

Survival estimates of western gray whales *Eschrichtius robustus* incorporating individual heterogeneity and temporary emigration

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ABSTRACT: Gray whales *Eschrichtius robustus* exist as 2 geographically and genetically distinct populations in the eastern and western North Pacific. Subjected to intensive commercial whaling during the 19th and 20th centuries, the western population presently numbers approximately 100 individuals and is regarded as one of the most endangered baleen whale populations in the world. Since 1997, ongoing studies of western gray whales have resulted in a photographic dataset that can be used for mark-recapture survival estimation. Pollock's robust design was applied to 129 individual whale encounter histories spanning 25 monthly capture occasions from 1997 to 2003. Using Akaike's Information Criterion (AICc) model selection, models incorporating individual heterogeneity in residency patterns and higher temporary emigration probabilities for younger whales provided better fits to the data. Non-calf and calf (1st year post-weaning) survival were estimated as 0.951 (SE = 0.0135, 95 % CI = 0.917 to 0.972) and 0.701 (SE = 0.0944, 95 % CI = 0.492 to 0.850), respectively, averaging across the best models (n = 13) in order to account for model uncertainty. The non-calf survival point estimate is similar to mark-recapture estimates for Gulf of Maine humpback whales, but lower than an indirect estimate for the eastern gray whale population. Although no statistically robust direct estimates of baleen whale calf survival exist for comparison to the current study, the calf survival estimate is markedly lower than a value suggested for Gulf of Maine humpback whales. Estimation of survival is necessary for assessing the status of western gray whales, which can contribute to increased protection, conservation, and management planning for this critically endangered population.

KEY WORDS: Survival estimation · Temporary emigration · Individual heterogeneity · Western gray whale · Robust design · Mark-recapture · Photo-identification · Sakhalin Island

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INTRODUCTION

Two populations of gray whales *Eschrichtius robustus* occur in the North Pacific, referred to as the eastern and the western populations (Rice & Wolman 1971).

The 2 populations can be differentiated genetically at the population level, and are considered geographically and genetically distinct population units (LeDuc et al. 2002). Eastern gray whales migrate along the western coast of North America from winter breeding

grounds off Baja California to summer feeding grounds in the Bering and Chukchi Seas (Pike 1962). Western gray whales, also annual migrators, return to summer feeding grounds in the Okhotsk Sea (Berzin 1990). Winter breeding grounds for this population are unknown, but are suspected to be along the coast of southern China (Wang 1984, Omura 1988, Kato & Kasuya 2002).

Throughout their range, gray whales typically do not occur outside the shallow waters of the continental shelf. Their coastal distribution made them accessible to both aboriginal and commercial whalers. Both populations were greatly reduced by intensive commercial whaling during portions of the 19th and 20th centuries. After receiving international protection over 50 yr ago, recovery of the eastern population was observed (e.g. Reilly 1992). Abundance estimates of over 20000 whales by the mid-1990s (e.g. Buckland & Breiwick 2002) suggest that this population recovered to its pre-commercial exploitation population size (Reilly 1992).

Not afforded the same degree of international protection, the western population has failed to exhibit the successful recovery demonstrated by its eastern counterpart (Clapham et al. 1999, Weller et al. 2002a). Western gray whales were proposed to be extinct as recently as the early 1970s (Bowen 1974), but are presently known to survive as a remnant population (Brownell & Chun 1977, Blokhin et al. 1985, Weller et al. 1999). Recent mark-recapture abundance estimates indicate that the population may currently consist of approximately 100 individuals (Wade et al. 2003). Western gray whales are one of the world's most endangered large whale populations (Clapham et al. 1999, VanBlaricom et al. 2001) and were recently listed as 'Critically Endangered' (Criterion D) by the World Conservation Union (IUCN) (Hilton-Taylor 2000, Weller et al. 2002a).

The use of marked individuals and mark-recapture theory in assessing biological populations is well documented (see Pollock 1991 for review). For many whale species, individuals can be identified from photographs of unique natural markings (e.g. scars and pigmentation patterns) in a method known as photo-identification (see Hammond et al. 1990 for overview). In the application of mark-recapture theory to photo-identification data, the first photographic sighting of an individual constitutes the 'mark' and subsequent sightings the 'recaptures.' The complete individual sighting record serves as the encounter history (White & Burnham 1999). An appropriate mark-recapture model (see Seber 1982 for examples) is fitted to the compiled encounter histories to estimate the population parameter of interest. Mark-recapture photo-identification studies can be used to estimate the

abundance (e.g. Hammond 1986), survival (e.g. Buckland 1990), and fecundity (e.g. Barlow & Clapham 1997) of whale populations. However, for most mark-recapture whale studies, care must be taken to reduce bias in the parameter estimates that can arise from individual heterogeneity in capture probabilities (Buckland 1990). Individual heterogeneity in capture probability can occur if some whales are more easily identified (e.g. possess distinctive markings or are more approachable) or spend more time in the study area than other whales (Buckland 1990). Temporary emigration, that is, the complete absence of individuals from the study area during a study period, can also bias mark-recapture parameter estimates if not properly accounted for in whale studies (Fujiwara & Caswell 2002).

Gray whales (including calves) are individually identifiable by natural pigmentation patterns and in some cases scarring from previously attached epizoid barnacles. Numerous multi-year studies have shown photo-identification to be a reliable and effective research technique for this species (Hatler & Darling 1974, Darling 1984, Swartz 1986, Jones 1990, Weller et al. 1999, Calambokidis et al. 2002). Whereas eastern gray whales are one of the better-studied baleen whale populations, western gray whales have only recently come under concerted study (e.g. Brownell et al. 1997, Weller et al. 1999). Concerns about the lack of recovery exhibited by western gray whales and the increase of anthropogenic threats in their known geographic range (i.e. coastal waters of Russia, Japan, the Korean peninsula, and China) prompted the initiation of a photo-identification study to evaluate basic western gray whale life history parameters, including survival, for integration into population assessments necessary for the appropriate conservation and management of this population (Weller et al. 1999, 2002a).

Since 1997, an ongoing collaborative Russia – U.S. photo-identification study of western gray whales has been conducted on their only known summer feeding ground, located off the northeastern coast of Sakhalin Island, Russia, in the Okhotsk Sea. This research has documented the regular use of the feeding ground by whales of both sexes and multiple age classes, including reproductive females and their calves (Weller et al. 1999, 2002a). When these females are post-parturient, they arrive on the feeding ground nursing a single calf, which is subsequently weaned during the feeding season at approximately 6 to 8 mo of age. This study has also demonstrated that many individuals exhibit a consistent annual return and strong seasonal fidelity to the study area, while others are absent for all or part of any given field season (Weller et al. 1999, 2002a, 2003). A multi-year (1997

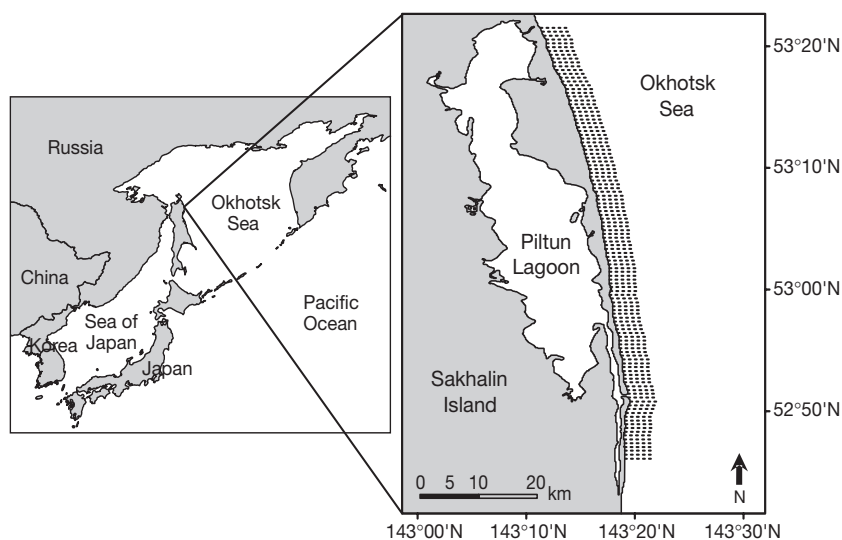


Fig. 1. Map of western gray whale study area (dashed lines) proximate to Piltun Lagoon, Sakhalin Island, Russia, in the Okhotsk Sea

to 2003) photographic dataset has been generated by the project.

