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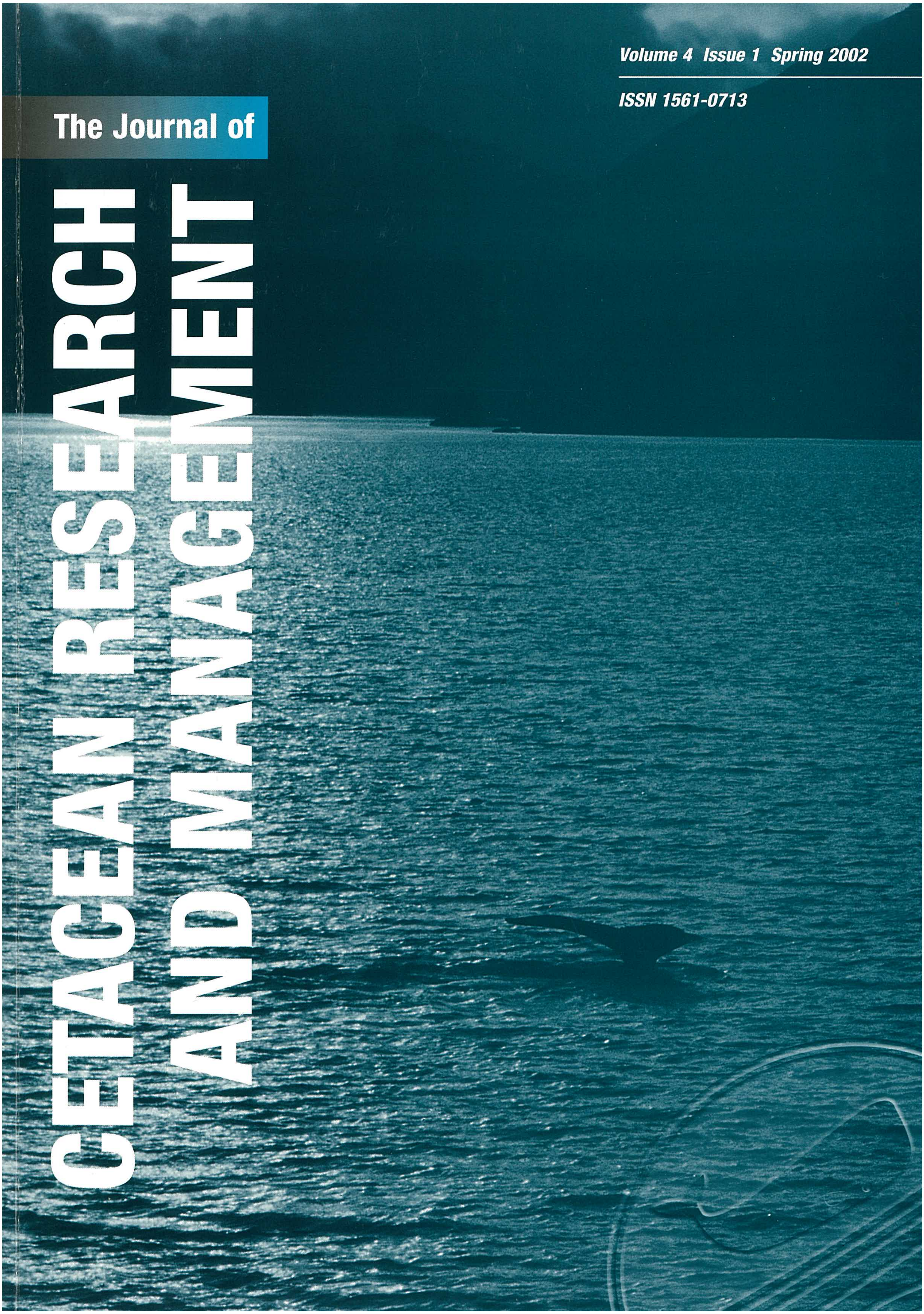

# Contents

# Editorial

Welcome to this the first issue of the fourth volume of the *Journal of Cetacean Research and Management.* The Editorial Board has decided to dedicate this issue to papers related to the status of the gray whale (*Eschrichtius robustus*). This is partly as there is to be a major assessment of this species at the forthcoming meeting of the IWC Scientific Committee and partly to publish a number of important papers that had at one time been intended to form a special volume in the old *Reports of the International Whaling Commission* special issue series, but which, for a number of reasons, did not materialise.

This issue therefore includes both recent papers and seminal papers that were originally written for previous gray whale assessments by the IWC, including some that formed the basis for the report of the gray whale workshop published in 1993 (*Rep. int. Whal Commn.* 43: 241-59).

The gray whale represents a fascinating case study. Although heavily depleted on both sides of the North Pacific by whaling in the 19th and earlier centuries, the eastern gray whale has recovered to at or near carrying capacity (over 20,000 animals), whilst the western gray whale remains at critically low levels (less than 100 animals) – and is perhaps the most endangered population of large whales in the world.

The opening paper in this issue (LeDuc *et al.*), for the first time examines genetic differences between these two management stocks and concludes *inter alia*, that they can be genetically differentiated at the population level.

The papers by Weller *et al.* review the history and status of the western gray whale, including results from the recent joint USA-Russia research programme. There is serious concern over the ability of this population to recover. Urgent and co-ordinated action is required to reduce to a minimum anthropogenic threats to these animals.

The following two papers examine aspects of critical habitat for the eastern gray whale. The first (Moore and Clarke) addresses the potential impact of offshore human activities on gray whales, including oil and gas exploration and development. These issues are also relevant to the western population. Findlay and Vidal examine records from two calving sites for the eastern gray whale in the Gulf of California, Mexico and discuss possible reasons for changes in the distribution and presence of gray whales in the study areas. In particular, they highlight the effect of local fishing practices on the whales.

Any assessment of the status of populations requires good estimates of abundance and ideally trends in abundance. Although estimating cetacean abundance is always difficult, the migratory behaviour of the eastern gray whale allows for shore-based censuses to be undertaken relatively easily during the southbound migration. This issue contains four papers of relevance to this topic. The first, by Buckland and Breiwick, presents a major analysis of estimates for almost a 30-year period. The second, by Turnock and Mizroch, examines the effect of different census frequencies on an ability to detect trends in abundance given certain assumptions about CVs of estimates and rates of change in the population. Although concentrating on early census data, the lessons to be learned remain relevant today when designing research programmes for management. The paper by Sheldon and Laake examines an important factor in the use of shore-based censuses – the offshore distribution of animals and how these may vary over time. The final paper related to abundance looks at a practical way in which to improve our ability to examine offshore distribution of migrating animals during censuses.

The final papers in this issue address various modelling exercises to determine the status of the eastern gray whale. The first paper by Butterworth *et al.* represents the primary analysis of a problem that has affected many attempts to model the eastern population: namely reconciling the observed increase in gray whales since systematic censuses began in the late 1960s with the historical catch information that suggested that the population was commercially extinct at the end of the 19th century. Simple density-dependent models find it impossible to reconcile the known catch history and recent increasing trends in the population.

The remaining three papers (Butterworth *et al.*, Wade, and Punt and Butterworth) consider alternative modelling approaches (dynamic response analysis (DRA) and Bayesian methodology) to examine the present status of the eastern gray whale, particularly in terms of the possibility that it is at or near carrying capacity. Butterworth *et al.* reviewed the results of an earlier DRA study that had concluded that the eastern gray whales had passed through its maximum net productivity level between 1967 and 1980. Their alternative approach suggested that in fact the data indicate that the population was still below that level in 1990.

Wade's paper used Bayesian methods to estimate probability distributions for both input and output parameters in two model types (one simple, the other age- and sex- structured). The exercise also provided evidence that CVs of earlier abundance estimates had been underestimated. The final paper, by Punt and Butterworth, examines this approach and the assumptions behind it, using a different population model.

The papers in this issue have benefited from the editorial work of a number of people and it is important here to particularly thank Howard Braham (now retired) and Marcia Muto of the National Marine Mammal Laboratory in Seattle, Washington USA, who have put in an enormous effort into many of the papers published here and into some of the gray whale papers that will be published in future issues. Similarly, John Bannister of the Western Australian Museum in Perth has assisted with several of the papers.

I would also like to thank all of the many scientists who act as anonymous reviewers for the Journal. Without their dedicated (and often unsung) work, the Journal would not exist. A list of reviewers is kept on the Journal website (http://www.iwcoffice.org/publications/JCRM), in addition to the contents of previous volumes.

Finally, I would like to thank Elaine Shield who has been responsible for the artwork and tabulae matter included in the Journal. She is leaving after 5 years to concentrate on her young family.

G.P. Donovan
*Editor*

# Genetic differences between western and eastern gray whales (*Eschrichtius robustus*)

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ABSTRACT

Molecular data were used to examine the differentiation between the western and eastern gray whale (*Eschrichtius robustus*) populations. Control region sequences were generated from samples collected in the western Pacific ($n = 45$) and eastern Pacific ($n = 120$). There were 36 unique haplotypes identified. Ten haplotypes were represented in the western samples, and 33 in the eastern samples. Seven of these haplotypes were shared between populations, leaving three haplotypes that were only seen in the western samples and 26 only in the eastern. Although there were no fixed (diagnostic) differences between the western and eastern groups, they were significantly different in their haplotype frequency distributions and should be considered as separate populations. None of the 33 haplotypes found in the eastern samples had a frequency of over 11%, yielding an estimated haplotypic diversity of 0.95. This finding indicates that the reduction in abundance due to whaling may not have had a great effect on the haplotypic diversity of the eastern population, although the loss of rare haplotypes may still have occurred and would be difficult to detect. In contrast, the western group was dominated by two haplotypes, which represented over 77% of all individuals sampled, resulting in a substantially lower haplotypic diversity of 0.70. The lack of fixed differences between the two populations and frequency of shared haplotypes renders these data inappropriate for forensic applications at the population level.

KEYWORDS: GRAY WHALE; GENETICS; POPULATIONS; CONSERVATION; NORTH PACIFIC

## INTRODUCTION

Although the gray whale (*Eschrichtius robustus*) once occurred in both the North Atlantic and North Pacific, it became extinct in the Atlantic several hundred years ago (Mead and Mitchell, 1984), is severely depleted in the western Pacific (e.g. Weller *et al.*, 2002), and was greatly reduced in the eastern Pacific before its recovery (IWC, 1998). Currently, gray whales are considered as two separate management stocks living along the eastern and western boundaries of the North Pacific. While both were reduced by historical whaling, only the eastern gray whale has recovered to near pre-exploitation levels (IWC, 1998). The western gray whale was thought to be extinct as recently as the early 1970s (Bowen, 1974) but is known to survive today as a remnant population (see review in Weller *et al.*, 2002). Although studies of the behaviour and biology of both eastern and western gray whales have been conducted (see Swartz *et al.*, 2000 for review), questions about the level of genetic differentiation between eastern and western gray whales, or how their exploitation may have affected genetic diversity, have remained largely unaddressed. Contemporary gene flow between them is not likely in that the geographic distributions do not overlap, and the migratory routes are disjunct and lead to opposite sides of the North Pacific basin. However, the possibility of dispersal has yet to be tested with genetic data. If gene flow is negligible or non-existent and the stocks have differentiated genetically since becoming allopatric, an additional question is whether they have diverged enough to allow individual whales from unknown localities (e.g. market samples of meat) to be characterised as eastern or western. As part of an ongoing US-Russia research project studying western gray whales in the Okhotsk Sea, biopsy samples have been routinely taken from animals summering off Sakhalin Island, Russia (Weller *et al.*, 2002). In addition, many samples are available from the eastern gray whale population. Together, these datasets provide an opportunity to characterise the genetic makeup of eastern and western gray whales and to quantify their degree of differentiation.

## MATERIALS AND METHODS

Samples from the western population were obtained as biopsies from free-ranging animals on their summer feeding grounds off the northeastern coast of Sakhalin Island, Russia, primarily during 1998 and 1999. Since the biopsied animals were photographed at the time of sampling, cross-matching with the photo-identification catalogue (Weller *et al.*, 1999) enabled the removal of duplicate samples prior to sequencing, giving a total of 42 samples. Three biopsy samples from the same study area were collected in 1995 (Brownell *et al.*, 1997). In the absence of identification photographs, these were only added to the western samples after microsatellite analysis (not described) confirmed they were not from individuals sampled in 1998-1999. This resulted in a total of 45 western samples. A total of 120 eastern samples were collected from many localities between southern California and the Chukotka Peninsula in Russia. These samples were taken primarily from strandings, as well as a few from directed subsistence takes, fishery bycatch and biopsies of living whales. A similar check of individual identity was not done for the eastern North Pacific samples due to the lack of a comprehensive photo-identification catalogue. However, given that over 90% of the eastern samples were collected from dead animals, and given an estimated population size of over 26,000 (Rugh *et al.*, 1999), the effect of any possible duplicate sampling is negligible.

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In addition to these samples, sequences of a 361 base pair (bp) segment of the mitochondrial control region from two gray whales that were sampled in Japan (M. Goto and L. Pastene, pers. comm.) are used here in our discussion of the gray whale market samples sequenced by Baker *et al.* (2002). One whale stranded on the eastern side of Hokkaido in 1995 (Anon., 1997), and the other was an animal harpooned in the Sea of Japan off western Hokkaido in 1996 (Brownell and Kasuya, 1999). These sequences were not used in the population genetic analyses.

Using standard protocols, DNA was extracted from each sample, and a 523 bp region of the 5' end of the mitochondrial control region was amplified and sequenced. The primers used for amplification and sequencing were 5'-TACCAAATGTATGAAACCTCAG-3' (Rosel *et al.*, 1995) and 5'-CCTCCCTAAGACTCAAGGAAG-3' (designed at SWFSC). Haplotypic diversity was calculated using the computer program Arlequin (Schneider *et al.*, 2000), which was also used to calculate the divergence between populations with $F_{ST}$, $\phi_{ST}$ (an $F_{ST}$ analogue) and $\chi^2$, as well as to create a minimum spanning tree based on the number of differences between haplotypes. Haplotypic diversity ($h$) is calculated by the formula $h = 1 - \Sigma\, p_I^2$, where $p_I$ is the frequency of the $I^{th}$ haplotype (Nei, 1987).

## RESULTS

A total of 36 haplotypes defined by 37 variable sites were found among the 165 samples examined. Thirty-three of these haplotypes occurred in eastern samples and 10 in the western samples; seven haplotypes were shared between the two samples. Fig. 1 shows the minimum spanning network of the 36 haplotypes. Fig. 2 shows the frequencies of the different haplotypes in the eastern and western samples. Haplotypic diversity differed greatly with the eastern samples showing a diversity of 0.95 +/- 0.01 and the western samples having a value of 0.70 +/- 0.05. The average percent difference (i.e. nucleotide diversity) between individuals differed little, with the eastern samples averaging 1.6% sequence difference from each other and the western samples averaging 1.7%. The average percent difference for between-population pairwise comparisons was 1.9%. In genetic studies, one must be cautious that some results, such as the much lower level of diversity found in the western gray whale population, are not caused by inadequate or biased sampling. However, it is doubtful that this is the case here. The 120 eastern samples actually represent a much lower overall proportion of the eastern gray whale population than the 45 samples do from the western population, which may number less than 100 animals (e.g. see Weller *et al.*, 2002). Therefore, the probability of there being appreciable amounts of unsampled variation in the western population is relatively low, despite the smaller number of samples. Finally, examination of the degree of genetic sub-division between the eastern and western samples indicated that they are significantly different from each other ($\phi_{ST} = 0.117, p < 0.001$; $\chi^2 = 65.9, p < 0.001$; $F_{st} = 0.087, p < 0.001$).

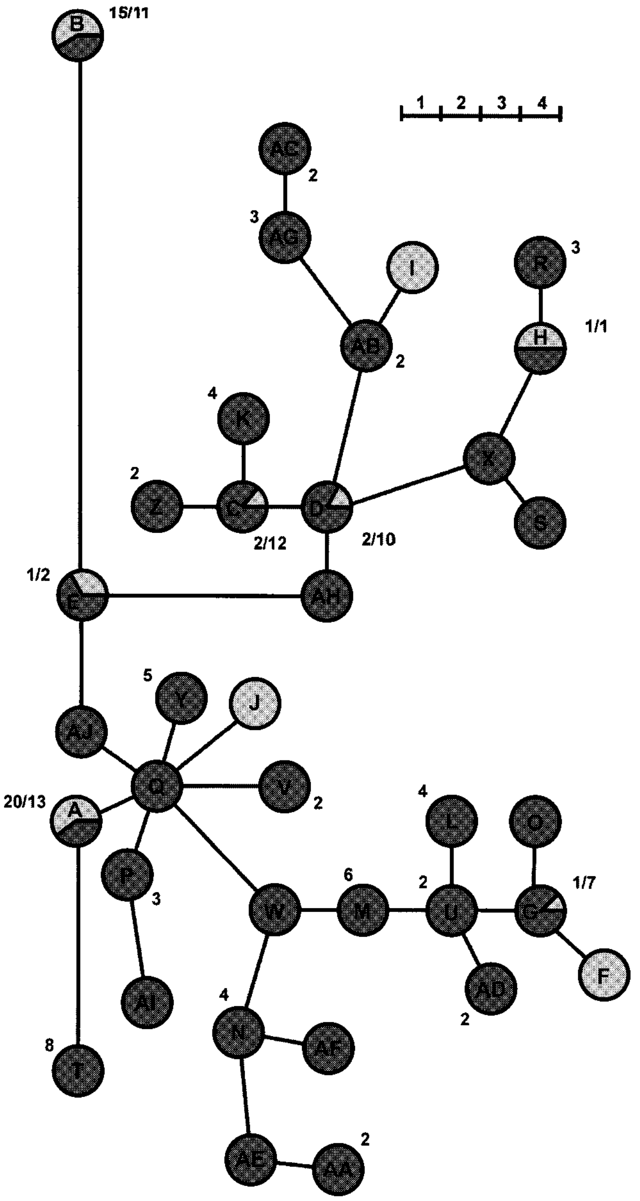

Fig. 1. Minimum spanning tree of the 36 haplotypes from this study. Numbers beside circles indicate the number of individuals having that haplotype in western (light gray) and eastern (dark gray) sample sets. Circles without numbers indicate haplotypes only represented by single individuals. The scale gives number of changes along connecting branches.

## DISCUSSION

The results presented here show that the eastern and western gray whales are genetically differentiated at the population level. The significant difference found between the two populations and the negligible levels of gene flow that it implies, agrees well with their very different recovery histories; dispersal that is significant in any management sense should not be expected to occur. However, the statistical population differentiation arises primarily from differences in haplotypic frequencies (Fig. 2) and reflected in their respective haplotypic diversity indices. The populations have apparently not been isolated for a sufficiently long period of time for the shared haplotypes to be removed via genetic drift, and therefore no diagnostic character or characters within the 523 bp region can be reliably used to distinguish one population from another, or to determine the source of a gray whale of unknown affinity (e.g. a forensic analysis of market meat). The case could be made that if a test animal has a haplotype unique to the eastern samples, then it probably arose from there, since the absence of that haplotype in the western population is based on a fairly thorough sampling scheme (perhaps 50% of the population sampled so far). However, the converse (a test animal having a haplotype unique to the western sample set being from the Okhotsk Sea population) is more difficult to

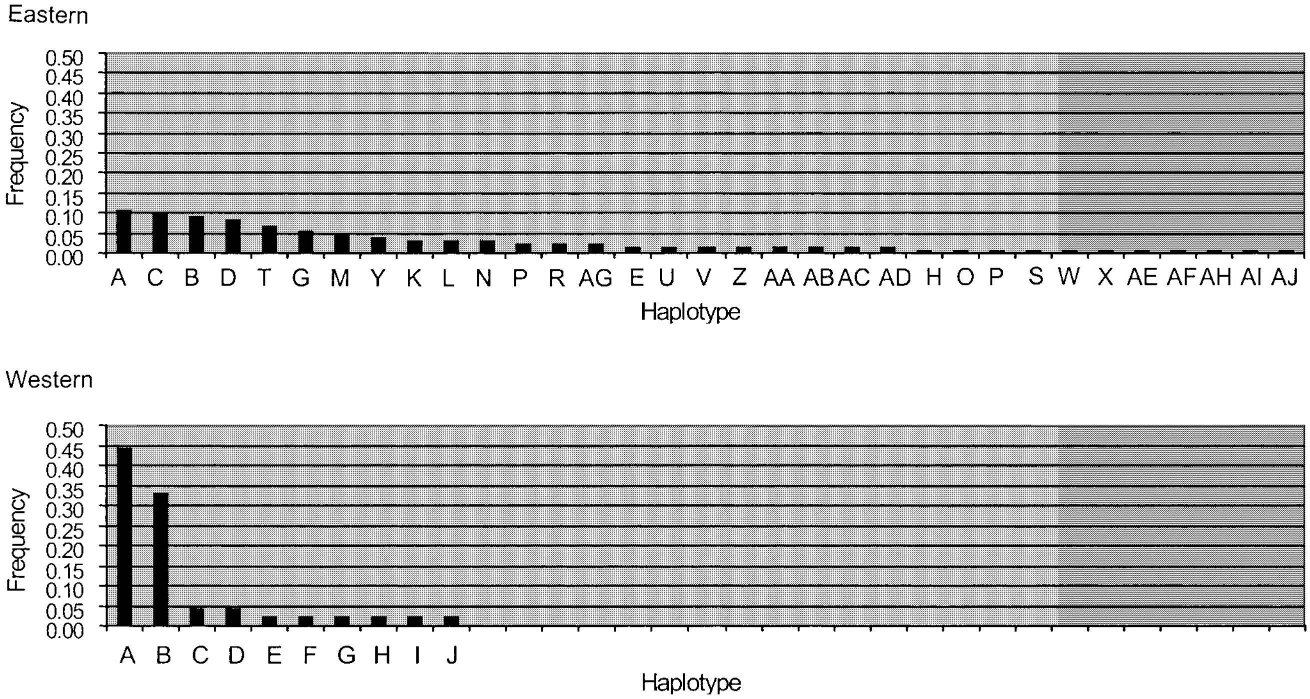

Fig. 2. Frequency distributions of haplotypes in each of the gray whale populations.

argue, since the very high diversity in the eastern population allows for the presence of many unsampled haplotypes. Although the genetic differences between the populations are modal rather than absolute, the differentiation is large, and demographically they should be treated as isolated population units, especially for management purposes as they have been and are by the International Whaling Commission (e.g. IWC, 1998).

The differences between the two populations in their haplotypic diversities may reflect differences in their past levels of abundance and effects of exploitation. Haplotypic diversity (*h*) is affected by both the numbers of haplotypes present in the population and their relative frequencies, with numerous haplotypes and equal frequencies both serving to increase the value of *h*. In the present dataset, the differing values of *h* arise primarily from the differences in haplotype frequency distributions, which differed dramatically between the two populations (Fig. 2). In the eastern samples, the most common haplotype was only represented in 10.8% of the individuals, and seven of the 33 haplotypes were represented in over 5% of the samples. The overall effect is one of a fairly even frequency distribution of haplotypes. In contrast, the two most common haplotypes in the 45 western samples were represented by 20 (44.4%) and 15 individuals (33.3%), with the remaining eight haplotypes appearing in single animals or in pairs. If the 10 western haplotypes were evenly distributed in the sample set, $h_{west}$ would increase from 0.70-0.90, but an equivalent redistribution of the 33 eastern haplotypes would only increase $h_{east}$ from 0.95-0.97. In other words, given the differences in sample sizes, the western and eastern sample sets contained comparable numbers of haplotypes, albeit with very different frequency distributions.

The haplotypic diversity value (0.95) calculated for the eastern samples in the present dataset is similar to the value (0.94) found by Steeves *et al.* (2001) in their study of 57 samples of eastern gray whales. These relatively high values for contemporary eastern gray whales seem to indicate that there was little loss of genetic variation in this population due to historical whaling. However, it is possible that some loss of diversity due to whaling may have occurred without a reduction in haplotypic diversity. In the calculation of haplotypic diversity, the frequencies of haplotypes are squared, so that the resulting value of *h* is not greatly affected by the occurrence or number of rare haplotypes, those contained in the population in very low frequencies. Therefore, although the eastern sample set contained 11 haplotypes only represented by single samples, the loss of other rare haplotypes cannot be ruled out.

In the western population, the lower haplotypic diversity value may be, but is not necessarily, a result of whaling. The lower value for the western animals may be related to their history of overexploitation, but it is also consistent with a smaller long-term effective population size ($N_e$). The amount of diversity that a population can maintain is directly determined by its $N_e$, which for the haplotypic and uniparentally-inherited mitochondrial genes, is approximately one-quarter of the $N_e$ of nuclear genes. Although there are no reliable estimates for the pre-exploitation size of the western gray whale population, it was very likely to have been smaller than the eastern population (Weller *et al.*, 2002). Furthermore, the ten haplotypes found in the western sample set are not closely related to each other. Indeed, the two dominant western haplotypes (A and B) are very different from each other (Fig. 1). In a statistical sense, the occurrence of relatively few, but quite divergent, haplotypes explains why the western population exhibits an equal level of average sequence divergence when compared to the eastern population, despite its lower haplotypic diversity. Biologically, this pattern is consistent with either a loss of haplotypes due to long-term genetic drift or a whaling-induced bottleneck.

Although the haplotypic diversity is lower in the western population, the fact that 10 haplotypes still remain in a population this small is encouraging. It may indicate that a considerable amount of variation is still contained within the gene pool. In comparison, only five haplotypes have been observed in the western North Atlantic population of right whales, currently estimated at approximately 300 individuals (Malik *et al.*, 2000). However, the retention of 10 haplotypes in the western gray whale population has some relevance to another important issue, namely whether or not the western population is recovering. Weller *et al.* (2002) estimated that less than 50 of the western gray whales are mature, and that the current sex ratio of this population is approximately 60% male:40% female. This translates into an estimate of approximately 19 reproductive females; probably even less according to Weller *et al.* (2002). The recovering eastern population has been estimated to have had a maximum growth rate of 3.3% per year (for the interval 1967/68 to 1987/88), even higher if the aboriginal take of approximately 180/yr was taken into account (IWC, 1998). Applying a 3.3% recovery rate, and assuming that there are 19 reproductive females today in the western population, there would have been only about six reproductive females in the western population when whaling ended in 1966. That is an extremely unlikely scenario considering that there were still 10 extant western haplotypes in 1999, two of which are now in very high frequency. Even if there had been ten reproductive females extant in 1966, each with a different haplotype, reproductive success would have had to be extremely skewed towards two of those matrilines.

There are a number of possible explanations for this many haplotypes persisting in such a small population. First, the current abundance estimate could be low. However, photographic identification data (Weller *et al.*, 1999; 2002 do not support the existence of an appreciably greater abundance off Sakhalin Island, although a still undiscovered feeding area cannot be ruled out. A second possibility is that the population has grown much more slowly than 3.3% since 1966 (i.e. the bottleneck was not as severe as six, or even ten, reproductive females). Although this scenario would bode well for the level of genetic diversity still contained in the population, it would nonetheless have serious implications for their viability. If the population in 1966 contained much more than six adult females, it raises the possibility that the population has only been holding steady or even continuing to decline since then rather than recovering. In other words, a population the size of the western gray whales that has been growing since 1966 would not be expected to contain as many as 10 haplotypes. These sub-optimal population trajectories suggest the existence of some yet to be determined source of mortality (e.g. bycatch in fisheries, direct kills, vessel strikes, etc.) or other impediment to recovery (e.g. habitat degradation as reviewed in Weller *et al.*, 2002).

Another possibility is that there is some dispersal from the eastern stock. In general, the gene pool of a small population is strongly influenced by even trivial amounts of gene flow from a larger neighbour, and the significant differences found between these populations would seem to contradict this possibility. However, given the maternal inheritance of the mitochondrial data examined here, male dispersal could still occur but would have little or no long-term effect on haplotype distributions (and mitochondrial differentiation). Indeed, of the eight western haplotypes represented by only one or two individuals, only two (*E* and *H*) came from females, with the remaining six only represented by males. Future work using microsatellite data may be able to test hypotheses of male dispersal. Because of the higher diversity and number of haplotypes in the eastern population, animals dispersing into the western population are most likely to carry haplotypes considered rare in the west (i.e. ones other than ‘A’ or ‘B’). Animals with these rare haplotypes could be the focus of microsatellite-based assignment tests (e.g. Paetkau *et al.*, 1995), to see if they show greater affinity to the eastern population than do the rest of the western animals. However, since it is the number of females that seems to have dropped to critical levels at present (Weller *et al.*, 2002), any influx of males that may occur would not be of immediate benefit to the western population, although it would mitigate any effects of inbreeding and loss of diversity in the nuclear genome. Overall, the present findings that the mitochondrial differentiation between eastern and western gray whales is large and female dispersal is negligible at best, coupled with the paucity of females in the western population (Weller *et al.*, 2002), underscores the critical status of the western gray whales (e.g. see IWC, 2002).

Based on molecular identification, Baker *et al.* (2002) determined that seven commercial market products purchased in Wakayama Prefecture, Japan in August and October 1999 were samples of gray whale meat. They noted that all seven products had the same haplotype as a GenBank gray whale sequence (Accession #L35611), from a whale sampled off the coast of Washington, USA. The GenBank sequence and the sequences from the Wakayama gray whale products are all identical to our haplotype ‘A’ (Figs 1 and 2), the most common haplotype in both the eastern and western sample sets (10.8% and 44.4%, respectively). The sequences are also identical to the sequence provided to us by M. Goto and L. Pastene (pers. comm.) for the whale harpooned off Hokkaido in 1996 (Brownell and Kasuya, 1999), the whale also referred to as the ‘Suttsu’ whale by Baker *et al.* (2002). This haplotype is shared between the two populations and it is not possible to definitively assign the Wakayama meat samples (or any given gray whale sample) to either population using mitochondrial sequence data. Nevertheless, given the match, and the apparent butchering of the carcass (Brownell and Kasuya, 1999), a reasonable explanation is that the meat from the Wakayama market originated from the whale harpooned off Hokkaido. This explanation can be tested by analysing both samples using microsatellite data, or any other molecular data that allow the genotyping of individual whales. Finally, the sequence sent to us by M. Goto and L. Pastene (pers. comm.) from the 1995 stranding in eastern Hokkaido matched both haplotype ‘G’ and ‘O’ of our dataset (the shorter sequence sent by Goto and Pastene did not include the variable sites that distinguish haplotype ‘G’ from haplotype ‘O’).

In summary, results presented here show that eastern and western gray whales can be genetically differentiated at the population level, and should be recognised as geographically isolated and demographically closed population units. However, because of shared haplotypes, it is not possible at this time to genetically identify an individual sample to either population. Furthermore, the presence of 10 western haplotypes in a population this small is inconsistent with a population that has undergone any appreciable growth.

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University of Alaska Fairbanks. We also thank T. Steeves of the National Zoological Park in Washington, D.C. for providing biopsy samples. In addition, we also thank the observers and ship captains in the California gillnet observer programme who collected samples from fishery bycatch. Lastly, we thank S. Blokhin for the samples of eastern gray whales collected in Chukotka, Russia.

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# The western gray whale: a review of past exploitation, current status and potential threats

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ABSTRACT

Gray whales (*Eschrichtius robustus*) occur along the eastern and western coastlines of the North Pacific as two geographically isolated populations and have traditionally been divided into the eastern (California-Chukchi) and western (Korean-Okhotsk) populations. Recent molecular comparisons confirm, based on differences in haplotypic frequencies, that these populations are genetically separated at the population-level. Both populations were commercially hunted, but only the eastern gray whale has returned to near pre-exploitation numbers. In contrast, the western population remains highly depleted, shows no apparent signs of recovery and its future survival remains uncertain. Research off Sakhalin Island, Russia between 1995 and 1999 has produced important new information on the present day conservation status of western gray whales and provided the basis for the World Conservation Union (IUCN) to list the population as 'Critically Endangered' in 2000. The information presented here, in combination with potential impacts from anthropogenic threats throughout the range of this population, raises strong concerns about the recovery and continued survival of the western gray whale.

KEYWORDS: GRAY WHALE; PACIFIC OCEAN; NORTHERN HEMISPHERE; CONSERVATION; OKHOTSK SEA; EXPLOITATION; POPULATION STATUS

## INTRODUCTION

Gray whales (*Eschrichtius robustus*) are known to occur along the eastern and western margins of the North Pacific (Andrews, 1914; Rice and Wolman, 1971); they have been extinct in the North Atlantic for several hundred years (Mead and Mitchell, 1984). Recent genetic studies show that animals from the eastern (California-Chukchi) and the western (Korean-Okhotsk) Pacific should be recognised as geographically and genetically separated at the population level (LeDuc *et al.*, 2002). Although both populations were greatly reduced by commercial whaling, only the eastern gray whale has returned to numbers approaching the suspected pre-exploitation population size (IWC, 1998). In contrast, the western gray whale was thought to be extinct as recently as the early 1970s (Bowen, 1974), but later published reports confirmed that the population was extant (Berzin, 1974; Brownell and Chun, 1977). Today, the western gray whale population remains highly depleted and shows no apparent signs of recovery (e.g. Weller *et al.*, 1999; IWC, 2002b). Information regarding the life history and biology of the western population is sparse (Andrews, 1914; Rice and Wolman, 1971) and only recently has it come under concerted study (e.g. Brownell *et al.*, 1997; Weller *et al.*, 1999).

Historic records and recent data suggest that summer feeding grounds for the western population are in the Okhotsk Sea, but the location(s) of the winter breeding grounds, suspected to be along the coast of southern China, remain unknown (Wang, 1984; Henderson, 1990). Contemporary findings from an ongoing US-Russia mark-recapture photo-identification project between 1995 and 2001 suggest that the total population size is $<100$ individuals (e.g. Weller *et al.*, 1999; IWC, 2002b). Low-level human-related mortality south of the Okhotsk Sea (Brownell and Kasuya, 1999; Baker *et al.*, 2002), and the onset of large-scale multinational oil and gas development programmes within Okhotsk waters, pose potential new threats to the continued survival of this population.

Serious concern over the status of this population has been expressed by the World Conservation Union (by assigning it 'Critically Endangered' - Hilton-Taylor, 2000) and by the International Whaling Commission (IWC, 2002b).

## RANGE AND DISTRIBUTION

Western gray whales occur off Russia, Japan, the Democratic People's Republic of Korea (North Korea), Republic of Korea (South Korea) and People's Republic of China (China). Although historic sighting and whaling records indicate that gray whales occurred in areas north of the presently described Okhotsk Sea feeding ground, the present day population range appears to be largely confined to the region between the west central Okhotsk Sea off the northeastern coast of Sakhalin Island (summer-autumn) and the South China Sea (winter). Individuals remain in shallow, mainly nearshore waters, year-round; except when crossing the La Perouse and Tartarskiy Straits off the southern end of Sakhalin Island or during north-south migrations in the Sea of Japan, and the Yellow and East China Seas. Although few records of gray whales are available south of Hong Kong (Wang, 1984; Zhu, 1998), it is presumed that they maintain a nearshore affinity throughout the southern portion of their range.

### Main habitat

Gray whales are known for their long-distance migrations between sub-tropical calving and mating grounds near continental coasts and high-latitude feeding grounds in the Arctic and sub-Arctic (e.g. Rice and Wolman, 1971; Swartz, 1986). As bottom-feeding specialists, gray whales aggregate during summer and autumn in shallow shelf waters and offshore banks where benthic and epibenthic invertebrate communities are concentrated (Nerini, 1984; Oliver *et al.*, 1984; Kim and Oliver, 1989). Traditional nearshore migratory routes connect high-latitude feeding areas with warm-water coastal and inshore wintering grounds. Today, the primary summer-autumn feeding habitat for western

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gray whales is located off the northeastern coast of Sakhalin Island (Weller *et al.*, 1999; 2002). The calving and mating grounds for this population are unknown, but records from sightings, strandings and whaling catches from 1933-1996 indicate that at least some western gray whales occur in coastal waters off China in the South China Sea (Wang, 1984; Zhu, 1998).

### Distribution

Key areas of distribution include the summer feeding grounds off northeastern Sakhalin Island (~52°50'N 143°20'E). Known portions of the north-south migratory route include regions off the eastern shore of Sakhalin Island in the Okhotsk Sea and along the eastern shores of mainland Russia near Peter the Great Bay and along the Korean peninsula in the Sea of Japan (Andrews, 1914; Brownell and Chun, 1977; Berzin, 1990). It is thought that prior to the 20th century, two groups of gray whales may have migrated to coastal waters off Japan (Omura, 1984). One of these groups was thought to travel along the eastern (Pacific) shore of Honshu during their southbound migration while en route for a supposed calving ground in the Seto Inland Sea (Omura, 1984). The other group was suspected to migrate along the eastern shore of Korea, cross the Korean Strait near Ulsan, and ultimately arrive at southwest Honshu and northwest Kyushu (Omura, 1984). Although gray whales were once hunted by net fishermen off the eastern shore of Honshu (Omura, 1984), present-day sightings of the species off Japan are very rare (Kato and Tokuhiro, 1997).

The winter distribution of this population is unknown. Whaling records indicate that peak gray whale numbers off southern Korea occurred in two seasonal pulses, one during the southward migration between December and January, and the other between March and April during the northward migration (Andrews, 1914; Kato and Kasuya, 2002). Whalers working off Ulsan, South Korea found that a majority of adult females taken between December-January were carrying near-term foetuses and were thought to be within two to three weeks of parturition (Andrews, 1914). Based on these observations, and his own measurement of one 4.76m foetus, Andrews suggested that calves were probably born somewhere off the southern end of the Korean Peninsula, and that this region represented the probable southern terminus of the winter migration (Andrews, 1914).

The idea that western gray whales overwinter off the southern coast of Korea, as suggested by Andrews (1914), was largely speculative (Rice, 1998). Several lines of evidence suggest that Andrews miscalculated the true position of the wintering grounds. Rice and Wolman (1971) reported an average near-term foetus size of 4.62m for eastern gray whales taken off central California between December and January. Thus, the observed foetus size, seasonal timing and latitudinal position (about 34°N) reported for Korea and central California closely corresponded. However, eastern gray whales migrate to breeding areas as far south as 20°-27°N off Baja California (Rice and Wolman, 1971; Swartz, 1986). Although Andrews suspected that western gray whales terminated their southern migration off southern Korea, a location approximately 7°-14° north of the eastern gray whale wintering grounds, historical records indicate that they occur as far south as the Yellow Sea, East China Sea and South China Sea (Henderson, 1972; 1984; 1990; Wang, 1978; 1984; Omura, 1988; Zhu, 1998; Kato and Kasuya, In press). Some evidence is available that western gray whales range at least as far south as 20°N off Hainan Island in southeastern China (Wang, 1984; Zhu, 1998). In addition, several unverified sighting reports led Omura (1974) to suggest that an alternative or additional calving and mating area was in the Seto Inland Sea (34°-35°N) off southern Japan, but little direct evidence is available to support this idea.

## EXPLOITATION

Groups of Koryak natives (Kamentsy, Parentsy and Itkantsy) living along the northeastern shores of the Okhotsk Sea hunted whales, although the particular species killed by these aboriginal whalers were not well documented (Krupnik, 1984); the author, however, believed that gray whales were hunted until the early 20th century. Whaling by Japanese hand-harpoon whalers was underway by at least the 16th century and Japanese net-whalers continued to take whales during the 17th-19th centuries (Omura, 1984). European and American whalers operating in the western North Pacific (mainly in the Okhotsk Sea) took gray whales from the late 1840s to perhaps the start of the 20th century (Henderson, 1984; 1990). Russian steam whalers took gray whales in the coastal waters of the Far East at the end of the 19th century (Andrews, 1914; Brownell, unpublished data). Japanese and Korean whalers continued to hunt gray whales until as recently as 1966 (Kasahara, 1950; Mizue, 1951; Brownell and Chun, 1977; Omura, 1984).

The reduction in the western Pacific gray whale population can be attributed largely to modern commercial whaling off Korea and Japan between the 1890s and 1960s. The population has been protected from commercial whaling since 1946, under the International Convention for the Regulation of Whaling. The Soviet Union and Japan joined the International Whaling Commission (IWC) in 1948 and 1951, respectively. The Republic of Korea and China, however, did not join until 1978 and 1980, respectively. Prior to their IWC membership, at least 67 gray whales were killed in the period 1948-1966 off the Republic of Korea (Brownell and Chun, 1977). Although no capture records are available from 1967 to the time that either the Republic of Korea or China joined the IWC, it cannot be assumed that gray whale catches did not occur during this period. Kasahara (1950) summarised whaling operations off northern Korea prior to 1945. Today, the Democratic People's Republic of Korea is not a member of the IWC and nothing is known about whaling in its waters since the end of World War II.

Western gray whales were probably never as numerous as their eastern counterparts. While pre-exploitation numbers for the western population are unknown, it has been speculated that they once may have numbered between 1,500-10,000 individuals (Yablokov and Bogoslovskaya, 1984). Berzin and Vladimirov (1981) estimated that only 1,000-1,500 gray whales remained in the population by 1910, after some commercial exploitation had already occurred. However, details of how these pre-exploitation and 1910 estimates were derived are not provided.

Kato and Kasuya (In press) estimated that some 1,800-2,000 whales (including 44 individuals killed by net whaling in the 1890s) were taken in the period 1891-1966, mostly off Korea and Japan. Peak annual catches of 100-200 whales began as early as 1907, but occurred primarily between 1911 and 1919 (no data were available for 1910) during which time at least 1,034 whales were killed, with a mean annual take of 115 whales. In the period 1920-1929, 289 whales were killed, with a mean annual take of 29 whales. By the 1930s, gray whale captures had greatly declined, with only 48 whales killed between 1930 and 1934 for a mean annual take of 10. No known additional catches occurred until 1942. Based on these catch data, it is apparent that by the early 1930s gray whales were far less abundant off the coasts of Korea and Japan and had likely reached commercial extinction. Continued low-level hunting between the 1940s and 1966, including the 67 whales captured in waters off South Korea, resulted in at least 71 whales killed. Kato and Kasuya (In press) hypothesise that the continued, albeit low-level, whaling pressure during this time is responsible for hindering the recovery of the western population. If the projected population size in 1910 was between 1,000-1,500, as estimated by Berzin and Vladimirov (1981), the removal of at least 1,442 whales recorded in the period 1911-1966 lends support to the above hypothesis offered by Kato and Kasuya (In press).

By the 1930s, the western gray whale was considered by many to be extinct (Mizue, 1951; Bowen, 1974). Nishiwaki and Kasuya (1970), believing the western population to be extinct and unaware of the Korean catches and sightings in the 1960s, suggested that sightings of two gray whales, one in about 1959 and one in 1968 off the coast of Japan, represented strays from the eastern population. However, Brownell and Chun (1977) described the probable existence of the western population based on catch records from the Korean coast during a nearly 20-year period between 1948 and 1966. These catch records, combined with the observation of four gray whales in the western Okhotsk Sea in 1967 (Berzin, 1974) and the sighting of a female gray whale and her calf in Korean waters in May 1968 (Brownell and Chun, 1977) indicated that western gray whales continued to survive in small numbers and that the observations reported by Nishiwaki and Kasuya (1970) were likely to be of western rather than eastern gray whales.

## CURRENT POPULATION STATUS

The western gray whale population survives as a small remnant population (Blokhin *et al.*, 1985; Weller *et al.*, 1999). Aerial and ship-based sighting records in the Okhotsk Sea between 1979 and 1989 indicated that gray whales aggregated predominantly along the shallow-water shelf of northeastern Sakhalin Island and were most common offshore of the southern portion of Piltun Lagoon (Blokhin *et al.*, 1985; Berzin *et al.*, 1988; 1990; 1991; Berzin, 1990; Blokhin, 1996). Two non-quantitative population estimates have been reported in the Russian literature (Vladimirov, 1994; Blokhin, 1996). An estimate of 250 by Vladimirov (1994) was derived from cetacean sighting records collected between 1979 and 1992 in the Okhotsk Sea; these records were collected from a variety of observation platforms, during different seasons, and employed mostly non-systematic sampling strategies. Although counts may be inflated by repeated observations of the same individuals, the highest number reported by Vladimirov (1994) during any sampling period was 34 gray whales observed in 1989 off northeastern Sakhalin Island. The author does not explain the origin of the estimate 250. An estimate of 100 by Blokhin (1996) was based on eight shore counts and one helicopter survey conducted between July and August of 1995 along the northeastern Sakhalin Island coast. The highest number of whales counted on any one day during that period was 42 but again, the author did not explain the origin of the estimate of 100. Therefore, both of these estimates must be considered unreliable.

Recent photo-identification studies conducted between 1994 and 1999 on the primary feeding ground off northeastern Sakhalin Island (Weller *et al.*, 1999; 2000; Würsig *et al.*, 1999; 2000) have identified a total of 88 individual whales (Table 1). These photo-identification data indicate high levels of annual return and pronounced seasonal site fidelity for most whales (Table 2). While new individuals continue to be identified annually, the rate at which this is occurring is low. Only 18 previously unidentified whales (excluding calves) were photographed during 91 days of effort between 1998 and 1999. This finding suggests that a majority of the population had been identified in the period 1994-1997 (Weller *et al.*, 2000). Between 1995 and 1999, 11 reproductive females and their

Table 1

Annual survey effort, number of groups encountered and whales identified in the period 1994-1999.

| Year | Sampling period | No. of surveys | Hours of direct observation | Rolls of film used | Groups encountered | Whales identified |
|---|---|---|---|---|---|---|
| 1994 | 7 Sep. - 12 Sep. | | | | | 10 |
| 1995 | 15 Aug. - 19 Aug. | 5 | 10.1 | 15 | 23 | 27 |
| 1997 | 9 Jul. - 8 Sep. | 22 | 33.4 | 72 | 114 | 47 |
| 1998 | 6 Jul. - 29 Sep. | 35 | 50.5 | 91 | 125 | 54 |
| 1999 | 29 Jun. - 13 Oct. | 56 | 122.0 | 160 | 434 | 70 |
| Overall | | 118 | 216.0 | 338 | 696 | 88* |

*The number of whales identified annually includes resightings of individuals from previous years, resulting in a total of 88.

Table 2

Annual sighting trends and resighting percentages of whales photo-identified in the period 1994-1999.

| Year | Whales identified | Calves/non-calves identified (crude birth rate) | New non-calves | Non-calves identified from previous years |
|---|---|---|---|---|
| 1994 | 10 | | 10 | |
| 1995 | 27 | 2/25* | 20 | 20.0% ($n = 5$) |
| 1997 | 47 | 2/45 (4.3%) | 25 | 44.4% ($n = 20$) |
| 1998 | 54 | 8/46 (14.8%) | 5 | 89.1% ($n = 41$) |
| 1999 | 70 | 3/67 (4.3%) | 13 | 80.6% ($n = 54$) |

* Insufficient data available to calculate crude birth rate.

15 calves were observed (Weller *et al.*, 2000). Two calves were observed in each of 1995 and 1997, eight in 1998 and three in 1999. Crude birth rates ranged between a low of 4.3% in 1997 and 1999, to a high of 14.8% in 1998. Of the 12 calves identified between 1995-1998, seven (58.3%) have not been resighted on the Sakhalin feeding grounds subsequent to their birth year.

### Mature population size[1]

Estimating the number of whales inferred to be capable of reproduction or 'number mature' is problematic for western gray whales because there are limited direct data, and demographic estimates depend on the population growth rate, which is currently unknown. Two approaches are used here to estimate plausible, albeit conservative, numbers mature. The first uses information from Rice and Wolman (1971), who found that 24% of the eastern gray whales in their sample were sexually immature and from this suggested that the total proportion of immature animals in the population was more likely to be 44%-61%. Using the minimum estimate of 88 western gray whales (Weller *et al.*, 1999; 2000) and using the estimated proportion immature from Rice and Wolman (1971), the number of mature whales in the western population ranges between 34 and 49.

However, the eastern gray whale population was growing at the time Rice and Wolman conducted their study and would therefore be expected to consist primarily of immature animals; this would not be the case for a stable population. The second method used here is based on the premise that the proportion mature for a stable population can be estimated using age-specific birth and mortality rates. Rice and Wolman (1971) reported the mean age of sexual maturity for eastern gray whales to be eight years (range = 5-11 years). Reilly (1992) estimated adult survival to be 0.95. Although there are no data for first year survival in gray whales, it is assumed here that survival does not differ strongly from that for humpback whales (*Megaptera novaeangliae*), which is 0.875 (Barlow and Clapham, 1997). For a stable population, therefore, the estimated proportion mature is 63%, which for the estimate of 88 whales in the present case results in 55 mature animals.

