997 and a relatively small estimated detection probability for 1998 (Fig. 7). The result for 1997 may reflect the fact that the watch teams for that year were the most experienced, whereas the result for 1998 may reflect a learning curve for new observers. Because the object of this analysis was to compare yearly estimates of calf production, we chose to fully stratify by year so that differences in annual estimated numbers of calves would be less likely the result of differences in annual detection

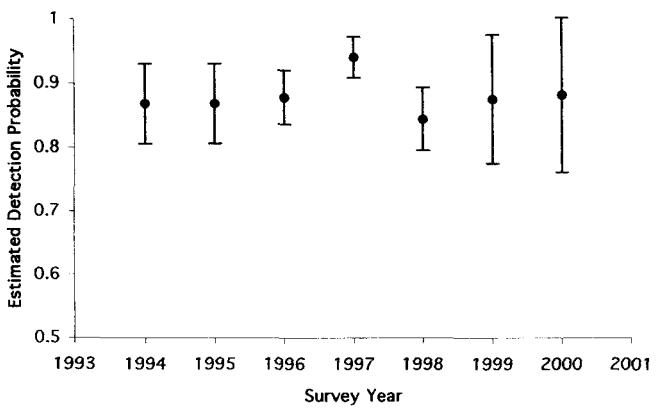

Figure 7. Annual estimates of detection probabilities for northbound gray whale cow/calf pairs. The 2000 estimate is pooled estimate for all previous years. Error bars are for ±1.96 SE.

Table 3a. Significance of adding main effects to the constant model. Change in deviance in each row of table represents the improvement in fit of model where detection probabilities p_{ij} depend on corresponding covariate, over model where the p_{ij} are constant. The P-value is from asymptotic χ^2 approximation to change in deviance.

Base model	Added covariate	Change in deviance	Change in df	P
Intercept only	—	(775.8)	(583)	—
	pod size: 1 *vs.* 2+	4.6	1	0.031
	Glare	3.7	1	0.056
	Year	11.2	5	0.047
	# Other pairs 0–3 *vs.* 4+	1.7	1	0.19
	Vis. code 1–2 *vs.* 3–4	1.7	1	0.19
	Path	0.82	1	0.36
	Watch station	0.29	1	0.59

probabilities. Stratifying fully by year did increase estimated standard errors over a partially stratified model, but it had little effect on estimated precision for the final calf abundance estimates. This was because most of the uncertainty in those final estimates was due to extrapolation to periods when the watch teams were off effort, *i.e.,* night and poor weather conditions.

After including year, the main effects for pod size and glare were no longer significant at the 5% level, although they were nearly so (Table 3b), and no other main effects or interactions were significant. It would have been possible to include terms for pod size and glare in the model, but we chose not to do so. One reason for this choice was that neither covariate could be measured precisely. Specifically, pod associations were often short-lived, and pairs along the same line of sight were sometimes recorded as groupings even though they were not. In addition, glare was defined by time of day, rather than being recorded directly by observers. There are two possible negative consequences of using a simpler model without terms for pod size and glare. First, ignoring covariates can introduce statistical dependence between watch stations and

Table 3b. Significance of adding main effects to year-stratified model. Change in deviance in each row of table represents improvement in fit of model where detection probabilities p_{ij} depend on both corresponding covariate and on year, over model where the p_{ij} depend only on year. The P-value is from the asymptotic χ^2 approximation to the change in deviance.

Base model	Added covariate	Change in deviance	Change in df	P
Intercept + Year	—	(764.6)	(578)	—
	Pod size: 1 *vs.* 2+	3.3	1	0.067
	Glare	2.5	1	0.11
	# Other pairs 0–3 *vs.* 4+	0.34	1	0.56
	Vis. code 1–2 *vs.* 3–4	1.8	1	0.18
	Path	1.2	1	0.28
	Watch station	0.29	1	0.59

Table 4. Estimates of detection probabilities p_{ij} as function of pod size and glare. Year-specific estimates were made, however estimates presented here are averaged over all years for simplicity of presentation. Final estimates used in our analysis depended only on year, and not pod size or glare; see text.

Factor	Level	Estimated average detection probability	Estimated SE
Pod size	1 pair	0.866	0.014
	2 or more pair	0.914	0.014
Glare	present	0.835	0.033
	absent	0.891	0.011

thus lead to biased estimates of detection probability. The effects of pod size and glare (Table 4), though practically significant for individual detections, were of a small enough magnitude that any bias in an estimated detection probability that ignores those factors was not important. This was confirmed by Monte Carlo simulation using a range of possible models, including ones with effects of larger magnitude than those actually estimated for pod size and glare. Second, the estimated detection probabilities come from data collected during the replicate watch period, but are applied to data from the remaining portion of the survey period as well. If covariates that were ignored have values that are, on average, different between the two periods, then the estimated average probabilities from the former period would not be applicable to the latter. There is no reason to expect that this is the case for either pod size or glare.