An unusually low return to the feeding ground of western gray whales first observed as calves had been noted in the earlier years of the study (Weller et al. 2002a). By 2001, only 6 of the 16 (37.5%) calves identified between 1997 and 2000 had been resighted subsequent to their year of weaning. Integrating 2002 to 2003 findings, 19 of the 29 (65.5%) calves identified between 1997 and 2002 have presently been resighted post-weaning. Specific results from these recent years reveal that the low return to the study area by whales first sighted as calves can partially be attributed to the temporary emigration of these whales. For example, 2 whales were resighted in 2002 that had not been observed since they were calves in 1997 and 1998, respectively. Anecdotally, a whale not seen in

Table 1. *Eschrichtius robustus*. Summary of annual survey effort and photo-identification from 1997 to 2003. Number of whales identified annually includes resightings of individuals from previous years

Year	Sampling period (mm/dd–mm/dd)	No. of months	No. of surveys	No. of whales identified	Photo-identification catalog size
1997	07/09–09/08	3	22	47	47
1998	07/06–09/29	3	35	54	67
1999	06/29–10/13	5	56	69	85
2000	06/25–09/16	4	40	58	91
2001	06/25–09/25	4	48	72	103
2002	07/01–09/25	3	36	76	116
2003	07/15–09/13	3	22	75	129
Overall		25	259	129	129

the study area since it was first observed as a calf during a 1995 pilot study (Brownell et al. 1997) was also resighted in 2002.

The mark-recapture estimation of western gray whale survival from 1997 to 2003 was the objective of the present analysis. In order to reduce bias in the resulting estimates, the noted individual heterogeneity in capture probability was addressed in the analysis. Likewise, the aforementioned temporary emigration of young whales was also considered.

MATERIALS AND METHODS

Photo-identification. Western gray whale photo-identification surveys were carried out annually during summer months off northeastern

Sakhalin Island, Russia, in the nearshore waters proximate to Piltun Lagoon (Fig. 1). The study area consisted of waters within 5 km of shore along approximately 70 km of the coastline. Recent aerial surveys (e.g. Weller et al. 2002c, Blokhin et al. 2004) have corroborated that the study area encompasses the majority of whales feeding in the vicinity of Piltun Lagoon. Thus, the study area can also be referred to as the Piltun feeding ground.

The photo-identification survey vessel was directed to encounter as many whales as possible throughout the study area and did not follow a systematic track. Surveys were conducted for as long as fuel, weather conditions, and availability of whales permitted. For additional information about the study area and a detailed description of the photo-identification data collection and analysis protocols, see Weller et al. (1999). From 1997 to 2003, 259 photo-identification surveys completed during 25 mo produced the 129 individual whale encounter histories utilized in the current analysis. A summary of annual survey effort and whale photo-identification is shown in Table 1.

Survival estimation. Pollock's robust design (Pollock 1982, Kendall & Pollock 1992, Kendall & Nichols 1995, Kendall et al. 1995, 1997), combining the Cormack-Jolly-Seber (CJS) open recapture model (Cormack 1964, Jolly 1965, Seber 1965) and Huggins' closed capture estimator (Huggins 1989, 1991), was used to estimate model para-

meters. The field seasons over the 7 yr study period were treated as the closed primary sampling periods (i.e. population additions and deletions are assumed to have occurred between field seasons). Months within a field season were considered the secondary sampling periods (i.e. whales were recorded as sighted or not sighted in each month), as monthly intervals provided a consistent and comparable way to temporally partition each field season. The following parameters were estimated, although non-calf and calf survival are the primary parameters of interest: ϕ_g = survival probability of group g , where g is either non-calf or calf (1st year post-weaning); γ_{gi} = probability of group g being unavailable for capture in primary period i , given that group g is alive during period i (i.e. temporary emigration), where g is either ≥ 2 yr old, < 2 yr old, ≥ 3 yr old, < 3 yr old, ≥ 4 yr old, or < 4 yr old and $i = 1998, 1999, \dots, 2003$; p_{hij} = probability of individual whale h being captured in secondary sample j of primary period i , given that individual whale h is alive and in the study area during period i , where $h = \text{Whale 1, Whale 2, } \dots, \text{ Whale 129}$; $j = \text{June, July, } \dots, \text{ October}$; and $i = 1997, 1998, \dots, 2003$.

Assumptions of the parameter estimation are: (1) all whales possess unique markings and were correctly identified; (2) the population was closed to births, deaths, immigrants, and emigrants within each primary sampling period; (3) all western gray whales used or passed through the study area during the study period, but not necessarily in each year; (4) constant non-calf and calf survival during the study period; and (5) random temporary emigration (Kendall & Nichols 1995, Kendall et al. 1997) that is either constant, group varying (between whales ≥ 2 yr old and < 2 yr old, ≥ 3 yr old and < 3 yr old, or ≥ 4 yr old and < 4 yr old), time varying, or group and time varying. Thus, one model of survival ($\phi(gc)$, where gc = group varying between non-calves and calves) was tested in conjunction with 8 models of temporary emigration: $\phi(\cdot)$, $\gamma(g2)$, $\gamma(g3)$, $\gamma(g4)$, $\gamma(t)$, $\gamma(g2 + t)$, $\gamma(g3 + t)$, and $\gamma(g4 + t)$; where \cdot = constant (no group or time influence), $g2$ = group varying between whales ≥ 2 yr old and < 2 yr old, $g3$ = group varying between whales ≥ 3 yr old and < 3 yr old, $g4$ = group varying between whales ≥ 4 yr old and < 4 yr old, t = time varying by primary period, and $+$ = additive model.

The $g2$ model was developed to account for the low return to the study area by whales first sighted as calves, by allowing the temporary emigration probability of yearlings (i.e. weaned in the previous year) to differ from older whales. Yet, given the observation that whales were absent from the study area for more than 1 yr after weaning, 2 more explicit models were constructed, which allowed whales first observed as calves to temporarily emigrate with a characteristic

probability for up to 2 and 3 yr post-weaning (i.e. $g3$ and $g4$ models, respectively).

Given the constant survival and variable temporary emigration parameters, the effects of various combinations of time, survey effort, and an individual residency covariate were examined in 9 models of capture probability: $p(t)$, $p(T)$, $p(Eff)$, $p(Res)$, $p(t + Res)$, $p(T + Eff)$, $p(T + Res)$, $p(T + Eff + Res)$, and $p(Eff + Res)$; where t = time varying by secondary period, T = trend over time; Eff = effort (time covariate); and Res = residency (individual covariate).