In addition to the uncertainty surrounding the estimated values of the population parameters, this estimate assumes that all mature adults are capable of reproduction. If, as suspected, the western population is not growing, then it is plausible that reproduction has been compromised because the population is so small. Data from another small population that has failed to recover provide a pessimistic comparative scenario. Only 70% of North Atlantic right whale (*Eubalaena glacialis*) females known to be mature are reproductively active (IWC, 2001). If it is assumed that all males reproduce but only 70% of the females do, then 85% of the sexually mature animals are capable of reproduction. Thus, of the 55 mature western gray whales estimated using this approach, only 47 would meet the IUCN definition of mature (see below).

Clearly, both these approaches are somewhat crude and are based on assumptions that may not be valid. However, both suggest a mature population size of less than 50 mature individuals, including only 11 known calf-bearing females documented between 1995 and 1999.

### Potential threats to the population

Although there is some evidence that an undetermined level of hunting may occur (e.g. Brownell and Kasuya, 1999; Baker *et al.*, 2002), it seems likely that the major threats for this population may stem from indirect mortality (e.g. bycatches and ship strikes) and habitat pollution and degredation.

Gray whales are known to be vulnerable to incidental catches in fisheries (e.g. IWC, 1994) and there are extensive coastal net fisheries off southern China, Korea and Japan (Zhou and Wang, 1994; Kato, 1998; Kim, 2000). The substantial nearshore industrialisation and shipping congestion throughout the migratory corridor(s) of this population also represent potential threats by increasing the likelihood of exposure to chemical pollution and ship strikes. Present and planned large-scale offshore gas and oil development in the South China Sea and in close proximity to the only known feeding ground for western gray whales off northeast Sakhalin Island in the Okhotsk Sea is of particular concern (e.g. see Brownell *et al.*, 1997; Brownell and Yablokov, 2001; IWC, 2002b). Activities related to oil and gas exploration, including high-intensity geophysical seismic surveying, drilling operations, increased ship and air traffic, and oil spills all pose potential threats to gray whales (e.g. Moore and Clarke, 2002). Disturbance from underwater industrial noise may displace whales from critical feeding, migratory and breeding habitat (e.g. Bryant *et al.*, 1984; Richardson *et al.*, 1995; Brownell and Yablokov, 2001). Physical habitat damage from drilling and dredging operations, combined with possible impacts of oil and chemical spills on benthic prey communities, also warrant concern.

A recent concern is the deterioration in physical condition of numerous individuals; during 1999, 2000 and 2001 whales have been observed that appeared to be unusually thin ('skinny') while on the summer feeding grounds (Weller *et al.*, 2000; authors' data). Morphological attributes correlated with this description varied among individuals, but consisted of at least one of the following: (1) an obvious sub-dermal protrusion of the top edge of the scapula from the body with associated thoracic depressions at the anterior and posterior insertion points of the flipper; (2) the presence of depressions near and posterior to the blowholes and head; and (3) a pronounced depression along the neural/dorsal spine of the lumbar and caudal vertebrae resulting in the appearance of a 'bulge' along the lateral flank.

While the causal mechanism(s) for the observed deterioration in physical condition and apparent health status of some whales is unknown, any of the following alone or in combination may be contributing factors: (1) natural or human produced changes in prey availability or habitat quality; (2) physiological changes related to stress; or (3) disease. Regardless of the cause, the loss of even a few whales (especially reproductive females) due to this deterioration in physical condition will greatly hinder population growth and ultimately prevent its recovery. Therefore, it is essential that this situation is carefully monitored and that all anthropogenic activities be reduced to an absolute minimum.

Although a natural occurrence, predation by killer whales (*Orcinus orca*) may also pose an additional threat to the recovery of this population at its currently reduced number. Killer whales are known to kill eastern gray whales, especially calves, off central and northern California (Rice and Wolman, 1971; Baldridge, 1972). Andrews (1914) found killer whale tooth raking on the flukes and flippers of a majority of the gray whales killed off Korea and

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[1] In terms of evaluating the western gray whale population under 'Criterion D' (population estimated to number less than 50 mature individuals) of the World Conservation Union (IUCN), the definition of 'mature individuals' in this context is defined as 'the number of individuals known, estimated or inferred to be capable of reproduction' – see section on 'International concern and conservation measures'.

documented numerous accounts of killer whales attacking both living and already captured gray whales. Although killer whales are somewhat common off the Sakhalin Island gray whale feeding ground, no aggressive interactions between the two species have been observed (Weller *et al.*, 2000). However, of 69 gray whales photographically identified between 1997 and 1998 on the feeding ground off Sakhalin, over 33% had tooth rakes from killer whales on their flukes, flippers or bodies (authors' data). This finding suggests that killer whales are at least threatening, and perhaps killing, western gray whales somewhere within their range but any associated mortality related to these observations is currently unknown.

Other factors, for which the cause is unknown but which give rise to concern for this population include low calf survival estimates ( < 42%) between 1995 and 1998; a male bias (59.4% males, 40.6% females; $n = 64$) in the [biopsy] sampled population and a more pronounced male bias (77.8% males, 22.2% females; $n = 9$) in sampled calves.

## INTERNATIONAL CONCERN AND CONSERVATION MEASURES

Largely on the basis of the recent information provided by the joint USA-Russia research programme (1995-2001) initiative and summarised here, the World Conservation Union (IUCN) listed the western gray whale population as 'Critically Endangered' in 2000 (Hilton-Taylor, 2000). In particular, this was due to the criterion that the population is estimated to have less than 50 mature individuals.

Serious concern over the status of the population has also been expressed by the Scientific Committee of the International Whaling Commission (IWC, 2002b). As a result of this, the Commission itself passed a Resolution in 2001 calling for concerted action by range states and others to pursue actions to eliminate anthropogenic mortality and disturbances on this population (IWC, 2002a). The IWC also strongly endorsed a continuation and expansion of the current research programme.

## CONCLUSION

It is apparent that long-term research and monitoring efforts of the western gray whale population need to be continued and expanded. The extensive past exploitation of this population, in combination with potential new threats from anthropogenic activities throughout its range, raises questions about the potential recovery and continued survival of the western gray whale. Future measures to protect this population will require international research collaboration between all range state countries and development of effective conservation measures and dedicated cooperation between science, industry and government.

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# A note on the spatial distribution of western gray whales (*Eschrichtius robustus*) off Sakhalin Island, Russia in 1998

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ABSTRACT

Three aerial surveys were conducted along a portion of the northeastern coast of Sakhalin Island, Russia between August and September 1998. They were conducted to examine the spatial distribution of western gray whales on their feeding grounds, and in relation to current and planned industrial activity. A total of 32 gray whale groups, consisting of 38 whales, was sighted during the surveys. Group sizes ranged from 1-3 individuals (mean = 1.2, SD = 0.54), with 87.5% ($n = 28$) composed of single whales. All groups detected were within 5km of the shore and 93.8% ($n = 30$) were sighted inside 4km. Sighting locations ranged from 0.6-4.8km offshore, with an overall mean distance from shore of 2.5km (SD = 1.11). These data suggest that western gray whales feed primarily in waters less than 20m deep and relatively close to shore. The nutrient-rich effluent from a large coastal lagoon is believed to significantly enrich the near-shore benthic environment of the northeastern Sakhalin Island coast, creating an area of particularly high food availability, and in turn contributing to the near-shore affinity of gray whales observed during this study.

KEYWORDS: GRAY WHALE; PACIFIC OCEAN; NORTHERN HEMISPHERE; FEEDING GROUNDS; DISTRIBUTION; SURVEY-AERIAL

## INTRODUCTION

The western (Okhotsk-Korean) North Pacific population of gray whales (*Eschrichtius robustus*) is one of the most endangered and little known populations of large whales in the world (Clapham *et al.*, 1999; Weller *et al.*, 2002). Western gray whales were thought to be extinct as recently as 1972 (Bowen, 1974), but are known to survive today as a small (*ca* 100 animals) remnant population (e.g. Weller *et al.*, 2002). Recent genetic studies show that eastern and western Pacific gray whales should be recognised as geographically and genetically separated at the population level (LeDuc *et al.*, 2002).

Reviews of Russian aerial and ship-based sighting records in the Okhotsk Sea during the late 1960s, 1970s and 1980s (Berzin, 1974; 1990; Vladimirov, 1994) indicated that gray whales were distributed predominantly along the shallow-water shelf off northeastern Sakhalin Island, Russia (Fig. 1) during summer-autumn, with particularly high numbers observed offshore of the southern portion of Piltun Lagoon (see also Blokhin *et al.*, 1985; Blokhin, 1996). Recent photo-identification (1994-1999) and shore-based studies (1997-1999) have also documented the annual occurrence of gray whales off Piltun Lagoon (e.g. Weller *et al.*, 2002). Photo-recognition research identified 88 individuals between 1994-1999, and documented high levels of annual return and seasonal site fidelity for a majority of all known whales (see Weller *et al.*, 2002). Shore-based counts and theodolite-determined sightings suggested that most gray whale groups occurred in coastal waters near the entrance to Piltun Lagoon and that 95% of all observed groups were located within 5km of shore; although feeding gray whales have been observed >15km from shore in the Piltun area, such sightings are considered to be unusual (Ivashchenko, 1999; Würsig *et al.*, 1999; 2000).

Gray whales aggregate off northeastern Sakhalin Island during summer-autumn to feed on benthic and epibenthic prey. The observed inter- and intra-annual occurrence and distribution patterns of known individuals emphasise the ecological importance of the Piltun region, and suggest that it is likely to be the primary feeding habitat for western gray whales. Activities related to oil and gas exploration and production, including increased vessel and aircraft traffic, geophysical seismic surveys, and well-drilling operations have recently been initiated near or on the feeding grounds. Given the critically endangered status of western gray whales and the potential for increased industry-related disturbance (Weller *et al.*, 2002), a joint USA-Russia research programme was initiated in 1995 to monitor the population (and other marine mammals) off the northeastern Sakhalin Island coast. Results reported here represent findings from three aerial surveys conducted along a portion of northeastern Sakhalin Island during the summer-autumn of 1998. These surveys were designed to examine the distribution of gray whales on their feeding grounds and in relation to current and planned industrial activity.

## METHODS

### Study area

Zaliv Pil'tun (referred to here as Piltun Lagoon) is located on the northeastern shore of Sakhalin Island, Russia (Fig. 1). It is approximately 80km long and 15km across (at its widest point) with only one entrance to the Okhotsk Sea. The near-shore environment is characterised by waters generally <20m deep, over a predominantly sand substrate. Although significant inter-annual variability exists, sea surface temperature during the summer varies between approximately 2-15°C, salinity ranges between 28-36ppt, and periods free of sea ice are usually between late May and December.

### Survey technique

Systematic flights were conducted on 6 August, 28 August and 29 September 1998. Visibility was excellent to good (>5km) during each survey and the sea state was always

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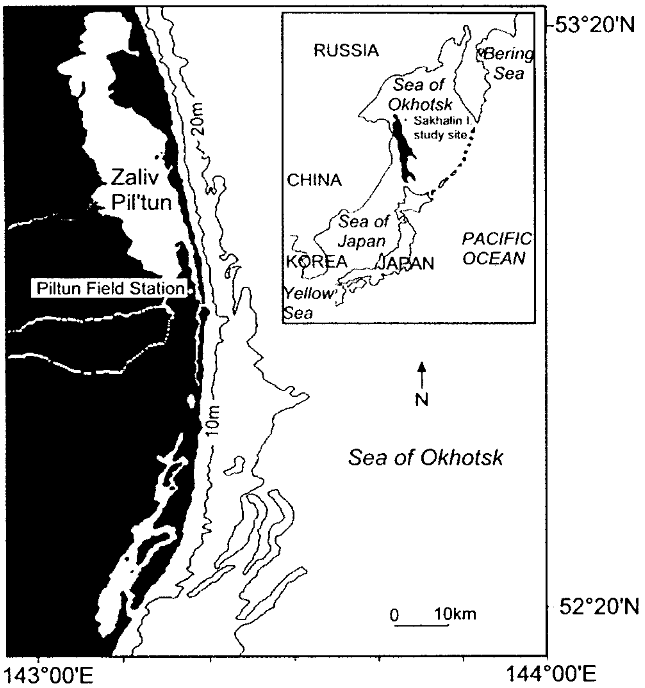

Fig. 1. Northeastern Sakhalin Island.

Beaufort 3 or less. Observations were made from a Russian MI-8 helicopter, travelling at an altitude of 450m and air speed of 150km/h. Four experienced observers, two on each side of the helicopter, were stationed behind the cockpit; a trackline observer and data recorder were in the cockpit. The MI-8 body configuration has poor visibility for aerial surveys; the right side observers could not search between 50-90°, and the left side observers could not search between 60-90°[1]. Fortunately, the trackline observer and data recorder had good below-aircraft visibility through downward-facing landing windows. Given the unacceptable downward visibility of the aircraft (and the track design, see below), no estimates of whale density or abundance have been attempted.

Transects consisted of five 50km north-south lines, with two 2.5km and three 5.0km east-west legs between lines (Fig. 2a). The total area covered by each flight was approximately 1,000km$^2$. This design allowed both longshore (north-south) and offshore (east-west) distribution to be evaluated, but not abundance estimates. The survey area included waters surrounding an exploratory oil drilling rig (Sakhalinskaya) and an offshore drilling and production platform (Molikpaq), located approximately 13 and 24km from the entrance to Piltun Lagoon, respectively. The Sakhalinskaya was present in the study area during all three surveys, while the Molikpaq was present only for the final survey. Each survey began at the Piltun Lighthouse field station, the helicopter then flew north along the tide line of the eastern seashore, allowing observers to search within approximately 500m of shore. The first two east-west legs were set at 2.5km (one-half of the remainder) to give greater coverage in the near-shore region where gray whales are known to concentrate (e.g. Weller *et al.*, 1999).

Standard survey techniques developed for gray whale aerial surveys were followed (Rice *et al.*, 1981; Rugh, 1984). An on-board Global Positioning System (GPS) was used for navigation and to determine cetacean sighting positions, vessel positions and oil platform locations. Observers followed a standard protocol. Upon first sighting, GPS position and time were recorded. Once the sighting was directly abeam, the angle of declination between the sighting and the helicopter was measured with a hand-held inclinometer (which could be used to calculate sighting distance - Lerczak and Hobbs, 1998). Information on species, number of animals, orientation relative to the aircraft and behaviour was also recorded. Environmental conditions such as visibility, sea state (Beaufort Scale), swell and glare were noted at the start of each transect line and updated as conditions changed.

## RESULTS

A total of 32 gray whale groups (38 whales) were sighted during the surveys (Table 1). The total number of whales sighted on 6 August, 28 August and 29 September was 9, 13 and 15, respectively. Group sizes ranged from 1-3 individuals (mean = 1.2, SD = ±0.54), with 87.5% ($n = 28$) of the groups sighted composed of single whales. Twenty-three (71.9%) of the groups were seen near the entrance to Piltun Lagoon, or to the north (Figs. 2b-d). All groups detected were within 5km of the shore, with 93.8% ($n = 30$) located inside 4km of shore (Fig. 3). Sighting locations ranged from 0.6-4.8km offshore, with an overall mean distance from shore of 2.5km (±SD = 1.11). Fig. 4 displays the mean and median group distances from shore for each of the three surveys. An analysis of group distance from shore revealed no significant effect of survey date ($F(2,29) = 0.598$, $p = 0.5563$).

The only other cetacean sighted during the aerial surveys was a pair of killer whales (*Orcinus orca*) approximately 16km from shore during the first survey (Fig. 2b).

## DISCUSSION

These data show that western gray whales on their summer-autumn feeding grounds generally remained within 5km of shore and in waters < 20m deep, were distributed mainly offshore of the entrance to Piltun Lagoon, and occurred in small groups. While caution is needed to avoid over-interpretation of the present results due to the limited downward visibility from the helicopter and the fact that only three flights took place, these findings complement the distribution patterns described by recent shore-based theodolite tracking research which also found most groups located within 5km of shore (Würsig *et al.*, 1999; 2000). The mean group size here (mean = 1.2) was lower than those reported from boat-based (mean = 2.0) and shore-based observations (mean = 1.7) during the same period (Weller *et al.*, 1999; Würsig *et al.*, 2000). This finding, in combination with several additional lines of evidence, suggests that the aerial surveys under-counted the number of whales in the study area. Concurrent boat-based research in the same study area in 1998 identified eight mother-calf pairs (Weller *et al.*, 2002), however, none were sighted during the aerial surveys. In addition, the high percentage of single animal groups (87.5%) recorded from the air is substantially higher than the percentage (52.9%) derived from the boat (Würsig *et al.*, 2000). These results are perhaps not unexpected given the poor visibility from the helicopter, and may also explain the absence of sightings of the more difficult to see common minke whales (*Balaenoptera acutorostrata*) and harbour porpoise (*Phocoena phocoena*) that have frequently been recorded from boats or the shore in this area.

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[1] The horizon is 0° and the line directly below the helicopter is 90°.

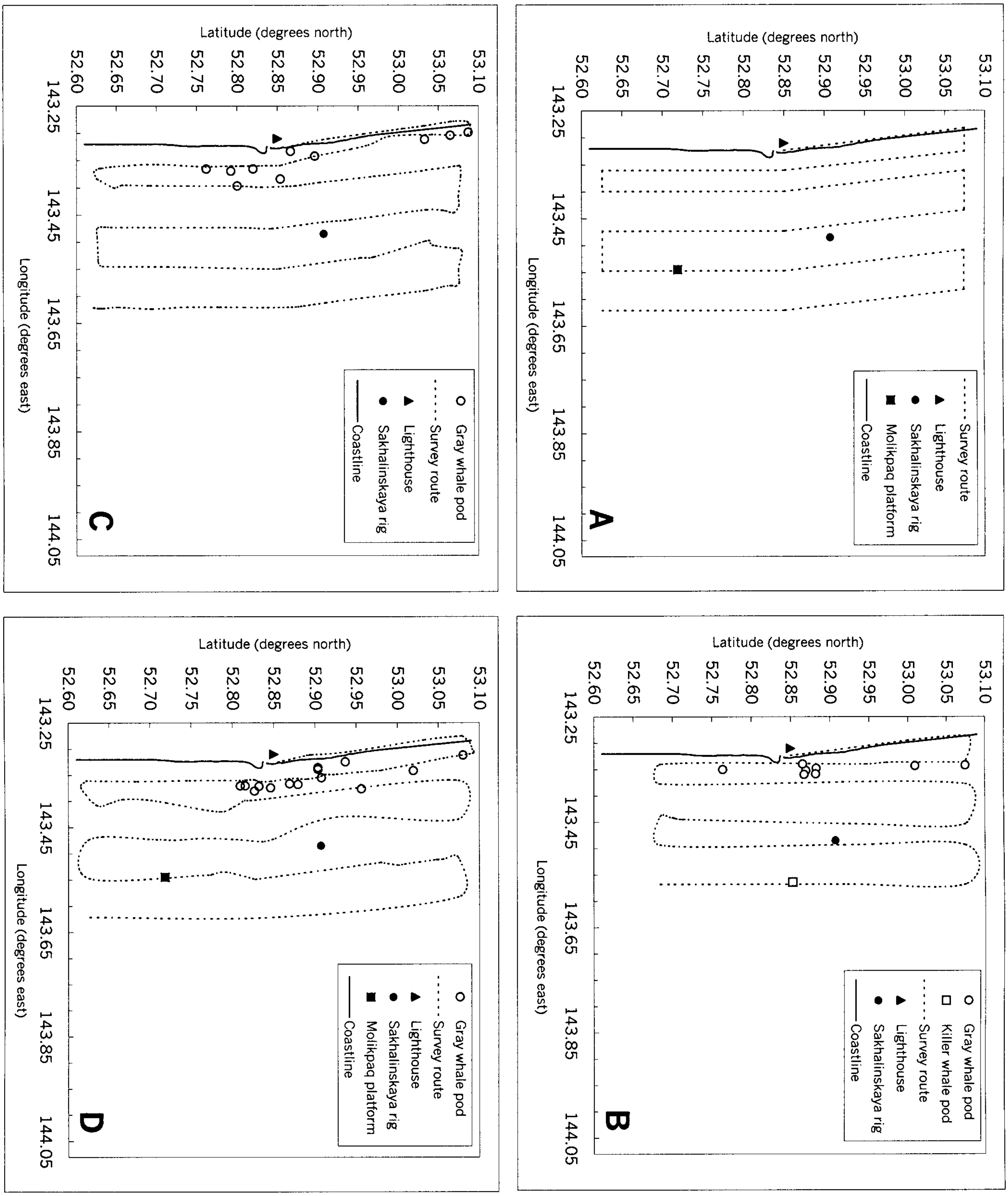

Fig. 2. Aerial survey plots: (a) transect lines; (b) Survey 1 (6 August); (c) Survey 2 (28 August); (d) Survey 3 (29 September). Latitude and Longitude are displayed in decimal degrees.

Since gray whales aggregate off Piltun during summer-autumn to feed, it is assumed that their nearshore distribution mirrors that of their prey. We hypothesise that nutrient-rich effluent from Piltun Lagoon significantly enriches the surrounding near-shore benthic environment, creating an area of particularly high food availability, and in turn contributing to the near-shore affinity of gray whales reported here. This hypothesis is supported by earlier studies that found some of the highest benthic biomass densities (1,000g/m$^2$) in all of the western Okhotsk Sea occurred near Piltun Lagoon (Koblikov, 1982). This apparent ecological relationship between prey biomass and whale distribution may help to explain why the relatively expansive Russian aerial and ship-based survey programmes during the 1970s and 1980s found the only major concentrations of gray whales in the Okhotsk Sea to be located along the

Table 1

Summary results from Aerial Surveys.

| Date | No. whales | Position (Lat.°N/Long.°E) | Distance from shore (km) |
|---|---|---|---|
| 6 Aug. 1998 | 1 | 53.074, 143.342 | 3.7 |
| 6 Aug. 1998 | 1 | 53.009, 143.343 | 3.0 |
| 6 Aug. 1998 | 1 | 52.883, 143.348 | 1.8 |
| 6 Aug. 1998 | 1 | 52.869, 143.352 | 2.0 |
| 6 Aug. 1998 | 1 | 52.865, 143.340 | 1.1 |
| 6 Aug. 1998 | 1 | 52.764, 143.350 | 1.7 |
| 6 Aug. 1998 | 3 | 52.867, 143.359 | 2.4 |
| 6 Aug. 1998 | 1 | 52.882, 143.358 | 2.5 |
| 28 Aug. 1998 | 1 | 53.033, 143.311 | 1.2 |
| 28 Aug. 1998 | 1 | 53.065, 143.304 | 1.1 |
| 28 Aug. 1998 | 1 | 53.087, 143.299 | 0.8 |
| 28 Aug. 1998 | 2 | 52.896, 143.342 | 1.6 |
| 28 Aug. 1998 | 3 | 52.866, 143.333 | 0.6 |
| 28 Aug. 1998 | 1 | 52.853, 143.384 | 4.0 |
| 28 Aug. 1998 | 1 | 52.820, 143.365 | 2.7 |
| 28 Aug. 1998 | 1 | 52.792, 143.369 | 3.0 |
| 28 Aug. 1998 | 1 | 52.762, 143.365 | 2.7 |
| 28 Aug. 1998 | 1 | 52.800, 143.396 | 4.8 |
| 29 Sep. 1998 | 1 | 52.937, 143.324 | 0.9 |
| 29 Sep. 1998 | 1 | 53.080, 143.312 | 1.7 |
| 29 Sep. 1998 | 1 | 53.019, 143.341 | 3.0 |
| 29 Sep. 1998 | 1 | 52.908, 143.355 | 2.6 |
| 29 Sep. 1998 | 1 | 52.903, 143.335 | 1.3 |
| 29 Sep. 1998 | 1 | 52.903, 143.339 | 1.5 |
| 29 Sep. 1998 | 1 | 52.879, 143.367 | 3.1 |
| 29 Sep. 1998 | 1 | 52.869, 143.366 | 2.9 |
| 29 Sep. 1998 | 1 | 52.846, 143.374 | 3.3 |
| 29 Sep. 1998 | 2 | 52.832, 143.371 | 3.1 |
| 29 Sep. 1998 | 1 | 52.827, 143.380 | 3.7 |
| 29 Sep. 1998 | 1 | 52.815, 143.370 | 3.0 |
| 29 Sep. 1998 | 1 | 52.810, 143.370 | 3.1 |
| 29 Sep. 1998 | 1 | 52.956, 143.376 | 4.6 |

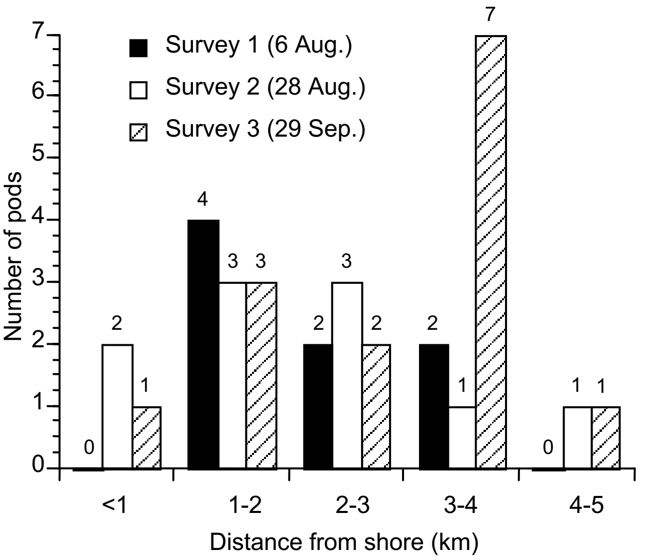

Fig. 3. Number of gray whale groups detected as a function of distance from shore (km). Value labels represent the number of groups sighted.

northeastern shore of Sakhalin Island, particularly off Piltun Lagoon.

In light of the critically endangered status of this remnant population of gray whales, we recommend that the ongoing oil and gas development along the northeastern Sakhalin Island shelf continue to be carefully monitored. In addition to the behavioural, genetic and photo-identification studies currently being conducted, research on the near-shore benthic environment, where whales annually return to feed is essential if the ecological factors that make this region attractive to gray whales are to be better described and the potential impacts of industrial activity further understood.

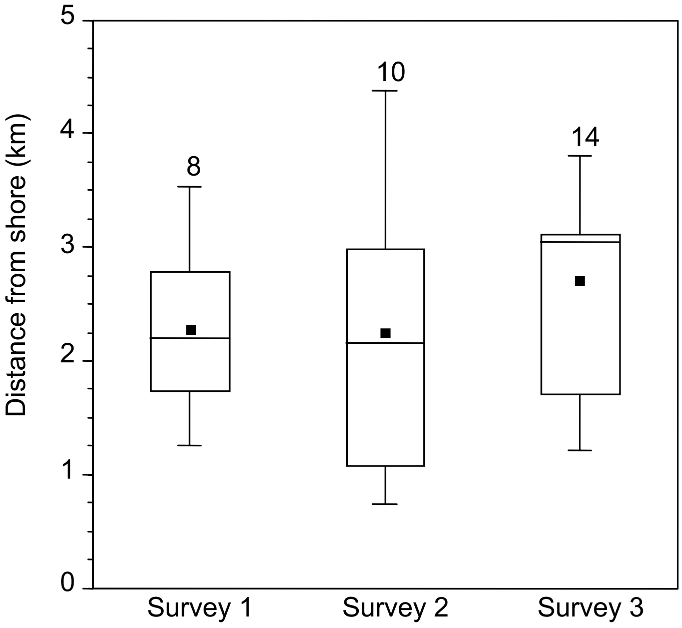

Fig. 4. Mean distance from shore (km) for gray whale groups detected during each survey. The lowest, second lowest, middle, second highest and highest box points represent the 10th, 25th, median, 75th and 95th percentiles, respectively. Means are represented by black squares. Value labels represent the number of groups counted.

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# Potential impact of offshore human activities on gray whales (*Eschrichtius robustus*)[1]

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ABSTRACT

Gray whale (*Eschrichtius robustus*) reactions to offshore human activities have been relatively well studied compared to those of other mysticetes. Studies of short-term behavioural responses to underwater noise associated with aircraft, ships and seismic explorations indicate a 0.5 probability that whales will respond to continuous broadband noise when sound levels exceed *ca* 120dB[2] and to intermittent noise when levels exceed *ca* 170dB, usually by changing their swimming course to avoid the source. Gray whales were 'startled' at the sudden onset of noise during playback studies, but demonstrated a flexibility in swimming and calling behaviour that may allow them to circumvent increased noise levels. Whales may be 'harassed' by noise from large commercial vessels, especially in shipping lanes or near busy ports. Gray whales sometimes change course and alter their swimming speed and respiratory patterns when followed by whalewatching boats. Conversely, some whales swim toward small skiffs deployed from whalewatching boats in breeding lagoons, seemingly attracted by the noise of idling outboard engines. Reported gray whale reactions to aircraft are varied and seem related to ongoing whale behaviour and aircraft altitude. Whale response to research involving tagging and biopsy sampling appears to be short term. Gray whales were seen swimming through surface oil from the *Exxon Valdez* oil spill along the Alaskan coast and showed only partial avoidance to natural oil seeps off the California coast. Laboratory tests suggest that gray whale baleen, and possibly skin, may be resistant to damage by oil, but spilled oil or oil dispersant in a primary feeding area could negatively affect gray whales by contaminating benthic prey. Gray whales are sometimes injured or killed in collisions with vessels or entanglement in fishing gear. Concern about the cumulative long-term impact of offshore human activities is particularly acute in the Southern California Bight, where many activities are often concurrent.

KEYWORDS: GRAY WHALE; NOISE; WHALEWATCHING; PACIFIC OCEAN; SHORT-TERM CHANGE; POLLUTANTS; ECOSYSTEM; LONG-TERM CHANGE; HUMAN IMPACT

## INTRODUCTION

The coastal habits of gray whales (*Eschrichtius robustus*) often bring them into direct contact with offshore human activities. During their annual migration along the North American coast, the eastern North Pacific (California) gray whale stock passes through US oil and gas exploration/development areas, shipping lanes, military test ranges and near coastal cities, from which 'whalewatchers' embark. The western North Pacific (Korean) stock probably encounters similar offshore human activities during its migration along the Asian coast, especially near Korea and Japan (see review in Weller *et al.*, 2002). In a review of the impact of offshore human activities on gray whales along the migration route and in the breeding lagoons in the eastern North Pacific, Reeves (1977) suggested that additional research, enforceable management procedures and public education were needed to mitigate human harassment of whales. Responses to this suggestion in the ensuing years are summarised here.

This review of information regarding human activities that may affect gray whales is presented in three sections: (1) offshore oil and gas development; (2) commercial fishing and vessel traffic; and (3) whalewatching and scientific research (Fig. 1). Underwater noise from each of these activities is often regarded as the primary source of disturbance. Gray whale reactions to underwater noise associated with oil and gas development have been directly observed, resulting in documented responses to sounds from aircraft, a variety of classes of vessels, airgun pulses used in seismic exploration and oil drilling and production operations (summarised in Malme *et al.*, 1989; Richardson *et al.*, 1989; 1995). Less attention has been focused on gray whale responses to oil on the sea surface (Kent *et al.*, 1983), on the potential fouling of the skin and baleen and on the contamination of prey by oil (Geraci and St. Aubin, 1985; 1990).

Gray whales are sometimes injured or killed by entanglement in commercial fishing gear (Heyning and Lewis, 1990). Commercial vessel traffic results in the ensonification of shipping lanes and occasionally leads to collisions with whales (Heyning and Dahlheim, 2002). Finally, harassment of animals due to whalewatching and scientific research has become a focus of concern, particularly as more commercial recreation vessels, private boats and researchers converge to 'watch' whales near large cities along the North American coast. Gray whale reactions to vessel noise observed during studies of oil- and gas-related noise impact are referred to in both the 'Commercial Fishing and Vessel' and the 'Whalewatching and Scientific Research' sections of this paper, as appropriate.

## OFFSHORE OIL AND GAS DEVELOPMENT

The potential impact of offshore oil and gas development on marine mammals was the focus of extensive research during the mid-1980s. Richardson *et al.* (1989) reviewed both acoustic and non-acoustic impacts of oil and gas exploration and development activities on marine mammals. Malme *et al.* (1989) used a modelling procedure to rank the impact of various petroleum-industry-related noise sources on gray whales and other marine mammals. Geraci and St. Aubin (1990) summarised the ecological and toxicological effects of oil on marine mammals. The potential impact of oil and gas development on gray whales is summarised in two

[1] A version of this paper was originally presented as SC/A90/G5.

[2] dB re 1 $\mu$Pa throughout manuscript.

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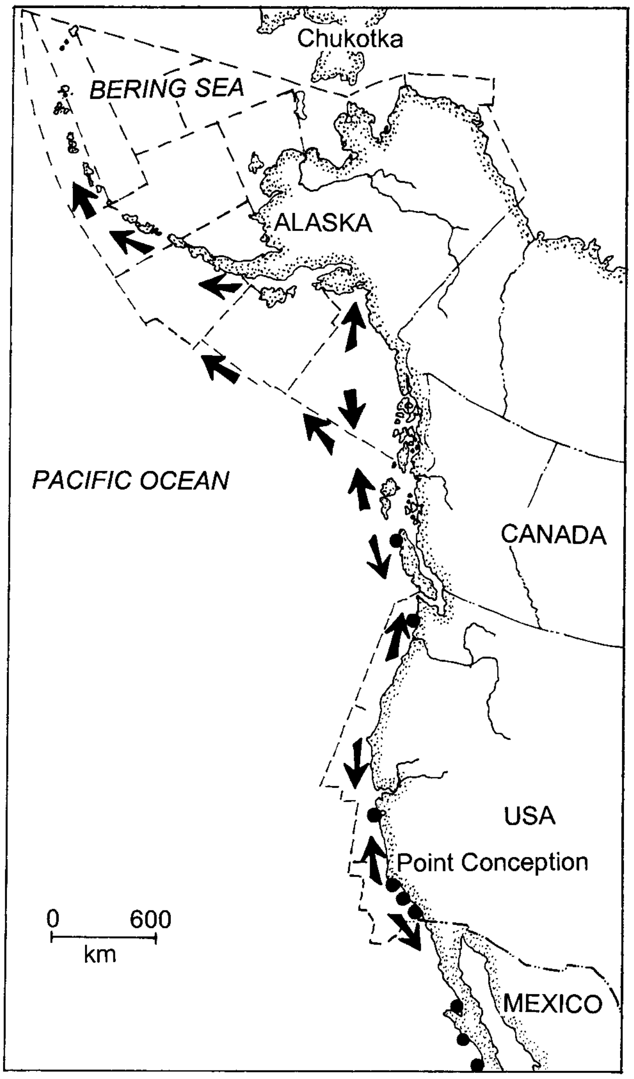

Fig. 1. US oil and gas planning areas (---), shipping lanes (→), and whalewatching centres (●) along the gray whale's northeast Pacific ranges.

sections, the first relating whale responses to noise associated with offshore operations and the second focusing on oil contamination of whales or their habitat.

## Noise

Short-term responses of gray whales to playback of noise associated with oil and gas development were studied during the migration past the central California coast in 1983-1984 (Malme *et al.*, 1984), near feeding whales in the Bering Sea in 1985 (Malme *et al.*, 1988) and in San Ignacio Lagoon, Baja California, Mexico in 1981-1984 (Dahlheim, 1987, summarised in Richardson *et al.*, 1995). Underwater noise sources recorded and used during playback trials included helicopter overflights, drillship operations, drilling and production platforms, a semi-submersible drilling rig and tripping operations (withdrawing drills from exploratory wells). In addition, Malme *et al.* (1984; 1988) conducted experiments using airgun arrays and single airguns as sources. It is important to recognise that although playback studies provide valuable information on specific responses of whales to a controlled noise source, they are hampered by the limitations of the sound projector and rarely fully simulate noise from the source, especially at low (<100Hz) frequencies.

Gray whale responses to noise playback and airgun blasts included: changes in swimming speed and direction to move away from the sound source, termed 'avoidance' (Malme *et al.*, 1984); abrupt behavioural changes from feeding to avoidance, with a resumption of feeding after exposure (Malme *et al.*, 1988); changes in calling rates and call structure (Dahlheim, 1987); and changes in surface behaviour, usually from travelling to milling. A 0.5 probability of avoidance was calculated for migrating gray whales exposed to continuous noise at levels ranging from 117-123dB (Table 1). When migrating or feeding gray whales were exposed to airgun pulses, a 0.5 probability of avoidance was calculated at levels of 170dB and 173dB, respectively. Overall, Malme *et al.* (1988) concluded that a 0.5 probability of avoidance occurred when continuous noise levels exceeded *ca* 120dB and when intermittent noise levels exceeded *ca* 170dB. While these values provide some useful baseline information on the levels of industrial noise to which gray whales respond, the distance from the source at which these levels occur varies with geographic region and sea condition.

Table 1

Gray whale response to various levels of playback of noise associated with offshore oil and gas development. Data from Malme *et al.*, 1984, except: [1] from Malme *et al.*, 1988; and [2] from Dahlheim, 1987. Tripping operations = sound of drillstring being drawn out of exploratory well hole.

| Source | Noise level (dB re 1μ Pa) | Response (avoidance probability) |
|---|---|---|
| Helicopter | 115 | 0.10 |
| | 120 | 0.50 |
| | >127 | 0.90 |
| Drillship | 110 | 0.10 |
| | 117 | 0.50 |
| | 122 | 0.90 |
| Semi-submersible | 115 | 0.10 |
| | 120 | 0.50 |
| | >128 | 0.90 |
| Drilling platform | 114 | 0.10 |
| | 117 | 0.50 |
| | >128 | 0.90 |
| Production platform | 120 | 0.10 |
| | 123 | 0.50 |
| | >129 | 0.90 |
| Airgun pulses | | |
| Migrating whales | 164 | 0.10 |
| (airgun array) | 170 | 0.50 |
| | >180 | 0.90 |
| Feeding whales[1] | 163 | 0.10 |
| (single airgun) | 173 | 0.50 |
| Tripping operations[2] | 110-130 | 'increased milling' |

Malme *et al.* (1989) subsequently prepared a disturbance ranking scheme for oil and gas noise sources in outer continental shelf (OCS) planning areas of offshore Alaska, based on a model of noise contribution and exposure rating. The ranking scheme indicated that gray whales had a high probability of being influenced by noise from oil and gas operations, particularly from large tankers, dredges and airgun arrays. The authors cautioned that the noise contribution and exposure rating models used in ranking were based upon several untested hypotheses regarding the properties of sound transmission in specific locales and the ability of gray whales to hear frequencies produced by offshore oil and gas operations.

Dahlheim (1987) studied the effects of man-made noise, including ship, outboard engine and oil-drilling sounds, on gray whale calling and surface behaviours. Statistically significant increases in gray whale calling rates and changes in calling structure, swimming direction and surface behaviours were associated with artificially-increased noise levels during playback experiments in San Ignacio Lagoon, Mexico. For example, when tripping noise was played back, gray whales decreased their calling rate and level and a greater proportion of whales milled near the playback transducer compared to the control periods. Whale responses varied with the type and presentation of the noise source. In general, as noise levels increased there was a corresponding increase in calling rates, level of calls received, number of frequency-modulated calls, number of pulses produced per pulsed-call series and call repetition rate. Whales responded more dramatically ('startled') to the sudden onset of sound compared to sound played back over a longer time period. Dahlheim (1987) emphasised that flexibility in swimming and calling behaviour may allow gray whales to circumvent increased noise levels in their environment, but cautioned that the combined effects of various disturbances could pose a problem.

The 'noisiest' period of offshore oil and gas operations occurs during exploration and site establishment (Richardson *et al.*, 1995). Many interrelated activities during these periods require support from aircraft, a variety of vessels, dredges and sometimes even explosive operations (University of California, 1990). Conversely, production activities are generally quieter and require fewer support operations. Gray whales have been migrating past oil exploration and production activities in the Santa Barbara Channel off California for decades, suggesting that they habituate to, or at least tolerate, noise associated with these activities (Richardson *et al.*, 1995). Although there are no published accounts of gray whale disturbance caused by production platform noise, Gales (1982) hypothesised that this noise could be detected by a mysticete from 37m to over 5km away, depending on propagation conditions in the Santa Barbara Channel and the hearing thresholds of the individual whales.

## Oil contamination

The effect of surface oil on gray whales has been the topic of more speculation than study (Geraci and St. Aubin, 1985; 1990). It is unclear whether gray whales can detect surface oil. Gray whales were observed lying in or swimming through oil slicks from the 1989 *Exxon Valdez* oil spill along Alaska's south-central coast (Table 2). Similarly, gray whales migrating past areas of natural oil seeps near Santa Barbara, California, often swam through oil (Kent *et al.*, 1983). In general, gray whales swimming through oil offshore of California swam faster, stayed submerged longer and took fewer breaths than whales that did not pass through oil. Whales sometimes changed direction to swim around surface oil, but it was not clear that the direction change was in response to the oil. Reactions of migrating gray whales to the 1969 Santa Barbara Channel oil spill were not documented (Brownell, 1971), but no deaths were attributed to the effects of oil pollution (Reeves, 1977). Six gray whale carcasses were recovered after the 1969 Santa Barbara spill and 25 after the 1989 *Exxon Valdez* spill (Geraci, 1990). Although the tally of dead whales was higher than previously recorded for both areas, researchers concluded that the higher counts were due to increased survey effort.

Table 2

Reports of gray whales associated with oil from the 1989 *Exxon Valdes* oil spill.

| Date | No. whales | Behaviour | Pers. comm. |
|---|---|---|---|
| 6 Apr. | 1 | Lying still in large oil slick <100m from shore | B. Morris |
| | 5-6 | Swimming through oil slicks *ca* 1km from shore | |
| 12 Apr. | 4 | Swimming in and out of oil slicks | |
| | 2 | Swimming through oil slicks | |
| | 1 | Swimming through oil slicks | |
| Apr./May | *ca* 20 obs. | Whales swimming near or through oil | M. Dahlheim |

Gray whales probably experience irritation to their eyes and tactile hair follicles upon contact with oil, but lasting effects on skin tissue may be less likely (Geraci, 1990). Although exposure of discrete areas of captive bottlenose dolphins' (*Tursiops truncatus*) skin to crude oil and gasoline for 0.5-1.25hrs initially resulted in 'small blisters' (Geraci and St. Aubin, 1982; 1990), normal colour returned within 2hrs. Geraci and St. Aubin (1985) concluded there was 'no evidence of damage or loss of integrity,' possibly because dolphins do not exhibit a vascular reaction to contact with petroleum products. Similarly, although the mid- and outer layers of the skin of a live-stranded sperm whale (*Physeter macrocephalus*) were damaged by a 7-12hr exposure to oil and gasoline, the basal layer and underlying dermis were undamaged. Geraci and St. Aubin (1985) also reported no difference in healing between two shallow epidermal wounds in uncontaminated dolphin skin and two wounds contaminated with oil for 0.5 or 1hr, suggesting that oil contamination did not seriously impair the healing process.

Geraci (1990) concluded that cetacean skin impeded the penetration of petroleum compounds by 'tight intercellular bridges, the vitality of the superficial cells and the extraordinary thickness of the epidermis.' However, there have been no laboratory tests of oil contamination of gray whale skin and inferences drawn from small sample-size studies on other species must be interpreted with caution. Specifically, Albert (1981) suggested that rough or damaged skin (such as the barnacle-covered skin of a gray whale) may be more susceptible to oil contamination and subsequent bacterial infection than the smooth skin of the majority of other cetaceans. This suggestion will probably remain untested for the foreseeable future, as funding for studies related to oil and gas impacts on marine mammals has diminished substantially in recent years.

In laboratory tests, water flow through gray whale baleen contaminated with various grades of oil was relatively unaffected (Geraci and St. Aubin, 1985; Geraci, 1990). Most of the oil (70%) was removed from the test baleen within 30 minutes of continuous flushing with sea water. Geraci and St. Aubin (1985) concluded that oil impact on baleen was slight and short term, but added that oil-coated baleen fibres could contaminate ingested food. Baleen fibres could remain oiled if an animal was feeding in an area so blanketed by oil that fouling outpaced the rate of cleansing, such as in the centre of a spill (Geraci, 1990). Ingested oil is toxic to marine mammals (Engelhardt, 1983). Although no cases of ingestion have been reported, gray whales could consume oil from fouled baleen, by engulfing floating tar balls (Geraci, 1990) or from contaminated bottom sediments (Hansen, 1985). Stranded gray whales, examined after the *Exxon Valdez* spill, had oil on their baleen but not in their digestive tracts, suggesting that the baleen was fouled after the animals died (M. Dahlheim, pers. comm.).

Oil and chemical dispersants, used to break up surface oil and cause it to sink, could impact gray whales by contaminating benthic prey (Neff, 1990; Würsig, 1990).

Although gray whales probably feed opportunistically throughout their range, they return annually to primary feeding areas in the northern Bering Sea and Chukchi Sea (e.g. Nerini, 1984; Moore *et al.*, 1986; Weller *et al.*, 1999). Any large-scale contamination by oil or oil dispersants of a primary feeding area could negatively impact the population. Increased activity by the oil and gas industry in offshore waters and recent large oil spills motivated the Scientific Committee of the International Whaling Commission to recommend the development of 'measures to prevent and mitigate the impact of petroleum exploration, development and transportation' (IWC, 1990a). As yet, plans on paper have not resulted in an effective clean-up of any offshore oil spill, leaving real the possibility of large-scale contamination somewhere within the gray whale range.

## COMMERCIAL FISHING AND VESSEL TRAFFIC

Many different classes of commercial fishing and transport vessels regularly transit shipping lanes and frequent busy marine ports along the North American coast. Gray whales are exposed to the combined noise from these vessels along their migration route and in feeding and breeding areas. Further, gray whales are sometimes struck by vessels and occasionally become entangled in fishing gear. As summarised in the subsequent two sections, potential negative impacts of commercial fishing and vessel traffic on gray whales include collisions, entanglement and noise harassment due to the ensonification of coastal waters by intense vessel traffic.

### Collisions and entanglement

Information on gray whale mortality or injury incidental to vessel traffic or fishing operations must be inferred from stranding records, which are not uniformly available for the species' entire range. Heyning and Dahlheim (2002) summarised instances of gray whales being struck by ships and stated that there are 'several documented cases of dead, stranded gray whales with cuts from the propellers of large ships', although they could not estimate ship collision-related mortality. Gray whale mortality due to entanglement in fishing gear is also difficult to substantiate because stranded animals often exhibit little or no evidence of entanglement (Baird *et al.*, 2002; Heyning and Dahlheim, 2002). Often stranded whales cannot be examined for cause of death because of geographic location (see, e.g. Kasamatsu and Ishikawa, 1990).

Gray whale mortality incidental to offshore fishing operations in British Columbia was estimated at 27% of all stranded whales, or roughly two gray whales per year (Baird *et al.*, 2002). The authors cautioned that biases in survey methods and stranding records may have resulted in under-representation of the actual number of whales taken incidentally. Gray whales were the species most frequently documented (94% of all records) as entangled, usually in set gillnets, off southern California (Heyning and Lewis, 1990). Of the 61 animals entangled, most were 3yrs of age or younger (< 10m in length). Many of the 41 live entanglements were released alive; however, it is unknown whether there are any long-term effects of entanglement on live-released whales.

### Ensonification

Commercial vessels range from cargo supertankers (> 250m) to small sports-fishing boats (*ca* 30m). Noise levels for these vessels range from *ca* 185-190dB re 1$\mu$Pa-m for the supertankers, to 169-180dB re 1$\mu$Pa-m for medium sized ships, to *ca* 145-170dB re 1$\mu$Pa-m at frequencies from *ca* 50-300Hz (Richardson *et al.*, 1995). Cybulski (1977) reported a maximum source level of 205dB at 2Hz for an oil tanker, but noted that measurement of such long wavelength sounds was highly dependent on water depth. The noise field from the combined output of several vessels has not been documented, but would be expected to be greatest near ports and along busy shipping lanes (Malme *et al.*, 1989).

Reactions of gray whales to vessels are summarised in Richardson *et al.* (1995) and Malme *et al.* (1989). Most accounts describe relative movements of whales and vessels, with little or no specific information on concomitant underwater noise. On the summer feeding grounds, gray whales fled when Soviet catcher vessels approached within 350-550m, but generally they paid no attention to vessels at distances > 550m (Bogoslovskaya *et al.*, 1981). Wyrick (1954) reported that migrating gray whales changed course at distances of 200-300m to avoid vessels. Although many whalewatching and private boats routinely approach within 200m of whales, there are no published accounts of the whales' responses at these distances. Vessels moving erratically or at high speeds in the breeding lagoons sometimes caused whales to swim rapidly away, but there was little or no whale response to slow-moving or anchored vessels (Swartz and Jones, 1979).