It is worth noting that partial residual plots for all of the covariates tested other than watch station showed a systematic pattern that, while not statistically significant, was consistent with what would be expected for those factors. For example, residuals plotted against visibility code showed that detection was somewhat less likely for higher codes (poorer visibility). The magnitude of the estimated coefficients for covariates whose main effects were not declared significant was of the same order as those for pod size and glare. In light of the residual plots, their lack of statistical significance may be caused by a difficulty, as with pod size and glare, in determining precise values for these covariates. For example, the path taken by a given cow/calf pair can include what would be considered both inshore and offshore areas. In any case, as with pod size and glare, their effects are of a small enough magnitude that any bias in estimating detection probabilities averaged over those factors would be small. Larger sample sizes (*i.e.*, more replicate watch effort) or a more objective or precise means of measuring those covariates might lead to smaller standard errors and statistically significant effects.

Calf Estimates

Our estimates of the total number of calves passing the survey site are based on counts from the standard watch, which were corrected for imperfect prob-

Table 5. Total calf estimates, estimates of detection probability, and indices of calf production for each survey years.

Survey year	Calf count	Detection probability	Total calf estimate	SE	Abundance estimate	Calf production index	SE
1994	325	0.868	945	68.21	22,710	4.2%	0.003
1995	194	0.868	619	67.19	23,281	2.7%	0.003
1996	407	0.878	1,146	70.67	23,875	4.8%	0.003
1997	501	0.894	1,431	82.02	24,484	5.8%	0.003
1998	440	0.844	1,388	94.84	25,109	5.5%	0.004
1999	141	0.875	427	41.10	25,750	1.7%	0.002
2000	96	0.889	279	34.79	26,407	1.1%	0.001

ability of detection estimated by analysis of the concurrent replicate watch data (Table 5). Although there were obvious and statistically significant (ANOVA, $F = 45.85$, $P < 0.001$, df = 6, 58) differences in total calf estimates between years, no predictable pattern or trend in gray whale reproduction is apparent from these results (Fig. 8).

Calf Production Indices

We divided our annual calf estimates by the corresponding fitted gray whale abundance estimates (Buckland and Breiwick, in press) to produce yearly indices of calf production (Table 5). We compared our indices of calf production with those derived by dividing the calf estimates from Poole (1984*a*) by the modeled abundance estimates for those years (Fig. 9) and again found significant differences between indices for some years (ANOVA, $F = 36.15$, $P < 0.01$, df = 8, 80). Pairwise comparisons (SNK) between yearly indices showed that the 1980 and 1981 indices were not significantly different ($P > 0.05$)

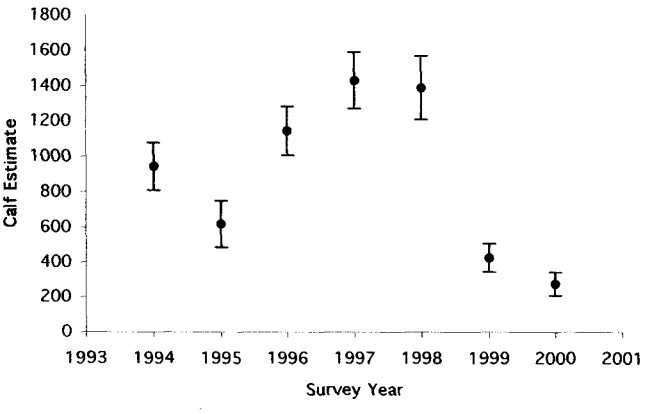

Figure 8. Estimates of the total number of gray whale calves passing Piedras Blancas during each survey year. Error bars are ±1.96 SE.

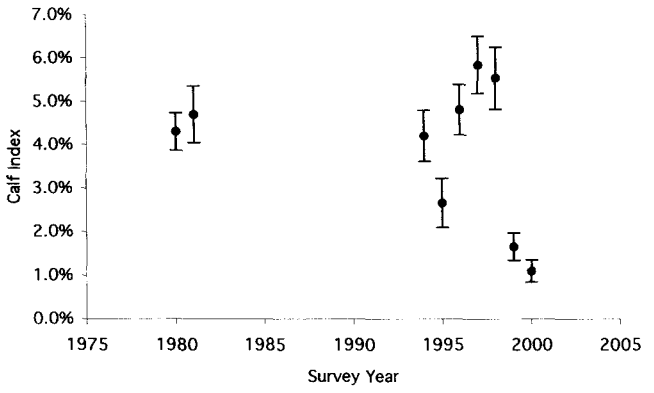

Figure 9. Indices of gray whale calf production derived from counts of northbound calves divided by modeled abundance estimates provided by Jeff Breiwick (AFSC, National Marine Mammal Laboratory). Calf estimates for 1980 and 1981 taken from Poole (1984*a*).

from those of 1994, 1996, and 1998. The clear outliers of the group of indices, 1995, 1999, and 2000, differed significantly from all other annual indices ($P < 0.05$). There was no evidence of a trend or detectable pattern in calf production over the period from 1980 to 2000.