Testing for a trend over time in capture probability served to address the hypothesis that capture probability increased over time because of improved efficiency in survey ability over the primary sampling period. Eff is the number of photo-identification surveys conducted each month, which are regarded as a comprehensive and comparable measure of monthly survey opportunity. Res is defined as the number of days a whale was captured in a given month divided by the mean number of days all whales were captured that month, averaged over all months that the whale was captured. This value acts as an index of the relative duration of residency of an individual whale in the study area during the study period, and should reduce the individual heterogeneity in capture probability associated with some whales spending more time in the study area than others (Fig. 2). In other words, Res indicates whether an individual whale tended to remain over longer periods in the study area, or to stay for shorter amounts of time before leaving the area. This type of individual heterogeneity was emphasized in the analysis because it was the only discernible source of individual heterogeneity in capture probability exhibited by whales on the Piltun feeding ground

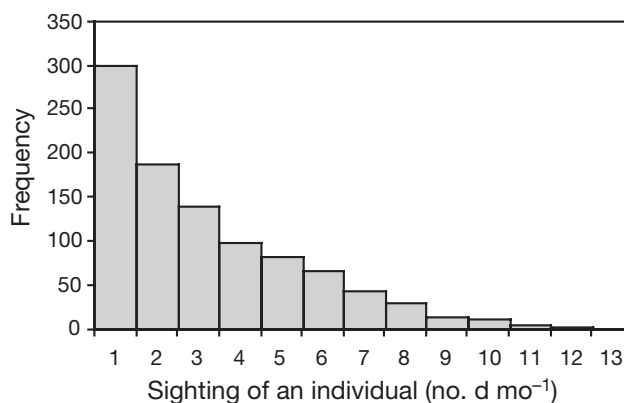


Fig. 2. *Eschrichtius robustus*. Histogram of number of days an individual was sighted per month ($n = 991$ occurrences of individuals seen 1 to 13 d mo^{-1}) pooled over all secondary sampling periods. Individual whales are represented in as many months as the individual was seen; monthly variation in survey effort is not reflected

during the study period. It should be noted that *Res* is based on the daily sighting records, as these data are considered to reflect the relative duration of whale presence in the study area and were not used to estimate model parameters. Likewise, the calculation is conditioned on the individual being seen in a given month, so the residency index does not repeat information in the encounter history used for parameter estimation. In calculating *Res*, scaling to the mean of each month allows the duration of residency detected monthly to be relative to sampling effort. A histogram of the residency values used to model capture probability is shown in Fig. 3.

With the one survival model, the 8 temporary emigration models, and the 9 models of capture probability, a total of 72 models were fitted to the encounter histories using maximum likelihood estimation. The analysis was conducted in Program MARK (White & Burnham 1999). Models were selected using Akaike's Information Criterion (Akaike 1973) corrected for small sample size (AICc) (Hurvich & Tsai 1989). Non-calf and calf survival estimates were averaged across the best models in order to account for model uncertainty (Burnham & Anderson 2002).

RESULTS

Incorporating *Res*, *t*, and *Eff* into models of capture probability provided the best fits to the data (Table 2). As expected, capture probability was positively correlated with *Res* and also varied by secondary sampling period (Fig. 4). That is, the positive correlation between capture probability and *Res* was characteristically represented during each secondary sample (Figs. 4 & 5). The pattern of monthly capture probabilities differed by primary sampling period, although monthly capture probabilities increased initially during 6 yearly field seasons, decreased eventually during 5 seasons, and tended to be highest during the month of August (Fig. 5).

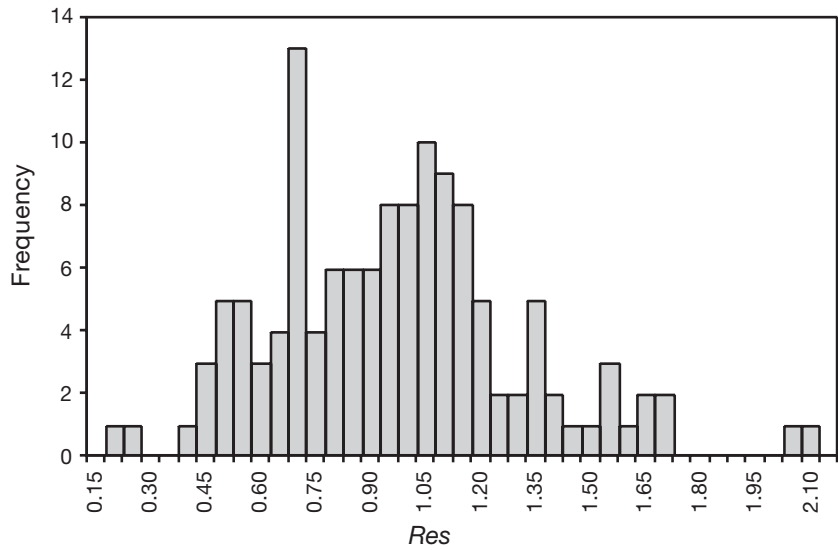


Fig. 3. *Eschrichtius robustus*. Histogram of individual residency (*Res*) covariates ($n = 129$) used in models of capture probability. Each individual whale in the study is represented by a single value

The influence of temporary emigration on model selection was secondary to the effect of capture probability (Table 2, Appendix 1). However, for each representation of capture probability, the constant and group-varying temporary emigration models fit the data better than models allowing temporary emigration to vary by time or by group and time. Specifically, allowing temporary emigration to differ between whales ≥ 4 yr old and < 4 yr old was primarily

Table 2. *Eschrichtius robustus*. Comparison of the best models ($n = 13$) used to estimate non-calf and calf survival of western gray whales from 1997 to 2003. Delta AICc: difference in the AICc of a model from the minimum AICc model; AICc weight: Akaike Weight (see Burnham & Anderson 2002 for description). See text for details of parameters and model notation. A comparison of all models ($n = 72$) used to estimate western gray whale survival is shown in Appendix 1

Model	AICc	Delta AICc	AICc weight	No. parameters
$\phi(gc) \gamma(g4) p(t+Res)$	2274.96	0.00	0.51288	36
$\phi(gc) \gamma(.) p(t+Res)$	2276.24	1.28	0.26996	35
$\phi(gc) \gamma(g3) p(t+Res)$	2278.02	3.06	0.11083	36
$\phi(gc) \gamma(g2) p(t+Res)$	2278.40	3.44	0.09197	36
$\phi(gc) \gamma(g4+t) p(t+Res)$	2283.92	8.96	0.00581	41
$\phi(gc) \gamma(t) p(t+Res)$	2284.45	9.49	0.00445	40
$\phi(gc) \gamma(g3+t) p(t+Res)$	2286.47	11.51	0.00162	41
$\phi(gc) \gamma(g2+t) p(t+Res)$	2286.63	11.67	0.00150	41
$\phi(gc) \gamma(g4) p(T+Eff+Res)$	2288.81	13.85	0.00050	32
$\phi(gc) \gamma(.) p(T+Eff+Res)$	2290.11	15.15	0.00026	31
$\phi(gc) \gamma(g3) p(T+Eff+Res)$	2291.88	16.91	0.00011	32
$\phi(gc) \gamma(g2) p(T+Eff+Res)$	2292.25	17.29	0.00009	32
$\phi(gc) \gamma(g4+t) p(T+Eff+Res)$	2297.63	22.67	0.00001	37