Evidence that vessel traffic can cause gray whales to abandon an area is equivocal. Gray whales stopped using Guerrero Negro Lagoon, Baja California, Mexico during a period of increased dredging and commercial shipping activity (1957-1967), but reoccupied the lagoon in later years after ship traffic abated (Bryant *et al.*, 1984). Conversely, Jones and Swartz (1984) reported no evidence that whales moved out of San Ignacio Lagoon when whalewatching vessels were present and suggested that gray whales became less sensitive to boats in the lagoons as the winter progressed. Notably, whalewatching boats remained at anchor in the seaward one-third of the lagoon with only their generators running while tourists made excursions in small outboard-powered skiffs to watch whales. Jones and Swartz (1984) noted an increasing tendency for whales to approach rather than flee from these skiffs since the late 1970s. Dahlheim *et al.* (1984) also reported that some whales were attracted to noise from idling outboard engines and that each whalewatching vessel and outboard-powered skiff in San Ignacio lagoon had a distinctive acoustic spectrum profile.

## WHALEWATCHING AND SCIENTIFIC RESEARCH

### Whalewatching

Whalewatching has become an important recreational industry in several communities along the North American coast from British Columbia, Canada, to the breeding lagoons of Baja California, Mexico, especially in the Southern California Bight (waters south of Point Conception, California, to the Mexican border) where day cruises are launched from at least 14 landings from Morro Bay to San Diego and hundreds of private vessels launch from the large metropolitan areas (Reeves, 1977). In addition, some expeditions sail from southern California ports to observe gray whales in the breeding lagoons. The Mexican government has designated the lagoons as a sanctuary and strictly controls the number and location of vessels in the lagoons. Whalewatching along the migration route is not as well regulated and it has been suggested that this activity, in combination with commercial fishing and vessel operations, may cause gray whales to migrate further offshore (Wolfson, 1977).

A Workshop to Review and Evaluate Whalewatching Programs and Management Needs was convened by the Center for Marine Conservation (CMC) and the National Marine Fisheries Service (NMFS) in Monterey, California, November 1988 (Center for Marine Conservation and National Marine Fisheries Service, 1989). Bursk (1989) reported that gray whales often changed speed and deviated from their course in the presence of whalewatching boats. In another evasive behaviour, 'snorkelling,' whales came to an almost complete halt to breathe in an inconspicuous manner. Similarly, migrating gray whales disturbed by vessels tended to exhale underwater and surface only long enough to inhale, making it difficult to see them (Hubbs and Hubbs, 1967). Because estimates of energy expenditure based on breathing patterns indicated that fast-moving whales breathe and use energy more rapidly than slow-moving whales (Sumich, 1983), Bursk (1989) suggested that these vessel-induced practices may increase gray whale energy consumption and thereby reduce migrating efficiency.

At the CMC/NMFS meeting, a distinction was made between commercial whalewatching vessels and private recreational boats. The general consensus was that commercial operators were effectively limiting their approach distances to whales, but private boaters often 'harassed' gray whales by approaching closely or by cutting in front of their path. The NMFS established whalewatching guidelines for all boat operators, effective during the 1990-1991 gray whale migration season (J. Lecky, pers. comm.). The guidelines stipulate that boaters maintain a 100yd (90m) distance from whales, avoid sudden changes in course or speed, not cross a whale's path or separate a whale from a calf, and not restrict whale movements or behaviour (University of California, 1990).

Observations of gray whales migrating further offshore in the Southern California Bight have been interpreted as either a response to increased human activities along the coast or a reoccupation of routes historically used by an increasing whale population (Rice and Wolman, 1971; Dohl and Guess, 1979). The route of the southbound migration along the North American coast bifurcates at Point Conception. Some whales (*ca* 20-35%) turn east and continue to follow the coast, while the others (*ca* 65-80%) swim south across open water to the northern Channel Islands (Leatherwood, 1974; Kent *et al.*, 1983). Most whales (*ca* 94%) pass the northern Channel Islands within 3 n.miles (5.5km) of shore and tend to cluster at points, reefs, headlands and inter-island passages (Jones and Swartz, 1990). The route between the northern and southern Channel Islands is poorly documented. Whales tend to pass the southern Channel Islands along the western shore, then turn southeastward, joining coastal migrants near the USA/Mexican border (Sumich and Show, 1990). Counts of whales passing San Clemente Island, the southernmost of the Channel Islands, indicate that there is broad interannual variability in the number of whales using that route (Graham, 1990). However, such variation is not necessarily related to human activities and Sumich and Show (1990) suggest that the use of offshore routes along the Channel Islands may reflect whale migration patterns established during the last glacial maximum.

### Scientific research

Research often requires observers to approach gray whales closely in aircraft or boats. Reported gray whale reactions to aircraft are varied and seem related to ongoing whale behaviour and aircraft altitude. For example, cow-calf pairs in the northern Chukchi Sea seemed particularly sensitive to a turboprop aircraft at 305m altitude; calves swam under adults and were subsequently hard to see (Ljungblad *et al.*, 1983). Conversely, a group of mating gray whales did not react to the arrival of the same aircraft, nor to its circling at 320m altitude for over 10 minutes (Ljungblad *et al.*, 1987). Malme *et al.* (1984) played back underwater noise recorded from a Bell 212 helicopter (estimated altitude = 100m), at an average of three simulated passes per minute, to migrating gray whales. Whales changed their swimming course and sometimes slowed down in response, but proceeded to migrate past the transducer. Migrating gray whales did not react overtly to a Bell 212 helicopter at $>$425m altitude, occasionally reacted when the helicopter was at 305-365m, and usually reacted when it was below 250m (Southwest Research Associates, 1988). Reactions included abrupt turns or dives or both.

Gray whale tracking and biopsy studies necessitate approaching whales (to within 10-25m) by boat and attaching tags or firing projectiles into them (e.g. Harvey and Mate, 1984; Swartz *et al.*, 1987; Mathews *et al.*, 1988). Gray whales sometimes responded to tag attachment by fluke slapping and rapid swimming, but usually returned to pre-tagging behaviours soon after the event (Harvey and Mate, 1984). The response of gray whales to biopsy darts was not described (Mathews *et al.*, 1988), but disruption of ongoing behaviours in other mysticetes has been brief, if sometimes dramatic (Brown *et al.*, 1991; Weinrich *et al.*, 1991). The long-term benefit of these activities to the population is generally accepted to outweigh the short-term discomfort to the subject whales (IWC, 1990b), although caution should be exercised for small populations such as the western gray whales (see IWC, 2002).

Oceanographic research often requires the use of low frequency sounds to investigate transmission loss and water mass properties. Specifically, during long-range acoustic tomography and acoustic thermometry studies, sounds to 190-220dB re 1 $\mu$Pa-m are commonly broadcast at 20-200Hz (Richardson *et al.*, 1995). Responses of gray whales to these sources are largely unknown. However, in August 1996, the US Navy began preparation of an Environmental Impact Statement (EIS) to support use of a low frequency active (LFA) sonar, which transmits signals as intense as 205dB re 1 $\mu$Pa-m in the 100-500Hz frequency range. Research to investigate the effect of this source was conducted offshore central California during the 1998 southbound gray whale migration (P. Tyack, pers. comm.). Preliminary results showed that gray whales avoided exposure to transmissions from this source at levels of 170 and 178dB re 1 $\mu$Pa-m by deviating their swimming path at ranges of 'several hundred meters', similar to avoidance behaviours described during playback of oil and gas-related sounds (Malme *et al.*, 1984). When the LFA source was transmitting at 185dB re 1 $\mu$Pa-m in the path of the migration (i.e. roughly 2km from shore), gray whales deviated their swimming path at significantly longer ranges ($>$1km) than when the source was broadcast farther offshore and out of the migration path. These results, and those of Malme *et al.* (1984), indicate that gray whales alter their behaviour to avoid exposure to loud low-frequency sounds.

## SUMMARY

When Reeves (1977) suggested that additional research, management and education were needed to mitigate human harassment of gray whales there were few quantitative accounts of whale responses to specific human activities. Much has been accomplished in the ensuing years. Overall, there is little evidence that gray whales disturbed by human activities travel far as a result of, or remain disturbed long after, the causal event. However, most research, management and educational efforts have focused on short-term responses by gray whales to single-stimulus trials. An example of event-related management is the warning given to spectator boats that were harassing migrating gray whales during the 1992 International America's Cup Regatta off San Diego, California (Marine Mammal Commission, 1993).

Assessing the cumulative, long-term effects of offshore human activities on gray whales should be the focus of future research. Specifically, Tyack (1989) suggested that management based on assessing long-term impacts of human activity on whale populations should take precedence over attempts to regulate individual acts of whale harassment. Gray whales often encounter stimuli from human activities simultaneously or sequentially, not in isolation. A case in point is the Southern California Bight, where gray whales are exposed to offshore oil and gas operations, a myriad of commercial shipping and fishing activities and various whalewatching and whale research efforts. The cumulative effects of several stimuli can be purely additive, or can lead to synergistic effects that result in changes greater than the sum of changes from individual stimuli.

Assessment of cumulative, long-term effects requires consistent data collection and analyses of multiple environmental factors over many years. A long-term (1957-1982) assessment of the effects of research vessels in Cape Cod Bay suggested that mysticete species differed in their response to vessels and there was no evidence that vessel interactions exerted a long-term negative impact on any population (Watkins, 1986). Similarly, an overview of the effects of whalewatching activities on mysticetes off Cape Cod suggested few negative impacts, provided that commercial vessels maintained safe guidelines for the approach and watching of whales (Beach and Weinrich, 1989). The recovery of the gray whale population in the face of long-term exposure to human activities along the North American coast suggests a strong degree of tolerance to such activities. Long-term research should be directed at investigating whether there is a limit to such tolerance by examining changes in relative abundance and migration routes near centres of human activities over a number of years.

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# Gray whale (*Eschrichtius robustus*) at calving sites in the Gulf of California, México[1]

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ABSTRACT

Records of gray whales (*Eschrichtius robustus*) at and near their two known calving sites in the Gulf of California (Sea of Cortés), México, are reviewed up to 1995. The sites of Tojahui/Yavaros (Sonora) and Bahía Santa María (Sinaloa) represented the most distant calving grounds regularly visited by the species. Prior observations (mainly in the 1950s and 1960s) revealed relatively small but seasonally consistent numbers of whales, with maximum counts, including calves, of 30 individuals at Bahía Santa María in 1954, and 17-19 at Tojahui/Yavaros in 1955, 1963 and 1971. Observations (initiated in 1979) as well as interviews with longtime local residents and fishermen, document a decline in numbers and occupancy times of whales, especially cow/calf pairs, visiting these sites. In contrast, 19th century whaling records indicate that many more gray whales were found seasonally along these coasts. The recent decline, leading to the apparent disappearance, is likely to be due to human-induced disturbances related to accelerated regional socio-economic development, with associated increases in artisanal and industrial fishing activities and other forms of maritime traffic. Within less than four decades of their 'discovery', it appears that no gray whales have returned to calve at these sites since the mid-1980s. Barring an unlikely change in regional fishing practices, this apparent abandonment of calving sites on the northwest coast of mainland México suggests that any anticipated further increase in population size of the eastern North Pacific stock may be unwarranted.

KEYWORDS: GRAY WHALE; GULF OF CALIFORNIA; ABUNDANCE; DISTRIBUTION; REPRODUCTION; POPULATION; TRENDS; HISTORY

## INTRODUCTION

The gray whale (*Eschrichtius robustus*) is well-known for its long-distance annual migration, from principal summer feeding grounds in boreal seas bordering Alaska and Siberia to principal winter reproductive areas along the west coast of the Baja California Peninsula in northwestern México. Many investigators have concentrated their observations on this coastal whale in its extensive bay and lagoon habitats of Baja California Sur, in sheltered waters that serve as major mating, calving and nursery sites, and where relatively large numbers of individuals can be observed, censused and studied during winter months. Much of what is known about the species in the southern part of its range derives from such studies (e.g. Gilmore, 1960; Norris *et al.*, 1977; Rice *et al.*, 1981; Jones and Swartz, 1984; Jones *et al.*, 1994; Urbán-R *et al.*, 1997). The major calving sites (Fig. 1) are: Laguna Ojo de Liebre (with 53% of the total calves), Laguna Guerrero Negro (9%), Laguna San Ignacio (11%) and Boca de la Soledad/Estero de Santo Domingo (12%), and the minor sites (each with less than 6%) of Ensenada de San Juanico, Bahía Magdalena, Bahía Almejas and Bahía Santa Marina (Rice *et al.*, 1984).

Less well known is the extended migration of a small portion of this eastern North Pacific gray whale stock around the tip of the Baja California Peninsula into waters of the Gulf of California. These whales enter the major part of what Gilmore (1960) termed the 'extra-limital wandering area' for the population, which also includes a few isolated sightings from more southern localities along the Pacific coast of mainland México and at the oceanic Revillagigedo Islands.

This paper reviews the available information on gray whales at their two calving sites in the Gulf of California.

Historical information comes from: (1) historical records of commercial whaling (*ca* 1850s-1870s) reviewed by Henderson (1972; 1984); (2) information that was forthcoming following the 'discovery' of these calving sites by scientists in 1954 (Gilmore and Ewing, 1954; Gilmore, 1960; Gilmore and Mills, 1962; Gilmore *et al.*, 1967; Gard, 1976; Gilmore Collection, no date; R.L. Brownell, Jr., pers. comm.); and (3) interviews with longtime local fishermen and residents, some of whom were living at Bahía Santa María between the late 19th century and the early years of the 20th.

Recent information is based on observations conducted for this study (1979-1995) as well as many interviews with fishermen and residents at both calving sites and nearby areas. Occurrence and abundance of gray whales at these sites has been discussed previously, in part, by Findley *et al.* (1982), Findley and Vidal (1983), Swartz (1986), Vidal and Findley (1988; 1989), Vidal (1989) and Vidal *et al.* (1993).

## CALVING SITES IN THE GULF OF CALIFORNIA

Observations conducted during this study focussed on the two localities along the northwestern coast of mainland México where gray whales were, until recently, known to consistently congregate and calve (mating behaviour has never been observed at either locality). These sites represent the extreme geographical limits consistently reached by the reproductive part of the southward-migrating stock: the relatively restricted area of open coast off Tojahui and the

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nearby lagoon (*laguna*, *estero*, *bahía*) of Bahía de Yavaros, Sonora; and the extensive coastal lagoon complex of Bahía Santa María (Reforma), Sinaloa (Fig. 1).

After reviewing 19th century whaling records, Henderson (1972: pp. 165-166, pp. 175-177, p.190, table 1; 1984: p.170, p.174, table 1) reported that whalers pursued the gray whale (and other species, mainly humpback whale, *Megaptera novaeangliae*) along the Pacific coast of northwestern México as far south as the Islas las Tres Marías and Bahía Banderas, Nayarit/Jalisco. Principally during the 1850s and 1860s, some vessels sailed to the Gulf of California and the Mexican mainland coast where relatively small catches were obtained; about 200 whales (not including calves) during approximately 25 trips (Henderson, 1972; 1984). Henderson (1972; 1984) noted that while catches were always more important along the west coast of Baja California, several trips were made into the Gulf of California. Dedina and Young (1996) cite an 1861 letter by the territorial governor of Baja California, T. Riveroll, sent to Mexican President Benito Juárez, that includes a complaint of whaling ships along both coasts of the peninsula, albeit mainly in the bays and lagoons of the Pacific coast. Henderson (1972, p.190) estimated that prior to commercial exploitation, a maximum of about 500 gray whales annually visited calving sites in the Gulf of California, sites almost certainly including the bays and coastal lagoons of Yavaros (Sonora) and Santa María, Altata/Pabellón, Navachiste/San Ignacio (Henderson, 1972, pp. 30-31) and Topolobampo/Ohiura (Sinaloa) and possibly other lagoons on the eastern side of the Gulf, such as Agiabampo on the coast between northernmost Sinaloa and southernmost Sonora (Fig. 1), and possibly even some of the (fewer) bays and lagoons along the largely rocky southeastern coast of Baja California Sur.

As noted by Henderson (1972, p.30), and evident during research visits to Tojahui/Yavaros and Bahía Santa María during this study, gray whales are well known to local fishermen, who refer to them as *ballenas pintas* ('spotted whales'). Gilmore and Ewing (1954) were the first to report

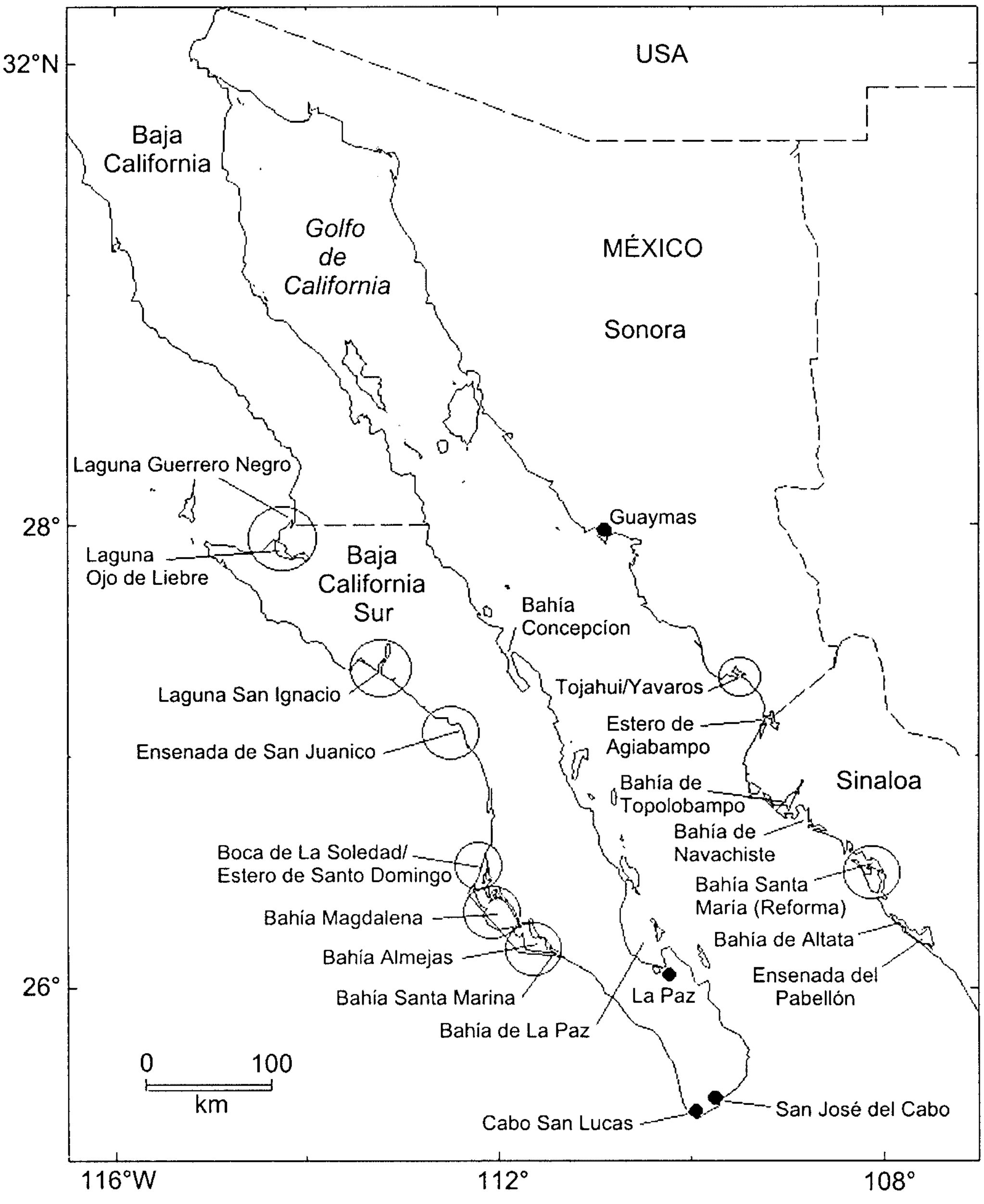

Fig. 1. Gray whale calving localities in northwestern México. Six circles on the west coast of Baja California Sur enclose principal mating/calving/nursery sites. Two circles on the west coast of mainland México enclose calving/nursery sites in Sonora and Sinaloa.

in modern literature the aerial observations of small numbers of gray whales, mainly cow/calf pairs, at or nearby these sites in 1954. During a few subsequent years, limited (mainly one overflight) censuses were continued by Gilmore and/or collaborators at these two calving/nursery sites (Gilmore, 1960; Hubbs and Hubbs, 1967). These observations terminated after the 1962 season at Bahía Santa María (Gilmore and Mills, 1962; Gilmore Collection, no date), but counts were continued (largely by Al Harrison) until the 1971 season at Tojahui/Yavaros (Gilmore *et al.*, 1967; Gilmore Collection, no date; R.L. Brownell, Jr., pers. comm.). A period of several years followed when no systematic observations were made, with the notable exception of counts for 1975 at both sites reported by Gard (1976). Although the majority of observations were short-term, they corroborated the seasonal presence of small numbers of whales at both sites, with the separate counts usually not exceeding 15 individuals, including calves, with maxima of 17-19 at Tojahui/Yavaros in 1955, 1963 and 1971 (Gilmore *et al.*, 1967) and 30 at Bahía Santa María in 1954 (Gilmore and Ewing, 1954).

## Tojahui/Yavaros, Sonora

### *Study area*

The main concentration of gray whales in this region (Fig. 2) has been the bight-like Ensenada de Tojahui (*ca* 26°37'N; 109°23'W), in an area about 10km SE of the major regional fishing port and bay of Yavaros. This relatively spatially restricted concentration seasonally occurred off that part of coastal Mayo Indian lands known as Tojahui, located between the fishing camp of Bajerobeta and the village of Las Bocas, in the Municipality of Huatabampo, Sonora. Viewed from a boat off Tojahui, the coast appears as a low, unmarked expanse of coastal thornscrub; the only topographical relief provided by the far-distant high mountain range of the Sierra de Alamos on the eastern horizon. At Tojahui, two abandoned and dilapidated houses of masonry (*Las Casonas de Tojahui*) stand on low (3-5m), eroding bluffs behind a narrow sand beach containing scattered small outcrops of mudstone. The bluffs (and soils inland) are of generally unconsolidated fine-grained alluvial sediments (likely deposited as part of an ancient distributary delta of the formerly large Río Mayo), and are occasionally intersected by outwashes such as the mouths of the Arroyos de Tojahui and Bajerobeta (Fig. 2). Seaward, the sandy-silty bottom slopes gradually; a depth of only 8m was measured at a distance of 2km offshore.

### *Sightings and strandings*

The gray whales observed from shore and small boats at this site tended to be about 1-1.5km offshore, although Gilmore *et al.* (1967) and local fishermen (pers. comm.) reported them slightly closer inshore in earlier years. Fishermen state that several years ago, when more whales visited the site, they were also frequently observed a short distance to the south, off Punta Jimarohuisa and Las Bocas (Fig. 2).

Table 1 (see p. 37ff.) presents gray whale counts in this area for the 1975-1995 seasons made during this study, and also includes those made during previous studies.

Two days during the 1980 season and one day during the 1981 season were spent in an unsuccessful shore watch at Las Bocas, but have been included in Table 1 to emphasise (what was not fully recognised at the time) the whales' preference for the site directly off Tojahui. Although a few recent sightings have been made nearby, such as off Huatabampito and near the mouth and inside Bahía de Yavaros (Table 1; Fig. 2), the main concentration of whales was consistently off Tojahui. The maximum number of gray whales observed by us at this site was eight (3 cow/calf pairs and 2 solitaries), during the first two days of March 1981. A good photographic record of these individuals was obtained.

A more intensive observational effort was undertaken at Tojahui during the 1982 season; a 7m observation tower was constructed at the larger abandoned house and one of the

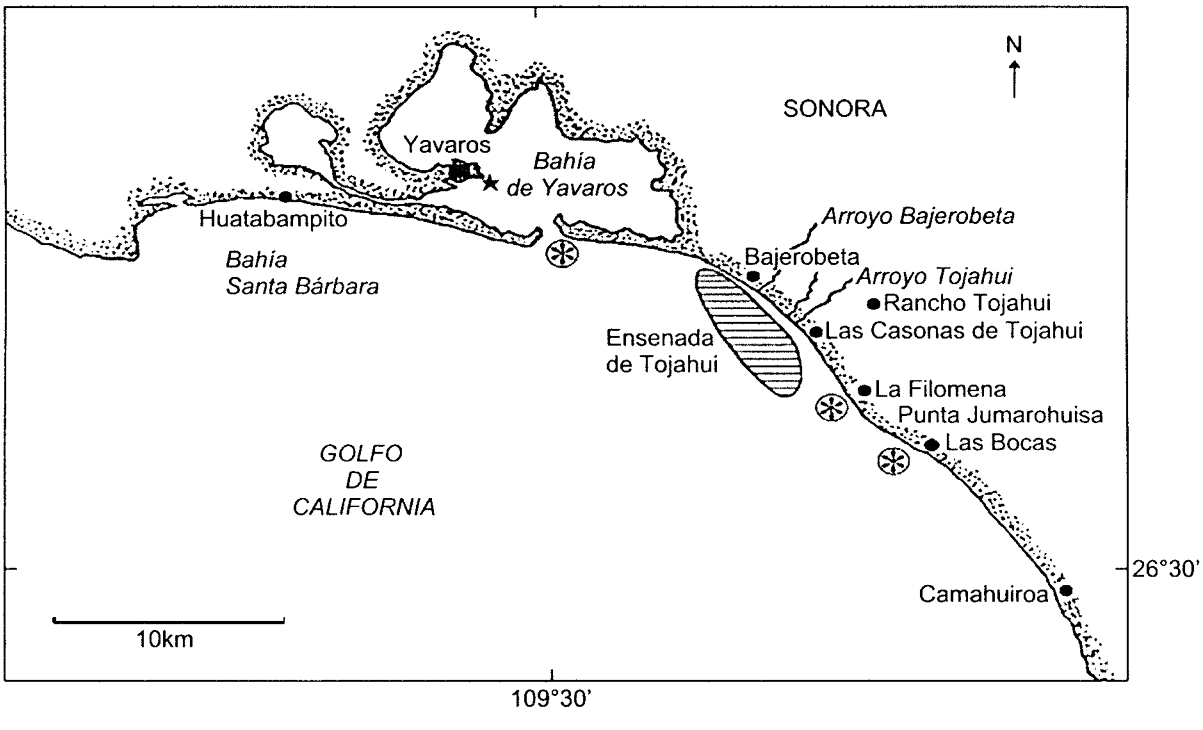

Fig. 2. Locality of gray whale calving site of Tojahui/Yavaros, Sonora. Hatched area encloses sightings during 1979-1987 seasons. Star in Bahía de Yavaros indicates sightings in 1983. Encircled asterisks indicate three strandings (one immature each) (see Table 1 and text).

authors (OV) took up semi-continuous residence. Several site visits were also made by the other author and students of the Instituto Tecnológico y de Estudios Superiores de Monterrey (ITESM)-Campus Guaymas. In addition, several reliable informants (principally longtime resident Sr. Gonzalo Rojo), who daily fish the area, reported their sightings or absence of sightings. However, even with the increased 1982 effort, during the 61 days spent at Tojahui, a total of only two cow/calf pairs and a solitary adult were seen (Table 1). The presence of these whales off Tojahui was often sporadic during the 36-day period between initial and final sightings (21 January and 25 February), with the cow/calf pairs and the solitary adult moving seemingly independently into and out of the observational area. During 16 days of this 36-day period, at least one cow/calf pair (probably the same pair) was present, but only occasionally along with the other pair and/or the lone adult. Most of these five whales were present during the period 21-30 January, but all had left the site on 31 January. On this and the following day, a pod of killer whales (*Orcinus orca*) including a large male, was observed in the area. Killer whales have been reported to harass and sometimes attack gray whales (e.g. Scammon, 1874; Morejohn, 1968; Poole, 1984), and the latter have been shown to avoid the underwater sounds of the former (Cummings and Thompson, 1971; Jones *et al.*, 1994). It is possible that the gray whales temporarily vacated the area off Tojahui due to the presence of these predators. Whether or not the gray whales took refuge inside Bahía de Yavaros or elsewhere is not known, but three days later, on 4 February, all five whales returned to the observational area off Tojahui. However, one of the cow/calf pairs departed the following day and was not seen again. For nine non-consecutive days during the period 5-25 February, the remaining cow/calf pair was observed at the site (temporarily absent, or no observers present, during the other days), but the solitary adult was present on only two of these days (16 and 17 February). This cow/calf pair was not seen again in the area after 25 February. Unfortunately, photographs suitable for identification were not obtained of any of these individuals.

To test the possibility that these whales had moved far offshore, on 2 March a transect was made in a fishing skiff (*panga*) directly off Tojahui to a distance of *ca* 15km. No gray whales were sighted, but a pod of three female or immature killer whales was encountered harassing a pair of fin whales, *Balaenoptera physalus* (Vidal and Pechter, 1989). It is unknown if any of these killer whales were the same as those sighted previously, but these sightings verify the (at least) temporary presence of this predatory species in the region, and may explain the sporadic presence and relative early departure of the five gray whales from the site.

Several months later, during November 1982, two small immature gray whales stranded in this region. These, and another such stranding in April 1976, are noted in Table 1 and Fig. 2, and are discussed below.

Although the 1983-season sighting effort at Tojahui was less than in 1982, several site visits, including several parallel-to-shore transects in *pangas* between Tojahui and Yavaros, were made by the authors and other ITESM personnel. Nevertheless, no whales were seen and all information on gray whales in the area was provided by local fishermen at Tojahui and residents of Yavaros (Table 1). At Tojahui, a total of only three or four whales, including at least one cow/calf pair, was reported, seen on only two days during late January. Notably, killer whales were again in the area; a pod of four individuals, including a large male, was seen by G. Rojo, on 24 January. Two residents of Yavaros reported gray whales inside Bahía de Yavaros (Table 1; Fig. 2) during the days *ca* 19 and 20, and 27 January. Although Gilmore *et al.* (1967) hypothesised that the original concentration of calving gray whales in this region was principally inside Bahía de Yavaros, and Henderson (1972) alluded to whales there, the 1983 reports constitute the first definitive sightings from inside this lagoon, and suggest that these individuals were seeking refuge from the killer whales. It is not known whether the presence of killer whales in the area was the cause of the apparent absence of these few gray whales from the area off Tojahui after 27 January.

The observations from 1984-1988 were also relatively restricted; all information for this period resulted from several short-term visits to the area and from personal communications with reliable local informants. For 1984, the maximum number of whales observed for one day was six (3 cow/calf pairs) on 29 January. Again, presence of the whales off Tojahui was sporadic between the initial and final sightings (20 January and 12 February), with at least one of the cow/calf pairs seen during a non-consecutive eight-day period. The last whale observed was an immature (estimated 7m) at Punta Jimarohuisa on 12 February. This was probably the same individual that had become entangled in a gillnet off Las Bocas and had been released by fishermen two days previously. For the 1985-1987 seasons, numbers of gray whales (all from reports by informants) were (Table 1): for 1985, two unaccompanied ‘adults’ off Tojahui on *ca* 11 January, and an ‘adult’ (one of the previously sighted two?) off Bajerobeta on 15 January; for 1986, one ‘adult’ off Bajerobeta in early January and ‘some cow/calf pairs’ during February; for 1987, ‘some whales’ (including at least one cow/calf pair) in late January and early February. It was not possible to visit Tojahui by land during the 1988 season, and thus no reports from informants were obtained. On 18 February, an aerial observation over Tojahui, Yavaros and nearby Bahía Santa Bárbara produced no gray whale sightings.

No data were forthcoming for the 1989 season, but information for the 1990-1995 seasons was obtained by interviewing (in 1994 and 1995) reliable informants and by on-site visits during the 1994 season by two students reporting to one of the authors (OV) (Table 1). The six resident fishermen, including G. Rojo, interviewed in February 1994, stated that no gray whales had been seen in the area during the prior four years, and one of them, R. Valenzuela, mentioned that the only inshore whale seen by him during that time was a juvenile *quila* (fin whale) which he witnessed (February 1993) stranding itself on the beach following a chase by a *bufeo* (killer whale) (a vertebra of the fin whale was later retrieved and deposited in the Marine Vertebrates Collection of ITESM-Campus Guaymas). No gray whales were sighted at Tojahui during a total of 116 hours of effort by the two ITESM-Campus Guaymas students, F. Cardoza and A. Romero, over a total of 10 days in February/March 1994, and none were seen during the 1995 season by the principal informant (G. Rojo) interviewed by one of the authors (OV) in June 1995 (Table 1).

### *Discussion*

A review of all sightings at Tojahui/Yavaros (Table 1; Gilmore *et al.*, 1967) shows no precise timing of arrival and departure dates (earliest definite sighting, 12 January 1957; latest, 1 May 1962). Nevertheless, it seems probable that whales normally arrived around the middle of January.

Despite some sightings in April and one on 1 May, the whales appeared to usually depart by the middle of March (Table 1). However, the sporadic presence and apparent early departures of the few individuals off Tojahui during the 1982-1987 seasons, if not due at times to the presence of killer whales, may indicate a trend of decreasing site fidelity for gray whales normally visiting the site. The Tojahui/Yavaros gray whales may have been relocating to other calving areas.

As in most other mysticetes, the gray whale is predominately a biennial breeder (e.g. Reilly, 1984). Photo-identification studies in the calving/breeding lagoons suggest that most adult females are site-specific, with the same females usually returning to the same lagoon to give birth on alternate years (e.g. Jones and Swartz, 1983; 1985). This biennial breeding trait led Gilmore *et al.* (1967) to speculate that two groups of females, of about the same group size, each occupy Tojahui/Yavaros in alternate years. But, lacking identifiable photographs of individual whales, these authors were unable to verify their hypothesis. Likewise, the hypothesis could not be tested in this study due to a poor photographic record of the increasingly less-abundant and more-difficult-to-approach whales in the years following 1981.

Since no mating behaviour had been observed among the gray whales at Tojahui, Gilmore *et al.* (1967) hypothesised that mating probably occurs in one year off Cabo San Lucas at the tip of the Baja California Peninsula (see also Norris *et al.*, 1983; Urbán-Ramírez *et al.*, 1990) or in the area of Bahía Magdalena, Baja California Sur (Fig. 1), and, subsequently, the pregnant females cross the Gulf of California to the ‘Yavaros’ area the following year (after their normal migration to and from northern waters) to give birth. It is not known from which direction the whales observed at Tojahui arrived during this study, but, if valid, the report of a sighting on 10 January 1983 of ‘a few gray whales (*ballenas pintas*) among several fin whales (*quilas*)’ far seaward of Tojahui/Yavaros, may indicate a more-or-less direct crossing of the southern Gulf of California by gray whales enroute to this area. However, this report may be suspect since pregnant females normally migrate as solitaries, and the report was of a ‘group’ of gray whales (number unspecified). No other reports of far-offshore sightings of this species are known in the Gulf of California.

No mating behaviour has been reported for gray whales in the Gulf of California and southward along the mainland coast of México (although a probable such observation exists for near Roca Partida, part of the oceanic Revillagigedo Archipelago, in April 1960 [notes in Gilmore Collection]). It appears that for northeastern Pacific gray whales the southern limit for this behaviour is off Cabo San Lucas at the tip of the Baja California Peninsula (Norris *et al.*, 1977).

Although occasional births of gray whales have been reported along the southerly migration route and outside the natal lagoons (e.g. Leatherwood and Beach, 1975; Sund, 1975; Shelden *et al.*, 1996), compared to the nearly landlocked lagoons of Baja California, the relatively exposed open-coast calving site at Tojahui is unusual. A plausible hypothesis offered by Gilmore *et al.* (1967) is that the original calving site in this region was located inside Bahía de Yavaros, but that increased fishing and other maritime activities at the rapidly developing port of Yavaros likely forced the whales to abandon this lagoon and relocate to the nearby area off Tojahui.

In 1920, Yavaros was an insignificant port serving as a fuel-storage depot, but later (beginning in the 1960s) developed into an important fishing centre in the economy of northwestern México (West, 1993, fig. 37 and p.158, footnote 97). In addition to high levels of contaminants in the form of domestic and industrial sewage from the town of Yavaros and nearby cities, pesticides and fertilisers from drainage canals of surrounding farmlands, and residual oils, fuels and waste waters from its many fishing boats and fish-processing plants (Segovia, 1997), the bay of Yavaros today serves as an important regional port for deep-draft vessels such as sardine purse-seiners (second in importance for this fishery in all of México) and shrimp trawlers, as well as for numerous 5-6m skiffs (*pangas*) utilised in the coastal artisanal (principally gillnet) fisheries. In September 1996, an aerial census revealed a total of 1,066 *pangas* working along the nearby short stretch of coast between Bahía Santa Bárbara and Camahuiroa[2] (Fig. 2).

Boat traffic continues to increase in this area, and semi-continuous dredging operations to clear and deepen the channel leading into the bay have added to an increasing level of underwater noise. Among other scientists, Myrberg (1990a; b) has cautioned that (presumably similar) increased noise levels create conditions of annoyance and disturbance for several species of marine animals, including gray whales. Since acoustical communication is almost certainly necessary to maintain contact between gray whale mothers and their newborn calves (Dahlheim, 1987), human-induced underwater noise may interfere with this and other important social behaviours. Dahlheim (1983) and Dahlheim *et al.* (1984) reported that gray whales in Laguna San Ignacio (evidently necessarily) became more vocal when exposed to man-made noises, and Jones *et al.* (1994) and Dahlheim *et al.* (1995) found that most gray whales, especially cow/calf pairs, abandoned Laguna San Ignacio for a year in response to a month of underwater playback experiments of noises from outboard motors of boats, industrial activities and other sources, including killer whale vocalisations. As mentioned previously, the only records of gray whales inside Bahía de Yavaros were at a time when killer whales were sighted in the area outside this coastal lagoon.

Although shrimp boats have occasionally been seen trawling close inshore at Tojahui, fishing activities there are mainly limited to close-inshore deployment and retrieval of gillnets by local fishermen working from outboard motor-powered *pangas*. Gillnet fishing is increasing along this entire stretch of coast, and may be the primary reason for the few gray whales once utilising this site to have apparently located slightly farther offshore as compared to earlier years and, also, why they were recently rarely seen even slightly farther south at Punta Jimarohuisa and Las Bocas. Disturbance from high-powered *pangas* and gillnet fishing may have played an important role in the decrease in number of gray whales that seasonally occupied, and now apparently avoid, this calving site. Table 1 includes two definite records of gillnet entrapment of individuals at or near Tojahui (a calf in 1978, and another immature on 10-11 February 1984), as well as three records of strandings of immatures (in 1976 and November 1982) for which cause of death is unknown but may or may not have involved gillnet entrapment. Incidental capture in gillnets may thus have been an important cause of mortality for calves and immatures at this and other areas in the Gulf of California (e.g. a videotape made in 1989 by K.C. Balcomb of an immature entangled and released from a gillnet in the region of La Paz, Baja California Sur), and has been documented in other parts of the migratory route of the species (e.g. Brownell, 1971; Talbot, 1985; Dedina and Young, 1995).

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[2] J.M. García and M.A. Cisneros, pers. comm.

Counts of gray whales (maximum number sighted/stranded per season) between 1954 and 1995 made at Tojahui/Yavaros are compared in Fig. 3. Notwithstanding considerable variability in sighting effort and observer bias over these years, the recent decrease in the number of gray whales is evident, and has led to the apparent abandonment of this calving site. A similar trend and result appears to have occurred at the other Gulf of California calving site of Bahía Santa María.

## Bahía Santa María (Bahía Reforma), Sinaloa

### *Study area*

This extensive lagoon complex (mid-point *ca* 25°03'N; 108°08'W), located in the Municipalities of Angostura and Navolato in central Sinaloa, fronts a wide, low-lying coastal plain almost totally dedicated to agriculture (Fig. 4). Behind the long and narrow, sand dune-crested barrier island of Altamura, several mangrove-lined islands and islets flank the major tidal channels and extensive sand and mud flats. In general, the entire lagoon complex is known as Bahía Santa María (or Bahía Reforma, especially the part fronting the major regional fishing town of La Reforma), but other names have been applied to certain sections (see Fig. 4). A linear distance of about 32km (the approximate length of Isla Altamura) separates the southern and northern mouths of the lagoon. At both entrances, especially the northern one, sand bars and shoal areas flank the relatively narrow tidal channels penetrating the interior of the lagoon.

### *Sightings and strandings*

Local fishermen reported that gray whales formerly arrived at the northern part of the lagoon in January-February and departed in March-April. Similar information was obtained from fishermen by James Mills during visits to the area in the 1960-1962 seasons (Gilmore Collection, no date). A few whales have stranded or been seen at or near the southern entrance to the lagoon, but the main concentration, at least in recent years, was at the northern extremity.

During transects of the lagoon in *pangas*, all sightings of cow/calf pairs (and almost all sightings of gray whales) were made around the northern entrance, in or near the main tidal channel (Fig. 4). Until early February 1989, when the stranding of a 12.37m male occurred, fishermen at the fishing camp of Yameto, near the southern entrance (Punta Varadito), reported that no gray whales had been seen there since about 1974. Evidently, another adult stranded there around that year. The only other known recent occurrence there was a small immature seen in the main tidal channel of that entrance on 12 February 1989.

### *Discussion*

Although, in comparison to the Tojahui/Yavaros site, observations at Bahía Santa María were more sporadic and of shorter duration, the number of gray whales visiting the latter site also has decreased to apparent abandonment. Notwithstanding the relatively high counts for 1954, 1960 and 1982, this conclusion is based on observations and interviews with several local informants who have fished the area for many years, including some elderly gentlemen who have lived in La Reforma their entire lives. All informants agree that gray whale numbers in Bahía Santa María have decreased drastically, especially since the early 1950s. Before that time, many more whales came into the lagoon, and several could even be seen in the innermost waters fronting La Reforma, where they are never seen today. One informant, A. Camacho, adamantly stated seeing 'hundreds' of gray whales in the lagoon around the year 1942. Another resident, P. Bohórquez, whose family was one of the first to settle at La Reforma, remembered his father telling him of a time (*ca* 1910) when so many whales were in the lagoon that it was necessary to be constantly alert while navigating his small fishing sailboat in order to avoid colliding with them. Similar information was obtained from fishermen by J. Mills (*in litt.* to Gilmore, 19 September 1962, Gilmore Collection, no date): A. Obezo remembered seeing gray whales in the lagoon from *ca* 1910, and J. Santos (88 years old at the time of the interview) remembered seeing the whales as a child, *ca* 1880.

These reports agree with the logs of whaling captains who, at times during the 1850s and 1860s, pursued the gray whale (and other species) along this mainland coast of México as

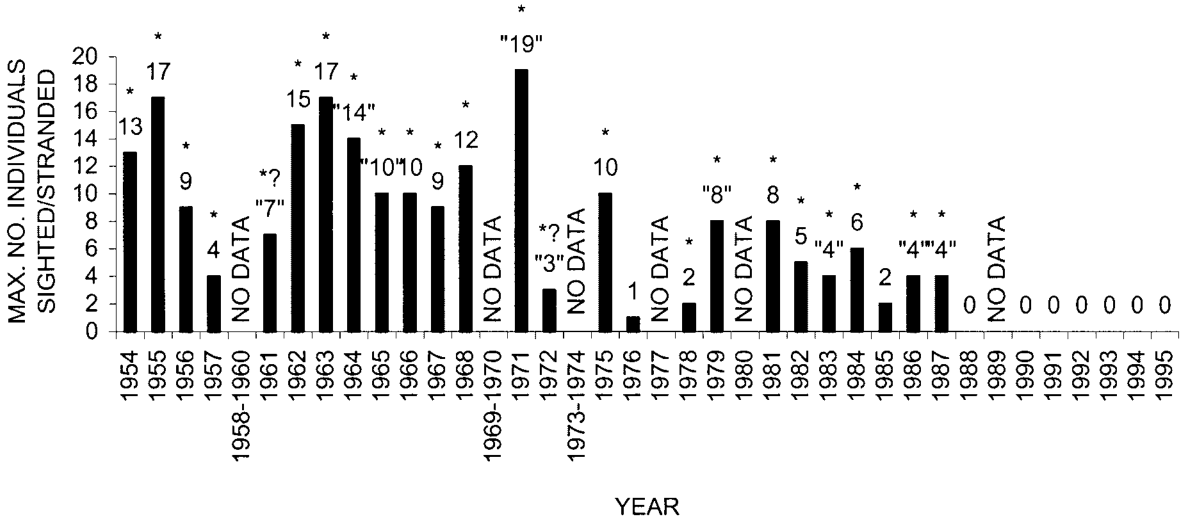

Fig. 3. Maximum number of gray whales sighted/stranded per season, 1954-1995, at Tojahui/Yavaros, Sonora (uncorrected for sighting effort). Numbers in quotation marks indicate close estimates (see Table 1 and text). Asterisks indicate at least one cow/calf pair included in count (but uncertainty of this indicated by question mark).

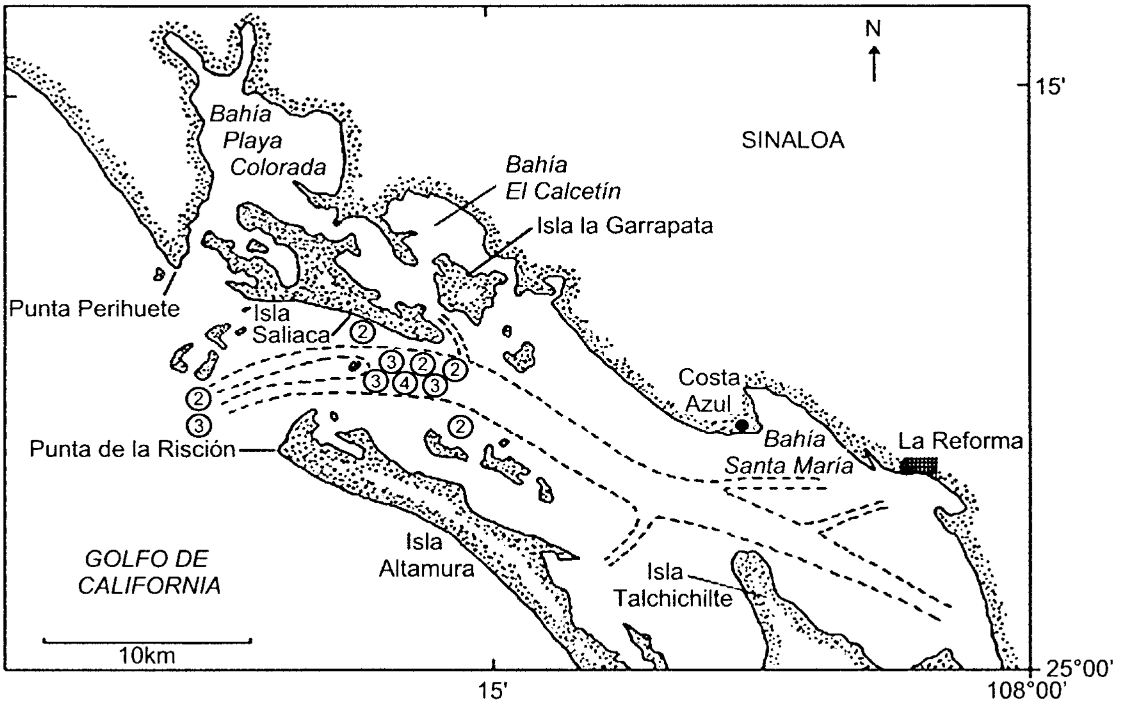

Fig. 4. Locality of gray whale calving site in northern half of Bahía Santa María (Reforma) lagoon complex, Sinaloa. Encircled numbers indicate sightings during 1982 ('2'), 1983 ('3') and 1984 ('4') seasons (see Table 2 and text). Broken lines approximate tidal channels, 10-14+m deep in area of sightings (Alvarez-Arellano and Gaitán-Morán, 1994, fig. 31). Hatching indicates the major regional fishing town of La Reforma.

far south as Bahía Banderas, Nayarit/Jalisco. As reviewed in the scholarly works by Henderson (1972; 1984), those records are not detailed, but lead to the conclusion that, in comparison to recent years, mainland México calving/nursery sites such as Bahía Santa María once hosted considerably larger numbers of gray whales.