Arctic Ice and Recruitment

The number of days that the selected reference point over the Chirikov Basin was free of seasonal ice varied from a high of 190 d (in 1993 and 1995) to a low of 147 d in 1999. We found a significant positive correlation between the ice (or feeding season) index and our estimates of calf production for the following spring ($r = 0.860$, $P = 0.010$). Thus, shorter ice-free seasons were followed by low estimated calf production, and longer ice-free periods were followed by higher estimated calf production (Fig. 10). When we introduced a one-year lag in our tests, we found no significant correlation between the ice index and calf production ($r = 0.289$, $P = 0.607$).

Discussion

Like Poole (1984*a*,*b*), we found that the northbound migration of gray whale cows with calves closely followed the coastline in the vicinity of Piedras Blancas, with pairs often swimming just outside the surf line. This phase of the gray whale migration generally extends from late March to late May, with a median date around the last week of April. Cows with calves were most often sighted as single pairs. As the pairs approached the point from the southeast, they swam directly towards the survey site providing an excellent perspective for detecting the presence of a calf alongside the associated cow, even when the whales were still over 4 km from the survey team.

Although the cows with calves passed so close to the survey site that they

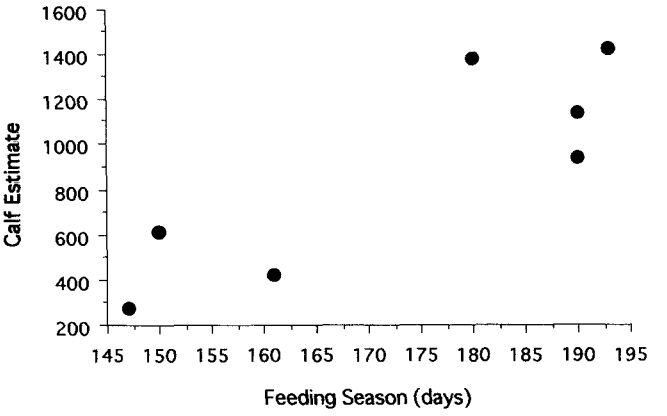

Figure 10. Number of days that gray whale feeding grounds on the Chirikov Basin were free of seasonal ice ("Feeding Season") and number of calves estimated from our surveys in subsequent spring.

could sometimes be heard as well as seen, we attempted to address each of the potential sources of bias raised from the much more difficult shore-based abundance surveys of southbound gray whales conducted from Granite Canyon, California (Reilly 1984). We scheduled the surveys to encompass the entire migration to avoid extrapolating the tails of the migration from whales counted during the core period. We conducted aerial surveys well offshore from the survey site and determined that correcting shorebased counts for whales passing far offshore was unnecessary. We excluded sightings and effort with poor visibility, codes >4, and our analysis of the replicate watch data revealed that the effect of visibility on sighting probabilities within the range of codes 1–4 was negligible. We estimated day and night migration rates from counts of whales detected with thermal sensors and found that the rates were not significantly different. We conducted concurrent replicate-watch effort each year and estimated the probability that gray whale cows and calves passing nearshore would be detected by the standard watch. Finally, as part of a complementary photogrammetric study, we used an aircraft to search for cows with calves among the adults and juveniles that constitute the first phase of the northbound migration and found none (Perryman, unpublished data). Based on these results, we assumed that passage rates measured during on-effort periods were representative of those during off-effort periods and only corrected our estimates for whales that passed nearshore but were missed by the survey team.

It would have been possible to include the replicate watch sighting counts directly in our estimates of three-hourly totals, as well as including them indirectly through the estimated detection probabilities. In fact, because the probability of detection by both watches together $(1 - (1 - p_{i,std})(1 - p_{i,rep}))$ was higher than that for the standard watch alone $(p_{i,std})$, the uncertainty due to random detection would have been somewhat smaller in our estimates of abundance. However, simulations indicated that because detection probability

was already high, the decrease in standard error by including replicate sightings was only a few percent, and we did not use this more complicated estimator.