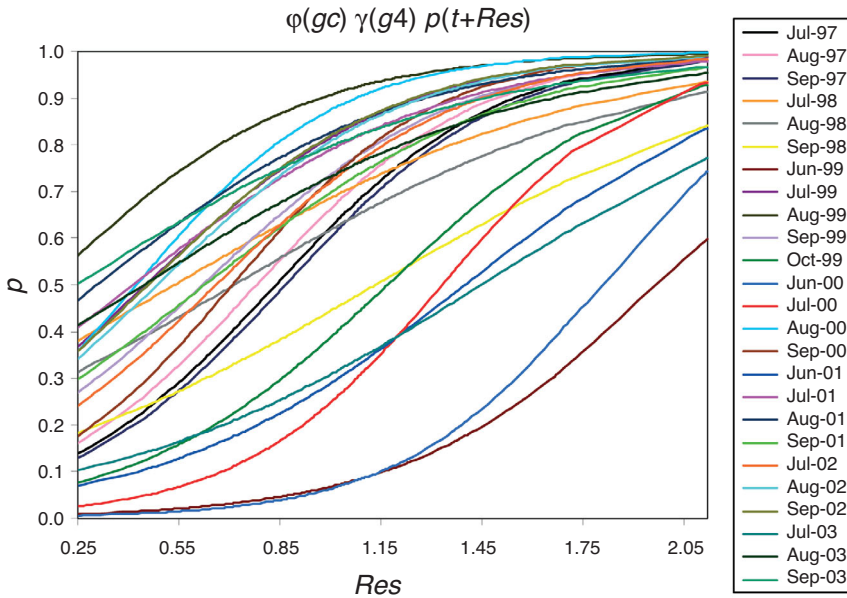


Fig. 4. *Eschrichtius robustus*. Capture probability (p) vs. residency (Res) for each secondary sampling period ($n = 25$) according to the highest AICc weighted model

selected in 5 of the 9 cases of capture probability. Values of all temporary emigration parameters estimated in combination with the highest weighted capture probability model are listed in Table 3 for the constant and group-varying temporary emigrations models and depicted in Fig. 6 for the time-varying and additive models. The reduced AICc weights of the time-varying models notwithstanding, the time-varying temporary emigration estimates exhibited a similar relative relationship as the constant and group-varying estimates. For each primary sampling period, estimates for whales <4 yr old and <3 yr old were higher than the corresponding estimates for older whales, while the all-whale, ≥ 2 yr old, and <2 yr old estimates were nearly equivalent (Fig. 6). The time-varying temporary emigration estimates varied by primary sampling period, and were lowest during the 1999 and 2001 field seasons.

Non-calf and calf survival estimates were averaged across the 13 best models and a weighted average point estimate, an unconditional SE (i.e. an SE estimate that is not conditional upon a particular model; see Buckland et al. 1997 for estimation method), and weighted 95% CIs (using logit transformation) were obtained. Results of model averaging are shown in Table 4. Non-calf and calf survival were estimated as 0.951 (SE = 0.0135, 95% CI = 0.917 to 0.972) and 0.701 (SE = 0.0944, 95% CI = 0.492 to 0.850), respectively.

DISCUSSION

Analysis assumptions

The present analysis depended on 5 assumptions (see the 'Survival estimation' section of 'Materials and methods') and possible violations to these assumptions should be considered. The first two, concerning markings and population closure, are general assumptions implicit in Pollock's robust design (Kendall et al. 1995). Given the established distinctiveness and reliability of gray whale pigmentation patterns (Hatler & Darling 1974, Darling 1984, Swartz 1986, Jones 1990, Weller et al. 1999, Calambokidis et al. 2002) and the careful examination of the western gray whale photographic dataset (Weller et al. 1999), a violation of the first assumption is regarded as unlikely. If any human errors remain undetected in the dataset, these mistakes would likely be at the level of the daily sighting records, which were not used to estimate model parameters.

As for the assumption of population closure during each primary sampling period, the assertion that births and deaths are not occurring during each field season is reasonable. In contrast, photo-identification studies have demonstrated that whales do immigrate to and emigrate from the Piltun feeding ground within a field season (Weller et al. 2003). While this movement

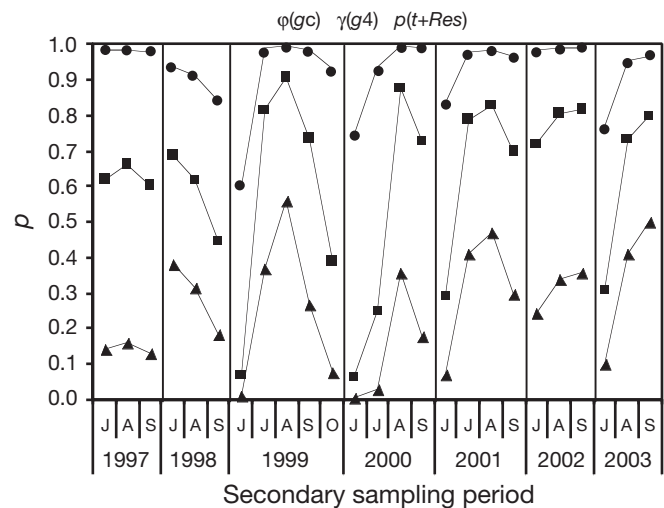


Fig. 5. *Eschrichtius robustus*. Capture probability (p) as a function of secondary sampling period ($n = 25$) for the whale with the (●) highest ($Res = 2.12$), (▲) lowest ($Res = 0.25$), and (■) average ($Res = 1.00$) residency time according to the highest AICc weighted model

Table 3. *Eschrichtius robustus*. Constant (all-whale) and group-varying temporary emigration (γ) parameters estimated in combination with the highest AICc weighted model of capture probability, with resulting estimates and associated SE. Estimates are presented in the order that their respective model was selected

Model	AICc weight	Parameter	Estimate	SE
$\phi(gc) \gamma(g4) p(t+Res)$	0.51288	$\gamma_{\geq 4}$ yr old	0.168	0.0256
		$\gamma_{< 4}$ yr old	0.311	0.0805
$\phi(gc) \gamma(.) p(t+Res)$	0.26996	$\gamma_{all-whale}$	0.185	0.0245
$\phi(gc) \gamma(g3) p(t+Res)$	0.11083	$\gamma_{\geq 3}$ yr old	0.180	0.0257
		$\gamma_{< 3}$ yr old	0.229	0.0804
$\phi(gc) \gamma(g2) p(t+Res)$	0.09197	$\gamma_{\geq 2}$ yr old	0.185	0.0252
		$\gamma_{< 2}$ yr old	0.186	0.0986

appears to violate the closure assumption, Kendall (1999) found that random movement in and out of a study area does not bias closed capture parameter estimates as long as the entire population (i.e. all individuals in and out of the study area) is closed to immigrants and emigrants, which is the case for western gray whales. However, the precision of such estimates is reduced (Kendall 1999).

The last 3 assumptions were made specifically for the current analysis and deal with interpretation of the findings. Given that individual whales can be absent from the study area for all or part of a field season, the third assumption, about whale presence in the study area during the study period, allows the resulting parameter estimates to be interpreted at the population level. If there is a portion of the western gray whale population that never uses the Piltun feeding ground, then the estimates reported here would not extend to that subset. This suggestion, though, is contrary to results from survey and photo-identification effort throughout the Okhotsk Sea, which indicate that the Piltun region is the only area where western gray whales reliably return to feed (Blokhin et al. 1985, Berzin et al. 1988, 1990, 1991, Blokhin 1996, Weller et al. 2003).