Based on his limited aerial observations and the also limited counts made from fishing *pangas* by Mills, and applying a theoretical rate of increase (11%) for the Baja California gray whales between 1953 and 1958, Gilmore (in Gilmore and Mills, 1962) calculated a theoretical 'population' of 72 adult gray whales for the year 1954, 145 for 1960, and 163 for 1961, for the whole Bahía Santa María lagoon complex. The latter two estimates more or less agreed with estimates made by local fishermen who reported to Mills, and it thus appeared to Gilmore that the number of gray whales visiting Bahía Santa María were increasing annually (while they were not increasing at the 'Yavaros' site). However, based on interviews with local residents for this study, it appears that Gilmore's estimate for 1954 was too low, and that rather than increasing, an actually larger number of whales had been visiting the lagoon but had begun to decline by the early 1960s or before. Comparing the earlier counts and estimates reported in Gilmore and Mills (1962) with his counts made in 1975, Gard (1976) also concluded that the number was decreasing. As with the Tojahui/Yavaros calving site, this decline in number of gray whales returning to Bahía Santa María may be correlated with dramatically increased fishing-boat traffic.

Although shoal areas at both entrances effectively bar safe passage of deep-draft vessels into the interior of the lagoon, several commercial shrimp boats have been seen trawling in the adjacent deeper waters. It is believed that the only semi-continuous dredging inside the lagoon has been at La Reforma, where an access channel was cut through the tidal mudflats to allow passage of the many artisanal fishing *pangas* to the dock area fronting a fish processing plant. Several fishermen at La Reforma, Yameto (at the southern entrance), and the fishing village of Costa Azul (Fig. 4) believe that the decrease in gray whales in the lagoon over the past several years is due to the increase in artisanal fishing and *panga* traffic. Interviews with these fishermen and the longtime resident Mexican government fisheries officer indicate that, around 1945, only approximately 50 fishing *pangas* (under sail or powered by relatively small outboard motors) were operating in the whole lagoon complex. Since then, a continual increase in fishermen (*ca* 3,000 in 1995), fishing cooperatives and modernised dockside facilities for processing catches (especially at La Reforma), brought the estimated number of *pangas* to about 1,000 in 1983 and to more than 2,000 in 1989.

Although a recent (September 1996) aerial census of *pangas* in and around Bahía Santa María by fisheries biologists M.A. Cisneros and J.M. García (pers. comm.) showed a lower number (1,385) than the estimate made in 1989 (perhaps due to a recently depressed regional economy), a still-high level of *panga* activity is evident. The majority of these *pangas* now use modern, high-powered (65-75hp) outboard motors, allowing high-speed transit over the entire lagoon complex. During autumn and winter months many of these *pangas* are involved in drift fishing for shrimp utilising relatively small fine-meshed trawl nets (*suriperas*) in the lagoon and potentially compete for space with cow/calf pairs of gray whales. A more negative effect on the whales, however, is the many *pangas* that daily exit and re-enter the lagoon. During early mornings and late afternoons, when gillnet (*red agallera*) and long-line (*cimbra*) fishermen are enroute to or returning from offshore fishing grounds, many high-speed *pangas* were seen transiting areas where observations of cow/calf pairs of gray whales were being made near the lagoon's northern entrance (Fig. 4). Almost invariably, this disturbance elicited an evasive reaction by the whales. This behaviour involves rapid diving ('sinking') and prolonged submergence, followed by quiet surfacing with little or no observable or audible spout when only exposing a small area around the blowholes above the waterline, then, again, rapid submergence. The same or similar behaviour (which has been termed 'snorkelling') was mentioned by Hubbs and Hubbs (1967) and has been seen in Laguna San Ignacio, Baja California Sur, where it was interpreted as a reaction indicating that the whales felt molested in the presence of boats (S.L. Swartz, pers. comm., 2 February 1984). Similar behaviour has been observed for gray and fin whales in the presence of killer whales or of sounds produced by these predators, and has been interpreted as a protective mechanism (Cummings and Thompson, 1971; Vidal and Pechter, 1989).

It seems likely that the increased level of high-speed fishing-boat traffic in Bahía Santa María has been a major factor in the decrease in the number of gray whales utilising this lagoon as a calving/nursery area. Increase in boat traffic has also been implicated in the temporary decrease in gray whale numbers in several of the Baja California lagoons. At various times in recent years, fewer whales returned to or even temporarily abandoned Laguna Guerrero Negro, Laguna Ojo de Liebre and Bahía Magdalena, until boat activity was terminated or variously regulated (Gard, 1974; 1976; Bryant *et al.*, 1984). Furthermore, the behavioural changes, especially in vocalisations, preceding the abandonment/avoidance of Laguna San Ignacio by most of the gray whales, especially cow/calf pairs, during underwater noise experiments (Jones *et al.*, 1994), and the avoidance by whales of fishing boats powered by 40hp outboard motors running at high speeds in the same lagoon (Jones *et al.*, 1994), confirm the disturbing effect of high-level underwater noise on gray whales. As mentioned previously, the more numerous outboard motors in use in Bahía Santa María are even higher powered (usually 65 or 75hp) than most of those utilised by fishermen in Laguna San Ignacio.

Table 2 (see p. 39ff.) presents counts of gray whales in Bahía Santa María. The counts for this study began in 1982, and the (combined daily) maximum number observed was 20-22 individuals (10-11 cow/calf pairs) on 22 and 23 February, and 8 March of that year, all at or near the northern entrance of the lagoon. In 1983, the (combined daily) maximum was less, 12 (6 cow/calf pairs) on 19 and 20 February, and 5 March; again all at the northern mouth. Unfortunately, observations for the 1984-1989 seasons were limited to relatively few visits, including aerial searches on one day each of 1985, 1986 and 1988, when no whales were seen. The only records of gray whales in or near the lagoon during those six years show a complete absence of cow/calf pairs, and, for 1984, include only one sighting of a lone individual at the northern entrance, and the stranding of an immature north of there, both reported by reliable informants. For 1989, only the small immature mentioned previously was seen swimming in the southern entrance to the lagoon on 12 February, whilst a necropsy was performed on the 12.37m male that had stranded there a short time earlier (Table 2). Data for the following six years (1990-1995) were reported to one of us (OV) during a June 1995 interview with Sr. Javier Torres, a longtime resident and artisanal fisherman of La Reforma and principal guide within the lagoon complex during this study. Since the last working visit there in 1989, neither he nor (to his knowledge) any of his many fishermen colleagues had seen any gray whales inside or at either entrance to the lagoon, and that recently the northern mouth was often almost completely closed by gillnets.

The available data for maximum numbers of gray whales sighted/stranded per season in Bahía Santa María for the period 1954-1995 are compared in Fig. 5. As with similar data for the Tojahui/Yavaros calving site (Fig. 3), and notwithstanding variability in sighting effort and observer bias, the recent decrease in number of gray whales visiting the lagoon appears evident, especially for cow/calf pairs (last pair sighted in 1983), as does the apparent absence of all gray whales there since the 1989 season.

Although the gray whale has proven itself to be a remarkably resilient species, in light of reports on the continued general increase in the eastern North Pacific stock (e.g. IWC, 1998), the apparent recent abandonment of the calving/nursery sites in Sonora and Sinaloa may be noteworthy with regards to further increase in that stock. If it is assumed that the major calving/nursery lagoons in Baja California are once again nearing or may have already reached their carrying capacity in terms of spatial and/or behavioural limits for further accommodation of calving gray whales (i.e. they are 'saturated'), and because all coastal lagoons and similar sites in the Gulf of California that would seem suitable as calving/nursery refuges are experiencing the disturbing effects of increasing artisanal and/or industrial-scale fishing, thus promoting avoidance of these sites by gray whales, we are led to conclude that, barring an

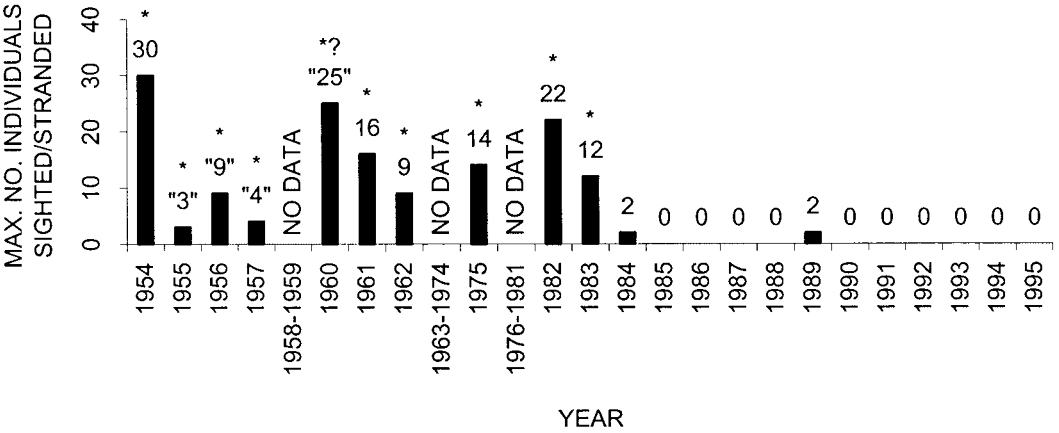

Fig. 5. Maximum number of gray whales sighted/stranded per season, 1954-1995, at Bahía Santa María (Reforma), Sinaloa (uncorrected for sighting effort). Numbers in quotation marks indicate close estimates (see Table 2 and text). Asterisks indicate at least one cow/calf pair included in count (but uncertainty of this indicated by question mark).

unlikely change in regional fishing practices, the present population in the eastern North Pacific will not substantially increase further.

## CALVING TIMES

One of the females observed on 5 March 1983 in Bahía Santa María was notably smaller (*ca* 11m) and easily distinguished by the almost complete absence of barnacles (*Cryptolepas rhachianecti*). Her calf was also relatively small (*ca* 4m), devoid of barnacles, and likely had been born only a short time previously (Table 2). Rice *et al.* (1981) reported that in Laguna Ojo de Liebre most births occur until around 15 February, and estimated 27 January as the mean date for births. Following five consecutive long-term study seasons in Laguna San Ignacio, when only two calves were born after 15 February, Jones and Swartz (1984) concluded that births after that date are relatively rare. Considering the longer distance that pregnant females would have to travel to reach calving sites in the Gulf of California, it seems probable that relatively 'late' births, such as the probable one mentioned above, would not be unusual for Bahía Santa María and for the Tojahui/Yavaros site.

Fishermen in Bahía Santa María told of sighting gray whales in April of some years. These reports, together with definite sightings of cow/calf pairs at the Tojahui/Yavaros site in April and May (Table 1), suggest that in some years pregnant females arrived, gave birth and departed with their calves relatively 'late' from these Gulf of California calving sites. Jones and Swartz (1984) estimated the calving period for gray whales in Laguna San Ignacio as 4-4.5 months, including sightings in late April, early May and even June, and Poole (1984) reports some northward-travelling cow/calf pairs passing central California in late May. It therefore seems probable that some records of gray whales in the southern Gulf of California that would normally be considered 'unseasonable,' represent these later-migrating cow/calf pairs that were tardily initiating their migration to feeding grounds in boreal seas.

## ACKNOWLEDGEMENTS

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We dedicate this paper to the memory of Raymond Maurice Gilmore (1 January 1907 to 31 December 1983).

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[Tables 1 and 2 on following pages]

Table 1

Counts, strandings and observational data on gray whales at Tojahui/Yavaros, Sonora, Mexico[1].

| | | | No. of whales | | |
|---|---|---|---|---|---|
| Year | Date | Observer(s) (method) | Cow/calf pairs | Others | Total |
| 'Before 1940s -1970's' | 'Arriving in Dec.' | F. Leyva (boats off Yavaros) | 'max. of *ca* 8 whales/year'[2] | | |
| 1954 | '2' Feb.[3] | R. Gilmore and G. Ewing (aeroplane) | 6[3] | 1 | 13[3] |
| | 16 Feb. | C. and L. Hubbs and G. Ewing (aeroplane) | 6 | 0 | 12 |
| 1955 | '14' Feb.[4] | R. Gilmore and G. Ewing (aeroplane) | 7 | 3 | 17 |
| 1956 | 26 Jan. | G. Ewing and F. Phleger (aeroplane) | 4 | 1 | 9 |
| 1957 | 12 Jan. | G. Ewing and F. Phleger (aeroplane) | 1 | 0 | 2 |
| | 25 Feb.[5] | R. Gilmore and G. Ewing (aeroplane) | 2 | 0 | 4 |
| 1958-1960 | No data | | | | |
| 1961 | 23 Feb. | A. Harrison (aeroplane) | 'some spouts seen' | | |
| | 1 Mar. | J. Mills (boat) | 'seven spouts'[6] | | |
| 1962 | 11 Feb. | A. Harrison (aeroplane) | '10 whales with some calves, *ca* 15?' | | |
| | 17 Feb. | J. Mills (boat) | 3 | 3 | 9 |
| | 18 Feb. | A. Harrison (aeroplane) | '5 or 6 adults'[7] | | |
| | 8 Mar. | A. Harrison (aeroplane) | 4 | 0 | 8 |
| | 11 Mar. | A. Harrison (aeroplane) | 6 | 3 | 15 |
| | 8 Apr. [7] | A. Harrison (aeroplane) | 4[8] | 0 | 8[8] |
| | 1 May[7] | A. Harrison (aeroplane) | 'cows with calves'[9] | | |
| 1963 | 3 Feb. | R. Brownell and R. Boice (boat) | 7 | 1 | 17 |
| | 'Feb.-Mar.' | A. Harrison (aeroplane) | 3-4 | *ca* 3 | 9-11 |
| 1964 | 28 Feb. | A. Harrison (aeroplane) | '5'[10] | 0 | '10'[10] |
| | 8 Mar. | A. Harrison (aeroplane) | '6'[10] | 2 | '14'[10] |
| | 22 Mar. | A. Harrison and R. Brownell (aeroplane) | 2 | 1 | 5 |
| 1965 | 1 Feb. | A. Harrison (aeroplane) | 1 | 0 | 2 |
| | 5 Feb. | A. Harrison (aeroplane) | 3 | 0 | 6 |
| | 21 Feb. | A. Harrison (aeroplane) | 4-5 | 0 | 8-10 |
| | 22 Feb. | A. Harrison (aeroplane) | 4-5 | 0 | 8-10 |
| 1966 | Early Feb. | A. Harrison (aeroplane) | 4 | 2 | 10 |
| | Mid-late Feb. | A. Harrison (aeroplane) | 4 | 2 | 10 |
| | 6 Mar. | A. Harrison (aeroplane) | 3 | 0 | 6 |
| 1967[11] | 12 Feb. | A. Harrison (aeroplane) | 4 | 1 | 9 |
| | 1 Mar. | A. Harrison (aeroplane) | 'whales present' (but not counted) | | |
| | 9 Mar. | A. Harrison (aeroplane) | 0 | 0 | 0 |
| | 16 Mar. | A. Harrison (aeroplane) | 'whales present' (but not counted) | | |
| 1968[11] | 18 Feb. | A. Harrison (aeroplane) | 3 | 5 | 11 |
| | 9 Mar. | A. Harrison (aeroplane) | 4 | 4 | 12 |
| | 30 Mar. | A. Harrison (aeroplane) | 2 | 0 | 4 |
| 1969[11] | 6 Apr. | A. Harrison (aeroplane) | 0 | 0 | 0 |
| | 13 Apr. | A. Harrison (aeroplane) | 0 | 0 | 0 |
| 1970 | No data | | | | |
| 1971[11] | 1 Feb. | A. Harrison (aeroplane) | 6-7 | 5 | 17-19 |
| | 1 Mar. | A. Harrison (aeroplane) | - | - | *ca* 19 |
| '*ca* 1972' | 'Winter' | M. Robinson[12] (shore at Huatabampito) | 'spouts seen, *ca* 2 or 3 whales' | | |
| 1973-1974 | No data | | | | |
| 1975 | 25 Feb. | R. Gard, S. White, H. Griese, B. Mate[13] (aeroplane) | 5 | 0 | 10 |
| 1976 | Early Apr. | Local newspaper[14] (stranded at Las Bocas) | - | 1[14] | 1 |
| 1977 | No data | | | | |
| 1978 | 'Winter' | G. Rojo (boat at Tojahui) | 1[15] | 0 | 2 |
| 1979 | 26 Feb. | L. and S. Findley, D. Arosemena, K. Crean *et al.*[16] (boat at Tojahui) | 3 | 1-2 | 7-8[17] |
| 1980 | 17-18 Feb. | L. Findley, O. Vidal and 13 students[16] (shore at Las Bocas)[18] | 0 | 0 | 0 |
| 1981 | 28 Feb. | L. Findley, O. Vidal, D. Arosemena, M. Hatziolos and 40 students[16] (shore at Las Bocas)[18] | 0 | 0 | 0 |
| | 1 Mar. | L. Findley, O. Vidal, D. Arosemena, M. Hatziolos and 40 students[16] (boat and shore at Tojahui) | 3 | 2 | 8 |
| | 2 Mar. | L. Findley, O. Vidal, D. Arosemena, M. Hatziolos and 40 students[16] (boat and shore at Tojahui) | 3 | 1 | 7 |
| | 'Mar.' | Local fishermen[19] (boat off Huatabampito) | 0 | 1[19] | 1 |
| 1982 | 24 Jan.-25 Feb.[20] | O. Vidal *et al.*[16] (boat and shore at Tojahui) | 2 | 1 | 5 |
| | *ca* 10 Nov. | G. Rojo, O. Vidal, P. Aguilar, L. Maroñas[16] (stranded at La Filomena) | 0 | 1 | 1[21] |
| | *ca* 25 Nov. | L. Findley, O. Vidal *et al.*[16] (stranded near mouth of Bahía de Yavaros) | 0 | 1 | 1[22] |
| 1983 | *ca* 10 Jan. | J. Cipriano López[23] (boat off Yavaros) | 'a few whales' | | |
| | *ca* 18-19 Jan. | F. Leyva (*cf.* footnote 2) (shore at Yavaros) | 1 | 0 | 2[24] |
| | 19 Jan. | G. Rojo[25] (shore at Tojahui) | 1 | 1 | 3 |
| | 26 Jan. | D. López[25] (shore and boat at Tojahui) | 'about 4 whales'[26] | | |
| | 27 Jan. | Local resident (shore at Yavaros) | '3 whales'[24] | | |
| 1984 | 20-21 Jan. | G. Rojo[25] (shore at Tojahui) | 1 | 0 | 2 |
| | 22 Jan. | O. Vidal, G. Rojo, G. Zuñiga, F. de Boer[16] (shore at Tojahui) | 1 | 0 | 2 |

cont.

Table 1 continued

| Year | Date | Observer(s) (method) | No. of whales | | |
|---|---|---|---|---|---|
| | | | Cow/calf pairs | Others | Total |
| 1984 (cont.) | 23-24 Jan. | G. Rojo[25] (shore at Tojahui) | 1 | 0 | 2 |
| | 26 Jan. | L. Findley and J. Valverde[16] (aeroplane at Tojahui) | 0 | 1? | 1?[27] |
| | 28 Jan. | O. Vidal, L. Findley, G. Rojo, M. Morrissey *et al.*[16] (shore at Tojahui) | 1 | 0 | 2 |
| | 29 Jan. | O. Vidal, L. Findley, G. Rojo, M. Morrissey *et al.*[16] (shore at Tojahui and boat between there and the mouth of Bahía de Yavaros) | 3 | 0 | 6 |
| | 8 Feb. | G. Rojo[25] (shore at Tojahui and Bajerobeta) | 2 | 0 | 4 |
| | 10-11 Feb. | Local fisherman[28] (shore and boat at Las Bocas) | 0 | 1 | 1[29] |
| | 12 Feb. | O. Vidal, G. Rojo, K. Gárate, R. Halffter[16] (boat at Punta Jimarohuisa) | 0 | 1 | 1[*cf.* 29] |
| 1985 | *ca* 11 Jan. | R. Valdéz [30] (boat at Tojahui) | 0 | 2 | 2 |
| | 15 Jan. | R. Flórez and D. Quijano [31] (shore at Bajerobeta) | 0 | 1 | 1 |
| 1986 | 'Early Jan.' | G. Rojo[25] (shore at Bajerobeta) | 0 | 1[32] | 1 |
| | 'Feb.' | G. Rojo[25] (shore at Bajerobeta) | 'some pairs'[33] | - | 4?[33] |
| 1987 | 'Late Jan.-early Feb. | G. Rojo and D. López[25] (shore and boat at Tojahui) | 1[34] | 'some others'[35] | 4?[35] |
| 1988 | 18 Feb. | O. Vidal, L. Findley, J. Morelli (aeroplane at Tojahui-Yavaros-Bahía Santa Bárbara) | 0 | 0 | 0 |
| 1989 | No data | | | | |
| 1990-1993 | 'Winters' | G. Rojo and D. López[25], R. Valenzuela, P. Sánchez, R. Rubio and Rosalino [36] (shore and boats at Tojahui, Bajerobeta and Las Bocas) | 0 | 0 | 0 |
| 1994 | 12-14 Feb. | F. Cardoza and A. Romero[37] (shore and boat at Tojahui) | 0 | 0 | 0 |
| | 26-27 Feb. | F. Cardoza and A. Romero[37] (shore at Tojahui) | 0 | 0 | 0 |
| | 5-6 Mar. | F. Cardoza and A. Romero[37] (shore at Tojahui) | 0 | 0 | 0 |
| | 12-13 Mar. | F. Cardoza and A. Romero[37] (shore at Tojahui) | 0 | 0 | 0 |
| 1995 | 'Winter' | G. Rojo[25] (shore and boat at Tojahui and Bajerobeta) | 0 | 0 | 0 |

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[1] Table, in part, modified from table 1 of Gilmore *et al.* (1967, p.202) for the period 1954-1966, but not including their dates on which no whales ('0') were seen (dates usually very early or very late in the season). The proper locality name for their counts is (Ensenada de) Tojahui [Gilmore *et al.*, 1967, p.201; Gilmore Collection in San Diego Natural History Museum, San Diego, California; R.L. Brownell, Jr., pers. comm., Apr. 1986]. Locality shown in Fig. 2. Data for years 'Before 1940s-1970s', 1967-1969, 1971, '*ca* 1972', and 1976-1995 published here for the first time.

[2] Long-time resident and former fisherman of Yavaros, reported this approx. max. number of whales seen around the mouth of Bahía de Yavaros for any one year, except *ca* 1966 when 'about 20 whales' were seen there. He further stated that 'fewer whales appeared in some years' (pers. comm., Jan. 1983).

[3] From Gilmore *et al.* (1967, table 1), but date appears as 'Feb. 3' in Gilmore and Ewing (1954, p.14). Notes in Gilmore Collection for 3 Feb. 1954 refer to five cow/calf pairs and solitary adult for total of 11 individuals; the additional cow/calf pair (to total 6 pairs) is explained in footnote '1' of table 1 in Gilmore *et al.* (1967, p.202) as being sighted nine miles south of the other whales.

[4] From Gilmore *et al.* (1967, table 1), but date appears as 'Feb. 27' in Gilmore (1960, p.28) and notes in Gilmore Collection.

[5] From Gilmore *et al.* (1967, table 1), but date appears as 'Feb. 27' in notes in Gilmore Collection.

[6] Not reported in Gilmore *et al.* (1967). Nevertheless, Mills (*in litt.*, including a photograph, to Gilmore, 15 Mar. 1961, in Gilmore Collection) believed the spouts to be from gray whales. Considering the sighting date and the inshore position of Mills, we accept his identification.

[7] Not reported in Gilmore *et al.* (1967); Harrison pers. comm. to Mills who reported to Gilmore (*in litt.*, 19 Sep. 1962, in Gilmore Collection).

[8] Harrison reported to Mills (*cf.* footnote 7) groups of 'two adults and a calf'. However, in a later communication to Mills, he was unable to verify if it had been 'four groups each of two adults and one calf, or four groups each of one adult and one calf' (Gilmore Collection). We accept the latter as more plausible.

[9] Harrison did not count the whales, but did take photographs of several cow/calf pairs that he forwarded (*via* Mills) to Gilmore, who identified them as gray whales (Gilmore, *in litt.* to Mills, 29 Sep. 1962, in Gilmore Collection).

[10] In Harrison, *in litt.* to Gilmore, 11 Apr. 1964 (Gilmore Collection), these counts are: '4-5' cows with calves and two solitaries for total of '12-14' individuals (for 8 Mar.).

[11] Data for these years provided by R.L. Brownell, Jr., communicated to him by A. Harrison (*in litt.*: 12 Feb., 1 and 6 Mar. 1967; 11 Mar. 1969; 12 Mar. 1971). The two dates for 1969 are late in the season, which may account for no whales being seen; thus this year is considered a 'no-data year' for purposes of Fig. 3.

[12] Then of Dept. Biol. Sci., Univ. Arizona, Tucson (pers. comm., Aug. 1982).

[13] From Gard (1976, p.8, table 2).

[14] A poor, but identifiable photograph of a stranded immature, with caption stating 'between 6 and 7m long, … just prior to Easter week,' appearing in newspaper *Informador del Mayo* (Navojoa, Sonora), No. 6772, 3 Apr. 1976, p.1. Otherwise, no data for this year.

[15] The calf, entangled in a gillnet near shore, liberated by G. Rojo and other fishermen assisted by a shrimp boat. Meanwhile, 'another whale [most likely the calf's mother] waited nearby' (G. Rojo, pers. comm., Mar. 1981).

[16] All then from ITESM-Campus Guaymas.

[17] Count not more exact due to limited observational time (L. Findley, field notes). Some whales photographed.

[18] A continuous daylight shore watch was maintained at Las Bocas (Fig. 2) without success. Although no whales were sighted, these dates are included to emphasise (what we did not realise then) the marked preference of the whales for the area directly off Tojahui. Tojahui site was not visited on these dates.

[19] Persons knowledgeable of gray whale characteristics, reporting (pers. comms) the whale as 'large' (adult).

[20] This period represents the first and last days whales were sighted by ITESM personnel (principally Vidal, in semi-continuous residence) at Tojahui, including 16 days when whales were present at the site and 17 days when observers were absent or whales were temporarily absent (see text). No whales sighted on site visits on 12, 24, 27-31 Dec. 1981 and 6-19 Jan. 1982. Principal informant, G. Rojo, reported whales arrived 21 Jan. and sightings on 22 and 23 Jan. No sightings on 26-28 Feb. and 1-15 Mar., when observers (principally Vidal) were present.

[21] An immature (*ca* 6.19m, reported as '6.0m' in Vidal, 1991, p.14) stranded at La Filomena (Fig. 2). G. Rojo (pers. comm., Nov. 1982) reported carcass first seen on beach about this date; decomposed remains not seen by us until 20 Nov.; partial skeleton retrieved 25 Nov. (by which time head had separated from body). Partial skull (condylobasal length 1.4m) and most of skeleton now housed at ITESM-Guaymas (ITESM 821125). Total length estimated by 'multiplying condylobasal length by 100/23 or 4.35, which should give an estimate of body length accurate to within a few inches' (D.W. Rice, *in litt.* to us, 16 Jan. 1986).

[22] Another immature (*ca* 7.4m, estimated by same method in footnote 21) stranded near mouth of Bahía de Yavaros (Fig. 2). G. Rojo (pers. comm., Nov. 1982) reported carcass first seen on beach about this date; remains not seen by us until 12 Feb. 1983 when skull (condylobasal length 1.7m) and most of anterior skeleton excavated from beach, and 26 Feb. when posterior skeleton excavated; now housed at ITESM-Guaymas (ITESM 830212) [in Vidal, (1991: 14) month of collection in error (should be II, not 'XI', which is month of stranding in 1982)]. Based on estimated length, this individual represents a weaned 'calf' or a juvenile (see Sumich, 1986).

[23] Captain of the shrimp boat *Indio Mayo*, reported (pers. comm.) 'a few gray whales among several fin whales,' *ca* 37km off mouth of Bahía de Yavaros.

[24] These whales reported (pers. comms) as being inside Bahía de Yavaros, *ca* 200m off main boat dock at Yavaros.

[25] Long-time Tojahui/Bajerobeta area fishermen and reliable informants cooperating in our sighting programme. Knowledgeable of gray whale characteristics.

[26] This sighting and that of 19 Jan. represent the only ones at Tojahui for the 1983 season and perhaps indicate decreasing site-fidelity of the whales normally visiting there. No other sightings reported by other local fishermen (who daily fish the area) or by several biologists (principally Vidal and Findley) during site visits: 15-16, 22, 29-30 Jan.; 5-6, 12-13, 19, 26-27 Feb.; and 29 Mar. Also, local fishermen at Las Bocas reported (pers. comms, through 27 Feb.) no sightings there.

[27] Identification not confirmed due to brevity of sighting, but this close-inshore whale was probably a gray whale.

[28] Mainly L. López and A. Sandoval (pers. comms, 12 Feb. 1984), longtime fishermen at Tojahui/Las Bocas and knowledgeable of gray whale characteristics.

[29] An immature (*ca* 7m) entangled in a gillnet *ca* 70m off Las Bocas on 10 Feb.; liberated by local fishermen the following day. Almost certainly the same individual sighted near Punta Jimarohuisa on 12 Feb.

[30] Fisherman and resident of Las Bocas (pers. comm., Jan. 1985).

[31] Longtime fishermen at Bajerobeta and knowledgeable of gray whale characteristics, reported the whale as 'large' (adult) (pers. comms, Jan. 1985).

[32] G. Rojo (pers. comm., Mar. 1987) reported the whale as 'large' (adult).

[33] 'Some cow/calf pairs' interpreted as at least two pairs (for total of '4?' individuals) for purposes of Fig. 3.

[34] This cow/calf pair, at least, remained at the site during *ca* 5 days (G. Rojo, pers. comm., Mar. 1987).

[35] 'Some others' interpreted as at least two individuals (for total of '4?') for purposes of Fig. 3.

[36] Longtime fishermen and residents of the area. When interviewed, with G. Rojo and D. López (*cf.* footnote 25) by F. Cardoza and A. Romero (*cf.* footnote 37) in Feb. 1994, all six informants reported the complete absence of gray whales in the area at that time and 'during the last four years' (i.e., 1990-1993) (see text).

[37] ITESM-Campus Guaymas students reporting to O. Vidal. Sighting efforts: Feb. 12-14 (32hrs), Feb. 26-27 (32hrs), Mar. 5-6 (32hrs), Mar. 12-13 (20hrs).

Table 2

Counts, strandings and observational data on gray whales at Bahía Santa María (Reforma), Sinaloa, Mexico.

| Year | Date | Observer(s) (method) | No. of whales | | |
|---|---|---|---|---|---|
| | | | Cow/calf pairs | Others | Total |
| 1954[1] | Early Jan. | G. Ewing and R. Menzies (aeroplane) | 0 | 1 | 1 |
| | 5 Feb. | R. Gilmore and G. Ewing (aeroplane at south entrance) | 2 | 3[2] | 7[3] |
| | 5 Feb. | R. Gilmore and G. Ewing (aeroplane at north entrance) | 10 | 3 | 23[3] |
| 1955 | *ca* '27' Feb.[4, 5] | R. Gilmore and G. Ewing[6] (aeroplane at north entrance) | 1 | 1[5] | 3[5, 7] |
| | 28 Feb.[8] | R. Gilmore and G. Ewing (aeroplane at both entrances) | 0 | 0 | 0 |
| 1956 | *ca* 15-16 Feb.[4, 9] | R. Gilmore and G. Ewing[6] (aeroplane at north entrance) | 4 | 1 | 9[10] |
| 1957[4, 11] | 12 Jan. | G. Ewing and F. Phleger (aeroplane at north entrance) | 0 | 1[12] | 1 |
| | *ca* 28 Feb.[4] | R. Gilmore and G. Ewing (?) (aeroplane)[13] | 2 | 0 | 4[4, 11] |
| 1958-59 | No data | | | | |
| 1960 | 23 Feb.[14] | J. Mills (boat at north entrance) | 'about 25 whales'[6, 15] | | |
| 1961 | 26 Feb.[16] | J. Mills (boat at north entrance) | 7[17] | 0 | 14 |
| | 27 Feb.[16] | J. Mills (boat at north entrance) | 8[17] | 0 | 16[18] |
| 1962[19] | 31 Dec. 1961 *or* 1 Jan.[20] and 4 Jan.[20] | Local fisherman[20] | 1[20] | 1?[20] | 3?[20] |
| | 19 Feb. | J. Mills (boat at north entrance) | 0 | 1 | 1 |
| | 20 Feb. | J. Mills (boat at north entrance) | 3 | 3 | 9 |
| 1963-74 | No data[21] | | | | |
| 1975 | 25 Feb. | R. Gard, S. White, H. Griese, B. Mate[22] (aeroplane at north entrance) | 7 | 0 | 14 |
| 1976-81 | No data | | | | |
| 1982 | 22-23 Feb. | L. Findley, O. Vidal, D. Arosemena, G. Pechter (boat at north entrance) | 7-8 | 0 | 14-16 |
| | 8 Mar. | L. Findley, O. Vidal, G. Pechter (boat at north entrance and outside) | 3[23] | 0 | 6 |
| | 8 Mar. | L. Findley, O. Vidal, G. Pechter (boat at south entrance and outside) | 0 | 0 | 0 |
| 1983 | 19-20 Feb. | L. Findley, O. Vidal (boat at north entrance) | 3 | 0 | 6 |
| | 5 Mar. | O. Vidal and five students (boat at north entrance) | 4[24] | 0 | 8[*cf.* 24] |
| | '*ca* 9, 14 + 21 Mar.' | Local fishermen (pers. comms) (boats at north entrance) | 1[25] | 0 | 2 |
| | 29-30 Mar. | O. Vidal and four students (boat at north entrance and outside) | 0 | 0 | 0 |
| | '*ca* 27 Dec.' | Local fishermen (pers. comms) (boats at north entrance) | 0 | 1 | 1 |
| 1984 | 'Jan.' | Local fishermen (pers. comms) (boats at north entrance) | 0 | 1 | 1 |
| | 'Early Mar.' | D. Ayón (shore north of north entrance) | 0 | 1[26] | 1 |
| 1985 | 2 Mar. | O. Vidal, M. Morrissey, J. Goodyear, J. Morelli (aeroplane at both entrances) | 0 | 0 | 0 |
| 1986 | Early Mar. | O. Vidal, L. Findley, J. Morelli (aeroplane at both entrances) | 0 | 0 | 0 |
| 1987 | 1 Mar. | O. Vidal, D. López, H. Medellín (boat at north entrance) | 0 | 0 | 0 |
| 1988 | 18 Feb. | O. Vidal, L. Findley, J. Maldonado, J. Morelli (aeroplane at both entrances) | 0 | 0 | 0 |
| 1989 | 5 Feb. | O. Vidal, P. Cendón, G. Alvarez-Manilla, A. Laborde (stranded at south entrance) | 0 | 1[27] | 1 |
| | 12 Feb. | L. Findley, O. Vidal and 14 students (shore at south entrance) | 0 | 1[28] | 1 |
| 1990-1995 | 'Winters' | J. Torres[29] and other local fishermen (boats at both entrances) | 0 | 0 | 0 |

[1] Gilmore and Ewing (1954, p.14).

[2] Includes one whale not seen during a previous flight on 3 Feb., other whales (including cow/calf pairs) probably the same ones seen on that date (*cf.* Gilmore, 1960, table 5).

[3] From these two counts, Gilmore (*cf.* footnote 6 below) estimated adult 'population' in the entire lagoon at this time as '72' (see text).

[4] From Gilmore (1960, table 5).

[5] *Ca* '27' Feb. (Gilmore, 1960, p.28 and table 5) appears as 'Feb. 27: one cow/calf pair and three solitaries (adults), for a total of five individuals' in notes in Gilmore Collection.

[6] From Gilmore and Mills (1962, p.27).

[7] This count reported [in error?, *cf.* footnote 5] as total for the entire lagoon in Gilmore (1960, table 5) and Gilmore and Mills (1962, p.27). Although flights were made over both lagoon entrances, whales were sighted only at the northern one.

[8] This flight, over both lagoon entrances, not reported in Gilmore (1960, table 5) or Gilmore and Mills (1962, p.27), but appears in notes in Gilmore Collection. Although only one day after the sightings on 27 Feb. no whales were seen.

[9] *Ca* 15 and 16 Feb. (Gilmore, 1960, table 5) appears as 'Feb. 3 and 4' in Gilmore and Mills (1962, p.27), and as 'Feb. 14 and 15' in notes in Gilmore Collection.

[10] Discrepancy in accounts: 'Nine whales' *ca*. 15 Feb [= 'Feb. 3' or 'Feb. 14'?, *cf.* footnote 9] in Gilmore (1960, pp.28-29; table 5) *vs* 'four whales' [probably the same individuals counted on 15 Feb.] *ca* 16 Feb. [= 'Feb. 4' or ' Feb. 15'?, *cf.* footnote 9] in Gilmore and Mills (1962, p.27).

[11] Another discrepancy in accounts: Gilmore and Mills (1962, p.27, 4th paragraph, 1st sentence) *vs* Gilmore (1960, pp.28-29; table 5). We have accepted the latter.

[12] An adult not reported in Gilmore (1960) and Gilmore and Mills (1962); pers. comm., Ewing to Gilmore (notes in Gilmore Collection).

[13] Not known if flight(s) covered only one or (probably) both lagoon entrances; counts given as totals in Gilmore (1960, table 5) and Gilmore and Mills (1962, p.27).

[14] 'Feb. 23' (Mills, *in litt.* to Gilmore, 30 Nov. 1960, Gilmore Collection) appears as 'one day in Feb.' in Gilmore and Mills (1962, p.27).

[15] 'The fishermen with Mills at N entrance estimated the entire 'population' [in whole lagoon] to be about 100' (Gilmore and Mills, 1962). From an estimate of 72 whales for 1954, Gilmore estimated the population in the whole lagoon to be 145 for the 1960 season (Gilmore and Mills, 1962, p.27) (see text).

[16] 26 and 27 Feb. (Mills, *in litt.* to Gilmore, 15 Mar. 1961, Gilmore Collection) appears as 'two days in Feb.' in Gilmore and Mills (1962, p.27).

[17] 'Seven cows with calves on the first trip, and eight on the second...' (Gilmore and Mills, 1962, p.27). We assume these represent the same individuals plus another cow/calf pair for total of eight pairs. However, Gard (1976, p.8) apparently assumed they represented different individuals, for a total of 15 (?) pairs.

[18] Local fishermen estimated 125 cow/calf pairs (no solitaries) in the whole lagoon at this time. From prior calculations (Gilmore and Mills, 1962), Gilmore estimated the population in the whole lagoon to be 163 for the 1961 season (see text).

[19] Mills, *in litt.* to Gilmore, 19 Sep. 1962, Gilmore Collection. Data for this season not reported in Gilmore and Mills (1962).

[20] 'Sr. Arturo Montoya of La Reforma reported this as the first day of the season when he saw a whale in the lagoon, and the first calf was seen Jan. 4' (Mills, *in litt.* to Gilmore, 19 Sep. 1962, Gilmore Collection); these thus represent minimum counts.

[21] *Ca* 1974, a 'large' gray whale stranded near fishing village of Yameto at the southern entrance to the lagoon; but 'none seen there in recent years' (resident fishermen, pers. comms, 8 Mar. 1982).

[22] Gard (1976, p.8 and table 2).

[23] Different cow/calf pairs than those seen 22 and 23 Feb. for total of 10-11 pairs seen in the 1982 season (Fig. 5).

[24] Includes a cow/calf pair seen 19 and 20 Feb. and three new pairs, one of which was a small cow and very small calf (apparently very recently born), for total of six pairs seen in the 1983 season (Fig. 5).

[25] Probably the same small cow and very young calf (*cf.* footnote 24) which arrived late and remained after departure of other pairs; last sighting was 21 Mar.

[26] Biologist D. Ayón (Facultad de Ciencias del Mar, Univ. Autónoma de Sinaloa, Mazatlán) reported this immature (*ca* 7m) stranded at La Casiona fishing camp, a few km north of the lagoon's northern entrance (pers. comm., 5 Mar. 1984).

[27] A recently stranded 12.37m male; necropsied by ITESM students and us (the skull, most of the skeleton and tissue samples housed at ITESM-Guaymas; ITESM 890212).

[28] An immature sighted during necropsy of the stranded male (*cf.* footnote 27).

[29] Long-time resident artisanal fisherman of La Reforma and often our guide within the lagoon complex (interviewed in June 1995 by O. Vidal), reported having seen no gray whales at either entrance, nor having heard of reports of any from his many fishermen colleagues, since our last working visit to the lagoon in 1989. He also mentioned that recently the northern entrance was often almost completely closed by gillnets.

# Estimated trends in abundance of eastern Pacific gray whales from shore counts (1967/68 to 1995/96)[1]

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ABSTRACT

Estimates of abundance of eastern Pacific gray whales (*Eschrichtius robustus*) are obtained from counts made during their southbound migration past a shore-based station near Monterey, California. Assuming an exponential rate of increase, the population is estimated to have increased at 2.5% per annum (SE = 0.3%) between 1967/68 and 1995/96. However, there is some indication that the population growth is slowing, so that an asymptotic growth curve may be more appropriate. The estimated asymptote from a logistic model is 26,046 (SE = 6,281) and the inflection point is approximately in 1971 (SE = 6.5). The onset of the migration, when 10% of the whales have passed the station, has occurred increasingly later through this sample period, by approximately one day every two years. Median dates show a similar trend of roughly one day every three years. However, there is no significant change in the date at which 90% of whales have passed the station.

KEYWORDS: ABUNDANCE ESTIMATE; GRAY WHALE; PACIFIC OCEAN; MIGRATION; SURVEY-SHORE-BASED; INDEX OF ABUNDANCE

## INTRODUCTION

Data from shore-based censuses of eastern Pacific gray whales, carried out between 1967/68 and 1979/80, were analysed by Reilly *et al.* (1980; 1983) to estimate trends in abundance. However, data from subsequent censuses in 1984/85, 1985/86, 1987/88, 1992/93, 1993/94 and 1995/96 have not been analysed in a way consistent with those of Reilly *et al.* (1980; 1983). In 1986, simultaneous counts were made for the first time by observers operating independently in different sheds with identical viewing areas (Rugh *et al.*, 1990). Since then that test has been repeated each season (Rugh *et al.*, 1993) and has resulted in refinements to abundance estimates by correcting for whales in the viewing area not recorded by single observers. Using the new correction factor, Breiwick *et al.* (1988) provided an initial abundance estimate for the 1987/88 census, later revised by Buckland *et al.* (1993). Absolute abundance estimates have also been made for the 1992/93 and 1993/94 censuses (Laake *et al.*, 1994), and 1995/96 (Hobbs *et al.*, 1996).

At the 1989 meeting of the Scientific Committee of the International Whaling Commission, a Working Group was set up 'to specify pre- and post-1980 Monterey shore censuses to allow tests for trend through 1988' (IWC, 1990). The recommendations of that Working Group were:

(1) A relative abundance estimate should be calculated for each survey year. Each estimate should be calculated as far as possible in a consistent manner. The Hermite polynomial model will be used for the time-density model to estimate the number of whales missed during periods of poor visibility, no watch and at the 'tails' of migration.
(2) The three aerial surveys (1978/79, 1979/80, 1987/88) will be compared. Average distance offshore is known to vary with year, hence it is necessary to test whether detection probability at any given distance varies with year. This detection probability may be estimated by taking the ratio of number of pods seen from shore to number seen from aerial surveys for each of several distance intervals. The probabilities may be arbitrarily scaled so that the maximum is unity, or scaled to be consistent with results from double counting. A test of whether the probabilities are constant across the three survey years will then be carried out. (Note: There will be four sets of probabilities since there was both a north and a south station in 1987/88.)
(3) If the above test is not significant (i.e. aerial:shore probabilities are not different among the four cases), the aerial survey data will be pooled and the detection curve will be estimated either by the probabilities calculated by interval or by a hazard-rate or Hermite polynomial model fitted to those probabilities (scaled so that their sum equals total sample size). If this test is significant, pool 1978/89 and 1979/80 data and model as above. Fit the 1987/88 data separately.
(4) Adjust the number of pods according to the estimated detection curve, as found above, so that pods missed are corrected for. Should the test in Step 2 be significant, use the adjustments calculated from the two earlier aerial surveys to apply to all shore surveys carried out without reticle binoculars and use the adjustments calculated from the 1987/88 aerial survey (averaged across the north and south stations) to correct the remaining surveys (i.e. 1984/85; 1985/86 and 1987/88).
(5) In recent surveys, periods with Beaufort $>4$ will be discarded. In earlier surveys (1967/68-1979/80), whole (5hr) watch periods in which Beaufort $>4$ was recorded will be discarded.
(6) Since it is only necessary to estimate relative abundance to test for a trend, no corrections for biased estimation of pod size will be made.
(7) Independent estimates will be made for the north and south stations for analysis of the 1987/88 survey data and the average across both stations used. This will give greater comparability between that survey and earlier surveys, for which there was just one station.
(8) Once the series of relative abundance estimates has been calculated, it will be rescaled so that it passes through the best absolute abundance estimate available - considered to be the 1987/88 estimate, when double-counting was carried out throughout the season.

In addition to the above, the National Marine Mammal Laboratory (NMML) requested that periods with visibility code $>4$ be treated as for periods with Beaufort $>4$ and that estimates would be presented to allow an assessment of whether there had been a trend in migration dates. This paper reports on the attempts to carry out the above analyses and tabulates estimates of abundance.

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[1] Paper originally submitted in 1992.

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## METHODS

The analysis methods used were as far as possible as laid down by the Working Group. They are reported in more detail by Breiwick *et al.* (1988) and by Buckland (1992).

Dates at which gray whale pods pass Monterey may be modelled as a probability density function of the following form:

$$f(y) \equiv \alpha(y_s) \cdot \left(1 + \sum_{j=1}^{m} a_j \cdot H_j(y_s)\right) \Big/ \beta$$

where:

$y$ is the date (measured to the nearest minute) a pod passes;
$y_s = (y-\mu)/\sigma$, a standardised $y$ value;
$\alpha(y_s) = \exp(-y_s^2/2)$;
$H_j(y_s)$ is the $j^{th}$ Hermite polynomial, $j = 1,...,m$;
$a_j = 0$, if term $j$ of $H_j(y_s)$ is not required, or is estimated by maximum likelihood;
$\beta$ is a normalising function of the parameters alone.

Apart from a scaling factor, $\alpha(y_s)$ is the normal density. Hence the parameters $\mu$ and $\sigma$ correspond to the first and second moments respectively, so that the first polynomial to be added is of order three, corresponding to an adjustment to the normal fit for skewness. The next term, of order four, adjusts the fit for kurtosis and so on.

Models with between zero (the normal density) and four terms were fitted to each dataset, except when convergence failed to occur after 1,000 iterations of the Newton-Raphson procedure. (Convergence problems occur when the likelihood surface is badly behaved, which happens with increasing frequency as more terms are added, indicating over-fitting.) Likelihood ratio tests were employed to select the 'best' fit. The resulting fits often yield a significantly high goodness-of-fit statistic. The variation in number of pods observed from one watch to another might be greater than Poisson for a variety of reasons. For example: speed of passage may vary with weather conditions; pods may not travel independently of each other; probability of detecting a pod depends on weather conditions, rate of passage, distance from shore, etc. We allow for this over-dispersion by multiplying the Poisson variance for the total count by a dispersion parameter, estimated as the ratio of the $\chi^2$ goodness-of-fit statistic divided by its degrees of freedom (McCullagh and Nelder, 1989, p.296).

The data analysed are numbers of pods passing within each count period, so that the data are grouped; the group endpoints are the start and end of each period for which visibility code and Beaufort did not exceed four. Pods recorded travelling north were excluded from analyses; such records were rare, except in 1972/73, when counting ended late and over 100 pods were recorded going north in February, largely in the last few days of the survey. To estimate the number of pods passing, the total number of pods sighted during the migration was multiplied by the ratio of the total area under the fitted curve to the sum of the areas under the curve corresponding to watch periods. Estimation of tail areas (before the first watch of the season and after the last) was improved by adding two zero counts to the data, one on day zero, defined to be 1 December, which is prior to the onset of migration and the second on day 90, which is 1 March (or 29 February in a leap year), after the migration is believed to be complete. This modification was found to be necessary for seasons in which counting started late or finished early.

To convert the estimated number of pods passing to an estimate of population size, an estimate of average pod size is required. Here the average of recorded pod sizes is used, first discarding pods sighted during poor visibility ( $>4$) or high Beaufort ( $>4$). The abundance estimates will be biased low unless two further corrections are made. One is an adjustment for underestimation of the size of pods detected and the other is a correction for pods missed during count periods, estimated for the 1987/88 season from independent sightings from two observers recording simultaneously. Details of these correction factors are given by Breiwick *et al.* (1988). The corrections are assumed to hold for all seasons, therefore allowing the conversion of our estimates of relative abundance to absolute abundance estimates.