Although our results are inconsistent with the negative trend in pregnancy rates suggested by data from the Russian hunt (Reilly 1992), we found significant fluctuations in calf production for this population (over five-fold between some years). We suggest that years with low calf production were associated with feeding seasons effectively shortened by extensive seasonal ice and that suboptimal nutritive condition in pregnant females was the link in this apparent biophysical connection.

There is a continuum in the degree of dependency animals place on stored fats for reproduction (Thomas 1990). Because they rely almost entirely on stored fats and other tissues for support through the final stages of pregnancy and most of the lactation period, gray whales are an example of one extreme of this relationship. Recognizing the physiologically demanding nature of this life history, Rice and Wolman (1971) suggested that selective pressure for suppression of ovulation at times when a female is incapable of carrying a pregnancy to term might exist. Lockyer (1986) reported a link between prey abundance and subsequent ovulation rates for eastern North Atlantic fin whales (*Balaenoptera physalus*). Because we have observed lower calf production in the spring immediately following ice-shortened feeding seasons (1994, 1998, 1999), we attribute the lower levels of calf production to a failure to carry existing pregnancies to term. This suggests that in this case it was existing pregnancies, rather than ovulations or conceptions, that were impacted.

In addition to the very low calf numbers reported here, unusually large numbers of dead gray whales were found along the North American coast in 1999 and 2000 (Moore *et al.*, in press). Le Boeuf *et al.* (2000) reviewed the strandings data and other unusual aspects of gray whale demographics and behaviors and suggested that gray whales were undernourished when they began their long two-way migration in 1999. We agree that the symptoms observed in this population in 1999 and 2000 are likely related to an overall reduction in nutritive condition of individuals within this population. We suspect that the dramatic nature of these events are the result of a synergistic interaction of lower overall food availability (Highsmith and Coyle 1992, Grebmeier and Dunton 2000) and reduced access to this already depleted resource caused by extensive seasonal ice. It is still unclear, however, whether the observed changes in productivity and mortality indicate that this population has exceeded the carrying capacity of its environment or whether they reflect reactions to shorter term environmental events.

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study. Richard Rowlett has been the leader of our observation team since the beginning of the study and his professionalism and unique skills are responsible in a large part for the consistent quality of our data set. Monica DeAngelis was a watch-team leader for several surveys and her leadership and attention to detail were critical to our success. We acknowledge Alexandra Von Saunder, LTJG, NOAA; Thomas Martin, LTJG, NOAA; and Todd Pusser for their long hours of valuable watch effort. We also thank Jeff Breiwick from the National Marine Mammal Laboratory, AFSC, who kindly provided abundance estimates for the years of our survey. This manuscript was improved by comments from Robert Brownell, SWFSC, and Richard Neal, SWFSC, and two anonymous reviewers.

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APPENDIX

COMPARISON OF METHODS WITH BUCKLAND *ET AL.* (1993)

Much of the work described here was based on methods developed by Buckland *et al.* (1993) to estimate gray whale abundance. However, our statistical analysis differs in three ways.

First, whereas we accounted for unobserved periods using a finite population model, they estimated the number of whales passing during those periods by fitting a smooth function to the time series of estimated daily totals. An advantage of smoothing the time series is that, with appropriate assumptions on the form of the smoothed data, passage rates can be extrapolated before and after the range of days when observers are present. Because observers in this study were present over the entire duration of the northbound migration, such extrapolation was not needed.

Second, we used conditional ML to estimate detection probabilities from paired watch data, by maximizing the likelihood (Equation 1) derived by Huggins (1989)

and Alho (1990) directly. In contrast, Buckland *et al.* (1993) developed a conditional ML algorithm that uses iterative maximization of a simpler likelihood (denoted by L, their page 239), in much the same spirit as the E-M algorithm (*e.g.*, Tanner 1996). However, their description inadvertently implies that their algorithm ultimately maximizes the simpler likelihood, when in fact that likelihood is used only as an intermediary. While not obvious, it can be shown that Buckland *et al.*'s iterative logistic regression algorithm does indeed maximize the correct conditional likelihood for the paired observer model (Equation 1). However, as with the E-M algorithm, using the simpler likelihood to derive the usual asymptotic variance estimators from ML theory leads to estimates of standard error that are too large, particularly with detection probabilities less than about 40.

Finally, the variance estimator given by Buckland *et al.* (1993, p. 240) accounts for variation in the estimate of abundance due to random detections of whales but does not account for variation due to using estimated (*i.e.*, random) detection probabilities. This component may or may not be a large portion of the total variance depending on the actual detection probabilities, which determine the magnitude of the first component of variance, and the sample size, which primarily determines the magnitude of the second component of variance. Our variance estimator for the hourly totals included components due to both sources of variance.