The fourth and fifth assumptions provide a framework for estimating the survival and temporary emigration parameters, which is unavoidably a simplification of reality. This generalization led to survival and temporary emigration estimates that are averaged over age-class and time, but as long as they are kept in the proper context, these estimates can be considered unbiased. No such explicit assumptions were made regarding capture probability, as numerous sources of variation were incorporated into models of this parameter. Nevertheless, with this variability in capture probability appropriately accounted for, an underlying assumption is that the remaining capture probability was equal for all whales in the study area, which is associated with a random sampling design. Due to logistical constraints, the survey vessel continuously entered

the study area at the same location and did not follow a systematic track, which could potentially lead to a violation of this assumption. However, particular whales were not targeted during surveys and whales are continually moving throughout the Piltun feeding ground (Weller et al. 2003), such that sampling was effectively random.

Capture probability

The individual *Res* covariate was included in the 24 best models, indicating that it helped to explain capture probability (Table 2 & Appendix 1). As anticipated, capture probability was higher for whales with longer relative residency times (Figs. 4 & 5). In other words, the more often whales used the study area, the more likely they were to be encountered. The 8 best models, which received the majority of the AICc weight, allowed capture probability to vary by *t* and *Res* (Table 2). Thus, capture probability differed between secondary sampling periods, but residency pattern was an important factor in determining the capture probability of an individual whale.

By allowing capture probability to vary by *Res*, bias resulting from individual heterogeneity in time spent in the study area was minimized. As previously described, other types of individual heterogeneity (e.g. prominent markings or greater approachability) have the potential to influence capture probability in whale studies (Buckland 1990). The presence of such forms of individual heterogeneity in capture probability within the current study would confound the calculated residency index, as the daily sighting records used to calculate *Res* would clearly encompass more individual heterogeneity than simply the relative duration of whales in the study area. However, although individual whales revealed differences in markings and behavior during the study period, a link between these characteristics and capture probability was not apparent.

The monthly capture probabilities tended to increase at the beginning of the primary sampling periods and decrease at the end, and were generally highest in August (Fig. 5). These patterns could reflect many sources of intra-seasonal variation that similarly affected the monthly capture probabilities of all whales. For instance, weather conditions influenced not only the number of photo-identification surveys conducted each month, but also survey duration and coverage. The typically milder weather conditions during August facilitated more frequent and extensive

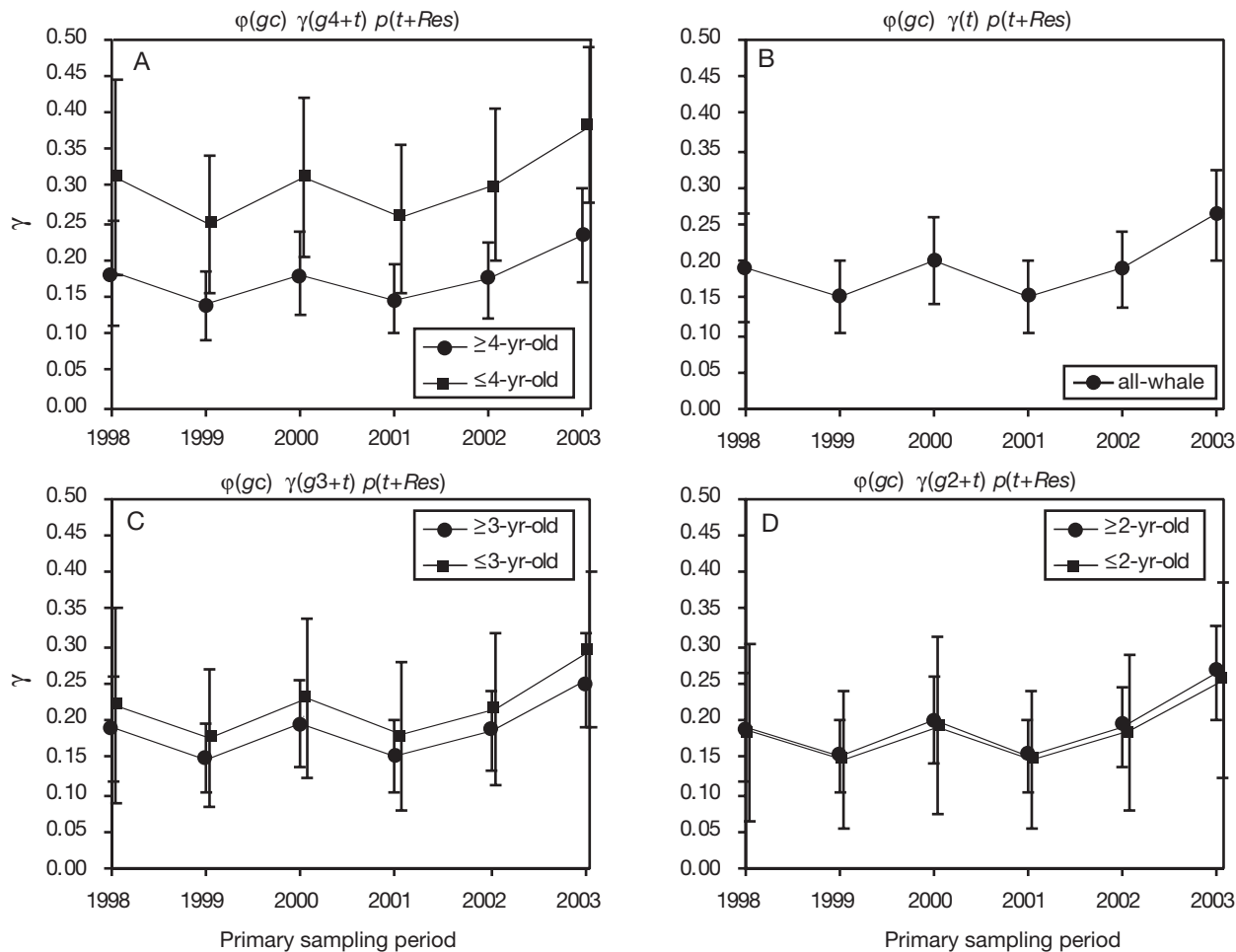


Fig. 6. *Eschrichtius robustus*. Temporary emigration (γ) as a function of primary sampling period ($n = 7$) for models considering (A) whales ≥ 4 yr old and < 4 yr old, (B) all whales, (C) whales ≥ 3 yr old and < 3 yr old, and (D) whales ≥ 2 yr old and < 2 yr old, according to the highest AICc weighted capture probability model. Note that a temporary emigration probability for the 1st primary sampling period cannot be estimated, as there are no marked individuals outside the study area at that time. Estimates are presented in the order that their associated model was selected. ●, ■: point estimate; error bars: SE

surveys, which may have contributed to the higher capture probabilities consistently observed during that month. The extremely low June capture probabilities are attributable to the small number of attempted surveys due to the late-June arrival of the research team (Table 1).

Other sources of intra-seasonal variation may have had a more direct effect on the overall distribution and abundance of whales in the study area, resulting in the apparent trends in monthly capture probabilities. For example, possible late-season changes in prey density and availability may have caused the foraging locations of whales to shift to regions towards the periphery of, or outside, the study area. This type of temporal change in the spatial distribution of whales would have generally lowered capture probabilities as the season progressed. Late-season decreases in capture probabilities may also have been attributable to the onset of

the southbound migration and the associated movement of some whales out of the study area, particularly during the lengthy 1999 field season.

Finally, the Piltun feeding ground overlaps with 2 major multinational offshore oil and gas development projects, and associated industrial activities have been observed to influence the behavior and distribution of whales in the study area (Weller et al. 2002b). For instance, whales shifted their distribution away from a region where geophysical seismic surveys were being conducted during August 2001 (Weller et al. 2002b). This shift concentrated whales in an easily accessible portion of the study area, and may have been a factor in the high capture probability noted during that month. The effects of other industrial activities (e.g. well-drilling, production operations, ship and aircraft traffic) have not yet been evaluated, but could also have played a part in shaping patterns of capture probability.