The estimate of trend developed in this study is considered valid if the following assumptions are met:

(1) there is no trend in the proportion of pods missed during count periods, for example as a result of increased efficiency of observers or of an increase in average distance offshore of pods passing the counting station;
(2) there is no trend in any bias in estimating average pod size;
(3) there is no trend in weather conditions across years. Alternatively, rate of passage is independent of weather conditions and probability of detection is independent of weather conditions up to Beaufort 4 and visibility code 4;
(4) there is no trend over time in the proportion of whales that pass seaward of the observers' viewing area, or in the proportion that fail to migrate south past the counting station.

The estimates of absolute abundance developed in this study are considered to be valid if the following assumptions are met:

(1) rate of passage is unaffected by poor visibility and rough weather;
(2) no whales pass seaward of the observers' viewing area and all whales in this stock migrate south past the counting station;
(3) adjustments for pods missed during count periods and for biased estimation of pod size are correct and appropriate for all years in which counts were made;
(4) the Hermite polynomial model has an appropriate form for fitting migration dates; in particular, it fits the tails of the distribution adequately.

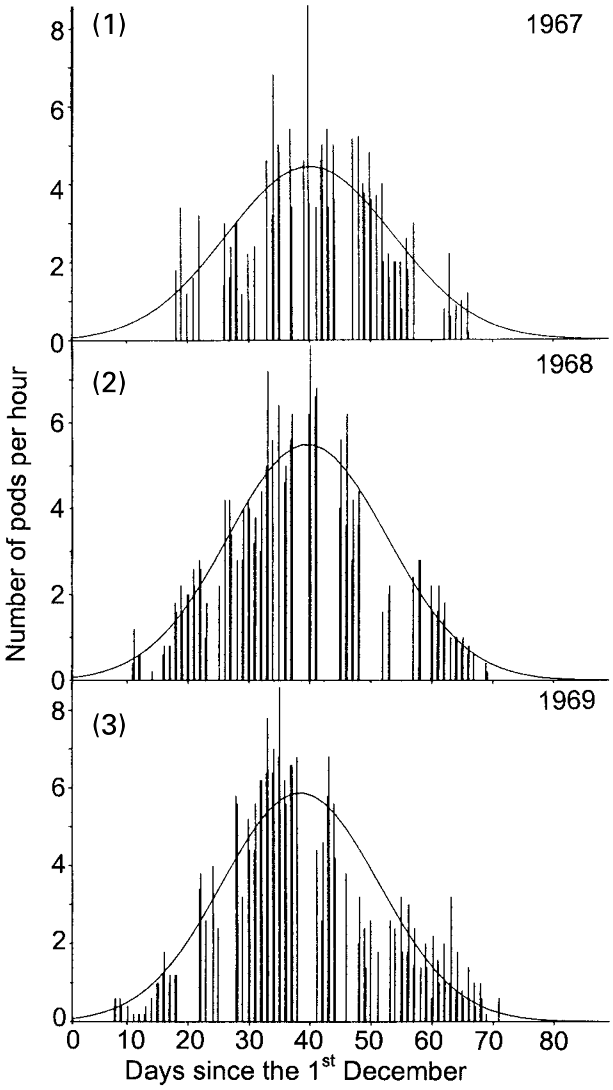
Adjustments to the abundance estimates to allow for changes in offshore distribution over time were requested by the Working Group. Since distances of pods from shore were recorded grouped, but the degree of grouping was not consistent, all distances were first grouped using the following group intervals: 0.01-0.25; 0.26-0.50; 0.51-0.75; 0.76-1.00; 1.01-1.50; 1.51-2.00; 2.01-8.00. These frequencies were then adjusted using data from aerial surveys as described in Recommendation 3 of the Working Group. A hazard-rate model was used to estimate the detection curve; since the distribution of offshore distances recorded from shore was markedly different in 1978/79 and 1979/80 from in 1987/88, separate detection curves were estimated for pre-1981 and post-1981 data. The estimated detection curves were used to evaluate, by numerical integration, the average distance expected in each of the above distance intervals; these average distances are in general smaller than the mid-points of the groups.

## RESULTS

Originally, this analysis examined the 1978/79, 1979/80 and 1987/88 aerial and shore-based sighting frequencies of pods by distance offshore; it was found that the offshore distribution of whales was similar in the three aerial surveys. Shelden and Laake (2002) and Withrow (1990) come to similar conclusions and extended the study by incorporating additional aerial survey data acquired since 1987/88. They found that the offshore distribution ( > 2.25 n.miles) of gray whale pods did not differ significantly between survey years (1979, 1980, 1988, 1993, 1994 and 1996). In our initial analysis there appeared to be a significant shift in mean estimated distance offshore from 1979/80 and earlier compared with subsequent estimates from shore surveys. However, it was subsequently discovered that the elevation of the counting site at Granite Canyon was overestimated and that an incorrect conversion factor was used to convert binocular reticles to distances (J. Laake, pers. comm.). Thus, the 1985/86 and 1987/88 shore-based mean distance estimates are now quite similar (1.23 n.miles *vs* 1.26 n.miles) and the probable explanation for the much smaller mean distance estimates prior to 1984/85 compared to the more recent estimates is that the latter were based on binoculars with reticles while the former were based on visual estimates by observers (without reticle binoculars). We have therefore omitted analyses of aerial and shore-based sighting frequencies of pods by distance.

Mean offshore distances of pods recorded from shore, calculated as described above, are given in Table 1. The estimated multipliers for pods missed during count periods are given in Table 2.

Given the inconsistencies in recorded offshore distances (discussed below), Hermite polynomial models were fitted to the unadjusted pod frequency counts. Although the intention of the Working Group was that only the parts of a watch for which Beaufort or visibility code exceeded four would be deleted for the more recent surveys, it was found that a change of conditions was frequently only noted when a sighting was made. Thus to avoid bias from including periods of search in unrecorded poor conditions and from ending watch periods immediately prior to a sighting, whole watches for which Beaufort or visibility code exceeded four at any time were discarded. Hermite polynomial fits to the remaining census data are shown for each survey in Figs 1-17.



Figs 1-17. Histograms of number of pods sighted, adjusted for watch length, by date. Counts made during watches in which either Beaufort or visibility code exceeded four are not included. Also shown are the Hermite polynomial fits to the histograms.
Fig. 1. 1967/68 survey; Fig. 2. 1968/69 survey; Fig. 3. 1969/70 survey.

Table 1

Mean estimated distance offshore (n.mile) of pods recorded from shore by year. ('67' represents the 1967/68 season etc.; 87N is the north station in 1987/88, 87S the south station.) Estimates for 1992/93 and 1993/94 are not available.

| Year | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 84 | 85 | 87N | 87S | 95 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean | 0.44 | 0.33 | 0.40 | 0.44 | 0.62 | 0.55 | 0.49 | 0.66 | 0.34 | 0.29 | 0.26 | 0.63 | 0.48 | 1.03 | 1.23 | 1.27 | 1.25 | 1.05 |

Table 2

Estimated adjustments to allow for whales missed during count periods, adopting the recommendations laid down by the Working Group. No adjustment corresponds to 1.0; a value of 2.0 would indicate that the abundance estimate should be doubled. ('67' represents 1967/68 season etc.; 87N is the north station in 1987/88, 87S the south station.)

| Year | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 84 | 85 | 87N | 87S |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Adj. | 2.89 | 1.44 | 1.76 | 2.44 | 3.51 | 4.00 | 3.51 | 5.61 | 1.83 | 1.37 | 1.27 | 3.49 | 2.16 | 1.002 | 1.002 | 1.008 | 1.007 |

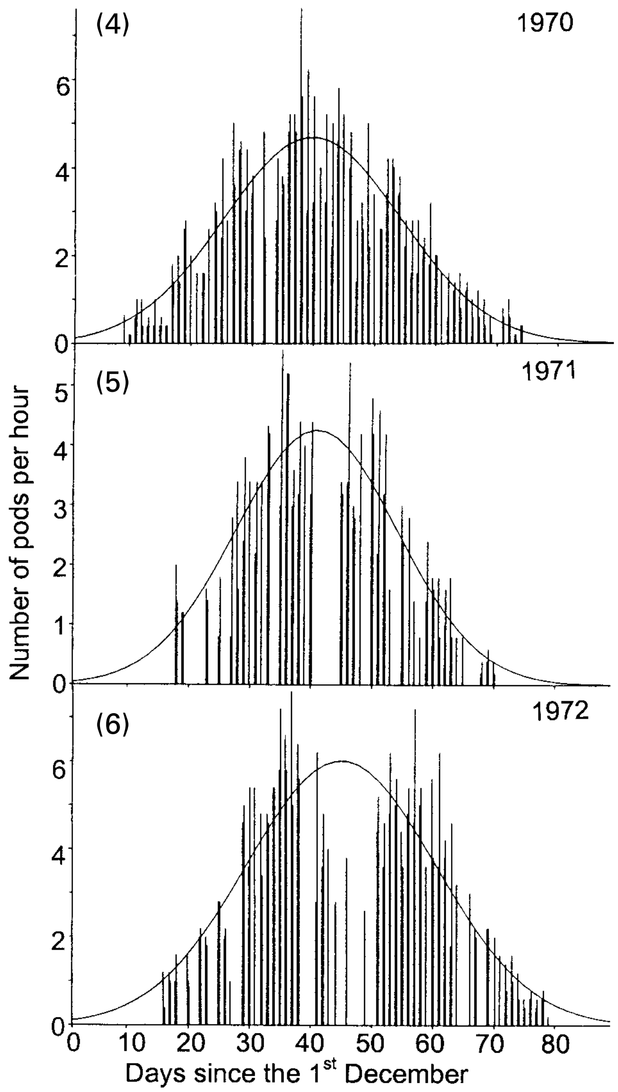


Fig. 4. 1970/71 survey; Fig. 5. 1971/72 survey; Fig. 6. 1972/73 survey.

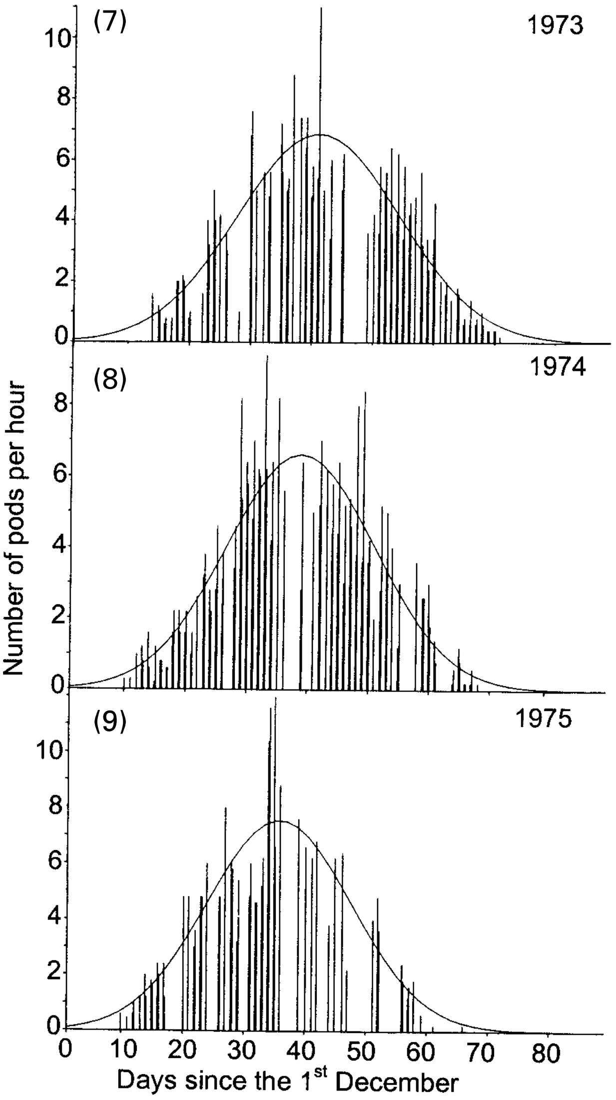


Fig. 7. 1973/74 survey; Fig. 8. 1974/75 survey; Fig. 9. 1975/76 survey.

In Table 3, estimates of the number of pods, the average pod size and the number of whales are given by year. As directed by the Working Group, no adjustment for biased pod size estimates is incorporated and, for reasons discussed below, no adjustments for pods missed during watch periods were made. Instead, the 'best' estimate of abundance available, given by Buckland *et al.* (1993), was taken and the relative abundance estimates in the penultimate column of Table 3 were rescaled to pass through this best estimate for 1987/88. Thus, the last column of Table 3 (adjusted abundance estimates) is the same as column 2 (absolute population size estimates) of table 3 in Buckland *et al.* (1993), through to 1987/88. They used double counting to estimate the number of pods missed during watch periods and also adjusted for underestimation of pod size. The CV of the product of these two adjustments was estimated by calculating the value required such that adjusting the relative abundance estimate for 1987/88 to the absolute estimate gave, via the delta method, the same standard error on the absolute estimate as that quoted by Buckland *et al.* (1993). Since the estimates of abundance from the south station and the north station for 1987/88 cannot be assumed independent, the worst possible assumption that the correlation between them was unity was made to obtain the estimated standard error for the average relative abundance estimate in that year. This yields a standard error close to the average of the standard errors of the two separate estimates.

A regression of abundance estimate on time (1967/68 to 1995/96), assuming a Poisson error distribution with over-dispersion, a logarithmic link function and the weighting of each estimate by the reciprocal of the squared coefficient of variation, yields an estimate of average annual increase of 2.53% (SE = 0.31%). The predicted abundance by year from this regression is shown in Fig. 18. The recent abundance estimates shown in Fig. 18 suggest that the rate of increase may be slowing. In this situation, a logistic curve would be more appropriate than an exponential curve. The abundance estimates were therefore fitted to a logistic model using unweighted non-linear regression, assuming an additive error model. The estimated asymptote is 26,046 animals (SE = 6,281) and the inflection point is approximately in 1971 (SE = 6.5 years). The predicted logistic curve, extrapolated back to 1900 and forward to 2025, is shown in Fig. 19.

For each Hermite polynomial fit, the 10th, 50th (i.e. median) and 90th percentile of the distribution was evaluated. These are given by year in Table 4. The date by

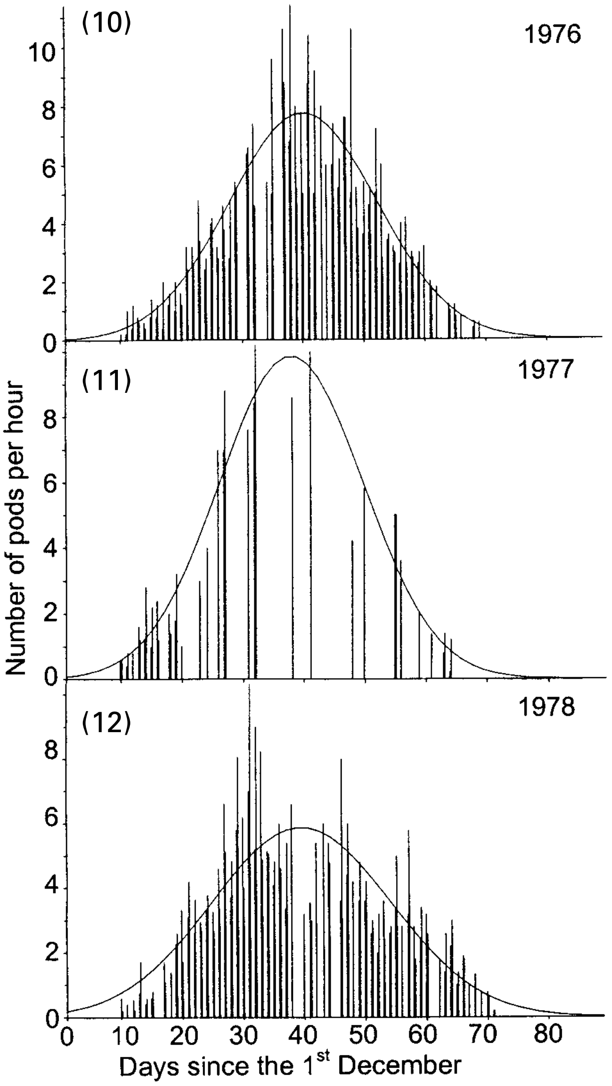


Fig. 10. 1976/77 survey; Fig. 11. 1977/78 survey; Fig. 12. 1978/79 survey.

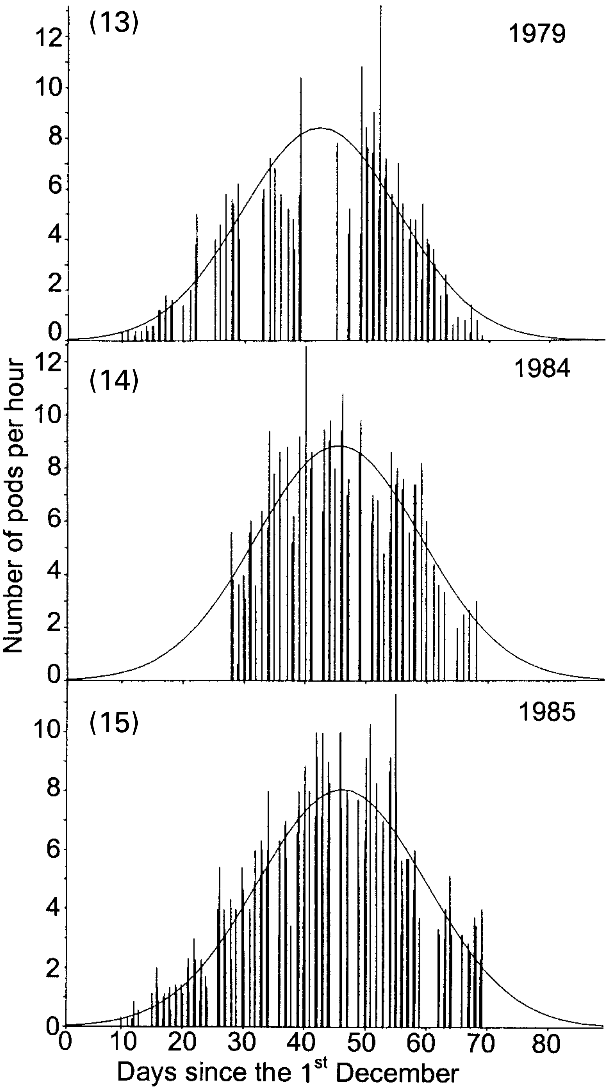


Fig. 13. 1979/80 survey; Fig. 14. 1984/85 survey; Fig. 15. 1985/86 survey.

which roughly 10% of whales had passed was typically around 24 December during the 1970s and became significantly later with time ($p < 0.001$), on average by a half-day per year. The change was greatest after 1979/80. The median passage date was typically around 10th January during the 1970s and also occurred later in more recent years ($p < 0.001$). The average change in date was around one day every three years and again the change is most apparent since 1979/80. On average, 90% of whales have passed by about 28 January, with no evidence of a trend with time.

## DISCUSSION

Changes to the procedures defined by the Working Group were found to be necessary on examination of the data. Recommendation 2 states that 'average distance offshore is known to vary with year' and the mean distances offshore of pods recorded from shore (Table 1) appear to confirm this statement. However, the estimated adjustments of Table 2 are wholly implausible. It now seems clear that estimated distances offshore from shore-based observers prior to 1984/85 are suspect. Offshore distances recorded by shore-based observers prior to 1984 appear to have been grossly underestimated. Although distance estimates were believed to be reasonably accurate (S.B. Reilly, pers. comm.), this remains by far the most plausible explanation of the data. If this explanation of the data is accepted, or if no satisfactory explanation can be found, then distance estimates prior to 1984 must be considered suspect and adjustment for whales missed during count periods cannot be made using a detection curve estimated from these recorded distances. An attempt to verify distance estimates using buoys at known distances was compromised when the buoys blew away six days after placement. Reilly *et al.* (1980) checked 542 distance estimates using an inclinometer. They found that shorter distances were significantly underestimated by observers and that some observers' estimates were more biased than others.

Therefore, Hermite polynomial models were fitted to unadjusted counts. In most cases, the Hermite polynomial fit seems to approximate the migration distribution adequately, even when migration started prior to the first watch period of the season or continued after the final watch period (Figs 1-17). Thus, estimates of the number of pods passing during night or poor conditions should be reliable, provided rate of passage is similar in these periods to watch periods and assuming that reliable adjustments for biased pod size estimation and for pods missed during watch periods are available. Evidence of over-dispersion is shown for example in Fig. 16, where the peak count per hour close to the mode

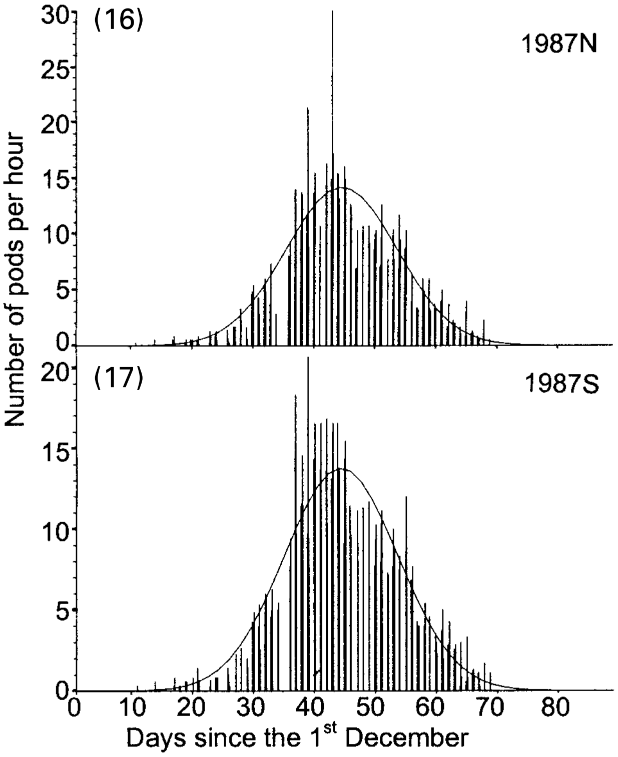


Fig. 16. 1987/88 survey, north station; Fig. 17. 1987/88 survey, south station.

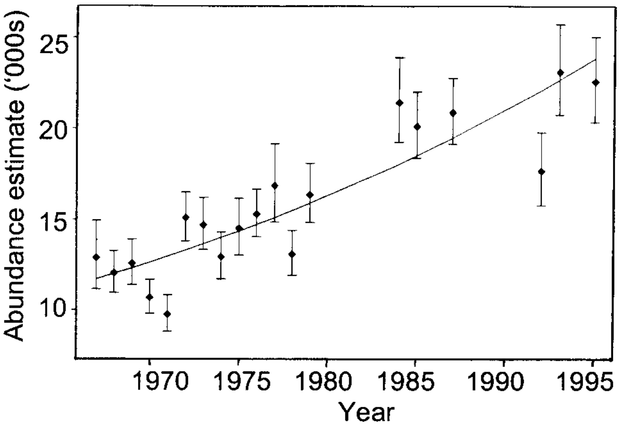


Fig. 18. Estimates of abundance of eastern Pacific gray whales and predicted abundance from a weighted exponential regression of abundance estimates on year. Vertical bars are approximate 95% confidence intervals. Year 1967 signifies season 1967/68, etc.

of the distribution is far in excess of counts either side of it. This should affect estimation little and its effect on variance estimation was reduced by scaling up the Poisson variance for counts.

Factors which may significantly affect the reliability of the abundance estimates and the estimated rate of increase of 2.5% per annum are as follows.

(1) The proportion of pods missed during count periods may have changed over time. For example, in 1987/88 there were two counting stations and the element of competition may have caused observers to concentrate harder for longer periods. Fig. 18 indicates that the estimate for that season is very similar to those for 1984/85 and 1985/86, suggesting that any such effect was small. If procedures in the last three surveys led to higher detection probabilities than in earlier surveys, the rate of increase will have been over-estimated.

(2) Rate of passage may vary with weather conditions. For example, the effect of slower passage during poor weather would be to generate positive bias in the abundance estimates. Since very few counts were lost through poor weather in some years, the bias would be low in those years. Fig. 11 shows that most counts were lost in the 1977/78 season, so if the rate is appreciably slower in poor conditions, the corresponding abundance estimate should be high. Fig. 18 shows that the estimate for 1977/78 is higher than predicted by the exponential model, but only by a small amount. Rate of increase will be biased only if there has been a trend in weather conditions over the period of the surveys. There is evidence that passage rate differs between night and day. Swartz *et al.* (1987) carried out radio-telemetry experiments to assess this, but concluded that the difference between day and night passage rates was not significant. Schweder (pers. comm.) found a significant difference by reanalysing their data using a paired *t*-test and pooling Monterey and Channel Islands data. Our absolute abundance estimates include a correction for a differential rate of passage between day and night, based on a reanalysis of the radio-tagging data (Buckland *et al.*, 1993). More recent work by Perryman and Laake (1994) allows for the estimation of a more reliable correction factor.

(3) Abundance would be underestimated if a proportion of the stock did not pass Monterey every year, or if some passed by far out to sea. The latter possibility would seem to be ruled out by the absence of records, even though efforts have been made to locate animals. The number of animals that remain north of Monterey is thought to be small. The estimated rate of increase would only be biased if there is a trend over time in the proportion staying north and, given the small numbers likely to be involved, bias is likely to be negligible.

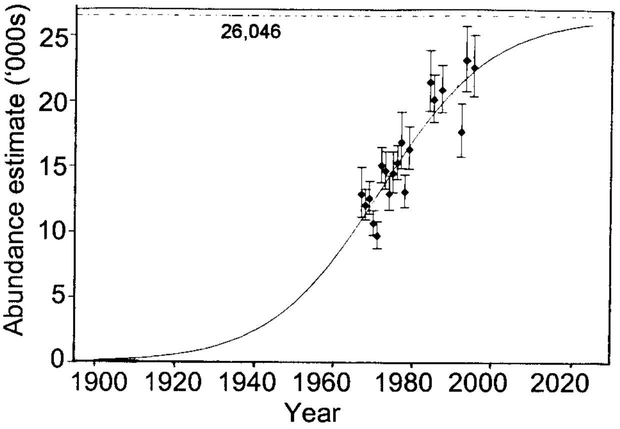


Fig. 19. Logistic curve fit to the abundance estimates. The predicted curve has been extrapolated back to 1900 and forward to the year 2025.

The Working Group recommended that relative abundance estimates should be rescaled to pass through the absolute abundance estimate for 1987/88 of Breiwick *et al.* (1988). That abundance estimate was obtained by retaining all periods for which the data indicated that both Beaufort and visibility code were $< 5$. Given that a change of conditions was usually only noted when a sighting was made, this procedure is potentially biased. Furthermore, the estimate

Table 3

Estimated number of pods, pod size and number of whales by year. The final column is found by using the multiplicative scaling factor that ensures that the 1987/88 average estimate is equal to the estimate of absolute abundance from Buckland *et al.,* 1993. (Standard errors in parentheses.)

| Year | No. of terms | $\chi^2$ [df] | Sample size (pods) | Estimated no. of pods | Estimated average pod size | Estimate of relative abundance | Adjusted abundance estimate[1] |
|---|---|---|---|---|---|---|---|
| 1967/68 | 4 | 83.0 | 903 | 4,051 | 2.438 | 9,878 | 12,921 |
| | | [45] | | (253) | (0.063) | (667) | (964) |
| 1968/69 | 0 | 70.6 | 1,079 | 4,321 | 2.135 | 9,227 | 12,070 |
| | | [61] | | (134) | (0.046) | (348) | (594) |
| 1969/70 | 1 | 104.5 | 1,245 | 4,526 | 2.128 | 9,630 | 12,597 |
| | | [67] | | (155) | (0.043) | (383) | (640) |
| 1970/71 | 2 | 116.2 | 1,458 | 4,051 | 2.021 | 8,185 | 10,707 |
| | | [90] | | (115) | (0.033) | (267) | (487) |
| 1971/72 | 0 | 71.3 | 857 | 3,403 | 2.193 | 7,461 | 9,760 |
| | | [56] | | (127) | (0.048) | (323) | (524) |
| 1972/73 | 4 | 91.5 | 1,539 | 5,279 | 2.187 | 11,543 | 15,099 |
| | | [71] | | (152) | (0.034) | (378) | (688) |
| 1973/74 | 4 | 133.7 | 1,496 | 5,356 | 2.098 | 11,235 | 14,696 |
| | | [66] | | (186) | (0.034) | (431) | (731) |
| 1974/75 | 0 | 159.2 | 1,508 | 4,868 | 2.034 | 9,904 | 12,955 |
| | | [74] | | (174) | (0.035) | (394) | (659) |
| 1975/76 | 2 | 101.1 | 1,187 | 5,354 | 2.073 | 11,100 | 14,520 |
| | | [47] | | (218) | (0.039) | (497) | (796) |
| 1976/77 | 0 | 139.7 | 1,991 | 5,701 | 2.052 | 11,700 | 15,304 |
| | | [87] | | (153) | (0.028) | (353) | (669) |
| 1977/78 | 0 | 50.2 | 657 | 7,001 | 1.843 | 12,904 | 16,879 |
| | | [31] | | (356) | (0.046) | (731) | (1,095) |
| 1978/79 | 4 | 152.9 | 1,730 | 4,970 | 2.016 | 10,018 | 13,104 |
| | | [84] | | (159) | (0.034) | (361) | (629) |
| 1979/80 | 4 | 109.3 | 1,451 | 6,051 | 2.068 | 12,510 | 16,364 |
| | | [55] | | (220) | (0.033) | (498) | (832) |
| 1984/85 | 3 | 105.2 | 1,756 | 7,159 | 2.290 | 16,393 | 21,443 |
| | | [49] | | (301) | (0.038) | (740) | (1,182) |
| 1985/86 | 1 | 141.4 | 1,796 | 6,873 | 2.237 | 15,376 | 20,113 |
| | | [104] | | (191) | (0.042) | (515) | (927) |
| 1987/88N | 3 | 205.9 | 2,426 | 7,756 | 2.040 | 15,825 | |
| | | [92] | | (221) | (0.027) | (497) | |
| 1987/88S | 3 | 152.8 | 2,404 | 7,642 | 2.104 | 16,082 | |
| | | [91] | | (194) | (0.029) | (464) | |
| 1987/88 | | | | | | 15,954 | 20,869 |
| (average) | | | | | | (481) | (913) |
| 1992/93[2] | | | | | | | 17,674 |
| | | | | | | | (1,029) |
| 1993/94[2] | | | | | | | 23,109 |
| | | | | | | | (1,262) |
| 1995/96[3] | | | | | | | 22,263 |
| | | | | | | | (1,078) |

[1] Absolute abundance estimates for 1967/68 to 1987/88 are from Buckland *et al.,* 1993.

[2] From Laake *et al.,* 1994.

[3] From Hobbs *et al.,* 1996.

Table 4

10th, 50th (median) and 90th percentiles of distribution of migration date. Units are days from midnight on 30 November; midnight on 31 December = 31.0 and midnight on 31 January = 62.0.

| Year | 10th percentile | Median | 90th percentile |
|---|---|---|---|
| 1967 | 17.0 | 39.5 | 58.9 |
| 1968 | 22.5 | 39.2 | 56.0 |
| 1969 | 22.2 | 36.9 | 56.2 |
| 1970 | 21.8 | 39.1 | 58.3 |
| 1971 | 23.5 | 40.5 | 57.5 |
| 1972 | 26.4 | 44.8 | 64.3 |
| 1973 | 24.0 | 40.4 | 56.9 |
| 1974 | 22.8 | 38.4 | 54.1 |
| 1975 | 20.3 | 35.5 | 50.1 |
| 1976 | 24.1 | 39.7 | 55.3 |
| 1977 | 22.5 | 37.6 | 52.7 |
| 1978 | 22.4 | 38.2 | 58.4 |
| 1979 | 24.3 | 41.7 | 56.6 |
| 1984 | 30.0 | 45.7 | 63.9 |
| 1985 | 28.3 | 45.9 | 65.7 |
| 1987N | 33.1 | 43.6 | 56.0 |
| 1987S | 32.9 | 43.5 | 56.2 |

was derived using data from the south station alone, except for calculation of the correction for whales missed during watch periods. We have thus used the revised estimate of Buckland *et al.* (1993), in which sighting heterogeneity was rigorously modelled and the data from both stations contributed equally to the analysis.

## ACKNOWLEDGEMENTS

The National Marine Mammal Laboratory at Seattle funded this work. We are very grateful to H. Braham for enabling the work to be carried out. We thank the many observers who, through the years, have collected the data making this analysis possible. S. Reilly, D. Withrow, D. Rugh and M. Dahlheim all responded promptly to requests for possible explanations of the discrepancies between aerial and shore-based estimates of distance offshore prior to 1984. S. Reilly (SWFSC, NMFS, California) and A. York (NMML) reviewed an earlier draft of the manuscript, leading to a much improved paper. We thank D. Rugh for his thorough review and helpful comments on the manuscript.

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# The effect of census frequency on the detection of trends in the abundance of eastern North Pacific gray whales[1]

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ABSTRACT

The ability to detect trends in gray whale abundance with various census frequencies is investigated. The number of surveys and years needed to detect a trend in abundance, and total change in abundance, are presented in graphs for various rates of change and census frequencies. The estimated annual rate of increase of the population during 1967 to 1980 using a linear model is 0.034. This rate of increase can be detected (power = 0.95) with 14 surveys over 13 years, 9 surveys over 16 years or 7 surveys over 18 years, for census frequencies of every year to every third year, respectively. Graphs are presented showing power of detecting different rates of increase with census frequencies from 1 to 3 years.

KEYWORDS: ABUNDANCE; GRAY WHALE; TRENDS; SURVEY; FREQUENCY

## INTRODUCTION

Shore-based censuses of migrating eastern North Pacific gray whales (*Eschrichtius robustus*) have been conducted regularly and often annually by the National Marine Mammal Laboratory since 1967/68. Reilly *et al.* (1983) estimated both abundance and rate of increase in population size for the early censuses (1967 to 1980). A number of other authors have estimated abundance using data from later surveys (e.g. see Buckland and Breiwick, 2002).

Censuses provide point estimates of abundance while long-term studies provide information about trend in population size over time. In many studies, estimating trend in population size is as important as estimating absolute population size in determining the status of the population. A number of papers have investigated the ability to detect trends in marine mammal abundance using regression models (de la Mare, 1984; Gerrodette, 1987; Holt *et al.*, 1987). This paper investigates the ability to detect trends for different frequencies of census.

With respect to eastern North Pacific gray whales, an impact issue is the number of times and how frequently surveys should be undertaken in order to detect when the population is approaching its carrying capacity (IWC, 1990).

If the growth of the population can be modelled by a logistic curve, and the population is approaching an asymptotic stable value (such as assumed by reaching ‘carrying capacity’), then as the slope of the curve, i.e. the growth rate, approaches zero, the number of surveys required to detect a trend will approach infinity. To determine if the population is ‘near’ its carrying capacity, some estimate is needed of that value, or the data must show the beginnings of an asymptote. The window of data available when this study was undertaken did not show an asymptote and may not be sufficient to fit the logistic model. Furthermore, if the population growth rate is near zero, it could be that recruitment failure has occurred owing to environmental or other causes, not necessarily that the population is near carrying capacity.

In this paper, the methods of Gerrodette (1987) are used to look at the power of detecting trends and the trade-off between the frequency of census and the number of surveys needed to detect a trend. The question regarding carrying capacity is not addressed directly, because the available data did not appear to fit a logistic curve.

## METHODS

The probability of detecting a trend, given that a trend exists, is defined as the power of the regression model. The power (1-$\beta$, where $\beta$ is the type II statistical error) of detecting a trend in abundance is affected by a number of factors: the coefficient of variation of the estimates of abundance; the magnitude of the change in abundance over time; the level for type I ($\alpha$) statistical error; and the number of estimates of abundance. By setting the values of four of these parameters, the fifth can be determined using formulae derived in Gerrodette (1987).

Gerrodette (1987) presents formulae for determining power for linear and exponential regression models and for three different relationships between coefficient of variation (CV) and abundance. This paper uses Gerrodette’s formula for linear rate of change with constant CV, based on data from Reilly *et al.* (1983).

One of the assumptions of this method is that abundance changes at a constant rate over regularly spaced intervals. This paper assumes that fluctuations in population estimates about the regression line are due to sampling variability alone, although this may not be fully realistic.

A linear model was chosen because the annual rate of change is assumed to decrease over time (when the slope is positive). The exponential model has a constant annual rate of change. If the population is approaching some asymptotic value, the linear model is more appropriate.

There appears to be no relationship between CV and abundance for the 13 years of gray whale data (Reilly *et al.*, 1983), with a mean CV = 0.1143 (Fig. 1). Reilly (1983) used a weighted exponential regression model to estimate a slope of 0.025 (SE = 0.00964) for the 1967-1980 abundance data (Fig. 2). An unweighted linear fit to the data gives an annual rate of increase of 0.034 ($Y = 11{,}112+390.29X$) (Fig. 2).

The formula relating the above listed parameters, for a linear rate of change with constant CV, is from Gerrodette (1987):

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[1] This paper was originally submitted as SC/A90/G14.

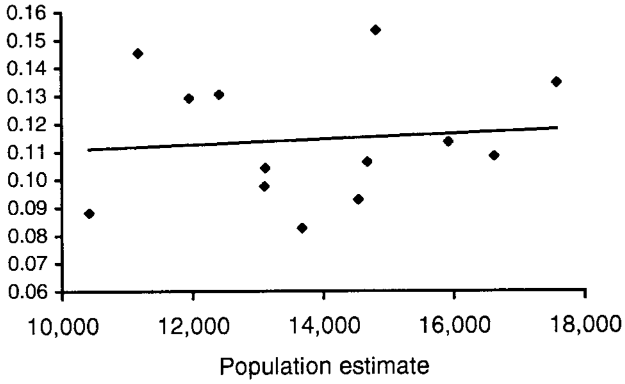

Fig. 1. Relationship between coefficient of variation and population estimates for the 1967/68-79/80 gray whale census data from Reilly *et al.* (1983).

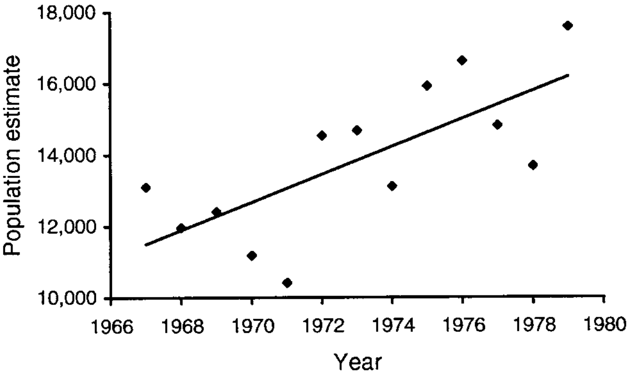

Fig. 2. Straight line regression fit to the gray whale population estimates for 1967/68-79/80. (Y = 11,112 + 390.29 X).

$$r^2 n(n-1)(n+1) \geq 12CV^2(Z_{\alpha/2}+Z_\beta)^2 \\ (1+r(n-1)[1+(\frac{r}{6})(2n-1)]) \qquad (1)$$

where:

$n$ is the number of surveys;
$r$ the annual rate of change in abundance;
$CV$ coefficient of variation;
$Z_{\alpha/2}$ the normal deviate for type I error; and
$Z_\beta$ normal deviate for type II error (power = 1-β).

The equation can be solved for one parameter given the other four parameters. The type I (α) and type II (β) errors were both set at 0.05, yielding a power of 0.95. $Z_{\alpha/2}$ is therefore equal to 1.96 and $Z_\beta = 1.65$. If a lower power is acceptable, fewer surveys would be needed. The CV was set at 0.1143, the mean from Reilly *et al.* (1983). The number of surveys to detect a trend was estimated for different values of $r$ and different intervals between surveys.

The number of years to detect a trend is estimated by:

$$ny = ([n]-1)\ t$$

Where:

$ny$ is the number of years;
[] indicates the next largest integer;
$n$ the number of surveys; and
$t$ the interval between surveys.

Total fractional change in abundance ($R$) is estimated by:

$$R = t\ r\ (n-1)$$

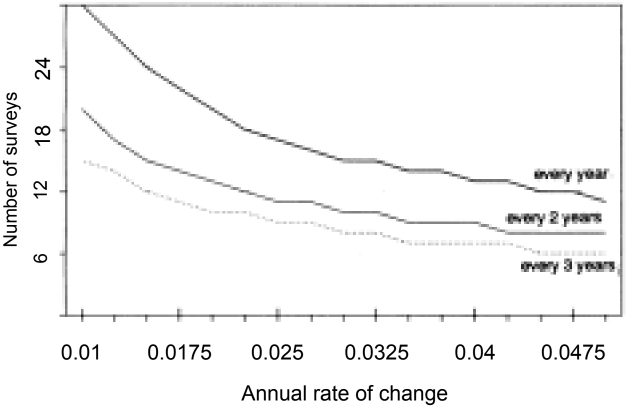

Fig. 3. Number of surveys to detect various positive rates of change and various survey intervals. CV = 0.1143, α, β = 0.05.

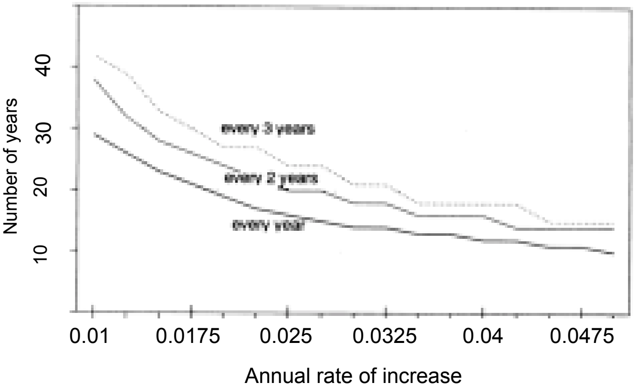

Fig. 4. Number of years before a trend is detected for various positive rates of change and various survey intervals. CV = 0.1143, α, β = 0.05.

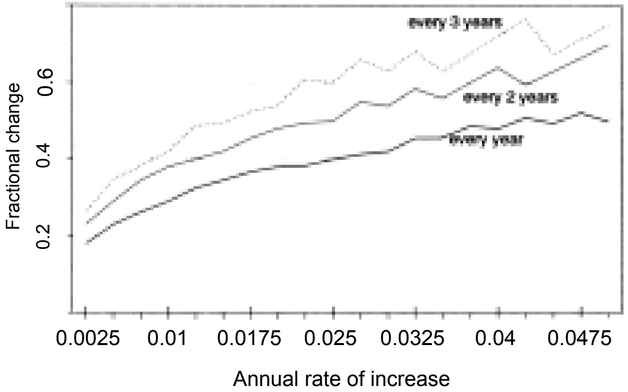

Fig. 5. Total fractional change in abundance over the years elapsed before a trend is detected for various positive rates of change and various survey intervals. CV = 0.1143, α, β = 0.05.

## RESULTS

The number of surveys needed to detect a particular rate of change in the population with power = 0.95, decreases as the time between censuses increases (Fig. 3); however, the number of years elapsed increases (Fig. 4). For example, to detect an annual rate of change of 0.034 with power = 0.95, 14 surveys over 13 years would be needed if surveys were conducted every year. The population would increase by 46% over this time period (Fig. 5). If surveys were conducted every other year, nine surveys over 16 years would be needed, and the population would increase by 56% over the time period. If surveys were conducted every three years, seven surveys over 18 years would be needed, and the population would increase by 63%.

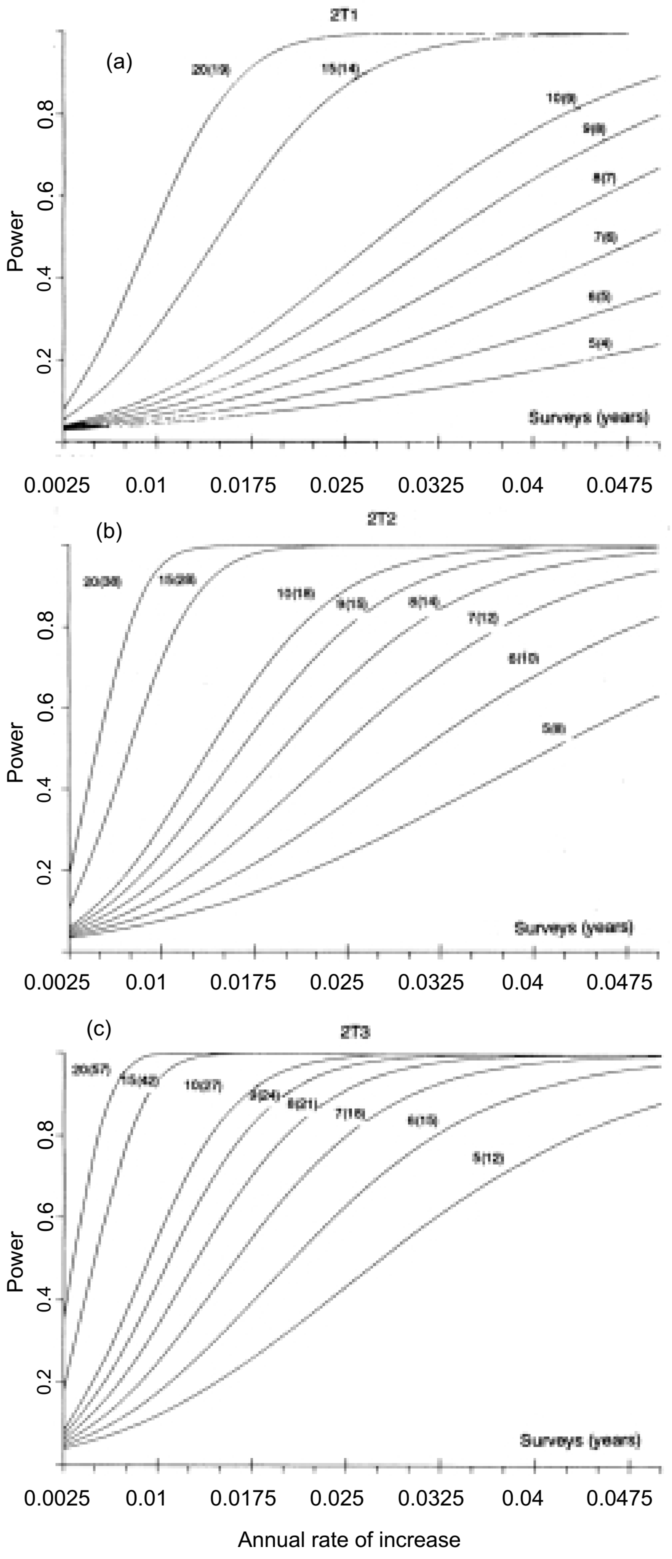

Fig. 6. Estimated power to detect various positive rates of change for surveys conducted (a) annually, (b) every second year and (c) every third year. CV = 0.1143, α, β = 0.005.

It is interesting to note how small an annual rate of increase can be detected. Fig. 6 shows the power of detecting different rates of increase using a linear model ($CV = 0.11$, $\alpha = 0.05$) for surveys every 1-3 years. With 20 annual surveys (19 years elapsed), an $r$ of 0.0175 can be detected with a power of 0.92. Approximately 13 surveys would be needed every other year (24 years elapsed), and 10 surveys every three years (27 years elapsed) to detect the same trend.