Temporary emigration

Although model selection was primarily controlled by capture probability, temporary emigration demonstrated a characteristic influence within each representation of capture probability (Table 2 & Appendix 1). Namely, in every case of capture probability, the constant and group-varying models of temporary emigration provided better fits to the data than the time-varying and additive models. This outcome could indicate that temporary emigration probabilities did not vary by primary sampling period. However, given that the latter models required the estimation of more parameters, a more likely interpretation is that the data could not support the additional model complexity. That is, the former models were more parsimonious (Burnham & Anderson 2002).

Out of the constant and group-varying temporary emigration models, the $g4$ model was predominantly selected in the 5 cases of capture probability incorporating Res , followed by the constant, $g3$, and $g2$ models (Appendix 1). During model fitting, the typically high residency values characteristic of younger whales seemingly contributed to interpretations of annual absences of individual whales <4 yr old from the study area, such that a distinct difference was found in the resulting temporary emigration probabilities of whales <4 yr old and older. Within the 4 capture probability models excluding Res , the constant temporary emigration model was principally selected, followed by the $g4$, $g2$, and $g3$ models. This shift in model selection suggests that without the influence of the individual covariate, the ≥ 4 yr old and <4 yr old temporary emigration probabilities did not differ enough to warrant the estimation of another parameter. The reversed order of the latter 2 temporary emigration models cannot as easily be explained.

The constant temporary emigration model was repeatedly selected over the $g2$ and $g3$ models, even when the data otherwise indicated that temporary emigration probability was different for younger whales. However, with the large SEs associated with the estimates for younger whales (resulting from small sample sizes) and the influence of whales 2 and 3 yr post-weaning on the samples of the corresponding older whale estimate, a clear enough

difference between the temporary emigration probabilities of older and younger whales was not likely detected in those 2 models to warrant the estimation of another parameter. Thus, model selection favored the constant temporary emigration model, even though the $g2$ and $g3$ models may have been more representative of whale temporary emigration patterns. Nonetheless, in each of the 3 group-varying models tested, temporary emigration probabilities were higher for younger whales, particularly for whales <4 yr old (Table 3).

The order of the time-varying and additive temporary emigration models closely resembled that of the constant and group-varying models (Table 2 & Appendix 1). Further, all the time-varying estimates of temporary emigration differed between primary sampling periods, with the lowest probabilities occurring during the 1999 and 2001 field seasons (Fig. 6). As discussed previously, the seasonal and annual dynamics of prey and increasing industrial activities on the Piltun feeding ground may have influenced the presence of whales in the study area. However, interpretation of this finding is difficult, given the lack of data related to the suggested hypotheses and the aforementioned uncertainty in the time-varying temporary emigration models.

The temporary emigration modeling results indicate that temporary emigration may play a significant role in the life history of young whales for at least up to 3 yr post-weaning. The abovementioned return in 2002 of the whale not seen in the study area since it was initially observed as a calf in 1995 suggests that tempo-

Table 4. *Eschrichtius robustus*. Model averaging of 1997–2003 western gray whale non-calf and calf survival estimates across the best models ($n = 13$) showing the weighted average point estimate, unconditional SE, and weighted 95% CI

Model	AICc weight	Non-calf estimate	SE	Calf estimate	SE
$\phi(gc) \gamma(g4) p(t+Res)$	0.51288	0.950	0.0136	0.712	0.0951
$\phi(gc) \gamma(.) p(t+Res)$	0.26996	0.952	0.0133	0.688	0.0917
$\phi(gc) \gamma(g3) p(t+Res)$	0.11083	0.951	0.0135	0.695	0.0932
$\phi(gc) \gamma(g2) p(t+Res)$	0.09197	0.952	0.0134	0.688	0.0927
$\phi(gc) \gamma(g4+t) p(t+Res)$	0.00581	0.955	0.0134	0.713	0.0944
$\phi(gc) \gamma(t) p(t+Res)$	0.00445	0.957	0.0129	0.693	0.0918
$\phi(gc) \gamma(g3+t) p(t+Res)$	0.00162	0.956	0.0131	0.698	0.0929
$\phi(gc) \gamma(g2+t) p(t+Res)$	0.00150	0.957	0.0129	0.692	0.0927
$\phi(gc) \gamma(g4) p(T+Eff+Res)$	0.00050	0.950	0.0136	0.712	0.0951
$\phi(gc) \gamma(.) p(T+Eff+Res)$	0.00026	0.952	0.0133	0.688	0.0917
$\phi(gc) \gamma(g3) p(T+Eff+Res)$	0.00011	0.951	0.0135	0.695	0.0933
$\phi(gc) \gamma(g2) p(T+Eff+Res)$	0.00009	0.952	0.0134	0.688	0.0927
$\phi(gc) \gamma(g4+t) p(T+Eff+Res)$	0.00001	0.955	0.0134	0.714	0.0944
Weighted average		0.951		0.701	
Unconditional SE			0.0135		0.0944
Lower weighted 95% CI		0.917		0.492	
Upper weighted 95% CI		0.972		0.850	

rary emigration from the Piltun feeding ground can function in the life history of juvenile whales for at least up to 6 yr post-weaning. However, estimating juvenile temporary emigration for up to only 3 yr post-weaning permitted the temporary emigration probability of younger whales to differ from older whales, but minimized potential positive bias to the non-juvenile estimate caused by the incorporation into that probability of young whales not first sighted as calves. Furthermore, a small number of whales would contribute to extending the estimate up to 4, 5, or 6 yr post-weaning (13, 10, and 2 whales, respectively), and a longer interval would exceed the length of the study.

Age-class segregation of eastern gray whales on their feeding grounds has been noted, with observations ranging from the complete separation of younger whales (Zenkovich 1937), to a less straightforward division (Bogoslovskaya et al. 1981), or a combination of both patterns (Darling et al. 1998). Thus, young western gray whales could be utilizing other feeding areas or parts of the Piltun feeding ground not regularly surveyed. Alternatively, perhaps some young whales did not migrate all the way to the Piltun feeding ground. Not all eastern gray whales migrate to Arctic feeding grounds, with both juvenile and adult whales spending the summer feeding along the west coast of North America (Rice & Wolman 1971, Hatler & Darling 1974, Darling et al. 1998). However, many juvenile western gray whales initially identified as calves did return to the study area and represented some of the most frequently sighted whales throughout each field season (e.g. Weller et al. 1999). With the exception of a potential preference for nearshore areas, these young whales did not appear to differ appreciably in overall distribution and habitat use from older whales. Thus, given the constant use of the Piltun feeding ground by juvenile whales and the lack of segregation by age exhibited there, the mechanism prompting relatively high temporary emigration probabilities for younger whales is unclear.

Survival

The estimates reported here are the first direct survival estimates for gray whales. The non-calf survival estimate of 0.951 (SE = 0.0135) is similar to mark-recapture estimates for non-calf humpback whales *Megaptera novaeangliae* in the Gulf of Maine (0.951, SE = 0.010 and 0.960, SE = 0.008; Buckland 1990 and Barlow & Clapham 1997, respectively), off West Greenland (0.957, SE = 0.028; Larsen & Hammond 2004), and in the central North Pacific (0.963, 95% CI = 0.944 to 0.978; Mizroch et al. 2004). Caswell et al. (1999) estimated survival of the highly endangered

western North Atlantic right whale *Eubalaena glacialis* population, but these time-varying mark-recapture estimates (from about 0.99 to about 0.94) are of crude survival and are not directly comparable to the non-calf survival estimate presented here. Likewise, a mark-recapture survival estimate for adult bowhead whales *Balaena mysticetus* of the Bering-Chukchi-Beaufort Seas stock (0.984, SD = 0.014; Zeh et al. 2002) and indirect survival estimates for adult female southern right whales *Eubalaena australis* off South Africa (0.986, 95% CI = 0.976 to 0.999; Best et al. 2001) and Argentina (0.981, SE = 0.005; Cooke et al. 2001) are not directly comparable. Finally, the western gray whale non-calf survival point estimate is lower than an indirect estimate of 0.987 (90% credibility interval = 0.972 to 0.998) by Wade & Perryman (2002) for the eastern gray whale population. However, the level of uncertainty in that estimate makes direct inter-population comparisons premature at this time.

Due to the small size of the western gray whale population, relatively few calves can be produced each year. Thus, the calf survival estimate of 0.701 (SE = 0.0944) presented here was expected to be imprecise, as only 29 calves were observed in the study area between 1997 and 2002. However, if the estimate is assumed to be accurate, it is markedly lower than a 'reasonable' 1st year post-weaning calf survival estimate of 0.875 (SE \approx 0.047) suggested by Barlow and Clapham (1997) for Gulf of Maine humpback whales. It is important to note that Barlow and Clapham (1997) were simply attempting to bracket the likely range of calf survival values, and the authors caution that 'little credence' should be placed in their estimate. However, it is the only known direct estimate of 1st year post-weaning calf survival currently available for comparison.

As the data used for the western gray whale survival estimation were collected during the feeding season, the resultant calf survival estimate represents survival of calves during their 1st year post-weaning. Gabriele et al. (2001) estimated the survival rate of central North Pacific humpback whale calves, from the breeding season to the subsequent feeding season, using sighting records of individually identified females with calves. Multiple rates were calculated in order to address the effects of various biases, leading to a range of estimates between 0.759 (95% CI = 0.566 to 0.897) and 0.850 (95% CI = 0.622 to 0.968; Gabriele et al. 2001). These calf survival estimates characterize survival of humpback whale calves from birth to weaning and are therefore not comparable to the 1st year post-weaning western gray whale calf estimate reported here. Similarly, an indirect estimate by Best et al. (2001) of 1st year survival (0.913, 95% CI = 0.601 to 0.994) for southern right whale calves born off South

Africa also cannot be compared. The survival rates of western gray whales from birth to weaning and 1st year post-birth are currently unknown, but are important for better understanding the dynamics of this population.

The estimate reported here suggests that survival of post-weaned western gray whale calves is low for a baleen whale population, which could be a result of both anthropogenic and natural factors. Potential anthropogenic causes of calf mortality are entanglement in fishing gear within the migratory corridor, direct catches (i.e. poaching), and inadequate nutritional reserves because of human-related shifts in prey availability. Possible sources of natural calf mortality are insufficient nutritional reserves due to natural changes in prey availability and killer whale *Orcinus orca* predation.

Migrating post-weaned western gray whale calves may be susceptible to entanglement in fishing gear, as has been reported for primarily young (i.e. calf and yearling) eastern gray whales off the California coast (Heyning & Lewis 1990). Although the level of western gray whale entanglement in fishing gear within the migratory corridor is currently unknown, incidental catches of other whale and dolphin species in coastal net fisheries off southern China, Japan, and Korea have been reported (Zhou & Wang 1994, Kato 1998, Kim 2000).

Despite international protection of western gray whales throughout most of their geographic range (i.e. in all range countries except North Korea), at least one direct take has occurred in recent years. In 1996, the anterior portion of a gray whale was found floating off Suttu, Hokkaido, presumably killed by Japanese Dall's porpoise fishermen (Brownell & Kasuya 1999). Although this whale was adult-sized, illegal hunting poses a risk to both non-calves and calves. Further heightening this concern is the discovery of gray whale products in Japanese commercial meat markets in 1999 (Baker et al. 2002). These products do not appear to have originated from local strandings or fisheries bycatch, and therefore potentially represent a violation of international agreements protecting gray whales (Baker et al. 2002).

Numerous, unusually thin, non-calf western gray whales have been observed in the Piltun study area since 1999 (Weller et al. 2002a), suggesting some degree of nutritional deficiency. The cause of this physical deterioration is unknown (Weller et al. 2002a), but could have directly or indirectly reduced the survival rate of calves. That is, if the poor physical condition of these whales was related to a lack of available prey, newly weaned calves, foraging independently for the first time, may also have directly experienced the nutritional consequences of not being able to find

and secure sufficient food. Alternatively, calves born to and nursing from abnormally thin females may have indirectly suffered the effects of compromised maternal nutrition.

Killer whale predation on eastern gray whale calves has been well documented (Baldrige 1972, Goley & Straley 1994). While killer whales are frequently sighted in the Piltun study area, aggressive interactions with western gray whales have not been observed. However, Weller et al. (2002a) recorded that at least 33% of identified western gray whales, including calves, had visible killer whale tooth rakes on their bodies, indicating that they are threatened by killer whales in some portion of their range (Weller et al. 2002a).

As survival probability is only a measure of 'apparent' survival (i.e. the probability a whale remains alive and available for recapture), an alternative explanation for low calf survival is that whales permanently emigrate from the Piltun feeding area after their first year. Yet, as stated previously, some juvenile whales initially sighted as calves have exhibited pronounced seasonal site fidelity to the study area (e.g. Weller et al. 1999). Additionally, aerial and ship-based surveys of the Okhotsk Sea between 1979 and 1989 found concentrations of gray whales only off the northeastern coast of Sakhalin Island near Piltun Lagoon (Blokhin et al. 1985, Berzin et al. 1988, 1990, 1991, Blokhin 1996). Furthermore, usable photographic sightings of eleven whales in other parts of the Okhotsk Sea have been matched to whales that regularly use the Piltun feeding ground, and have not yet included any whales first sighted as calves that were not resighted in the study area (Weller et al. 2003). Therefore, the study area is regarded as the only known location where western gray whales consistently aggregate to feed (Weller et al. 1999).

Given the aforementioned low return to the Piltun feeding ground by whales first sighted as calves characteristic of the 1997 to 2001 field seasons, an estimate of calf survival made during or after that period would clearly have been much lower than the estimate reported here. Similarly, if even a few of the 10 calves identified between 1997 and 2002 that have yet to be resighted in the study area eventually return there, an updated calf survival estimate would likely be higher than the present estimate. Contrasting results from the temporal addition of data are not unexpected for a small population of long-lived animals with demographic variation, highlighting the importance of continuing the western gray whale study so that accurate and precise estimates of both non-calf and calf survival can be obtained. Future data will also facilitate the refined estimation and additional hypothesis testing of temporary emigration probabilities for younger and

older whales. Such clarification is important, given the influence the various models of temporary emigration had on corresponding estimates of survival in the present analysis. That is, within each case of capture probability, the different models of temporary emigration lead to a range of resultant survival estimates (Table 4). Consequently, if higher temporary emigration probabilities are not really a significant part of the life history of younger whales, then calf survival is actually lower than the model-averaged estimate presented here (Table 4).

While the reported survival estimates do not quantitatively determine the status of western gray whales (i.e. degree of depletion and whether the population is growing or declining), they can be used in population modeling that is needed for such an assessment. Undoubtedly, the assessment should be made before drawing any conclusions from these estimates. However, the low calf survival estimate in conjunction with the small population size, small number of known reproductive females identified during the study period ($n = 23$), and recent predominance of a 3 yr calving interval (Brownell & Weller 2002) already raises questions about the potential for western gray whale recovery. A quantitative population assessment of western gray whales, incorporating all available life history information, can contribute to plans for the increased protection, conservation, and management of this critically endangered population.