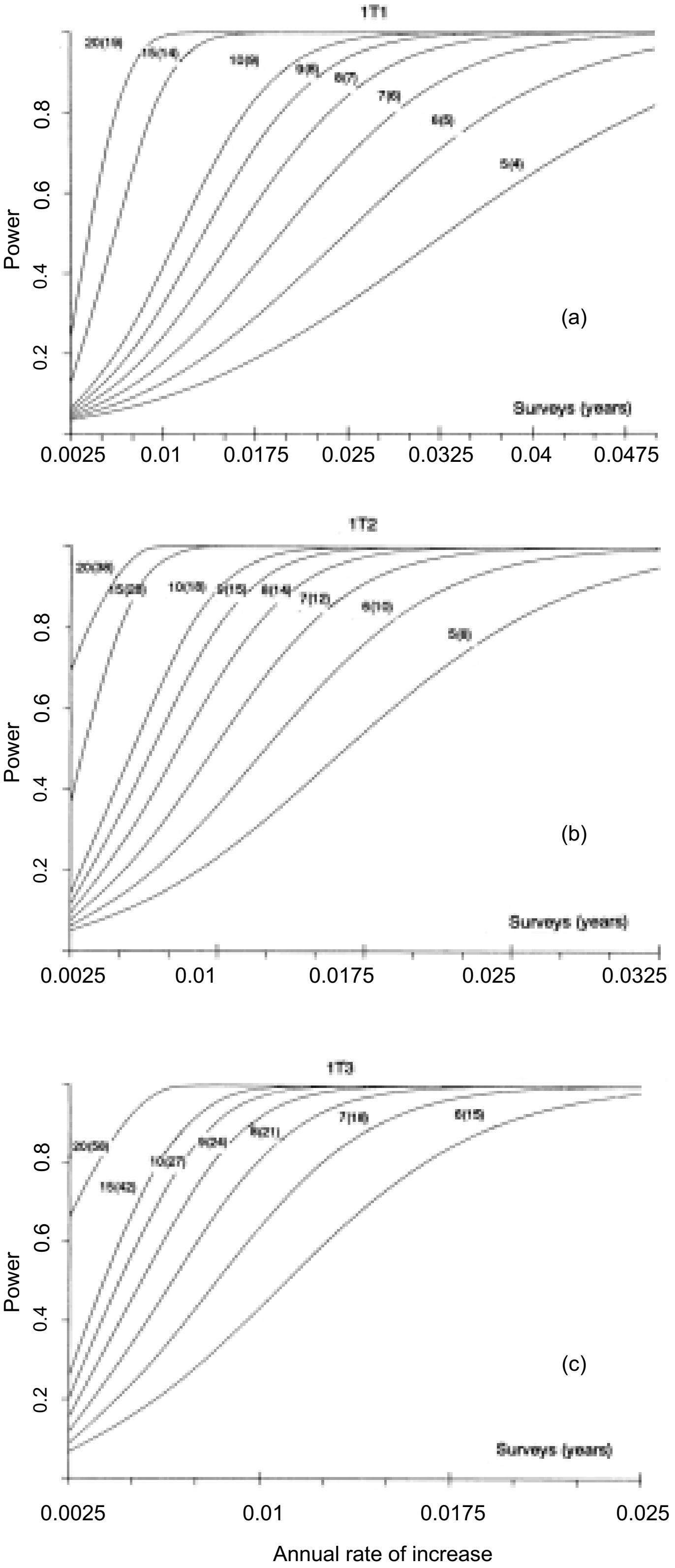

Fig. 7. Estimated power to detect various positive rates of change for surveys conducted (a) annually, (b) every second year and (c) every third year. CV = 0.05, α, β = 0.005.

The CV of recent surveys is estimated to be smaller than for the 1967-80 surveys (Breiwick *et al.*, 1988). A smaller CV, such as 0.05, will result in higher power and a need for fewer surveys to detect a given change in the population (Fig. 7). However, that estimate may be too low because no allowance has been made for uncertainty in the matching of pods of gray whales in the mark-recapture methods.

## DISCUSSION

A relatively long series of surveys is needed to detect trends in the population, especially if the rate decreases from the present estimate. The analysis shows that at least 13 years (14 annual surveys) would be needed to detect rates of increase similar to those estimated for the 1967-1980 surveys. It is possible to detect the same rate of increase using fewer surveys (e.g. 7 surveys), but it would take 18 years if surveys were conducted every three years.

More time would be required to detect smaller rates of increase. If a smaller CV can be obtained, or if a larger $\alpha$ or a smaller power is acceptable, then a smaller rate of change could be detectable. This paper assumes that the change in true abundance follows a linear trend. If this assumption is not valid, then the power of detecting a trend will be lower than estimated here.

When the interval between surveys increases, the number of surveys in a given time period decreases, and the number of years needed to detect a trend in abundance increases. For an increasing gray whale population, an undetected change in the population will not be as critical as for a decreasing population. If, however, the population is declining, one may want to sample at a frequency that allows detection of a certain percentage decline over the time needed to detect the trend, so that there is time for some action or more intensive study before too large a decline in the population has occurred. We have assumed a normal distribution for the abundance estimates. A bootstrap method (Efron and Tibshirani, 1993) could be used to avoid making assumptions about the underlying distribution.

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# Comparison of the offshore distribution of southbound migrating gray whales from aerial survey data collected off Granite Canyon, California, 1979-96[1]

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ABSTRACT

Aerial surveys provide an assessment of the offshore distribution of gray whales and an estimate of the proportion of whales that migrate beyond the visual range of shore-based observers. Six surveys were conducted concurrent with shore-based surveys during 1979, 1980, 1988, 1993, 1994 and 1996. Annual differences were tested for in the distribution of whales within an area 3 n.miles north and south of Granite Canyon, and it was found that the distributions within 3 n.miles of the shore differed by year but the shifts in the distribution were minor ( < 0.3 n.miles). The inshore ( < 2.25 n.miles) and offshore ( > 2.25 n.miles) distribution of gray whale pods did not differ significantly between survey years. An average of 4.76% (SE = 0.85%) of the whale pods were observed beyond 2.25 n.miles and only 1.28% (SE = 0.07%) beyond 3 n.miles.

KEYWORDS: GRAY WHALE; PACIFIC OCEAN; SURVEY-AERIAL; DISTRIBUTION; MIGRATION

## INTRODUCTION

Since 1977, scientists from the National Marine Mammal Laboratory (NMML) have been monitoring gray whale (*Eschrichtius robustus*) abundance from a shore-based site at Granite Canyon, California (36°26′41″N). Shore-based surveys have been conducted regularly (often annually) during the migration (e.g. see Reilly *et al.*, 1983; Buckland *et al.*, 1993; Buckland and Breiwick, 2002). Without an aerial survey or equivalent approach, the assessment of the gray whale population size from shore-based surveys at Granite Canyon would be contingent on the assumption that all whales migrate within visual range of the observers. Shore-based observers are able to see gray whales as far away as the horizon (8.93 n.miles) under ideal conditions, but most searching is conducted without the aid of binoculars, so whale surfacings occurring at distances of 5 n.miles or greater may go undetected. To assess the importance of this loss in sightings, and to examine the offshore distribution of gray whales, aerial surveys were conducted concurrent with the shore-based surveys in January 1979, 1980 (Reilly *et al.*, 1983), 1988 (Withrow, 1990), 1993, 1994 and 1996.

The results of the 1996 aerial survey are described and the results of all surveys conducted since 1979 are compared to test for annual differences in the distribution of whales within 3 n.miles of the shore and the proportion of whales migrating beyond 2.25 n.miles.

## METHODS

Aerial surveys were conducted 13-24 January 1996 during the peak of the gray whale southbound migration. Two survey aircraft were used: both were twin-engine *Partenavias* (model P68C)[2]. The first aircraft (N3832K), used from 12-19 January, was replaced with the ‘observer’ model (N6602L), used from 20-24 January. The survey altitude was 305m (1,000ft) and ground speed was 185km/hr (100kts). Each aircraft was equipped with a global positioning navigation system (GPS)[2], radar altimeter and bubble windows at the left and right observer positions. High wings allowed for a clear line of sight beneath and forward of the aircraft. The field of view for each observer was restricted to 19° below the horizon, which defined a strip width of 1 n.mile (0.5 n.miles on each side) at the flight altitude of 305m. The flight crew consisted of the pilot, two observers and a computer operator. One to four flights were conducted each day, with a 1-1.5hr interval between adjacent surveys to allow most of the observed whale pods to move south of the survey area.

Data were collected using a portable laptop computer with positional data downloaded from the GPS unit. Environmental conditions (Beaufort state, visibility, glare and percent cloud cover) and sighting information (observer, species, pod size and behaviour) were updated throughout the flight. A numerical waypoint was designated for the start and end of each trackline.

Tracklines were positioned perpendicular to the shoreline in close proximity to the shore-based site at Granite Canyon, with the southernmost tracklines flown first on each series (tracklines were numbered sequentially from south to north). This reduced the chance that a southbound whale would be seen on more than one trackline. In 1979 and 1980, 16 tracklines (each up to 10 n.miles offshore and 1 n.mile apart) with a 0.5 n.mile strip width were surveyed between Point Sur and Point Lobos (Reilly *et al.*, 1983; Fig. 1a). For the 1988 and 1993 surveys, transects were flown between the same two points but the distance between the tracklines was increased to 2-2.5 n.miles, thereby halving the number of tracklines surveyed (Withrow, 1990; Fig. 1b). To better characterise the distribution of whales near the shore-based site, the survey area was narrowed to within 3 n.miles north and south of the site in 1994 (Fig. 1c). In general, flights consisted of six tracklines (between 10 and 20 n.miles in length) with a maximum strip width of 0.5 n.miles on each side of the aircraft. The 1994 survey design was modified only slightly for the 1996 survey (Fig. 1d). Two types of transects were conducted throughout the sampling period in 1996, one consisting of six tracklines each 10 n.miles long,

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[1] A version of this paper was originally presented as SC/48/AS11.
[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

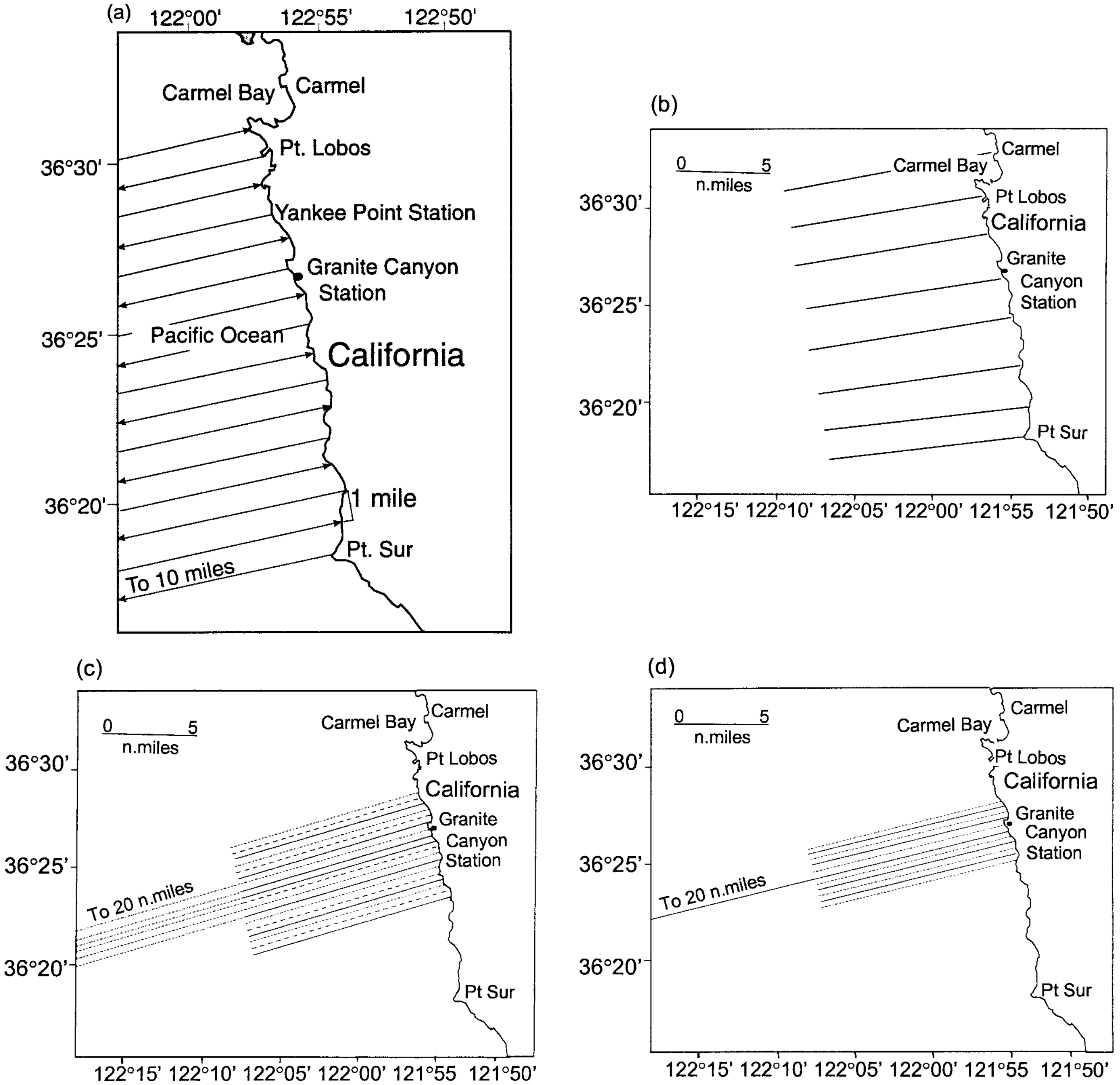

Fig. 1. Survey tracklines flown between Pt Sur and Carmel Bay, California, in January during the southbound migration of gray whales: (a) 1979 and 1980 (modified from Reilly *et al.*, 1983); (b) 1988 and 1993; (c) 1994; and (d) 1996.

the other with four 10 n.mile tracklines and two 20 n.mile tracklines (Fig. 1d). The 20 n.mile tracklines overlapped each other and started or ended directly over the Granite Canyon site. If sightings were made on the inbound leg, within the outer 10 n.mile zone, they were examined for potential duplication with sightings on the outbound leg. Duplication was not expected within the inner 10 n.mile zone because whales, travelling at the average speed of three knots (Swartz *et al.*, 1987), would have had sufficient time to move south of the transect strip. Likewise, 10 n.mile tracklines were separated by 0.66 n.miles between inbound and outbound legs, and pairs of legs were separated by 1 n.mile. This spacing allowed a contraction of the survey to within 2.5 n.miles north and south of the shore-based site, such that duplication of observations within 5 n.miles of the shore was not expected.

Comparisons of survey data between years were restricted to tracklines flown within a 3 n.mile perimeter north and south of the shore-based site. This included tracklines 4-9 for the 1979 and 1980 surveys, tracklines 4-6 for the 1988 and 1993 surveys, and all tracklines from the 1994 and 1996 seasons. Original survey records and raw data from the earlier surveys were obtained for the analysis. Chi-square contingency tests were used to examine changes in whale migration patterns within 3 n.miles of shore (four bins of 0.75 n.miles each) and proportion nearshore (within 2.25 n.miles) *versus* offshore (beyond 2.25 n.miles). The comparison within 3 n.miles of shore was arbitrarily established, as that distance was the expected outer viewing limit of shore-based observers (Withrow, 1990). To achieve reasonable power for the inshore-offshore comparison, 2.25 n.miles was chosen as the cutoff because few aerial observations were made beyond 3 n.miles.

The power of the chi-square test for the inshore-offshore comparison was computed empirically by repeatedly (1,000 times) simulating data under the alternative hypothesis and tallying the rejection frequency of the null hypothesis. Two types of alternative hypotheses were considered in the power calculations: (1) that the true offshore proportions for whales passing beyond 2.25 n.miles in each year were the measured values; and (2) that the proportions were random variables drawn from a uniform distribution with a lower bound of 0.02 and upper bounds of 0.09, 0.12, 0.15 and 0.22. In each case, the number of offshore pods for a year was a binomial random variable with parameters $N_y$, the sample size observed during that year and $p_y$, the probability specified by the alternative hypothesis. The probability ($P^*$) that the largest order statistic from the distribution (Mood *et al.*, 1974) was less than or equal to the observed maximum percentage during the six survey years was computed for each uniform distribution alternative.

## RESULTS

### 1996 survey

In 1996, a total of 108 tracklines 10 n.miles in length and 12 tracklines 20 n.miles in length were run (22.2 flight hours). On-effort sightings included 171 gray whale pods (325 individuals), of which 10 were cows with calves. Pod sizes ranged from one to seven individuals with the largest percentage of pods (52%) consisting of only one animal. The mean number of pods observed per flight (six tracklines) was 9 (SE = 1.04, median 8, range 1-23), and the average sighting distance offshore was 1.21 n.miles (SE = 0.06, median 1.14 n.miles, range 0.16-8.46 n.miles). Within 3 n.miles of shore, sightings occurred at an average distance of 1.13 n.miles (an area referred to as the 'migration corridor' by shore-based observers; Table 1). No sightings occurred beyond 10 n.miles.

Table 1

Offshore distribution of gray whale pods within 3 n.miles of shore near Granite Canyon, California, in January of each year (**bold** font indicates cells that contributed to the overall significance of the chi-square test). Column percentages (b) are derived from the corresponding columns in (a).

| Bin width (n.miles) | 1979 | 1980 | 1988 | 1993 | 1994 | 1996 | Totals |
|---|---|---|---|---|---|---|---|
| **(a) Number of pods** | | | | | | | |
| 0.00-0.74 | 15 | 26 | **43** | **5** | **32** | 31 | 152 |
| 0.75-1.49 | 36 | 47 | 101 | 45 | 159 | 113 | 501 |
| 1.50-2.24 | 17 | 26 | **15** | 21 | 67 | 22 | 168 |
| 2.25-2.99 | 3 | 1 | **11** | 4 | 9 | 2 | 30 |
| Totals | 71 | 100 | 170 | 75 | 267 | 168 | 851 |
| **(b) Column percentages** | | | | | | | |
| 0.00-0.74 | 21.13 | 26.00 | 25.29 | 6.67 | 11.99 | 18.45 | 17.86 |
| 0.75-1.49 | 50.70 | 47.00 | 59.41 | 60.00 | 59.55 | 67.26 | 58.87 |
| 1.50-2.24 | 23.94 | 26.00 | 8.82 | 28.00 | 25.09 | 13.10 | 19.74 |
| 2.25-2.99 | 4.23 | 1.00 | 6.47 | 5.33 | 3.37 | 1.19 | 3.53 |
| **(c) Expected counts** | | | | | | | |
| 0.00-0.74 | 12.68 | 17.86 | 30.36 | 13.40 | 47.69 | 30.01 | |
| 0.75-1.49 | 41.80 | 58.87 | 100.08 | 44.15 | 157.19 | 98.90 | |
| 1.50-2.24 | 14.02 | 19.74 | 33.56 | 14.81 | 52.71 | 33.16 | |
| 2.25-2.99 | 2.50 | 3.52 | 5.99 | 2.64 | 9.41 | 5.92 | |
| **(d) Migration corridor location** | | | | | | | |
| Median | 1.15 | 1.12 | 1.13 | 1.39 | 1.28 | 1.12 | |
| Mean | 1.20 | 1.14 | 1.07 | 1.35 | 1.25 | 1.13 | |
| SE | 0.06 | 0.05 | 0.04 | 0.05 | 0.03 | 0.03 | |

Weather conditions varied from flight to flight as storm fronts moved through the survey area during the sampling period. Beaufort states ranged from 2 (as far as 20 n.miles offshore on some flights) to 6. Of the twelve 20 n.mile legs, 8 were flown during Beaufort 2-3 states, 2 during Beaufort 4-5 and 2 during Beaufort 6. Light penetration and water clarity were generally good enough to view whales clearly beneath the surface.

Other species observed during the survey included one killer whale (*Orcinus orca*), Risso's dolphins (*Grampus griseus*: in groups ranging from 5-100+ animals, sometimes including calves), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*: with group sizes of 5-20 animals, some with calves), common dolphins (*Delphinus delphis*: in groups of 350 to over 1,000), northern right whale dolphins (*Lissodelphis borealis*: in mixed schools with Risso's and Pacific white-sided dolphins), and one minke whale (*Balaenoptera acutorostrata*).

### 1979-96 survey comparisons

The distributions of gray whale pods within 3 n.miles (Table 1) differed between years ($\chi^2 = 57.61$, df = 15, $p << 0.001$). Partitioning the table yielded similarities between the surveys conducted in 1979 and 1980 ($\chi^2 = 2.45$, df = 3, $p = 0.48$) and 1993 and 1994 ($\chi^2 = 2.32$, df = 3, $p = 0.51$). The 1988 and 1996 distributions were different ($\chi^2 = 10.16$, df = 3, $p = 0.02$), and each differed from the other surveys ($p < 0.005$ in all comparisons).

The nearshore (< 2.25 n.miles) and offshore (> 2.25 n.miles) distribution of gray whale pods (Table 2) did not differ significantly between survey years ($\chi^2 = 5.91$, df = 5, $p = 0.31$). The average percentage of pods beyond 2.25 n.miles was 4.76% (SE = 0.85%). The largest contributor to the chi-square statistic was the 1993 offshore cell. With the sample sizes obtained for the inshore-offshore comparison, the power of the chi-square test was reasonably good for small differences in the proportions offshore (0.02-0.09). For the alternative that the true offshore proportions are the measured values, the power was 0.45. Power calculations for the alternatives described by uniform distributions (Table 3) suggest that it was very unlikely that the proportion offshore varied by more than 0.02-0.15.

Table 2

Nearshore (within 2.25 n.miles) and offshore (beyond 2.25 n.miles) distribution of gray whale pods during the southbound migration near Granite Canyon, California, in January of each year.

| Bin width (n.miles) | 1979 | 1980 | 1988 | 1993 | 1994 | 1996 | Totals |
|---|---|---|---|---|---|---|---|
| **(a) Number of pods** | | | | | | | |
| 0.00-2.24 | 68 | 99 | 159 | 71 | 258 | 166 | 821 |
| 2.25-20.00 | 3 | 4 | 11 | 7 | 11 | 5 | 41 |
| Totals | 71 | 103 | 170 | 78 | 269 | 171 | 862 |
| **(b) Column percentages** | | | | | | | |
| 0.00-2.24 | 95.77 | 96.12 | 93.53 | 91.03 | 95.91 | 97.08 | 95.24 |
| 2.25-20.00 | 4.23 | 3.88 | 6.47 | 8.97 | 4.09 | 2.92 | 4.76 |
| **(c) Expected counts** | | | | | | | |
| 0.00-2.24 | 67.62 | 98.10 | 161.91 | 74.29 | 256.21 | 162.87 | |
| 2.25-20.00 | 3.38 | 4.90 | 8.09 | 3.71 | 12.79 | 8.13 | |

Table 3

Power calculations for the alternative hypothesis of a uniform distribution of tail probabilities with varying ranges and the probability ($P^*$) that a maximum of 9% (observed during the 1979-1996 aerial surveys) or less would be observed from the distribution.

| Range | Power | $P^*$ |
|---|---|---|
| 2-9% | 0.38 | 1.000 |
| 2-12% | 0.60 | 0.120 |
| 2-15% | 0.70 | 0.020 |
| 2-22% | 0.82 | 0.003 |

## DISCUSSION

To investigate what is occurring in the distribution of gray whales near the Granite Canyon station, the comparison of offshore distributions was restricted to within a narrow area north and south of the site. This reduced the sample sizes collected in all years except 1994 and 1996 and made comparisons between the results presented here and those in other publications (e.g. Reilly *et al.*, 1983; Withrow, 1990) inappropriate.

Even though significant differences between years were found in the distribution within 3 n.miles, this result should not be over-interpreted. First, the differences amount to no more than a 0.2-0.3 n.mile shift in the median distance (Table 1). Second, variations in distributional data within 3 n.miles of shore may, in part, result from differences or errors in methods used to gather positional data. In 1979 and 1980, the locations of whales relative to shore were 'calculated from the time difference between their position and the shore edge, and the plane's speed' (Reilly *et al.*, 1983, p.271). In 1988 and 1993, positions were determined by 'dead-reckoning' (Withrow, 1990); based on trackline starting time/position and ending time/position, with the position of the pod computed from the time of the sighting. GPS positions were used for the 1994 and 1996 surveys. All positional data were converted to distances relative to the coastline. Prior to 1993, the same way points were used for each survey. In 1994 and 1996, tracklines were staggered along the coast to average out irregularities in the coastline. However, indentations between points of land range from 0.10-0.20 n.miles and the irregularity of the coastline, in addition to the method used to determine pod locations, may account for some of the inter-year differences observed within 3 n.miles.

Inter-year comparison of proportions inshore and offshore of 2.25 n.miles is more important in assessing the impact on population estimates than are comparisons of sighting rates within 3 n.miles. If the shore-based observers saw no whales beyond 2.25 n.miles and the proportion exceeding 2.25 n.miles varied between 0.02 and 0.15, with a population of 20,000 gray whales, the estimate would vary from 17,000-19,600. However, shore-based observations to 3 n.miles are used in the abundance estimate, and the decrease in detection probability at larger offshore distances is already incorporated into the estimate (Laake *et al.*, 1994). Ignoring observations beyond 3 n.miles is of little consequence to the abundance estimate or an assessment of inter-year trend because the average percentage of aerial observations beyond 3 n.miles for all years combined was only 1.28% (SE = 0.07%) with a range of 0.0-3.8%.

## ACKNOWLEDGEMENTS

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# Evaluation of high-powered binoculars to detect inter-year changes in offshore distribution of eastern North Pacific gray whales

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ABSTRACT

Paired, independent searches for gray whales (*Eschrichtius robustus*) were conducted through fix-mounted, 25-power binoculars during January 1995 and 1996 at Granite Canyon, California. The study was a test of an efficient method for documenting inter-year changes in the offshore distribution of the migration. The research site has been used most years since 1975 by the National Marine Mammal Laboratory to make counts for abundance estimates of gray whales. Matching sightings between the paired observation efforts showed a very high agreement between observers (detection probability 0.97) for whale groups apparently of more than one animal within 1-3 n.miles of shore and a fairly high agreement (0.87) for animals travelling alone (5% of the sampled population) within 1-3 n.miles of shore. Sighting probability thus remained high up to 3 n.miles, a distance which includes most (98.7%) of the whale migration. For the critical sighting range of 1-3 n.miles, the method applied here is considered a feasible, cost-effective technique for detecting inter-year differences in the offshore tail of the distribution.

KEYWORDS: GRAY WHALE; SURVEY-SHORE-BASED; DISTRIBUTION; NORTH PACIFIC

## INTRODUCTION

The National Marine Mammal Laboratory (NMML) has been conducting shore-based counts of southbound migrating gray whales most winters over the past four decades. Since 1975, all of these counts have been made at Granite Canyon, near Carmel, central California (Reilly, 1992; Shelden *et al.*, 1997). The counts have formed the basis for estimates of and trends in abundance for this species (e.g. Buckland *et al.*, 1993; Buckland and Breiwick, 2002). The estimates are corrected for whales missed during watch periods using a sight-resight (double count) analysis of information from independent observers (Rugh *et al.*, 1990; 1993). However, the validity of the abundance estimates depends on the assumption that the sight-resight model incorporates all variables affecting detection probability. If whales pass at distances which effectively make them undetectable, abundance will be underestimated. Trend analysis assumes that there is no time dependence in any bias (Buckland *et al.*, 1993). If the offshore distribution of gray whales was to shift significantly beyond the shore-based observers' visual range (approximately 3 n.miles), bias could develop. Aerial surveys have been used to measure offshore distribution in the vicinity of the counting station (Reilly *et al.*, 1983; Withrow, 1990; Shelden and Laake, 2002) because there has been concern that the migratory corridor shifts significantly between years and needs to be assessed during each survey (Reilly, 1981).

Prior to using reticled binoculars (in 1985), distances to whale sightings were simply estimated. Results suggested there were large inter-year variations in offshore distribution (Reilly, 1981); however, on closer examination there appears to be little basis for using the estimated values as they were not calibrated. For example, from 1967-1980, observers estimated that 13.0% to 62.8% of the whale groups passed within 0.25 n.miles of shore (Reilly, 1981, table 7); yet, after reticled binoculars were in use, no more than 7% were sighted that close to shore (NMML, unpubl. data). Buckland and Breiwick (2002), in their analysis of gray whale counts from Granite Canyon, concluded 'that estimated distances offshore from shore-based observers are suspect'. It seems that offshore distances were grossly underestimated by shore-based observers before the use of reticled binoculars.

Six seasons of aerial survey effort near Granite Canyon showed that the nearshore ($<2.25$ n.miles) and offshore ($>2.25$ n.miles) distribution of gray whale pods did not differ significantly among survey years (Shelden and Laake, 2002). Only 4.76% of the pods were beyond 2.25 miles, and only 1.28% were beyond 3 miles (Shelden and Laake, 2002). Aerial surveys are clearly the most accurate method of assessing the offshore distribution of gray whales because the probability of detection is constant for all offshore distances, whereas shore-based observers will have a loss in detection probability as distance increases. However, aerial surveys are very costly, requiring approximately 40% of the annual survey budget and sample size may be limited. As a cost-effective replacement for aerial surveys, this study evaluated 25-power, reticled binoculars as a technique for detecting inter-annual changes in the offshore tail of the whale distribution. Because most (approximately 99%) of the gray whales passing Granite Canyon have been within 3.0 n.miles of shore (Shelden and Laake, 2002), 25-power binoculars may be a useful tool if the probability of detecting surfacing whales is high and relatively uniform up to 3 n.miles. This study estimates the detection probability of observers using 25-power binoculars with sight-resight data collected from paired, independent counts.

## METHODS

The paired, independent observer effort using two fix-mounted, 25-power binoculars ('Big Eyes') was conducted 6-25 January 1995 and 7-25 January 1996 during the gray whales' southbound migration past Granite Canyon (elevation 20.5m). Concurrent with the high-powered binocular study, standard counts were made for abundance estimations as in previous surveys (Rugh *et al.*, 1990; 1993). During the standard count effort, searches for whales were made across a 40-50° field of view, primarily without optic aids but assisted by handheld 7-power binoculars with compasses and reticles. In addition to the shore-based studies, an aerial survey was conducted in January 1996 (Shelden and Laake, 2002). Results from the 1995/96 standard counts are reported in Hobbs *et al.* (1996).

### Paired binoculars

Each 25-power binocular was housed in a separate observation shed. These sheds were approximately 2m apart and separated from sheds used for the standard census. The binoculars were supported on 1.2m wooden frames so that observers could view through them while comfortably seated. Fine vertical and horizontal adjustments allowed the binoculars to be set to nearly identical fields of view, which was critical for the paired effort. The horizontal orientation was along the 241° magnetic line, equivalent to the primary sighting angle on the standard watch. The 25-power magnification and narrow field of view (2.7°) made the system very sensitive to misalignment. Slow moving targets, such as distant ships, were used to check horizontal alignment and make adjustments if necessary. Alignment of the two binoculars was kept accurate to within 0.03° (1% of the field of view).

### Horizontal sectors

The horizontal field of view in the binoculars was divided into 6 *ad hoc* sectors. This provided an assessment of the horizontal component of a sighting. As the sectors were not etched onto the eyepieces, they had to be approximated by observers with the assistance of a drawing (Fig. 1). Whales seen to the extreme left or right (sectors 1 or 6) may have been missed by one of the two observers if the two binoculars were not exactly aligned; in the paired-record analysis, these entries were examined relative to sightings made in the mid-range (sectors 2-5).

### Vertical increments

The binoculars had scribed marks to delineate most of the vertical field of view. These showed whole and half increments for each of 20 reticles (0.077° each; Kinzey and Gerrodette, 2001), with the uppermost reticle sub-divided into fifths (Fig. 1). The uppermost line was set on the horizon, and the vertical angle was established as the number of reticles counted from the horizon down to the waterline where a whale surfaced. The vertical viewing perimeter of the search effort ranged from 9.0 n.miles (the horizon) to $<0.4$ n.miles, the closest perimeter in which a whale may have been seen. Calculations for offshore distance included a correction for dip to the horizon (the angle between absolute horizontal and the apparent horizon) and curvature of the earth. Distances were checked with an array of calibrations conducted in cooperation with a US Coast Guard vessel.

### Observers

At different times during the two research seasons, 12 observers took part in the study. All were experienced cetacean survey observers, and several had previous experience with gray whale counts at Granite Canyon. During periods with acceptable sighting conditions, standard and fixed-binocular watches were conducted continuously and simultaneously such that two to four observers were on effort at a time. Effort on the fixed-binoculars was divided into 45min watches and generally ran from 07:30 to 16:30. Watch rotations gave each observer equal pairing with all other available observers over the respective season. Observers were given at least a 1.5hr rest before and after each standard watch and a minimum of 45min rest between watches on the fixed binoculars.

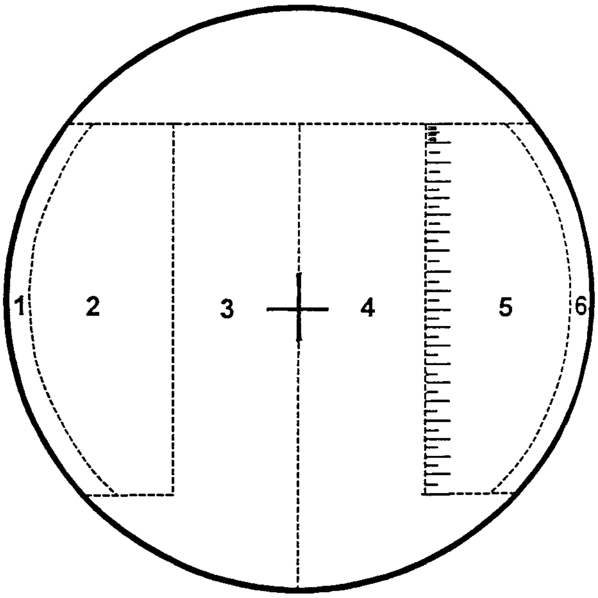

Fig. 1. Horizontal sectors (bordered by dashed lines) and vertical reticle marks (solid bars) used to describe locations of whale sightings in fix-mounted, 25-power binoculars. The dashed line across the top of the field of view demarks the horizon. Other dashed lines represent subjective borders. Solid lines represent marks permanently etched in the binocular optics.

### Independent effort

To keep the search efforts independent, no cues were communicated between observers while on watch. Visual isolation was provided by the walls of the observation sheds. Surf and wind noise or portable headsets blocked out other observers' voices. In an attempt to maximise search effort through the binoculars and minimise the time spent looking away, data were collected through voice-actuated tape recorders. After each 45min observation period, data were transcribed from tapes onto standard recording forms.

### Timing

Precise timings of surfacings were required to minimise discrepancies and potential ambiguities when making matches between the paired observers' records. At the start of each day, time pieces were synchronised to within 1sec. During the search through the binoculars, whale surfacings were recorded on audio tapes along with information on the vertical reticles and horizontal sectors in which the sightings occurred. The exact time was then reported to the second by a glance at a nearby digital watch. Pod sizes were estimated after each whale group left the field of view. During data transcription, the exact time of each surfacing was back-calculated from the recorded times. The precision in recording time was within 6sec. When an observer felt a time could not be estimated to within 10sec, a 'T' was entered to indicate 'time estimated'. When time could not be estimated closer than 60sec, a 'U' was entered for 'unknown time'. Only one surfacing per whale group was recorded in the primary dataset; other surfacings were usually tallied and later aided in the matching process. The surfacing tally was a record of the number of times each whale in the respective pod was visible.

### Visibility

Visibility was recorded as the apparent sightability of whales. It was subjectively appraised into one of six categories from excellent (1, an uncompromised view of the search area) to useless (6, very low likelihood that a surfacing whale could be seen). Because visibility through the binoculars often changed dramatically as a function of distance, the first 4 reticles below the horizon ( > 0.5 n.miles) were each assigned separate visibility ratings, while all distances inshore of reticle 4 ( < 0.5 n.miles) were given a single rating; therefore, there were five visibility zones designated from the horizon down.

### Establishing matches between paired sighting records

The paired records were manually searched for matches (i.e. whale groups recorded by both observers). To establish parameters in which a pair of sightings might be considered a match, several people independently reviewed each season's data, looking for sightings that were within a few seconds, reticles and sectors of each other. This *ad hoc* process also allowed for the possibility that different sightings were recorded of the same whale group as it passed southward through the viewing area. The independent reviews were then compared, first to establish obvious matches (within 6sec, 1 reticle and 1 sector) and then to work out appropriate rulings for ambiguous cases. Most matchings (98.3%) were unequivocal. Surfacing times proved to be the most important data used for recognising matches. Vertical measures (reticles) and horizontal sectors were used to locate positions of sightings, while information on group size, behaviour (e.g. breaching or fluking) and number of sighting cues, helped support decisions on matches.

Only periods when two observers were systematically searching were reviewed. When an entry had time recorded as estimated (T) or unknown (U), the observer's record was treated as 'off watch' for the time between the previous timed entry and the following timed entry. Sightings within the corresponding time period in the paired observer's record were also deleted. Summarising both sets of records for both years, 88 sightings were deleted because of time recording problems. That represents only 4% of the recorded sightings, so any potential bias in terms of a higher probability of deleting matched rather than unmatched records is minimal.

### Analysis

Once the matching record was established, a sight-resight type analysis was performed using the logistic regression approach of Buckland *et al.* (1993). With this method, the sensitivity of the sighting probability to different covariates can be reviewed.

For the 1995 dataset, the covariates considered were horizontal sector, pod size, distance offshore (expressed in reticles), visibility, observer and location (south or north sheds) (Table 1). The visibility code for a sighting was the single visibility code assigned to the reticle range within which the sighting was made. Counts of sighting cues were considered to approximately equate pod size estimates and therefore were not treated separately in the covariate analysis. All covariates were treated as categorical data. All covariates were entered into the model, and a backward step-wise model selection was used until no step decreased the Akaike's Information Criterion (AIC).

The 1996 data were analysed as for 1995 except that horizontal sector was dropped as a covariate (parts of sectors 1 and 6 were potentially not in view in both binoculars, so they were not used in the analysis), sea state and wind direction were added, and distance was treated as distance offshore rather than reticles below the horizon, thus increasing compatability with other studies (Table 1). All covariates were initially examined individually as categorical data, with numeric covariates treated as binned data. Numeric data were then assigned a functional form, or bins were combined to represent the data with as few parameters as possible. A visibility threshold was determined from the result of this categorical analysis; sightings from effort periods with lower than the threshold visibility were removed, while higher visibilities were uniformly included, without separate treatments for each visibility category. All covariates were then entered into the model and a backward step-wise model selection was used until no step decreased the AIC.

Table 1

Data collected while using paired, high-powered binoculars to observe gray whales migrating south past the shore-based station at Granite Canyon, California.

| Data fields | Covariates analysed[1] 1995 | 1996 | Covariates included in the model |
|---|---|---|---|
| Location (N or S Shed) | 2 | 2 | - |
| Date | - | - | - |
| Observer | 7 | 13 | - |
| Effort (start and stop time) | - | - | - |
| Visibility | 6 | 6 | 6 *vs* <6 |
| Wind direction | - | 16 | - |
| Wind force | - | 5 | - |
| Sighting time | - | - | - |
| Sighting sector (horizontal) | 6 | - | sectors 1 and 6 *vs* 2-5 |
| Sighting reticle (vertical) | >20 | >20 | reticles 0-2 *vs* 2-3 *vs* >3 |
| Size of whale group | 5 | 8 | 1 *vs* >1 |
| Presence of a calf | - | - | - |
| Travel direction | - | - | - |
| Behaviour | - | - | - |
| Number of sighting cues | - | - | - |
| Comments | - | - | - |

[1] Column entries are the number of categories recorded for each covariate.

## RESULTS

### Watch effort

During 6-25 January 1995, there was a total of 76.3 hours of observation in the south binocular and 74.7 hours in the north (of which 69.7 hours were paired). During 9-25 January 1996, there was a total of 124.9 hours in the south binocular and 119.1 hours in the north (of which 108.9 hours were paired). Effort was greatly compromised by weather conditions in 1995; unusually intense winds, rains and flooding dominated portions of the season. Weather in 1996 was considered fairly typical for winters in the study area.

### Sample size

In 1995, 381 pods (543 whales) were seen from the south binocular and 360 pods (502 whales) from the north. In 1996, 631 pods (1,038 whales) were seen from the south binocular and 613 pods (981 whales) from the north. Between the two seasons, peak counts reached 21 pods/hr but averaged 2.4 pods/hr, and on 20 of the 45-minute watches (8 in 1995; 12 in 1996) no whales were recorded. Based on the recorded number of sighting cues, whales surfaced an average of 1.7 times through the field of view.

Table 2 shows the number of sightings in each distance bin (0.25 n.miles) as used in the analysis after removing sightings from sectors 1 and 6, entries with timing problems, data collected during low visibility periods and any but unequivocal matches between observers' records.

Table 2

Number of gray whale sightings made during a study with high-powered binoculars at Granite Canyon, California. Sightings are shown as a function of distance from shore (n.miles) and observation shed. When paired observers recorded different offshore distances for a sighting they made in common, the data were split between the respective distance bins in this table.

| | 1995 | | | 1996 | | | Both sheds in both years (%) |
|---|---|---|---|---|---|---|---|
| Distance offshore | North shed | South shed | Both | North shed | South shed | Both | |
| 0-0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| 0.5 | 1 | 1 | 1 | 5 | 6 | 4 | 0.8 |
| 0.75 | 10 | 11 | 9 | 16 | 17 | 15 | 3.5 |
| 1.0 | 9 | 10 | 7 | 61 | 54 | 53 | 8.6 |
| 1.25 | 27 | 45 | 29 | 99 | 105 | 95.5 | 17.6 |
| 1.5 | 68 | 53 | 51.5 | 108 | 106 | 97.5 | 21.4 |
| 1.75 | 71 | 71 | 57.5 | 75 | 79 | 72 | 18.9 |
| 2.0 | 49 | 49 | 43.5 | 74 | 66 | 65.5 | 15.2 |
| 2.25 | 24 | 17 | 18 | 22 | 25 | 21 | 5.6 |
| 2.5 | 12 | 9 | 7 | 9 | 15 | 10.5 | 2.9 |
| 2.75 | 3 | 10 | 4.5 | 8 | 8 | 6.5 | 1.9 |
| 3.0 | 8 | 6 | 4 | 5 | 6 | 5.5 | 1.6 |
| 3.25 | 4 | 3 | 2.5 | 1 | 1 | 0.5 | 0.6 |
| 3.5 | 0 | 0 | 0 | 1 | 0 | 0.5 | 0.1 |
| 3.75 | 2 | 2 | 0.5 | 1 | 0 | 0 | 0.3 |
| 4.0 | 0 | 3 | 1 | 1 | 2 | 1 | 0.4 |
| 4.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| 4.5 | 3 | 0 | 1 | 0 | 0 | 0 | 0.2 |
| 4.75 | 1 | 1 | 1 | 0 | 0 | 0 | 0.1 |
| 5.0 | 0 | 1 | 0.5 | 0 | 0 | 0 | 0.1 |
| 5.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| 5.5 | 2 | 1 | 0.5 | 0 | 0 | 0 | 0.2 |
| >5.5 | 0 | 0 | 0 | 0 | 1 | 0 | 0.1 |
| Totals | 294 | 293 | 239 | 486 | 491 | 448 | |

Of the sightings matched between paired records, most (87%) were $< 6$sec apart, 96% were within 1 sector of each other and 96% were within 1 reticle. Of the sightings seen while two observers were on watch in 1995, 239 pods were recorded by both observers and 109 pods were recorded by only one. In 1996, 448 sightings were matched and 81 unmatched. This makes a total of 687 pods seen by both observers compared to 190 seen by only one observer.

### Covariates

The significant covariates in the logistic regression of the 1995 data were horizontal sector, pod size, distance offshore and visibility. To keep the model simple and relatively easy to interpret, no interaction terms were considered. Horizontal sectors (1 and 6 *vs* 2-5), pod size (1 *vs* $> 1$) and visibility (6 *vs* $< 6$) were each separated into two different categories, while distance offshore was divided into three categories (reticles 0-2, 2-3 and $> 3$). The extreme horizontal sectors (1 and 6) had some distortion, therefore the associated sightings (58 unmatched pods and 30 matched pods) were removed from further analysis, increasing the probability that both observers were studying the same viewing area.

Analysis of the 1996 data indicated a significant drop in sighting probability with visibility $> 4$, which was chosen as the visibility threshold. The seven pods sighted at visibility 5 were discarded from the analysis; none were seen in visibility 6. The significant covariates in the logistic regression were pod size, distance offshore and observer. Interactions of these three terms were considered and none were significant. A functional form was assigned to distance offshore which was modelled with linear, quadratic and inverse terms. The inverse of distance was included to model a steep drop in sightability near shore. The squared term dropped out and the linear and inverse terms remained. The detectability of pods of size one was significantly less than that of pods of size two or greater, but no significant difference in detectability occurred among the categories for pods $> 1$, so bins of 1 and $> 1$ were used. Observers were treated individually and were found to be significant covariates as a group, though no observer was found to be significantly different from the average observer; observer was thus dropped as a covariate.

### Detection probabilities

In 1995, the proportion of sightings seen by an average observer was 0.87 when pod size was $= 1$ (visibility $< 6$; sectors 2-5; distance $< 1.88$ n.miles) and 0.95 when pod size was $> 1$. In 1996, the proportion of sightings seen by an average observer was 0.87 when pod size was $= 1$ (visibility $< 5$; sectors 2-5; distance 1-3 n.miles) and 0.97 when pod size was $> 1$. Detection probabilities are shown as a function of distance offshore (Fig. 2), with pod sizes $= 1$ and $> 1$ segregated. The mean offshore distance of pod sightings, when visibility was $< 5$, was 1.94 n.miles ($n = 302$ pods; SD = 0.66 n.miles) in January 1995 and 1.72 n.miles ($n = 667$ pods; SD = 0.53 n.miles) in January 1996. These mean distances are not comparable to those obtained from aerial surveys because the nearshore sighting probability is low within the binoculars' field of view. In summary, then, the paired-observer sighting records showed a very high agreement between observers (detection probability 0.97) when whale group size was $> 1$ within 1-3 n.miles of shore and a fairly high agreement (0.87) for single whales (5% of the sampled population) within 1-3 n.miles of shore. Sighting probability thus remained high up to 3 n.miles, a distance which includes most (98.7%) of the whale migration (Shelden and Laake, 2002).

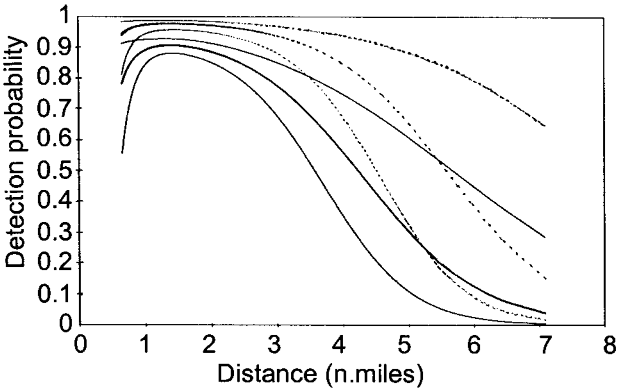

Fig. 2. Detection probabilities of gray whale pods migrating south past Granite Canyon, California, shown as a function of distance offshore. Detection is determined through rates of sightings matched or not matched between independent, paired observations on high-powered binoculars. The solid lines ($\bar{x}$ with 95% CI) show sightings where pod size $= 1$, and the dashed lines ($\bar{x}$ with 95% CI) show pod size $> 1$. Data are from all but the extreme horizontal sectors (1 and 6) and from all but the worst visibilities (5 and 6).

## DISCUSSION

The process of comparing paired, independent observation records is not new (e.g. Magnusson *et al.*, 1978; Maxim *et al.*, 1981; Rugh, 1984; Rugh *et al.*, 1990; 1993), but the application of this process to determining probability of detection in high-powered binoculars led to greater precision. The field of view for an observer on the standard watch was approximately 160° while the field of view through the 25-power binoculars was less than 3°. Although observers on the standard watch had many more opportunities to see each whale group passing through the search area, the likelihood that two observers would be looking in the same direction was small relative to two observers looking through the two aligned binoculars. The test with fix-mounted binoculars was therefore a relatively accurate assessment of sightability of whales in the common field of view (detection probability $>0.9$) in comparison with the paired standard watch (0.8; Rugh *et al.*, 1993). By locking down the binoculars on their frames and making fine adjustments for alignment, both observers should have been studying the same area. In the analysis, small amounts of misalignment were compensated for by removing records of sightings made in the extremes of the field of view (sectors 1 and 6). By using tape recorders and keeping the search effort to only 45 minutes at a time, the chance that one observer would have been looking away when the other made a sighting was minimised. The system improves the likelihood of detecting distant whales and increases the precision of location data. Through sight-resight type analysis, detection probability as a function of distance from shore may be calculated, and significant shifts in offshore distribution of the migratory corridor should be evident. With these refinements, paired binoculars provide an accurate mechanism for monitoring the offshore distribution of gray whales within the viewing area.

Detection probabilities calculated here might be overestimated as they do not account for all sources of heterogeneity, such as differences in number and size of sighting cues per whale at a given distance. Some surfacings are high, and the blows are distinct, while others are low and cryptic. However, even if this bias is significant (as much as 20%), the detection probability is sufficiently high for high-powered binocular surveys to be used instead of aerial surveys in detecting inter-year shifts in the offshore tail of the distribution of migrating gray whales.

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# What is needed to make a simple density-dependent response population model consistent with data for eastern North Pacific gray whales?[1]

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ABSTRACT

Census estimates indicate that the eastern North Pacific gray whale population showed an increase rate of some 3.2% per annum from 1968-1988. Further, historic records suggest that the population was 'commercially extinct' at the end of the 19th century. The standard HITTER-FITTER population model trajectories which pass through the 1987-88 census estimate of some 21,113, and utilise the customary historic commercial catch series, are inconsistent with both of these features; in particular, they generally show a decrease over the 1968-1988 period. The quantitative extent of various possible adjustment factors that would be needed to resolve these inconsistencies is examined. Depensation effects alone cannot account for the inconsistencies, while a model used to incorporate an additional response delay in recovery from exploitation produces unrealistic population oscillations. Other adjustment factors can, however, produce a 1968-1988 annual population increase rate of 2% or more, and all also correspond to a depletion of the population in 1900 to less than 25% of its size at the onset of commercial whaling in 1846. These are: an increase in the carrying capacity from 1846-1988 of at least 2.5 times; an underestimation of the historic commercial catch from 1846-1900 of at least 60%; or annual aboriginal catch levels prior to the commercial fishery at least three times those estimated by the 1990 Special Meeting of the Scientific Committee (IWC, 1993). These limits weaken if the adjustment factors are considered in combination rather than separately. The results appear insensitive to values assumed for the biological parameters of the population model (natural mortality, age at first parturition, age at recruitment and MSY level). However, they are sensitive to assumptions concerning data inputs, *viz* the accuracy of the 1987-88 census estimate used, and a 2:1 female:male ratio assumed for the commercial catches for which this information is not available. All trajectories which reflect a 1968-88 annual increase rate of 2% or more correspond to MSYR values (in terms of a 5+ exploitable population) of at least 4%. Fits of the population model to the series of gray whale census estimates are mis-specified, unless either or both of the historic commercial and aboriginal catches have been substantially underestimated (or carrying capacity has increased). The precision of these fits, conditional on fixed levels for such underestimation, is quite high, with coefficients of variation of about 10% for historic population sizes and about 20% for MSYR. There are indications that even if allowance was made for the uncertainty about these levels of underestimation, MSYR would remain relatively robustly estimated to be some 5% (or about 4% if expressed in terms of uniform selectivity on the 1+ population).

KEYWORDS: GRAY WHALE; NORTH PACIFIC; ASSESSMENT; WHALING-HISTORICAL; WHALING-ABORIGINAL; MSY

## INTRODUCTION

The problem of reconciling the commercial catch history for the eastern North Pacific gray whale (*Eschrictius robustus*) population with the population increase rate deduced from censuses carried out at Monterey from 1967-68 to 1979-80 when using a simple density dependent response population model is well known (Reilly, 1981; Cooke, 1986; Lankester and Beddington, 1986).

Fig. 1 captures the essence of the problem. It shows population model trajectories for this stock for a number of choices for the maximum sustainable yield rate (MSYR) parameter (expressed in terms of the 'exploitable' component of the population throughout this paper except where indicated otherwise). All of these trajectories are constrained to pass through ('hit') a total (1+) population size of 21,113 in 1988, which corresponds to the 1987-88 census estimate (Breiwick *et al.*, 1988)[2]. Further details concerning the calculation of these trajectories are given in the following section of the paper. Note first that for this 'standard model', the average annual growth rate over the 1968-1988 period for every one of the trajectories shown is *negative*. This is in contrast to the *positive* growth rate of 2.5% per annum over the 1968-1980 period indicated by the census estimates reported in Reilly *et al*. (1983) and to the estimate of 3.2% (SE = 0.5%) per annum for the 1968-1988 period (IWC, 1993). Further, Fig. 1 (and Table 3) show that none of these trajectories indicates substantial depletion of the population by the commercial catches over the latter half of the 19th century. This hardly seems consistent with the history of a population 'commercially extinct' by the end of that period (Reilly, 1981), unless a large part of the stock ceased to frequent the lagoons in Baja California where much of the commercial whaling took place (Lankester and Beddington, 1986).

All the authors referenced above suggest factors that could resolve these inconsistencies. Lankester and Beddington (1986) allude to possible increases in carrying capacity or the lack of an immediate start to recovery after the cessation of whaling. Cooke (1986) intimates that the latter effect might have been a consequence of the disruptive influence of intensive whaling temporarily depressing the breeding rate (equivalent here to the depensation effect referred to below). Cooke himself adds the possibilities of under-recorded historical catches, an overestimate of the recent growth rate of the population, the population being held at a low level by aboriginal whaling prior to the onset of commercial whaling in 1846, and the recent population increase not constituting

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[1] Originally presented as paper SC/A90/G10, updated to take account of data revisions agreed at the 1990 Special Meeting of the Scientific Committee on the Assessment of Gray Whales (IWC, 1993).

[2] A more recent reanalysis (Buckland *et al.*, 1993) published after this paper was finalised, provides an estimate for the 1987-88 census of 20,869 and an alternative 'modelled' estimate of 21,296. This does not affect the conclusions of this paper.

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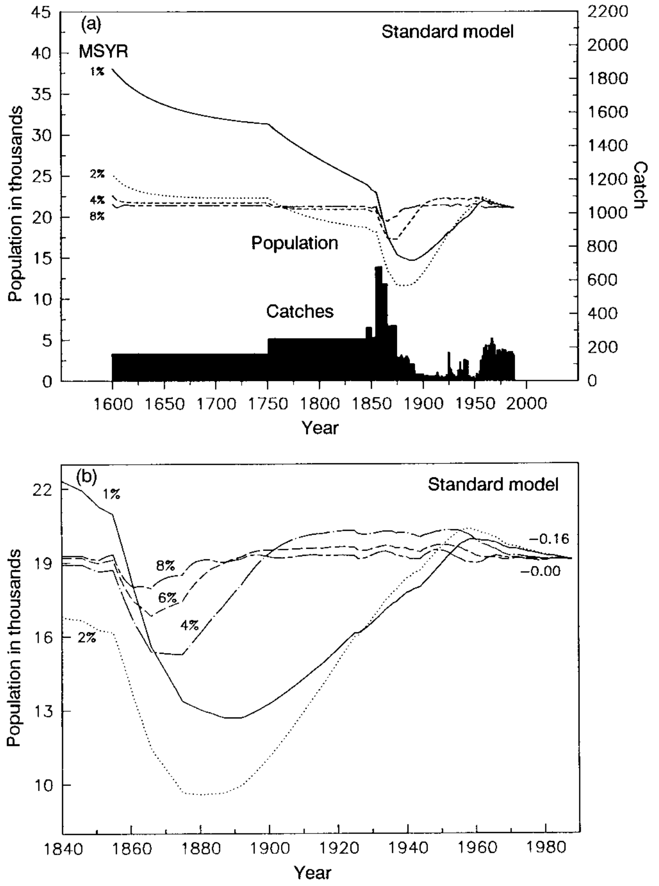

Fig. 1. The standard population model results, which incorporate the aboriginal catches of Table 2(b), for various MSYR values (1%, 2%, 4%, 6% and 8% as indicated in the Figure) for trajectories which hit a 1988 total population size of 21,113. In (a), the annual catches are also shown (on a different scale). A magnification of the population trajectories in (a) is shown in (b); the figures on the right hand extremities of the trajectories give the percentage annual increase ('Slope') of the total population from 1968-1988 as estimated from a linear regression fit to the logarithms of the model estimates of population size over this period.

a simple density-dependent response to previous exploitation. Reilly (1981) also considers the implications of earlier aboriginal whaling.

Only one of these possibilities appears to have been investigated quantitatively to any real extent. Lankester and Beddington (1986) considered the consequences of a constant annual aboriginal catch level ($C_{abo}$) prior to 1846, and concluded that this did not appear to influence the resultant population trajectory markedly (in particular, the trajectory still showed a decline over recent years). However, the case they illustrate (their fig. 3) has $C_{abo}$ = 250 only. In contrast, Reilly (1981) provides results (his fig. 3) which indicate that a recent population increase is compatible with a population model if $C_{abo}$ had increased to 600 by the year 1800, and comments that he is 'aware of nothing in the literature to clearly refute or substantiate' this possibility.

Clearly the factors mentioned, and indeed other possibilities, may well be able to reconcile the inconsistencies mentioned above. The important question though, is how *large* such factors would have to be to provide the requisite reconciliation; this must then be followed by the second question of whether there is any independent evidence for factors of that magnitude. The purpose of this paper is to attempt to answer the first of these questions, so that the second may be addressed by taking account of other evidence relating to those factors, including that presented in IWC (1993).

To this end, this paper considers the quantitative consequences of five possible adjustments to the 'standard model' (and associated datasets). These are depensation and additional time-lags in the density-dependent response (either of which could delay recovery after the cessation of commercial whaling in the late 19th century), an increase in carrying capacity, underestimation of historic commercial catches and aboriginal catches prior to the commercial fishery. These possibilities are investigated using the HITTER-FITTER (or BALEEN II) population model (de la Mare, 1989) commonly applied in assessments conducted for the IWC Scientific Committee; the associated parameter estimation procedure is a development of an approach of matching the slope of a time-series of a relative abundance index while also hitting an estimate of absolute abundance, which was pioneered by Holt (1985; 1986). Sensitivity of the results to the input data and to choices for the values of the biological parameters for this model is explored to a limited extent. Similarly, there is a limited investigation of the consequences of combinations of the adjustment factors listed above. Finally, the population model is 'fit' to the series of census estimates up to 1987-88 for some of these combinations, and bootstrap confidence intervals are calculated for one of these 'fits' to indicate the precision of the values of the model parameters estimated in this process.

## DATA AND METHODOLOGY

### Data

The census estimates used for the final 'fits' of the population model, taken from Buckland and Breiwick (2002), are listed in Table 1. Breiwick (pers. comm.) advises that the fraction of cow-calf pairs in the census data is very

Table 1

Gray whale estimates, with standard errors in parentheses.

| Year | Relative estimate | Absolute estimate |
|---|---|---|
| 1967-68 | 9,871 (667) | 13,012 (893) |
| 1968-69 | 9,289 (350) | 12,244 (484) |
| 1969-70 | 9,693 (381) | 12,777 (525) |
| 1970-71 | 8,474 (603) | 11,170 (806) |
| 1971-72 | 7,466 (323) | 9,841 (442) |
| 1972-73 | 12,868 (477) | 16,962 (660) |
| 1973-74 | 11,241 (429) | 14,817 (592) |
| 1974-75 | 9,964 (392) | 13,134 (540) |
| 1975-76 | 11,236 (506) | 14,811 (690) |
| 1976-77 | 12,100 (371) | 15,950 (524) |
| 1977-78 | 12,993 (716) | 17,127 (966) |
| 1978-79 | 10,090 (361) | 13,300 (501) |
| 1979-80 | 12,579 (500) | 16,581 (668) |
| 1984-85 | 16,646 (728) | 21,942 (994) |
| 1985-86 | 15,514 (520) | 20,450 (727) |
| 1987-88 | 16,017 (486) | 21,113 (688) |

Data source: see Buckland and Breiwick (2002), table 8; the absolute estimates above are the 'adjusted abundance estimates' of that table, i.e. the relative estimates scaled so that the absolute estimate for 1987-88 equals the 21,113 abundance estimate of Breiwick *et al.* (1988).

The values listed above, which were used for the calculations of this paper, were taken from an earlier version of Buckland and Breiwick (2002). There are minor changes to these values in the final version of that paper published in this volume, but the effect of these on the results reported in this paper is negligible.

small, so that these estimates of abundance have been taken to refer to age classes 1+ when comparing to the output from the population model.

As discussed in IWC (1993), the analysis by Breiwick *et al*. (1988) of data from the 1987-88 census is considered to provide the most reliable estimate of *absolute* abundance. Estimates of absolute abundance for other years were obtained by scaling a relative abundance series to this value, as detailed in Buckland and Breiwick (2002) and IWC (1993).

A sex-differentiated catch series is required for application of the HITTER-FITTER model to calculate population trajectories. What will be termed the ‘commercial catch’ data (actually, these are augmented by some small aboriginal catches which had been identified prior to the 1990 Special Meeting on gray whales (IWC, 1993)) are listed in Table 2(a), which also details the sources for these data and further assumptions which have been made in their compilation. An earlier version of this Table has now been amended to incorporate the modifications to the commercial catch data considered appropriate in IWC (1993). It has also been extended (Table 2(b)) to show the specifications of aboriginal catch levels until 1930 given in IWC (1993) and appropriate additions to the known aboriginal catch data from 1931-1943.

It is conventional in the case of this gray whale population to label the time of the various census estimates in the form of, for example, ‘1967-68’. For the rest of this paper, such an estimate will be labelled by the latter of the two years, i.e. ‘1968’ for the example given, and will be taken to correspond to the number of whales aged 1 and above provided by the population model for the ‘beginning of the year’.

## Population model

The HITTER-FITTER population model used is described in de la Mare (1989), Punt and Butterworth (1991) and Punt (1999), so that the details will not be repeated here. However, to aid in the explanation of certain subsequent model adjustments, it is useful to provide a simplified generic form of the basic population dynamics model (this

Table 2

Annual gray whale catches used for the population model. Data sources for commercial catches: Total catch: 1846-1854 = IWC (1993), Annex E; 1855-1962 = Lankester and Beddington (1986); 1963-1988 = C. Allison (IWC document dated 16/1/90); Sex ratio of catch: 1965-1970 = Lankester and Beddington (1986); 1972-1976 = Lankester and Beddington (1986); 1977-1988 = C. Allison (IWC document dated 16/1/90). Notes: (1) struck and lost whales are included in the totals; (2) the sex ratio of unknown sex or lost animals is assumed to be the same as that of animals of known sex in the catch that year; (3) for years for which no sex ratio information is indicated above, a ratio of 2:1 female:male is used (as in Lankester and Beddington, 1986); Reilly (1981) argues for a similar female preponderance (60%) in the 19th century catches. Data source for aboriginal catches: Total catch and assumed 1:1 sex ratio = IWC (1993), Annex E.

| Year | Male | Female | Total | Year | Male | Female | Total | Year | Male | Female | Total | Year | Male | Female | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **(a) Commercial catches** | | | | | | | | | | | | | | | |
| 1846 | 23 | 45 | 68 | 1885 | 21 | 41 | 62 | 1924 | 5 | 11 | 16 | 1963 | 60 | 120 | 180 |
| 1847 | 23 | 45 | 68 | 1886 | 17 | 33 | 50 | 1925 | 50 | 99 | 149 | 1964 | 70 | 140 | 210 |
| 1848 | 23 | 45 | 68 | 1887 | 7 | 13 | 20 | 1926 | 19 | 38 | 57 | 1965 | 68 | 108 | 176 |
| 1849 | 23 | 45 | 68 | 1888 | 7 | 13 | 20 | 1927 | 16 | 32 | 48 | 1966 | 123 | 97 | 220 |
| 1850 | 23 | 45 | 68 | 1889 | 7 | 13 | 20 | 1928 | 9 | 18 | 27 | 1967 | 94 | 156 | 250 |
| 1851 | 23 | 45 | 68 | 1890 | 7 | 13 | 20 | 1929 | 6 | 12 | 18 | 1968 | 67 | 134 | 201 |
| 1852 | 23 | 45 | 68 | 1891 | 7 | 13 | 20 | 1930 | 5 | 10 | 15 | 1969 | 59 | 155 | 214 |
| 1853 | 23 | 45 | 68 | 1892 | 7 | 13 | 20 | 1931 | 5 | 11 | 16 | 1970 | 26 | 125 | 151 |
| 1854 | 23 | 45 | 68 | 1893 | 0 | 0 | 0 | 1932 | 5 | 10 | 15 | 1971 | 51 | 102 | 153 |
| 1855 | 162 | 324 | 486 | 1894 | 0 | 0 | 0 | 1933 | 3 | 7 | 10 | 1972 | 22 | 160 | 182 |
| 1856 | 162 | 324 | 486 | 1895 | 0 | 0 | 0 | 1934 | 18 | 36 | 54 | 1973 | 97 | 81 | 178 |
| 1857 | 162 | 324 | 486 | 1896 | 0 | 0 | 0 | 1935 | 11 | 23 | 34 | 1974 | 94 | 90 | 184 |
| 1858 | 162 | 324 | 486 | 1897 | 0 | 0 | 0 | 1936 | 34 | 68 | 102 | 1975 | 58 | 113 | 171 |
| 1859 | 162 | 324 | 486 | 1898 | 0 | 0 | 0 | 1937 | 5 | 9 | 14 | 1976 | 69 | 96 | 165 |
| 1860 | 162 | 324 | 486 | 1899 | 0 | 0 | 0 | 1938 | 18 | 36 | 54 | 1977 | 86 | 101 | 187 |
| 1861 | 162 | 324 | 486 | 1900 | 0 | 0 | 0 | 1939 | 10 | 19 | 29 | 1978 | 93 | 91 | 184 |
| 1862 | 162 | 324 | 486 | 1901 | 0 | 0 | 0 | 1940 | 35 | 70 | 105 | 1979 | 56 | 127 | 183 |
| 1863 | 162 | 324 | 486 | 1902 | 0 | 0 | 0 | 1941 | 19 | 38 | 57 | 1980 | 53 | 128 | 181 |
| 1864 | 162 | 324 | 486 | 1903 | 0 | 0 | 0 | 1942 | 34 | 67 | 101 | 1981 | 36 | 100 | 136 |
| 1865 | 162 | 324 | 486 | 1904 | 0 | 0 | 0 | 1943 | 33 | 66 | 99 | 1982 | 56 | 112 | 168 |
| 1866 | 79 | 159 | 238 | 1905 | 0 | 0 | 0 | 1944 | 0 | 0 | 0 | 1983 | 46 | 125 | 171 |
| 1867 | 79 | 159 | 238 | 1906 | 0 | 0 | 0 | 1945 | 10 | 20 | 30 | 1984 | 59 | 110 | 169 |
| 1868 | 79 | 159 | 238 | 1907 | 0 | 0 | 0 | 1946 | 7 | 15 | 22 | 1985 | 54 | 116 | 170 |
| 1869 | 79 | 159 | 238 | 1908 | 0 | 0 | 0 | 1947 | 3 | 6 | 9 | 1986 | 45 | 126 | 171 |
| 1870 | 79 | 159 | 238 | 1909 | 0 | 0 | 0 | 1948 | 6 | 13 | 19 | 1987 | 47 | 112 | 159 |
| 1871 | 79 | 159 | 238 | 1910 | 0 | 0 | 0 | 1949 | 9 | 17 | 26 | 1988 | 43 | 108 | 151 |
| 1872 | 79 | 159 | 238 | 1911 | 0 | 0 | 0 | 1950 | 4 | 7 | 11 | | | | |
| 1873 | 79 | 159 | 238 | 1912 | 0 | 0 | 0 | 1951 | 4 | 9 | 13 | **(b) Aboriginal catches** | | | |
| 1874 | 79 | 159 | 238 | 1913 | 0 | 1 | 1 | 1952 | 15 | 29 | 44 | 1600-1750 | 80 | 80 | 160 |
| 1875 | 17 | 33 | 50 | 1914 | 6 | 13 | 19 | 1953 | 13 | 25 | 38 | 1751-1850 | 130 | 130 | 260 |
| 1876 | 17 | 33 | 50 | 1915 | 0 | 0 | 0 | 1954 | 13 | 26 | 39 | 1851-1860 | 95 | 95 | 190 |
| 1877 | 17 | 33 | 50 | 1916 | 0 | 0 | 0 | 1955 | 20 | 39 | 59 | 1861-1880 | 45 | 45 | 90 |
| 1878 | 17 | 33 | 50 | 1917 | 0 | 0 | 0 | 1956 | 41 | 81 | 122 | 1881-1891 | 40 | 40 | 80 |
| 1879 | 21 | 42 | 63 | 1918 | 3 | 5 | 8 | 1957 | 33 | 65 | 98 | 1892-1900 | 20 | 20 | 40 |
| 1880 | 17 | 34 | 51 | 1919 | 1 | 1 | 2 | 1958 | 49 | 99 | 148 | 1901-1915 | 15 | 15 | 30 |
| 1881 | 17 | 33 | 50 | 1920 | 1 | 1 | 2 | 1959 | 65 | 131 | 196 | 1916-1930 | 10 | 10 | 20 |
| 1882 | 17 | 33 | 50 | 1921 | 1 | 1 | 2 | 1960 | 58 | 115 | 173 | 1931-1939 | 5 | 5 | 10 |
| 1883 | 19 | 39 | 58 | 1922 | 2 | 3 | 5 | 1961 | 71 | 141 | 212 | 1940-1943 | 10 | 10 | 20 |
| 1884 | 23 | 45 | 68 | 1923 | 5 | 11 | 16 | 1962 | 49 | 98 | 147 | | | | |

simplified form assumes equivalence of the components of the population which are exploitable and past the age at first parturition):

$$P_{t+1} = (P_t - C_t)e^{-M} + (1 - e^{-M})P_{t-t_m+1}[1 + A\{1 - (P_{t-t_m+1}/P_0)^z\}] \tag{1}$$

where:

| | |
|---|---|
| $P_t$ | is the exploitable population size at the beginning of year $t$; |
| $C_t$ | is the catch taken in year $t$; |
| $M$ | is the natural mortality rate; |
| $t_m$ | is the age at first parturition; |
| $A$ | is the resilience parameter (related to MSYR); |
| $z$ | is the density-dependent exponent (related to the MSY level, MSYL, expressed in terms of the exploitable population size); and |
| $P_0$ | is the equilibrium exploitable population size in the absence of exploitation. |

Two points should be noted at this stage to avoid possible confusion.

(1) De la Mare (1989) *defines* the age at maturity for females as identical to the age at first parturition ($t_m$ above); the HITTER-FITTER output of a female 'age at maturity' is thus actually referring to an 'age at first parturition'. This may differ from usage by other authors, who intend female 'age at maturity' to mean 'age at first parturition less the gestation period'. Reilly (1984) states that the gestation period for gray whales is most likely to be somewhat greater than 12 months, and Rice (1990) reports an estimate of 418 days.

(2) $P_0$ above applies to the exploitable component of the population (both sexes combined). In this paper, $K$ is used for the corresponding value for the '*total*' population, $N^{tot}$, comprising all whales aged 1 and above. For model adjustments where an increase in carrying capacity is considered, this strictly refers to an increase in $P_0$ in equation (1); however, $K$ will increase by the same proportion (if other parameters remain unchanged), so that the multiplicative increase factor has been labelled $\mu_K$.

The 'base case' choice of parameter values for the trajectories calculated for this paper is as follows:

MSYL = 0.6 (related to choice of $z$, after other parameters have been fixed);
$t_m$ = 8 yr (knife-edge and pertinent only to females);
$M$ = 0.04 yr$^{-1}$ (age and sex invariant); and
$t_r$ = 5 yr (knife-edge and sex invariant)
where $t_r$ is the age at recruitment.

These choices were made to relate to the ranges of parameter values examined by Lankester and Beddington (1986). Obviously cases could be made for other choices. Reilly (1984) reports a median age at sexual maturity of 8 years, with a minimum of 5 and a maximum of 11; in addition he estimates $M = 0.055$ yr$^{-1}$ for females using age structure data, but this estimate also depends on his estimates of recent population growth rate and fishing mortality. However, the results of applications of the HITTER-FITTER model are generally not greatly sensitive to variations in these parameters, as indeed is demonstrated for a particular case later in this paper. For this reason, IWC (1993) decided to maintain this 'base case' choice for the calculation of population trajectories, although providing some additional estimates of biological parameters.

It has been conventional to apply and report results of the HITTER-FITTER package on the basis that density-dependence (the term multiplying the parameter $A$ in equation (1)) is related to the exploitable component of the population, and MSYR is expressed in terms of this same component. Subsequent to the 1990 Special Meeting, it was discovered that the calculations of a previous version of this paper, and the results listed in tables 3 and 4 of the Special Meeting report (IWC, 1993) had used a version of the package whose code had been amended so that MSYL and MSYR related to the component of the population past the age at first parturition, rather than the exploitable component. The results that follow have been recalculated on the conventional basis.

## HITTER model applications

The great majority of the results reported in this paper relate to population trajectories for given values of MSYR, which are constrained to pass through ('hit') a particular population estimate. The estimate chosen was the 1988 census estimate (i.e. 21,113), because this was regarded as the most reliable *absolute* abundance estimate (IWC, 1993). Thus, all the trajectories for such analyses have $N^{tot}_{1988}$ = 21,113. For applications ignoring the aboriginal catches of Table 2(b), the population is assumed to be at its unexploited equilibrium level (with the associated equilibrium age structure) at the beginning of 1846. When earlier aboriginal catches are also taken into account, these assumptions apply to the year in which those catches are assumed to commence.

The value of MSYR (corresponding to the exploitable component of the population) was varied to ascertain the effect on the trajectories. The HITTER-FITTER program effects this variation internally, essentially by changing the value of the resilience parameter, $A$, of the model. (The density-dependent exponent, $z$, also needs to be changed slightly in this process, to maintain a fixed MSYL.) For most calculations, only two readily interpretable summary statistics have been reported:

(i) 'Slope'– the average annual increase of population size from 1968-1988 as estimated from a linear regression fit to the logarithms of the model output for $N^{tot}$ over those years; and

(ii) the ratio $N^{tot}_{1900}$ / $N^{tot}_{1846}$

The first of these statistics can be related to the population growth rate estimate of 3.2% per annum (IWC, 1993) obtained from the results of the censuses listed in Table 1; the second assists in assessing the consistency of the particular trajectory with the commercial extinction of the population at the turn of the century.

## Model/dataset adjustments

### *Depensation*

Depensation is the phenomenon of a decrease in the *per capita* growth rate of a resource when population size is reduced below a certain level. If commercial whaling in the 19th century did deplete the population to a level at which depensation was operative, this could account for what may have been a slow initial recovery rate of the stock.

Depensation was modelled by adjusting the final term in equation (1):

$$A\{1 - (P_{t-t_m+1}/P_0)^z\} \quad \rightarrow \quad A\{1 - P_{t-t_m+1}/P_0)^z\}f(P_{t-t_m+1}) \tag{2}$$

where $f(P_t) = \begin{cases} f_0 + (1 - f_0)(P_t / P^*) & P_t < P^* \\ 1 & P_t \geq P^* \end{cases}$

Although, strictly, there will be a small domain of $P$ below $P^*$ for which the *per capita* growth rate still increases as $P$ is reduced, for convenience, $P^*$ will be referred to as the 'depensation level'.

*Additional response time-lag*
This was modelled in the same manner as suggested by IWC (1990):

$$A\{1 - P_{t-t_m+1} / P_0)^z\} \qquad A\{1 - (P_{t-t_m+1-T} / P_0)^z\} \qquad (3)$$

where $T$ is the 'additional time-lag'. The introduction of such a parameter might be a way of mimicking the effect of population sub-structure (such as 'herds' within a stock) in an aggregated model representation such as equation (1).

*Increase in carrying capacity*
For this adjustment, equation (1) was modified as follows:

$$[P_{t-t_m+1} / P_0]^z \quad \rightarrow \quad [P_{t-t_m+1} / P_0(t)]^z \qquad (4)$$

where:

$$P_0(t) = \begin{cases} P_0(1846) & t \leq 1846 \\ P_0(1846)+(t–1846)[\{P_0(1988) – P_0(1846)\} /(1988–1846)] & t > 1846 \end{cases}$$

$P_0(1988) = \mu_K P_0(1846)$

i.e. carrying capacity increases linearly over the period 1846-1988 by a multiplicative factor $\mu_K$.

*Underestimation of historic commercial catches*
The commercial catch data in Table 2(a) are not equally reliable throughout the complete period detailed. For 1846-1874 they are based on oil yields and struck-but-lost inferences, while from 1875-1943 only scarce data are available (Reilly, 1981). It is therefore not impossible that the historic commercial catch data listed are underestimates (see also IWC, 1993). This has been examined in this paper by the adjustment:

$$C_t \rightarrow \begin{cases} \mu_C C_t & 1846 < t < 1900 \\ C_t & t > 1900 \end{cases} \qquad (5)$$

where $\mu_C$ is termed the historic catch multiplicative factor. The sex ratio assumed for the catches (see footnotes to Table 2(a)) is kept unchanged in this adjustment.

*Aboriginal catches prior to the commercial fishery*
Both Reilly (1981) and Lankester and Beddington (1986) attempt to show the effect of such catches. Reilly also takes account of a likely reduction in such catches subsequent to 1800.

The approach adopted here is as follows. First, the effect of adding the aboriginal catch estimates specified in IWC (1993) and listed in Table 2(b) has been examined. Then, to allow for the possibility that these may be underestimates, their values have been adjusted by:

$$C_{abo}(t) \quad \rightarrow \quad \mu_A C_{abo}(t) \qquad t \geq t_s \qquad (6)$$

where:

$N_{t_s}^{tot} = K$

$t_s = 1600$ (see Table 2(b)); and

$\mu_A$ is termed the aboriginal catch multiplicative factor.

In addition to $t_s = 1600$, calculations have been carried out for $t_s = 1200$ and 1700, with the annual catch level of 160 from 1600-1750 specified in Table 2(b) then assumed to commence instead in year $t_s$. There is no intention here to suggest that the level of aboriginal catch was precisely constant over the period from $t_s$ to 1750. Rather, since historic catch levels and the time of their inception are not well known, alternative values of $t_s$ reflect variations in the assumptions of a population at carrying capacity and with equilibrium age-structure in 1600.

**Combinations of adjustments, and sensitivity tests**
Naturally, numerous combinations of the adjustment factors listed above could be investigated. Only one of these has been analysed in this paper: the combination of underestimation of both the historic commercial and aboriginal catches. The reason for this choice is that it is possible to exercise some judgement regarding the reality of the magnitudes of these factors needed to resolve the fundamental inconsistencies between the population model analysis and the data, whereas there is no direct evidence to support (or to allow independent estimation of the possible magnitude of) a change in carrying capacity (IWC, 1993).

The possibilities for sensitivity tests to the numerous assumptions and parameter value choices for the implementation of the HITTER-FITTER model are even more voluminous. To keep these within reasonable bounds, only one instance of the combination of the two adjustments mentioned in the paragraph above has been investigated in this context: $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) for various values of MSYR, with trajectories 'hitting' a given value of $N_{1988}^{tot}$. Sensitivity tests have been carried out for two variations in the data input for the HITTER procedure: changes to $N_{1988}^{tot}$ and changes to the sex ratio assumed for commercial catches for which this information is not available. Similar tests have been carried out for variations in the values assumed for the model parameters $M$, $t_m$, $t_r$ and MSYL.

**FITTER model applications**
Naturally all the adjustments considered above could be investigated in a 'fitting' as well as a 'hitting' context. Again, to keep computations within reasonable bounds, only three cases have been analysed in this paper. These are a subset of those chosen for the sensitivity tests discussed above, *viz.* ($\mu_C = 1.5$; $\mu_A = 1.5$), ($\mu_C = 2$; $\mu_A = 2$) and ($\mu_C = 2.5$; $\mu_A = 2.5$). Table 8(a) indicates that a 1968-88 annual average growth rate of some 3.2% can be attained within the MSYR range investigated for the last of these cases, so that model mis-specification problems are less likely in this instance. Further, Table 8(b) shows that results consistent with commercial extinction of the population at the end of the 19th century can be obtained for all three cases.

The population estimates to which the model was 'fitted' are listed in Table 1. The fitting procedure needs to take cognisance of the manner in which the absolute abundance estimates ($N_t^{tot}$) of that Table were derived. These are of the form:

$$N_t^{tot} = b\, I_t \qquad (7)$$

where:

$I_t$ is the relative abundance estimate for year $t$; and
$b$ is a scaling factor which was estimated for the 1988 census only.

The error structure assumed for model fitting purposes:

$$b\ I_t = N_t^{tot}\ e^{\varepsilon_t} \qquad \varepsilon_t \text{ from } N(0;\sigma^2) \tag{8}$$

where:

$\hat{N}_t^{tot}$ is the population model estimate of the number of whales aged 1 and above at the start of year $t$; and
$N(0;\sigma^2)$ is a normal distribution with mean 0 and variance $\sigma^2$.

The corresponding sum of squares functional minimised was therefore:

$$SS(K, MSYR, b) = (1/\sigma_1^2)\sum_{t-1968}^{1988}[\ln\ (bI_t) - \ln\ \hat{N}_t^{tot}]^2 + (1/\sigma_2^2)[\ln\ b_{obs} - \ln\ b]^2 \tag{9}$$

where $b_{\text{obs}}$ is the estimate of $b$ obtained independently from data from the 1988 census. The first term on the right hand side of equation (9) is taking account of the information on trend in abundance provided by the series of relative abundance estimates ($I_t$), while the second incorporates the information available on the absolute level of abundance.

The variance estimate ($\sigma_1^2$) used to weight the first term was obtained from the (bias-corrected) residuals about a quadratic fit to the ln $I_t$ series, which yielded $\sigma_1 = 0.134$. The variance ($\sigma_2^2$) associated with the estimate $b_{\text{obs}}$ followed from comparison of the two columns of Table 1, which indicates $b_{\text{obs}} = 1.318$, $\sigma_2 = 0.012$.

This procedure gives equal weights to each of the relative abundance estimates, despite their differing standard errors, SEs (and coefficients of variation CV). The reason for this is that these SE estimates correspond to the sampling contribution to the overall variance only, and are certainly not capturing most of the variability about the underlying trend (see discussion in Butterworth *et al.*, 2002). Note that this implies a CV for the 1988 absolute abundance estimate of $\sqrt{\sigma_1^2+\sigma_2^2} = 0.135$; this corresponds to an SE of 2,840, which indicates rather lesser precision than does the SE estimate of 688 given in Table 1. Buckland *et al.* (1993) took into account more sources of variability and indeed found a larger value for this SE (913 or 1,288, depending on methodology).

Differentiating equation (9) partially with respect to $b$, and setting the result to zero, provides a closed form expression for the estimate of $b$:

$$\ln\ \hat{b} = \{n/\sigma_1^2 + 1/\sigma_2^2\}^{-1}\ [(1/\sigma_1^2)\sum_{t=1968}^{1988}\{\ln\ \hat{N}_t^{tot} - \ln I_t\} + (1/\sigma_2^2)\ \ln b_{obs}] \tag{10}$$

where $n$ ( = 16) is the number of censuses over the 1968-1988 period. In consequence, the non-linear minimisation search is over two parameters only: $K$ and MSYR. The HITTER model applications discussed above are all of the form known as 'Hitting with fixed MSYR'. Given the series of census estimates, it becomes possible to estimate MSYR while still 'hitting' the 1988 census estimate. The non-linear minimisation search is then reduced to one parameter only.

A bootstrap technique was used to estimate SEs and confidence intervals (CIs) for the resultant fit. In place of the actual set of results from the censuses: $\{b_{\text{obs}};\ I_t: t = 1968,...,1988\}$, a large number of bootstrap sets was generated: $\{b_{obs}^S; I_t^S: t = 1968,...,1988\}$ where $S = 1,...,S_{\text{max}}$. The individual elements of these sets were generated as follows:

$$\begin{aligned} \ln\ I_t^S &= \ln(\hat{N}_t^{tot}/\hat{b}) + \in_{1,t}^S \qquad \in_{1,t}^S \text{ from } N(0;\sigma_1^2) \\ \ln\ b_{obs}^S &= \ln b + \in_2^S \qquad \in_2^S \text{ from } N(0;\sigma_2^2) \end{aligned} \tag{11}$$

The bootstrap distribution of a quantity of interest was then provided by minimising equation (9) for each of these alternative bootstrap data sets, which provides an estimate of the quantity for each set $S$. Bootstrap CIs were then obtained by ordering the resultant $S_{\text{max}}$ estimates of the quantity, while an SE estimate was provided by the SD of these $S_{\text{max}}$ estimates. For the results reported here, $S_{\text{max}} = 500$.

## RESULTS AND DISCUSSION

The results of HITTER model applications for the various model/dataset adjustments considered are presented in a standard format in most cases. First, a table containing two matrices is given, the one providing values of 'Slope', and the other values of $N_{1990}^{tot}$ / $N_{1846}^{tot}$. The rows in these tables correspond to MSYR values from 0% to 10%, and the columns to different values of the relevant adjustment factor.

'Slope' values relate to the corresponding estimate from the 1968-1988 censuses of an average annual growth rate of 3.2% over the period. As an aid for inspection of the tables, all 'Slope' values greater than 1.0% have been entered in italics. $N_{1990}^{tot}$ / $N_{1846}^{tot}$ entries of less than 0.30 are also entered in the same way, to draw attention to sets of parameter combinations which better reflect the commercial extinction of the population at the end of the 19th century.

Clearly it would be unreasonable to provide graphical representations of the trajectories for every parameter combination listed in the Tables described above. Figures have therefore been presented in two ways: first, the set of trajectories for a fixed MSYR for various adjustment factor values; and secondly, the set for a fixed adjustment factor value for various MSYRs. The fixed MSYR chosen was 5%, because this is usually the smallest MSYR value for which 'Slope' values of at least 3% can be achieved. Similarly, the fixed adjustment factor value normally chosen was the smallest for which a 'Slope' approaching 3% was possible. As an aid in relating the Tables and Figures, the Table entries for which Figures are provided (in most cases) are shown between dashed lines. Note that because the post-1840 period is of greater interest, the scale of the horizontal year axis has been reduced for the 1600-1840 period in many cases, to allow for better discrimination of the results for later years.

### Aboriginal catches prior to the commercial fishery

Table 3(a) gives results for the application of the basic population model including only the 'commercial' catches of Table 2(a), i.e. corresponding to a resource at its carrying capacity level at the onset of commercial harvesting in 1846. None of these results is able to reflect a recent growth rate

Table 3

Results for the basic population model (and catch data of Table 2) for various values of MSYR for trajectories which hit a 1988 total population size ( $N_{1988}^{tot}$ ) of 21,113. 'Slope' is the average annual increase of the total population from 1968 to 1988 as estimated from a linear regression fit to the logarithms of the model estimates of population size over this period. The unexploited equilibrium total population size $K = N_{1846}^{tot}$ for (a), which incorporates only the commercial catch data of Table 2(a); for (b), for which the aboriginal catches of Table 2(b) are included as well, $K = N_{1600}^{tot}$. The lowest size over 1846-1988 period is indicated by $N_{min}^{tot}$.

| | | | | $N_{min}^{tot}/K$ | |
|---|---|---|---|---|---|
| MSYR (%) | Slope (%) | $K$ | $N_{1900}^{tot}/N_{1846}^{tot}$ | Estimate | Year occurs |
| **(a) Commercial catches only (Table 2a)** | | | | | |
| 0 | -0.90 | 40,869 | 0.73 | 0.52 | 1988 |
| 1 | -0.45 | 27,568 | 0.78 | 0.74 | 1877 |
| 2 | 0.29 | 24,529 | 0.88 | 0.77 | 1875 |
| 3 | -0.14 | 23,316 | 0.95 | 0.81 | 1875 |
| 4 | -0.05 | 22,555 | 0.98 | 0.85 | 1866 |
| 5 | -0.01 | 22,061 | 0.99 | 0.88 | 1866 |
| 6 | -0.00 | 21,738 | 0.99 | 0.91 | 1866 |
| 8 | -0.02 | 21,346 | 0.99 | 0.96 | 1860 |
| 10 | 0.02 | 21,261 | 0.99 | 0.97 | 1859 |
| **(b) Addition of aboriginal catches (Tables 2a and 2b)** | | | | | |
| 0 | -0.89 | 96,491 | 0.64 | 0.22 | 1988 |
| 1 | -0.12 | 38,032 | 0.64 | 0.39 | 1890 |
| 2 | -0.16 | 25,127 | 0.70 | 0.46 | 1881 |
| 3 | -0.14 | 23,320 | 0.95 | 0.66 | 1875 |
| 4 | -0.05 | 22,555 | 1.02 | 0.77 | 1875 |
| 5 | -0.01 | 22,061 | 1.03 | 0.82 | 1866 |
| 6 | -0.00 | 21,739 | 1.02 | 0.87 | 1866 |
| 8 | -0.02 | 21,345 | 1.00 | 0.93 | 1866 |
| 10 | 0.03 | 21,278 | 0.99 | 0.97 | 1860 |

('Slope') which exceeds 0.3% (let alone 3%) and the extent of the estimated reduction in abundance between 1846 and 1900 is scarcely compatible with commercial extinction.

The consequences of including the levels of (additional) aboriginal catch (principally prior to the commercial fishery) that were specified in IWC (1993)[3], are shown in Table 3(b) and Fig. 1. Although marginally greater proportional reduction over the 1846-1900 period is rendered possible by their inclusion, there are no qualitative differences from the results of Table 3(a), so that these levels of aboriginal catch alone are unable to resolve the conflicts between the population model and observations.

The model and data used to produce the results of Fig. 1 and Table 3(b) will henceforth be referred to as the 'standard model'. All further model fits reported in this paper *include* the aboriginal catches listed in Table 2(b).

## Depensation

Table 3(b) (and Fig. 1) also provides results for the 'standard model' for the lowest depletion ($N_{\min}^{tot}/K$) over the back-projection period considered. Disregarding the unrealistic MSYR = 0% result (which is included only to provide values associated with a lower bound for MSYR), the lowest depletion shown by any of these trajectories is 0.39 and most other values are substantially higher than this.

Thus, depensation can have an effect only if the depensation level $P^*$ exceeds at least 0.39 $P_0$ (see equation 2). It hardly seems realistic to invoke depensation effects at population levels $N^{tot}$ that are not considerably lower than the 0.6*K* conventionally assumed for MSYL. Accordingly depensation *alone* does not appear to be a candidate for resolving the inconsistencies related to the population model, although it could of course play a role in combination with some other adjustment factor.

## Additional response time-lag

Results for the adjustment indicated by equation (3) are shown in Fig. 2. The larger of the values chosen for the additional time-lag *T* lead to marked oscillations in the population trajectories. Although these trajectories can produce 'Slope' values in the range indicated by the censuses, none correspond to a population which could be regarded as commercially extinct at the turn of the century.

Thus, none of these results appears to provide a reasonable representation of the gray whale population history, and the Table corresponding to Fig. 2 has accordingly been omitted. The manner in which the response time-lag is modelled in equation (3) therefore does not seem to hold any promise for resolving the inconsistencies in question.

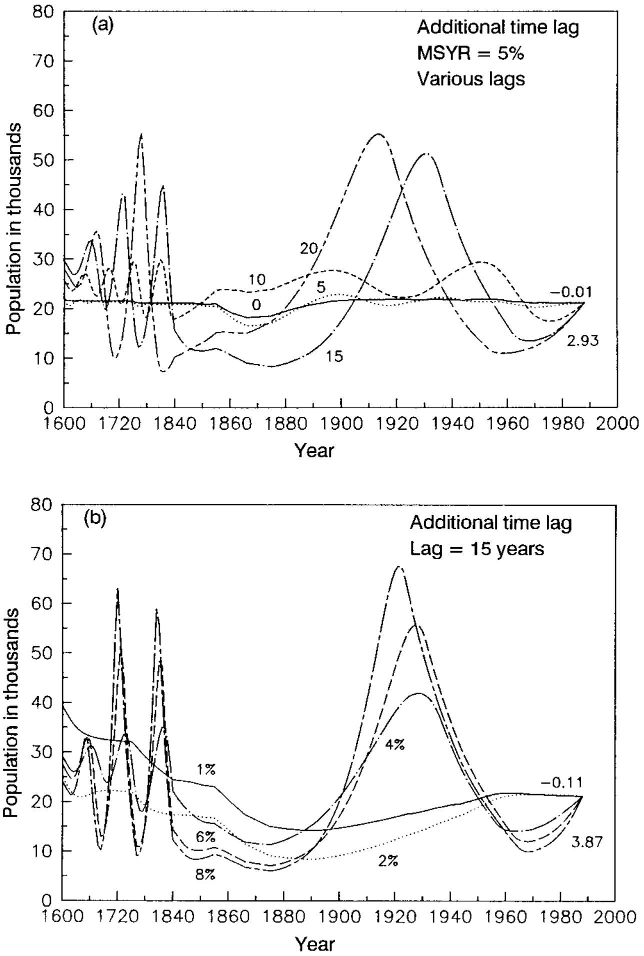

Fig. 2. The effect on population trajectories of introducing an additional time-lag into the density-dependent response term in the population model: (a) MSYR = 5%, additional time-lags from 0-20 years as indicated on each trajectory; (b) additional time-lag of 15 years, MSYR from 1% to 8%. (Note that the scale of the horizontal axis changes from 1840 in this and some following Figures.)

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[3] See Table 2(b).

Table 4

Results of allowing carrying capacity to increase linearly over the period 1846-1988 by a multiplicative factor $\mu_K$. Carrying capacity is constant prior to 1846. 'Slope' and '$N^{tot}$' are as for Table 3. Fig. 3 shows the trajectories corresponding to the row and the column between dashed lines.

| | $\mu_K$ | | | | | | |
|---|---|---|---|---|---|---|---|
| MSYR(%) | 1.0 | 1.5 | 2.0 | 2.5 | 3.0 | 4.0 | 5.0 |
| **(a) Slope** | | | | | | | |
| 0 | -0.90 | -0.90 | -0.90 | -0.90 | -0.90 | -0.90 | -0.90 |
| 1 | -0.45 | 0.01 | 0.06 | 0.08 | 0.09 | 0.10 | 0.10 |
| 2 | -0.28 | 0.58 | 0.81 | 0.90 | 0.95 | 0.99 | *1.01* |
| 3 | -0.14 | 0.63 | *1.35* | *1.59* | *1.70* | *1.80* | *1.84* |
| 4 | -0.05 | 0.18 | *1.72* | *2.18* | *2.38* | *2.54* | *2.61* |
| 5 | -0.01 | 0.23 | *1.88* | *2.72* | *3.00* | *3.24* | *3.33* |
| 6 | -0.00 | 0.25 | 0.77 | *3.22* | *3.60* | *3.89* | *4.01* |
| 8 | -0.02 | 0.23 | 0.36 | *4.08* | *4.72* | *5.12* | *5.27* |
| 10 | 0.02 | 0.26 | 0.38 | 0.44 | *5.74* | *6.22* | *6.37* |
| **(b) Total population in 1900 as a proportion of that in 1846** | | | | | | | |
| 0 | 0.73 | 0.64 | 0.64 | 0.64 | 0.64 | 0.64 | 0.64 |
| 1 | 0.77 | 0.61 | 0.60 | 0.60 | 0.60 | 0.60 | 0.60 |
| 2 | 0.88 | 0.49 | 0.45 | 0.44 | 0.44 | 0.43 | 0.43 |
| 3 | 0.95 | 0.39 | 0.32 | 0.31 | 0.30 | 0.30 | 0.30 |
| 4 | 0.98 | 0.73 | *0.24* | *0.23* | *0.23* | *0.22* | *0.23* |
| 5 | 0.99 | 1.09 | *0.19* | *0.18* | *0.18* | *0.18* | *0.19* |
| 6 | 0.99 | 1.20 | *0.18* | *0.16* | *0.16* | *0.16* | *0.17* |
| 8 | 0.99 | 1.19 | 1.38 | *0.14* | *0.15* | *0.15* | *0.15* |
| 10 | 1.00 | 1.17 | 1.36 | 1.27 | *0.14* | *0.15* | *0.15* |

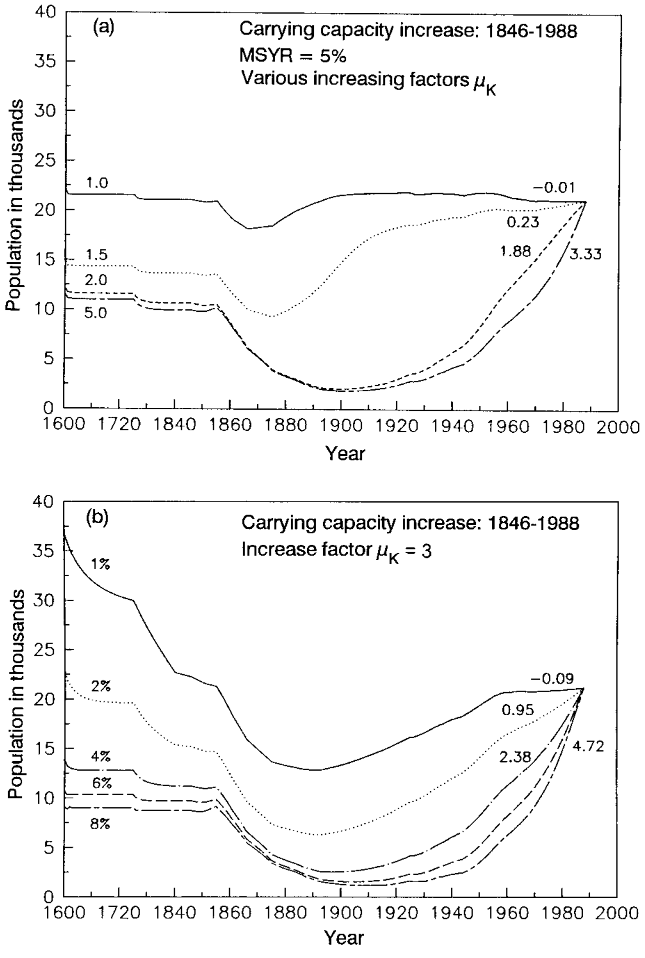

Fig. 3. The effect on population trajectories of a linear increase in carrying capacity over the period 1846-1988 by a multiplicative factor $\mu_K$: (a) MSYR = 5%, $\mu_K$ = 1.0, 1.5, 2.0 and 5.0; (b) $\mu_K$ = 3.0, MSYR from 1% to 8%.