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Appendix 1. *Eschrichtius robustus*. Comparison of models (n = 72) used to estimate non-calf and calf survival of western gray whales from 1997 to 2003. Delta AICc: difference in AICc of a model from the minimum AICc model; AICc Weight: Akaike Weight (see Burnham & Anderson 2002 for description). See text for details of parameters and model notation.

Model	AICc	Delta AICc	AICc weight	No. parameters
$\phi(gc) \gamma(g4) p(t+Res)$	2274.96	0.00	0.51288	36
$\phi(gc) \gamma(.) p(t+Res)$	2276.24	1.28	0.26996	35
$\phi(gc) \gamma(g3) p(t+Res)$	2278.02	3.06	0.11083	36
$\phi(gc) \gamma(g2) p(t+Res)$	2278.40	3.44	0.09197	36
$\phi(gc) \gamma(g4+t) p(t+Res)$	2283.92	8.96	0.00581	41
$\phi(gc) \gamma(t) p(t+Res)$	2284.45	9.49	0.00445	40
$\phi(gc) \gamma(g3+t) p(t+Res)$	2286.47	11.51	0.00162	41
$\phi(gc) \gamma(g2+t) p(t+Res)$	2286.63	11.67	0.00150	41
$\phi(gc) \gamma(g4) p(T+Eff+Res)$	2288.81	13.85	0.00050	32
$\phi(gc) \gamma(.) p(T+Eff+Res)$	2290.11	15.15	0.00026	31
$\phi(gc) \gamma(g3) p(T+Eff+Res)$	2291.88	16.91	0.00011	32
$\phi(gc) \gamma(g2) p(T+Eff+Res)$	2292.25	17.29	0.00009	32
$\phi(gc) \gamma(g4+t) p(T+Eff+Res)$	2297.63	22.67	0.00001	37
$\phi(gc) \gamma(t) p(T+Eff+Res)$	2298.18	23.22	0	36
$\phi(gc) \gamma(g3+t) p(T+Eff+Res)$	2300.18	25.22	0	37
$\phi(gc) \gamma(g2+t) p(T+Eff+Res)$	2300.34	25.38	0	37
$\phi(gc) \gamma(g4) p(Eff+Res)$	2304.23	29.27	0	25
$\phi(gc) \gamma(.) p(Eff+Res)$	2305.43	30.47	0	24
$\phi(gc) \gamma(g3) p(Eff+Res)$	2307.20	32.24	0	25
$\phi(gc) \gamma(g2) p(Eff+Res)$	2307.54	32.58	0	25
$\phi(gc) \gamma(g4+t) p(Eff+Res)$	2312.68	37.72	0	30
$\phi(gc) \gamma(t) p(Eff+Res)$	2313.10	38.14	0	29

Appendix 1 (continued)

Model	AICc	Delta AICc	AICc weight	No. parameters
$\phi(gc) \gamma(g3+t) p(Eff+Res)$	2315.10	40.14	0	30
$\phi(gc) \gamma(g2+t) p(Eff+Res)$	2315.23	40.27	0	30
$\phi(gc) \gamma(.) p(t)$	2370.18	95.22	0	28
$\phi(gc) \gamma(g4) p(t)$	2370.49	95.53	0	29
$\phi(gc) \gamma(g2) p(t)$	2372.22	97.26	0	29
$\phi(gc) \gamma(g3) p(t)$	2372.26	97.30	0	29
$\phi(gc) \gamma(t) p(t)$	2376.94	101.98	0	33
$\phi(gc) \gamma(g4+t) p(t)$	2377.73	102.77	0	34
$\phi(gc) \gamma(g2+t) p(t)$	2378.99	104.03	0	34
$\phi(gc) \gamma(g3+t) p(t)$	2379.09	104.12	0	34
$\phi(gc) \gamma(.) p(T+Eff)$	2382.18	107.22	0	24
$\phi(gc) \gamma(g4) p(T+Eff)$	2382.48	107.52	0	25
$\phi(gc) \gamma(g2) p(T+Eff)$	2384.20	109.24	0	25
$\phi(gc) \gamma(g3) p(T+Eff)$	2384.25	109.29	0	25
$\phi(gc) \gamma(t) p(T+Eff)$	2388.78	113.82	0	29
$\phi(gc) \gamma(g4+t) p(T+Eff)$	2389.57	114.61	0	30
$\phi(gc) \gamma(g2+t) p(T+Eff)$	2390.81	115.85	0	30
$\phi(gc) \gamma(g3+t) p(T+Eff)$	2390.91	115.95	0	30
$\phi(gc) \gamma(.) p(Eff)$	2394.02	119.06	0	17
$\phi(gc) \gamma(g4) p(Eff)$	2394.26	119.29	0	18
$\phi(gc) \gamma(g2) p(Eff)$	2395.99	121.03	0	18
$\phi(gc) \gamma(g3) p(Eff)$	2396.06	121.10	0	18
$\phi(gc) \gamma(t) p(Eff)$	2400.16	125.20	0	22
$\phi(gc) \gamma(g4+t) p(Eff)$	2400.90	125.94	0	23
$\phi(gc) \gamma(g2+t) p(Eff)$	2402.15	127.19	0	23
$\phi(gc) \gamma(g3+t) p(Eff)$	2402.26	127.30	0	23
$\phi(gc) \gamma(g4) p(T+Res)$	2458.03	183.07	0	25
$\phi(gc) \gamma(.) p(T+Res)$	2459.33	184.37	0	24
$\phi(gc) \gamma(g3) p(T+Res)$	2461.07	186.11	0	25
$\phi(gc) \gamma(g2) p(T+Res)$	2461.43	186.47	0	25
$\phi(gc) \gamma(g4+t) p(T+Res)$	2466.30	191.34	0	30
$\phi(gc) \gamma(t) p(T+Res)$	2466.80	191.84	0	29
$\phi(gc) \gamma(g3+t) p(T+Res)$	2468.80	193.84	0	30
$\phi(gc) \gamma(g2+t) p(T+Res)$	2468.92	193.96	0	30
$\phi(gc) \gamma(.) p(T)$	2538.56	263.60	0	17
$\phi(gc) \gamma(g4) p(T)$	2538.93	263.97	0	18
$\phi(gc) \gamma(g2) p(T)$	2540.54	265.58	0	18
$\phi(gc) \gamma(g3) p(T)$	2540.60	265.64	0	18
$\phi(gc) \gamma(t) p(T)$	2544.71	269.75	0	22
$\phi(gc) \gamma(g4+t) p(T)$	2545.62	270.66	0	23
$\phi(gc) \gamma(g2+t) p(T)$	2546.68	271.72	0	23
$\phi(gc) \gamma(g3+t) p(T)$	2546.80	271.84	0	23
$\phi(gc) \gamma(g4) p(Res)$	2597.84	322.88	0	18
$\phi(gc) \gamma(.) p(Res)$	2599.48	324.52	0	17
$\phi(gc) \gamma(g3) p(Res)$	2601.04	326.08	0	18
$\phi(gc) \gamma(g2) p(Res)$	2601.53	326.57	0	18
$\phi(gc) \gamma(g4+t) p(Res)$	2607.00	332.04	0	23
$\phi(gc) \gamma(t) p(Res)$	2607.97	333.01	0	22
$\phi(gc) \gamma(g3+t) p(Res)$	2609.81	334.85	0	23
$\phi(gc) \gamma(g2+t) p(Res)$	2610.07	335.11	0	23