## Increase in carrying capacity

Table 4 and Fig. 3 show the results of the adjustment of equation (4), which corresponds to a linear increase in carrying capacity over 1846-1988. Introduction of this factor can remove the inconsistencies, as typically $\mu_K > 2$ and MSYR $\geqslant$ 3% provide 'Slope' values exceeding 1%. Note that a saturation effect comes into play for high $\mu_K$ : once $\mu_K$ exceeds 3, little change is evident in the resultant population trajectories.

Thus, this particular analysis provides a simple answer to the first question of how large an adjustment factor needs to be to remove the inconsistencies: the multiplicative increase in carrying capacity must be at least 2 and probably about 3. However, this alone cannot be regarded as an entirely satisfactory resolution of the problem, given that there is no independent evidence for an effect of this size (IWC, 1993).

Naturally, increases in $K$ differing from the linear trend examined could be envisaged. Specific choices are problematic in the absence of independent evidence relating to the probable periods of greatest change. However, as a first approximation, $\mu_K$ will still remain meaningful as typical of the magnitude of adjustment factor necessary.

## Underestimation of historic commercial catches

Results for a multiplicative increase (by $\mu_C$) of the commercial catches between 1846 and 1900 (see equation 5) are given in Table 5 and Fig. 4. Once again the inconsistencies can be removed - in this instance 'Slope' values exceeding 1% are obtained provided $\mu_C \geqslant 2.25$ and MSYR $\geqslant$ 3%. A saturation effect is evident for $\mu_C > 3$, larger values having little effect on the post-1900 sections of the population trajectories.

To achieve a 'Slope' of at least 2% from historic commercial catch underestimation *alone* requires $\mu_C \geqslant 2.5$ (i.e. at least 60% underestimation). IWC (1993) discussed problems associated with the data and methods used to

Table 5

Results of increasing all historic commercial catches over the period 1846-1900 by a multiplicative factor $\mu_C$. 'Slope' and '$N^{tot}$' are as for Table 3. Fig. 4 shows the trajectories corresponding to the row and the column between dashed lines.

| MSYR | $\mu_C$ | | | | | | |
|---|---|---|---|---|---|---|---|
| (%) | 1.0 | 2.0 | 2.25 | 2.5 | 3.0 | 4.0 | 5.0 |
| **(a) Slope** | | | | | | | |
| 0 | -0.90 | -0.90 | -0.90 | -0.90 | -0.91 | -0.91 | -0.92 |
| 1 | -0.45 | -0.04 | -0.03 | -0.01 | 0.00 | 0.03 | 0.04 |
| 2 | -0.28 | 0.47 | 0.56 | 0.64 | 0.74 | 0.84 | 0.89 |
| 3 | -0.14 | 0.69 | 0.99 | *1.18* | *1.41* | *1.61* | *1.70* |
| 4 | -0.05 | 0.41 | *1.32* | *1.70* | *2.07* | *2.35* | *2.46* |
| 5 | -0.01 | -0.01 | *1.50* | *2.21* | *2.71* | *3.06* | *3.19* |
| 6 | -0.00 | -0.00 | 0.00 | *2.67* | *3.34* | *3.74* | *3.87* |
| 8 | -0.02 | -0.02 | -0.02 | 0.01 | *4.53* | *5.00* | *5.14* |
| 10 | 0.02 | 0.02 | 0.02 | 0.05 | *5.64* | *6.13* | *6.29* |
| **(b) Total population in 1900 as a proportion of that in 1846** | | | | | | | |
| 0 | 0.73 | 0.53 | 0.51 | 0.49 | 0.45 | 0.40 | 0.35 |
| 1 | 0.77 | 0.44 | 0.41 | 0.39 | 0.34 | *0.28* | *0.25* |
| 2 | 0.88 | 0.33 | *0.29* | *0.27* | *0.23* | *0.19* | *0.17* |
| 3 | 0.95 | *0.24* | *0.21* | *0.19* | *0.17* | *0.14* | *0.13* |
| 4 | 0.98 | *0.20* | *0.16* | *0.15* | *0.13* | *0.12* | *0.11* |
| 5 | 0.99 | 0.47 | *0.14* | *0.13* | *0.12* | *0.11* | *0.10* |
| 6 | 0.99 | 0.81 | *0.17* | *0.12* | *0.11* | *0.10* | *0.10* |
| 8 | 0.99 | 1.00 | 0.96 | *0.13* | *0.11* | *0.10* | *0.10* |
| 10 | 1.00 | 0.98 | 0.97 | 1.01 | *0.11* | *0.11* | *0.11* |

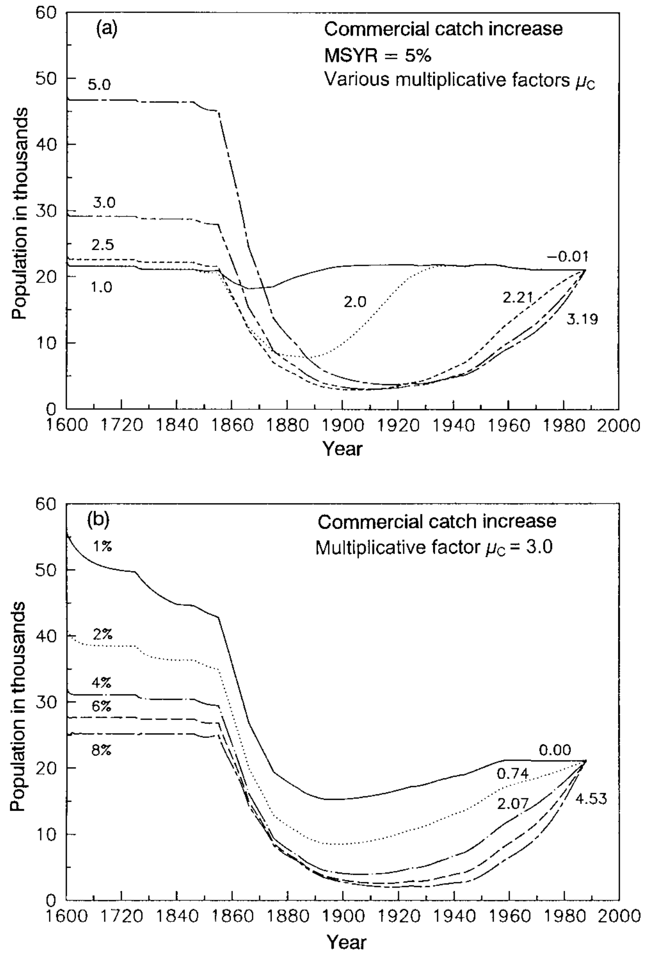

Fig. 4. The effect on population trajectories of increasing all historic commercial catches over the period 1846-1900 by a multiplicative factor $\mu_C$: (a) MSYR = 5%, $\mu_C$ = 1.0, 2.0, 2.5, 3.0 and 5.0; (b) $\mu_C$ = 3.0, MSYR from 1% to 8%.

estimate the 19th century commercial catches and the extent to which these might have been underestimated. Readers are invited to use those comments as a basis for judging whether underestimation by as much as 60% is a realistic possibility.

### Underestimation of aboriginal catches

Results for such catches over the period commencing in 1600 are shown in Table 6 and Fig. 5. Table 7 shows that the effect of changing the period considered for such catches to 1200-1845 or 1700-1845, for the case $\mu_A = 3$, makes no difference to the results of interest. It should be noted that some of the aboriginal catch levels considered are greater than the associated MSY for the resource, as is evident from inspection of Fig. 5a.

From Table 6, it is clear that $\mu_A \geqslant 2$ is needed to achieve a 'Slope' of at least 1%, and $\mu_A \geqslant 3$ for a 'Slope' exceeding 2%. For $\mu_A > 3$, a saturation effect is evident, with minimal change in the post-1900 trajectories.

### Combinations

Results for combinations of the last two adjustment factors above are reported in Table 8 and Fig. 6. The primary objective of investigating this combination is to assess to what extent the separate requirements of $\mu_C \geqslant 2.5$ and $\mu_A \geqslant 3$ to achieve a 'Slope' of at least 2% might be relaxed.

Table 6

Results for multiples of $\mu_A$ of the annual aboriginal catch ($C_{abo}$) given in Table 2(b). 'Slope' and '$N^{tot}$' are as for Table 3. Fig 5 shows the trajectories corresponding to the row and column between dashed lines.

| MSYR | $\mu_A$ | | | | | | |
|---|---|---|---|---|---|---|---|
| (%) | 1.0 | 2.0 | 2.25 | 2.5 | 3.0 | 5.0 | 10.0 |
| **(a) Slope** | | | | | | | |
| 0 | -0.90 | -0.90 | -0.90 | -0.90 | -0.90 | -0.90 | -0.90 |
| 1 | -0.45 | 0.04 | 0.05 | 0.07 | 0.08 | 0.10 | 0.11 |
| 2 | -0.28 | 0.72 | 0.80 | 0.85 | 0.91 | *1.00* | *1.03* |
| 3 | -0.14 | *1.09* | *1.31* | *1.45* | *1.61* | *1.81* | *1.89* |
| 4 | -0.05 | 0.53 | *1.45* | *1.82* | *2.17* | *2.56* | *2.69* |
| 5 | -0.01 | -0.01 | -0.01 | *1.67* | *2.58* | *3.24* | *3.44* |
| 6 | -0.00 | -0.00 | -0.00 | -0.00 | *2.69* | *3.86* | *4.14* |
| 8 | -0.02 | -0.02 | -0.02 | -0.02 | -0.02 | *4.96* | *5.44* |
| 10 | 0.02 | 0.03 | 0.03 | 0.03 | 0.04 | *5.83* | *7.22* |
| **(b) Total population in 1900 as a proportion of that in 1846** | | | | | | | |
| 0 | 0.73 | 0.58 | 0.56 | 0.55 | 0.53 | 0.45 | 0.35 |
| 1 | 0.77 | 0.52 | 0.50 | 0.48 | 0.45 | 0.37 | *0.28* |
| 2 | 0.88 | 0.40 | 0.38 | 0.36 | 0.34 | *0.28* | *0.23* |
| 3 | 0.95 | 0.30 | *0.28* | *0.27* | *0.25* | *0.22* | *0.19* |
| 4 | 0.98 | *0.27* | *0.23* | *0.22* | *0.21* | *0.19* | *0.17* |
| 5 | 0.99 | 1.13 | 1.03 | *0.19* | *0.18* | *0.17* | *0.16* |
| 6 | 0.99 | 1.09 | 1.13 | 1.20 | *0.17* | *0.16* | *0.16* |
| 8 | 0.99 | 1.02 | 1.03 | 1.05 | 1.10 | *0.16* | *0.15* |
| 10 | 1.00 | 0.99 | 0.99 | 0.99 | 1.01 | *0.16* | *0.15* |

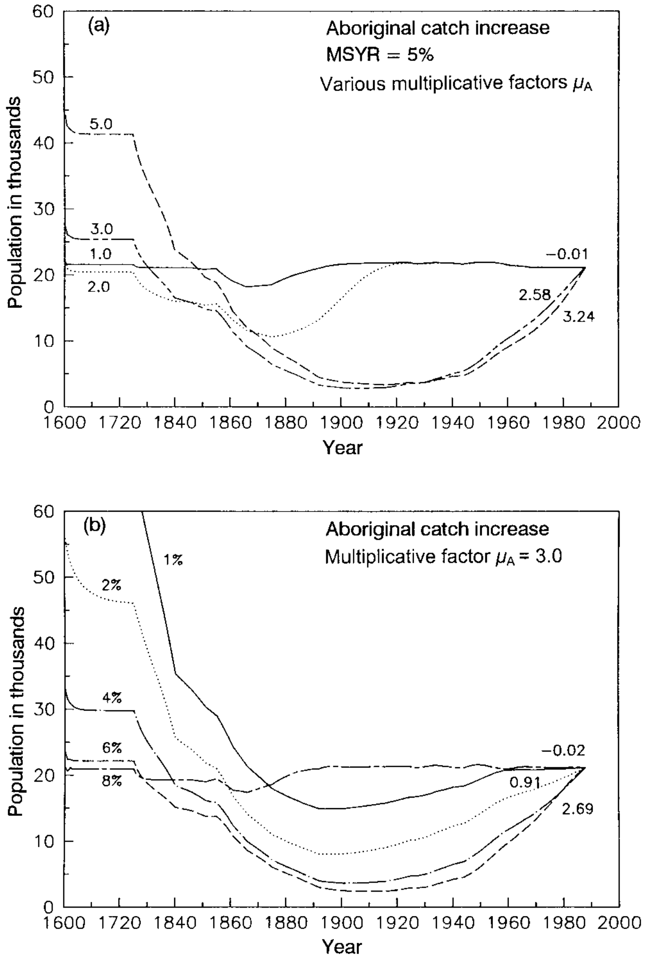

Fig. 5. The effect on population trajectories of increasing the aboriginal catches ($C_{abo}$) of Table 2(b) over the period from 1600 by a multiplicative factor $\mu_A$: (a) MSYR = 5%, $\mu_A$ = 1.0, 2.0, 3.0 and 5.0; (b) $\mu_A$ = 3.0, MSYR from 1% to 8%.

Table 7

Comparison of results for a change from 1600 of the year in which an aboriginal catch commences (see Table 2 (b)). Results are shown for the case $\mu_A = 3$, so that the commencing level of annual catch is 480 whales. 'Slope' and '$N^{tot}$' are as for Table 3.

| MSYR | Year $C_{abo}$ commences | | | MSYR | Year $C_{abo}$ commences | | |
|---|---|---|---|---|---|---|---|
| (%) | 1200 | 1600 | 1700 | (%) | 1200 | 1600 | 1700 |
| **(a) Slope** | | | | **(b) 1900 pop'n/1846 pop'n** | | | |
| 0 | -0.90 | -0.90 | -0.90 | 0 | 0.53 | 0.53 | 0.53 |
| 1 | 0.08 | 0.08 | 0.07 | 1 | 0.45 | 0.45 | 0.45 |
| 2 | 0.91 | 0.91 | 0.91 | 2 | 0.34 | 0.34 | 0.34 |
| 3 | *1.61* | *1.61* | *1.61* | 3 | *0.25* | *0.25* | *0.25* |
| 4 | *2.17* | *2.17* | *2.17* | 4 | *0.21* | *0.21* | *0.21* |
| 5 | *2.58* | *2.58* | *2.58* | 5 | *0.18* | *0.18* | *0.18* |
| 6 | *2.69* | *2.69* | *2.69* | 6 | *0.17* | *0.17* | *0.17* |
| 8 | -0.02 | -0.02 | -0.02 | 8 | 1.10 | 1.10 | 1.10 |
| 10 | 0.04 | 0.04 | 0.04 | 10 | 1.01 | 1.01 | 1.01 |

Table 8

Results for the combined effects of increasing all historic commercial catches over the period 1846-1900 by a multiplicative factor $\mu_A$ and aboriginal catches of Table 2(b) by a multiplicative factor $\mu_A$. 'Slope' and '$N^{tot}$' are as for Table 3.

| MSYR | $\mu_A$ | | | MSYR | $\mu_A$ | | |
|---|---|---|---|---|---|---|---|
| (%) | 1.5 | 2.0 | 2.5 | (%) | 1.5 | 2.0 | 2.5 |
| **(a) Slope** | | | | **(b) 1900 pop'n/1846 pop'n** | | | |
| $\mu_C$ (1846-1900) = 1.5 | | | | | | | |
| 0 | -0.90 | -0.90 | -0.90 | 0 | 0.55 | 0.53 | 0.50 |
| 1 | 0.00 | 0.04 | 0.07 | 1 | 0.48 | 0.45 | 0.42 |
| 2 | 0.57 | 0.76 | 0.86 | 2 | 0.36 | 0.33 | 0.31 |
| 3 | 0.66 | *1.24* | *1.49* | 3 | *0.29* | *0.25* | *0.23* |
| 4 | -0.05 | *1.34* | *1.95* | 4 | 0.54 | *0.20* | *0.19* |
| 5 | -0.01 | -0.01 | *2.14* | 5 | 0.91 | 0.47 | *0.17* |
| 6 | -0.00 | -0.00 | -0.00 | 6 | 1.02 | 0.99 | *0.24* |
| 8 | -0.02 | -0.02 | -0.02 | 8 | 1.00 | 1.02 | 1.05 |
| 10 | 0.03 | 0.03 | 0.04 | 10 | 0.98 | 0.99 | 0.99 |
| $\mu_C$ (1846-1900) = 2.0 | | | | | | | |
| 0 | -0.90 | -0.90 | -0.90 | 0 | 0.51 | 0.49 | 0.47 |
| 1 | 0.02 | 0.05 | 0.06 | 1 | 0.42 | 0.40 | 0.38 |
| 2 | 0.67 | 0.80 | 0.87 | 2 | 0.30 | *0.29* | *0.27* |
| 3 | *1.11* | *1.38* | *1.54* | 3 | *0.22* | *0.21* | *0.21* |
| 4 | *1.38* | *1.82* | *2.09* | 4 | *0.17* | *0.17* | *0.17* |
| 5 | *1.33* | *2.16* | *2.56* | 5 | *0.15* | *0.15* | *0.15* |
| 6 | -0.00 | *2.31* | *2.94* | 6 | 0.43 | *0.13* | *0.14* |
| 8 | -0.02 | -0.02 | -0.01 | 8 | 1.00 | 0.93 | 0.32 |
| 10 | 0.02 | 0.03 | 0.04 | 10 | 0.97 | 0.98 | 0.99 |
| $\mu_C$ (1846-1900) = 2.5 | | | | | | | |
| 0 | -0.90 | -0.90 | -0.90 | 0 | 0.47 | 0.45 | 0.44 |
| 1 | 0.02 | 0.05 | 0.06 | 1 | 0.37 | 0.36 | 0.34 |
| 2 | 0.75 | 0.83 | 0.89 | 2 | *0.26* | *0.25* | *0.25* |
| 3 | *1.36* | *1.49* | *1.59* | 3 | *0.19* | *0.19* | *0.19* |
| 4 | *1.93* | *2.10* | *2.23* | 4 | *0.15* | *0.15* | *0.15* |
| 5 | *2.48* | *2.68* | *2.83* | 5 | *0.13* | *0.13* | *0.14* |
| 6 | *3.01* | *3.24* | *3.40* | 6 | *0.12* | *0.12* | *0.13* |
| 8 | *3.98* | *4.29* | *4.50* | 8 | *0.12* | *0.12* | *0.12* |
| 10 | -0.02 | 0.05 | *5.50* | 10 | 0.82 | *0.14* | *0.12* |

Table 8 shows that underestimation of the historic commercial catch is the dominant of the two factors. To achieve a 'Slope' of 2%, $\mu_A$ can be reduced to 2.5 if $\mu_C$ = 1.5. Similarly, relaxing the requirement that $\mu_C \geqslant 2.5$ requires that $\mu_A \geqslant 2$.

The sensitivity tests that follow have been carried out for the ($\mu_C$ = 2; $\mu_A$ = 2) combination. These are provided for illustrative purposes and do not imply any reason for especially preferring this case as a representation of reality.

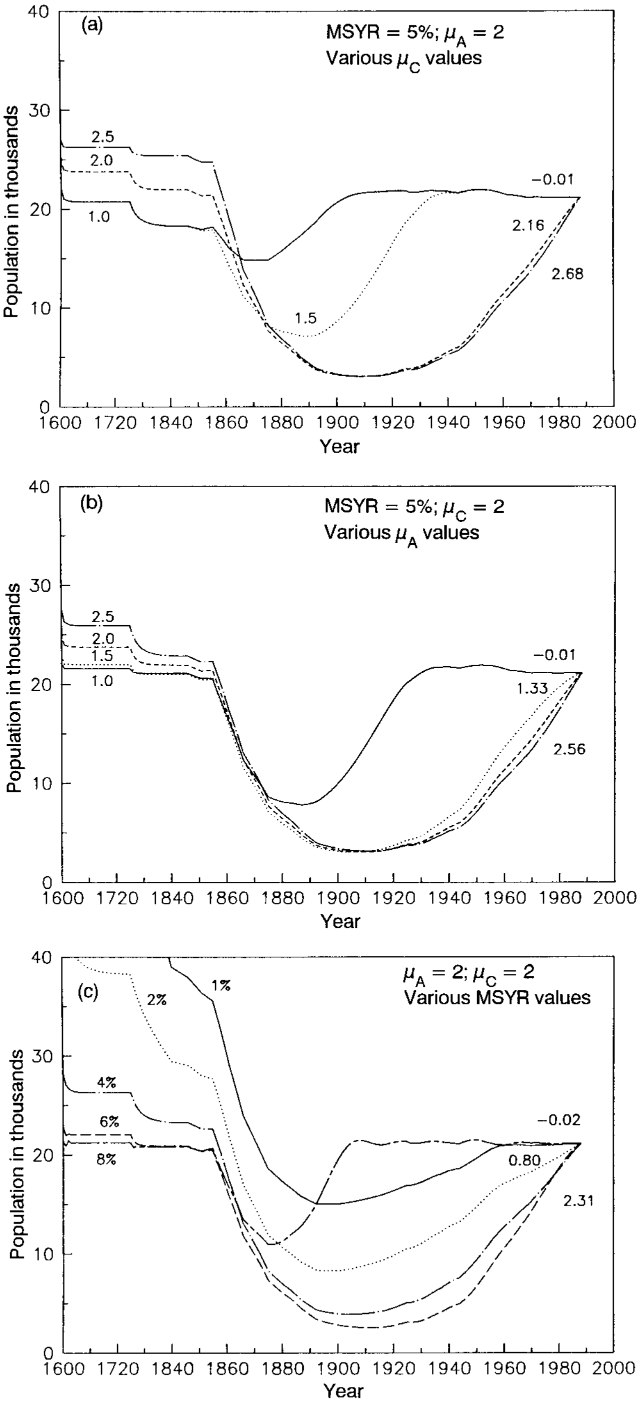

Fig. 6. The combined effects on population trajectories of increasing all historic commercial catches over the period 1846-1900 by a multiplicative factor $\mu_C$, and also multiplying the aboriginal catches by a factor $\mu_A$: (a) MSYR = 5%, $\mu_A$ = 2.0, $\mu_C$ from 1.0 to 2.5; (b) MSYR = 5%, $\mu_C$ = 2.0, ; $\mu_A$ from 1.0 to 2.5; (c) $\mu_C$ = 2.0, $\mu_A$ = 2.0, MSYR from 1% to 8%.

## Sensitivity tests

The results of sensitivity tests to variations in the data input and the chosen model parameter values for the case $\mu_C$ = 2 (for 1846-1900) and $\mu_A$ = 2 (for 1600+) are shown in Tables 9-14. These reflect variations in $N^{tot}_{1988}$, the assumed female:male catch ratio in the earlier commercial catches, $M$, $t_m$, $t_r$ and MSYL, respectively.

Table 9

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value of $N^{tot}_{1988}$ which the trajectory hits. 'Slope' and '$N^{tot}$' are as for Table 3.

| MSYR (%) | $N^{tot}_{1988}$ | | | MSYR (%) | $N^{tot}_{1988}$ | | |
|---|---|---|---|---|---|---|---|
| | 19,113 | 21,113* | 23,113 | | 19,113 | 21,113* | 23,113 |
| **(a) Slope** | | | | **(b) 1900 pop'n/1846 pop'n** | | | |
| 0 | -0.99 | -0.90 | -0.83 | 0 | 0.47 | 0.49 | 0.50 |
| 1 | -0.04 | 0.05 | 0.12 | 1 | 0.38 | 0.40 | 0.41 |
| 2 | 0.73 | 0.80 | 0.84 | 2 | *0.27* | *0.29* | 0.30 |
| 3 | *1.36* | *1.38* | *1.35* | 3 | *0.20* | *0.21* | *0.22* |
| 4 | *1.90* | *1.82* | *1.64* | 4 | *0.16* | *0.17* | *0.18* |
| 5 | *2.38* | *2.16* | *1.54* | 5 | *0.14* | *0.15* | *0.15* |
| 6 | *2.82* | *2.31* | -0.00 | 6 | *0.13* | *0.13* | 0.53 |
| 8 | *3.49* | -0.02 | -0.02 | 8 | *0.13* | 0.93 | 1.02 |
| 10 | 0.05 | 0.03 | 0.03 | 10 | 1.01 | 0.98 | 0.98 |

* Used for previous calculations.

Table 10

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value assumed for the female:male sex ratio in the catches for years for which this information is not available for commercial catches (see Table 2(a)). 'Slope' and '$N^{tot}$' are as for Table 3.

| MSYR (%) | Female:male ratio in catches | | | MSYR (%) | Female:male ratio in catches | | |
|---|---|---|---|---|---|---|---|
| | 1:1 | 2:1* | 4:1 | | 1:1 | 2:1* | 4:1 |
| **(a) Slope** | | | | **(b) 1900 pop'n/1846 pop'n** | | | |
| 0 | -0.75 | -0.90 | -1.05 | 0 | 0.50 | 0.49 | 0.48 |
| 1 | -0.25 | 0.05 | -0.16 | 1 | 0.40 | 0.40 | 0.40 |
| 2 | *1.04* | 0.80 | 0.56 | 2 | *0.27* | *0.29* | 0.30 |
| 3 | *1.59* | *1.38* | *1.13* | 3 | *0.18* | *0.21* | *0.23* |
| 4 | *1.80* | *1.82* | *1.64* | 4 | *0.13* | *0.17* | *0.19* |
| 5 | 0.03 | *2.16* | *2.13* | 5 | 0.43 | *0.15* | *0.17* |
| 6 | 0.02 | *2.31* | *2.60* | 6 | 1.08 | *0.13* | *0.16* |
| 8 | -0.01 | -0.02 | *3.47* | 8 | 1.03 | 0.93 | *0.15* |
| 10 | 0.01 | 0.03 | *4.23* | 10 | 0.98 | 0.98 | *0.16* |

* Used for previous calculations.

Table 11

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value of natural mortality $M$. 'Slope' and '$N^{tot}$' are as for Table 3.

| MSYR (%) | $M(\text{yr}^{-1})$ | | | MSYR (%) | $M(\text{yr}^{-1})$ | | |
|---|---|---|---|---|---|---|---|
| | 0.02 | 0.04* | 0.06 | | 0.02 | 0.04* | 0.06 |
| **(a) Slope** | | | | **(b) 1900 pop'n/1846 pop'n** | | | |
| 0 | -0.89 | -0.90 | -0.93 | 0 | 0.50 | 0.49 | 0.47 |
| 1 | 0.08 | 0.05 | -0.03 | 1 | 0.42 | 0.40 | 0.38 |
| 2 | 0.82 | 0.80 | 0.71 | 2 | 0.33 | *0.29* | *0.27* |
| 3 | *1.36* | *1.38* | *1.30* | 3 | *0.26* | *0.21* | *0.19* |
| 4 | *1.74* | *1.82* | *1.77* | 4 | *0.23* | *0.17* | *0.14* |
| 5 | *1.97* | *2.16* | *2.16* | 5 | *0.21* | *0.15* | *0.12* |
| 6 | *1.64* | *2.31* | *2.45* | 6 | *0.21* | *0.13* | *0.10* |
| 8 | -0.03 | -0.02 | -0.00 | 8 | 1.01 | 0.93 | 0.58 |
| 10 | 0.00 | 0.03 | 0.01 | 10 | 0.97 | 0.98 | 0.99 |

* Used for previous calculations.

Table 12

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value of the age at first parturition $t_m$. 'Slope' and '$N^{tot}$' are as for Table 3.

| MSYR (%) | $t_m$(yr) | | | MSYR (%) | $t_m$(yr) | | |
|---|---|---|---|---|---|---|---|
| | 5 | 8* | 11 | | 5 | 8* | 11 |
| **(a) Slope** | | | | **(b) 1900 pop'n/1846 pop'n** | | | |
| 0 | -0.88 | -0.90 | -0.91 | 0 | 0.49 | 0.49 | 0.48 |
| 1 | 0.04 | 0.05 | 0.05 | 1 | 0.41 | 0.40 | 0.39 |
| 2 | 0.77 | 0.80 | 0.82 | 2 | 0.30 | *0.29* | *0.28* |
| 3 | *1.32* | *1.38* | *1.41* | 3 | *0.23* | *0.21* | *0.20* |
| 4 | *1.72* | *1.82* | *1.86* | 4 | *0.19* | *0.17* | *0.16* |
| 5 | *2.00* | *2.16* | *2.16* | 5 | *0.16* | *0.15* | *0.14* |
| 6 | *2.05* | *2.31* | *2.17* | 6 | *0.15* | *0.13* | *0.13* |
| 8 | -0.01 | -0.02 | 0.07 | 8 | 0.95 | 0.93 | 0.98 |
| 10 | -0.06 | 0.03 | 0.38 | 10 | 0.99 | 0.98 | 1.11 |

* Used for previous calculations.

Table 13

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value of the age at recruitment $t_r$. 'Slope' and '$N^{tot}$' are as for Table 3.

| MSYR (%) | $t_r$(yr) | | | MSYR (%) | $t_r$(yr) | | |
|---|---|---|---|---|---|---|---|
| | 3 | 5* | 7 | | 3 | 5* | 7 |
| **(a) Slope** | | | | **(b) 1900 pop'n/1846 pop'n** | | | |
| 0 | -0.89 | -0.90 | -0.90 | 0 | 0.49 | 0.49 | 0.48 |
| 1 | 0.14 | 0.05 | -0.04 | 1 | 0.39 | 0.40 | 0.41 |
| 2 | 0.95 | 0.80 | 0.64 | 2 | *0.27* | *0.29* | 0.31 |
| 3 | *1.54* | *1.38* | *1.18* | 3 | *0.19* | *0.21* | *0.24* |
| 4 | *1.90* | *1.82* | *1.60* | 4 | *0.15* | *0.17* | *0.19* |
| 5 | *1.91* | *2.16* | *1.97* | 5 | *0.14* | *0.15* | *0.16* |
| 6 | -0.00 | *2.31* | *2.30* | 6 | *0.26* | *0.13* | *0.15* |
| 8 | 0.00 | -0.02 | -0.22 | 8 | 1.03 | 0.93 | 0.56 |
| 10 | 0.00 | 0.03 | -0.86 | 10 | 1.02 | 0.98 | 1.02 |

* Used for previous calculations.

Table 14

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value of the MSY level (MSYL). 'Slope' and '$N^{tot}$' are as for Table 3.

| MSYR (%) | MSYL | | | MSYR (%) | MSYL | | |
|---|---|---|---|---|---|---|---|
| | 0.5 | 0.6* | 0.7 | | 0.5 | 0.6* | 0.7 |
| **(a) Slope** | | | | **(b) 1900 pop'n/1846 pop'n** | | | |
| 0 | -0.90 | -0.90 | -0.90 | 0 | 0.49 | 0.49 | 0.49 |
| 1 | 0.14 | 0.05 | -0.05 | 1 | 0.37 | 0.40 | 0.42 |
| 2 | 0.84 | 0.80 | 0.70 | 2 | *0.25* | *0.29* | 0.31 |
| 3 | *1.34* | *1.38* | *1.35* | 3 | *0.18* | *0.21* | *0.24* |
| 4 | *1.69* | *1.82* | *1.90* | 4 | *0.14* | *0.17* | *0.19* |
| 5 | *1.94* | *2.16* | *2.36* | 5 | *0.13* | *0.15* | *0.17* |
| 6 | *2.07* | *2.31* | 0.07 | 6 | *0.12* | *0.13* | 0.40 |
| 8 | *1.09* | -0.02 | -0.18 | 8 | *0.11* | 0.93 | 0.98 |
| 10 | -0.00 | 0.03 | -0.24 | 10 | 0.97 | 0.98 | 0.77 |

* Used for previous calculations.

By and large, the results indicate insensitivity to these changes, except occasionally for the larger of the MSYR values listed. The only major exceptions to this are the cases of changed $N^{tot}_{1988}$ values and female:male catch ratios (Tables 9 and 10). The inconsistencies between the population model and the other evidence become more difficult to resolve (in the sense of necessitating larger values of $\mu_C$ or $\mu_A$, say) for a higher value of $N^{tot}_{1988}$, or for a smaller fraction of females in the catches. The results of the latter sensitivity test are also shown in Fig. 7 and serve to emphasise that it is the catch of *females* in particular that drives the model.

These tests suggest that the factors which are of most importance for further investigation involve the sex ratio of the catches and the accuracy of the 1988 census estimate ($N^{tot}_{1988}$) which the trajectories 'hit'. Improving estimates for $M$, $t_m$, $t_r$ and MSYL is of much less consequence.

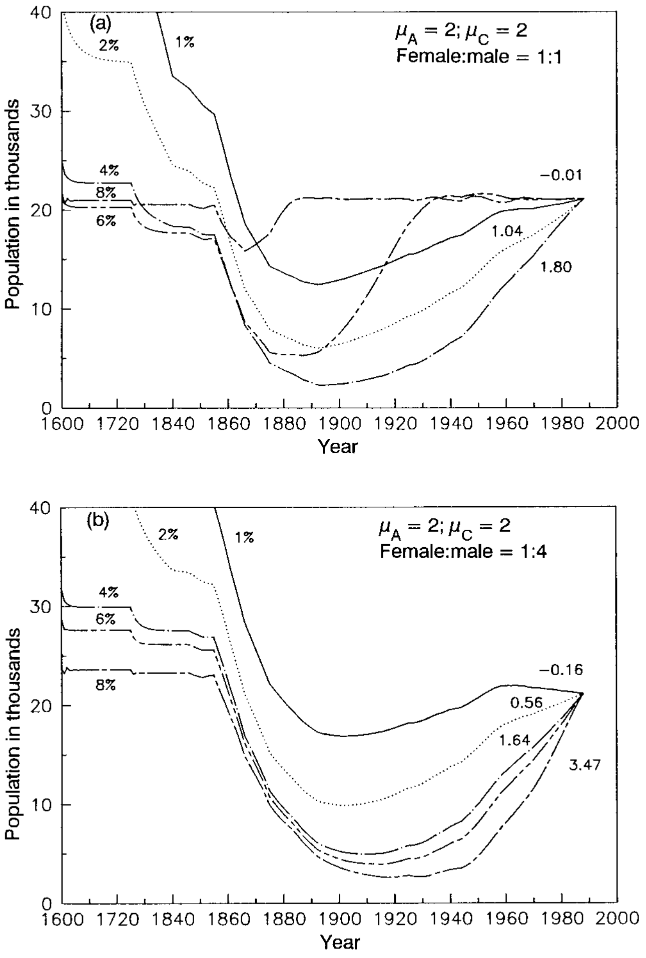

Fig. 7. Illustrations of the consequences of changing the female:male ratio from 2:1 as previously assumed for commercial catches for which this information is not available, for the case $\mu_C$ = 2.0 and $\mu_A$ = 2.0. Trajectories are shown for various MSYR values for female:male ratios of (a) 1:1 and (b) 4:1.

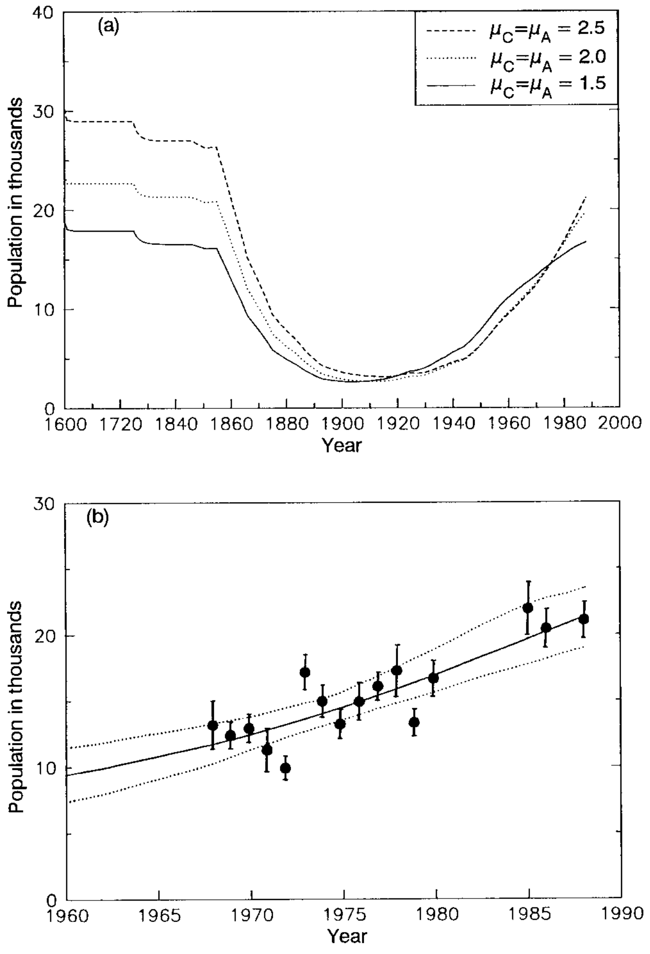

Fig. 8. In (a), population trajectories are shown for the model fitted to the census estimates up to 1987-88 for the cases ($\mu_C$ = 1.5; $\mu_A$ = 1.5), ($\mu_C$ = 2; $\mu_A$ = 2) and ($\mu_C$ = 2.5; $\mu_A$ = 2.5). Only the last of these cases is shown in (b), which reflects only the 1960-1988 period. There the estimated trajectory is shown by the solid line, and the bootstrap 95% CI about this by the dotted lines. Further, the absolute estimates from the censuses (Table 1) are shown by large dots, together with their 95% CIs (assumed to be ±2 SE). $\sigma_2$ = 0.012 for all the results shown.

Table 15

Results for fitting the population model to the census estimates as described in the text for various choices for $\mu_C$ and $\mu_A$. The HITTER fit is constrained to pass through the 1988 census estimate of 21,113 exactly. The FITTER results are for the choice $\sigma_2$ = 0.012 unless otherwise indicated. Quantities in parentheses are CV estimates, evaluated using the bootstrap technique described in the text. 'Slope' and '$N^{tot}$' are as for Table 3. MSYR$_{1+}$ is the MSY rate in terms of uniform selectivity harvesting on the 1+ population, rather than the 5+ population to which MSYR refers. $N^{f}_{1988}$ refers to the number of females past the age at first parturition in that year and $K^f$ is the corresponding number at unexploited equilibrium.

| Quantity | $\mu_C = 1.5$; $\mu_A = 1.5$ | $\mu_C = 2$; $\mu_A = 2$ | $\mu_C = 2.5$; $\mu_A = 2.5$ | | |
|---|---|---|---|---|---|
| | FITTER | FITTER | HITTER | FITTER | FITTER; $\sigma_2 = 0.01$ |
| $N^{tot}_{1600} = K$ | 18,825 | 23,584 | 29,637 | 29,729 (0.10) | 29,726 (0.11) |
| $N^{tot}_{1846}$ | 16,514 | 21,294 | 26,681 | 26,725 (0.05) | 26,723 (0.06) |
| $N^{tot}_{1900}$ | 2,655 | 2,910 | 3,501 | 3,517 (0.12) | 3,515 (0.13) |
| $N^{tot}_{1968}$ | 12,843 | 11,884 | 11,382 | 10,658 (0.07) | 11,496 (0.11) |
| $N^{tot}_{1988}$ | 16,657 | 19,715 | 21,113 | 21,347 (0.06) | 21,238 (0.09) |
| $b$ | 1.314 | 1.317 | 1.318 | 1.318 | 1.310 |
| Slope | 1.32 | 2.58 | 3.14 | 3.11 (0.18) | 3.12 (0.17) |
| $N^{tot}_{1900} / N^{tot}_{1846}$ | 0.16 | 0.14 | 0.13 | 0.13 (0.07) | 0.13 (0.08) |
| $N^{tot}_{1988} / K$ | 0.88 | 0.84 | 0.71 | 0.72 (0.16) | 0.71 (0.19) |
| $N^{f}_{1988} / K^f$ | 0.69 | 0.61 | 0.49 | 0.49 (0.16) | 0.49 (0.23) |
| MSYR (%) | 5.0 | 5.6 | 5.5 | 5.5 (0.21) | 5.5 (0.26) |
| MSYR$_{1+}$ (%) | 3.8 | 4.2 | 4.2 | 4.2 (0.19) | 4.2 (0.22) |

### FITTER model applications

The results of ‘fitting’ the model to the census estimates of Table 1 are shown in Table 15 and Fig. 8a for three different combinations of values for $\mu_C$ and $\mu_A$. Essentially all three trajectories pass close to the centroid of the series of absolute estimates in Table 1. However, the fits for the cases ($\mu_C = 1.5$; $\mu_A = 1.5$) and ($\mu_C = 2$; $\mu_A = 2$) are unable to achieve the observed population growth rate estimate of 3.2% over the 1968-1988 period, so that the corresponding population trajectories pass through lower total abundance estimates for 1988 than the 21,113 used above for HITTER evaluations. Clearly some model mis-specification remains for ($\mu_C = 1.5$; $\mu_A = 1.5$) and to a rather lesser extent for ($\mu_C = 2$; $\mu_A = 2$).

All three cases indicate a resource that is at present not far below its unexploited equilibrium level in terms of total numbers ($N^{tot}_{1988}/K$ between 0.70 and 0.88). However, this ratio is somewhat less for the ‘mature’ female component of the population ($N^{tot}_{1988}/K^f$ between 0.48 and 0.69). A resource of relatively high productivity is indicated, with MSYR in terms of the 5+ population in the vicinity of 5%, which corresponds to about 4% for uniform selectivity harvesting on the total (1+) population.

Because of the model mis-specification indicated for two of the cases considered, bootstrap variance estimation was carried out for the ($\mu_C = 2.5$; $\mu_A = 2.5$) scenario only. The results are shown as 95% CIs about estimated trajectories in Fig. 8b and as CVs in Table 15.

These results suggest that the data are able to provide reasonably precise estimates, with CVs for the various quantities listed in Table 15 ranging between about 5 and 20%. A concern, however, is that the results of Buckland and Breiwick (2002) in Table 1 suggest that the scaling factor $b$ has been independently estimated with a coefficient of variation ($\sigma_2$) only slightly in excess of 1%. This is unrealistically precise (as confirmed by subsequent analyses (Buckland *et al.*, 1993)), so that the ‘fitting’ was repeated for a larger (and possibly more realistic) value: $\sigma_2 = 0.1$. The results for this exercise are also shown in Table 15, and suggest that the level of precision originally indicated is not markedly dependent on a small value for $\sigma_2$.

To test the reliability of the bootstrap procedure used for variance estimation, 95% CIs for MSYR were computed for this same case ($\mu_C = 2.5$; $\mu_A = 2.5$) by means of both the bootstrap and a likelihood ratio method (Mood *et al.*, 1974). The results are shown in Table 16 and are encouragingly similar, with the bootstrap intervals being slightly larger.

Naturally, these estimates of precision are conditioned on fixed values of $\mu_C$ and $\mu_A$, and would increase if uncertainty in these values was also taken into account. A quantitative evaluation of the extent of this increase is beyond the scope of this paper. However, the point estimates of Table 15 for the variety of ($\mu_C$; $\mu_A$) combinations considered suggest that although CV estimates for historic population sizes would increase substantially given such an evaluation, the estimate of MSYR would remain reasonably robustly determined in the vicinity of 5% (in terms of the 5+ population).

Table 16

Estimates of 95% CIs for the estimate of MSYR (in terms of the exploitable component of the population) obtained from the applications of FITTER for $\mu_C = 2.5$ and $\mu_A = 2.5$ whose results are reported in Table 15. Estimates obtained from both the bootstrap and likelihood ratio methods (see text) are shown for the two values of $\sigma_2$ considered in Table 15. MSYR values are expressed as percentage.

| | MSYR: 95% CI | |
|---|---|---|
| | Bootstrap | Likelihood ratio |
| $\sigma_2 = 0.012$ | [3.7; 8.1] | [3.7; 7.9] |
| $\sigma_2 = 0.1$ | [3.7; 10.3] | [3.7; 8.1] |

The point estimate of $\text{MSYR}_{1+}$ (MSY rate in terms of uniform selectivity harvesting on the 1+ population) is 4.2%. In terms of the Pella-Tomlinson model used (see equation 1), this corresponds to a growth rate of some 6% per annum for the stock when at a very low level and protected. This is not incompatible with direct estimates of growth rate of other heavily depleted stocks; Best (1993) provides a list of these estimates which range from 5 to 14% per annum[4].

## CONCLUSIONS

It is convenient to summarise the results of the HITTER analyses above for various possible adjustment factors, by reporting the lower limits necessary to achieve an average population increase rate from 1968-1988 of at least 2% per annum. The resultant bounds (where appropriate) are as follows.

*(i) Depensation*
Cannot alone account for inconsistencies.

*(ii) Additional response time-lag*
Model used produces unrealistic population oscillations.

*(iii) Carrying capacity increase (1846-1988)*
$\mu_K \geqslant 2.5$ (and MSYR $\geqslant$ 4%).

*(iv) Underestimation of historic commercial catches (1846-1900)*
$\mu_C \geqslant 2.5$ (and MSYR $\geqslant$ 5%), or MSYR $\geqslant$ 4% (and $\mu_C \geqslant 3.0$).

*(v) Underestimation of aboriginal catches*
$\mu_A \geqslant 3$ (and MSYR $\geqslant$ 4%).

*(vi) Combination of $\mu_C$ and $\mu_A$*
For $\mu_C$ = *2.0:*
  $\mu_A \geqslant 2.0$ (and MSYR $\geqslant$ 5%)
  $\mu_A \geqslant 2.5$ (and MSYR $\geqslant$ 4%).

Note that each one of these cases corresponds to a depletion of less than 23% of the 1846 population over the 1846-1900 period. In all the cases listed which have a $\mu_C$ adjustment factor, this depletion level is of 17% or less. These cases therefore all seem reasonably consistent with the commercial extinction of the resource at the turn of the 19th century.

IWC (1993) discussed problems associated with the estimates of historic commercial and aboriginal catches and the extent to which these might have been underestimated. Readers are invited to form their own judgements, based upon these comments, as to whether there is supportive evidence for adjustment factors as large as $\mu_C$ of about 2 and/or $\mu_A$ of about 2, which would resolve the inconsistencies between simple density-dependent response population models for the gray whale and other information such as the population growth rate deduced from censuses. However, consideration needs to be given to the assumptions of the HITTER analyses that $N^{tot}_{1988} = 21{,}113$, and that the female:male ratio of commercial catches in years for which this information is not available is 2:1. Inferences

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[4] The choice of 5% for the lower end of this range excludes the estimate for Bering-Chukchi-Beaufort Seas bowhead whales from Best’s list, as the rate he quotes was for a period well after that during which this population was at a very low level.

concerning lower bounds for $\mu_C$ or $\mu_A$ to resolve inconsistencies are sensitive to these two assumptions. In contrast, such inferences are not particularly sensitive to the values chosen for the population model parameters $M$, $t_m$, $t_r$ and MSYL, so that rather less attention need be given to the determination of appropriate values for these parameters.

Relatively 'high' MSYR values (typically 4% or more) are required to obtain recent population growth rates of 2% per year. [Note that an MSYR of 4% for the recruited (5+) component of the population corresponds to one of about 3% for uniform selectivity harvesting on the 1+ population.] Such 'high' values are not altogether surprising, given recent fishing mortalities of about 1% per year coupled with an annual growth rate of about 3%.

'Fitting' the population model to the census estimates gives rise to model mis-specification unless $\mu_C$ and/or $\mu_A$ are fairly large, because the model cannot otherwise reflect the 'high' observed growth rate. For ($\mu_C = 2.5$; $\mu_A = 2.5$), the estimates of historic population sizes are determined with quite high precision (CVs about 10%), while estimates of recent growth rate and MSYR are also reasonably precise (CVs about 20%). This estimated precision is, of course, conditional on fixed values for $\mu_C$ and $\mu_A$, but results suggest that the MSYR estimate of some 5% (or 4% in terms of the 1+ population) is relatively robust to the uncertainty about these levels of underestimation.

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# Dynamic response analysis for the eastern North Pacific gray whale population: an alternative approach[1]

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ABSTRACT

Gerrodette and DeMaster (1990) conclude that dynamic response analysis indicates that the gray whale population passed through its maximum net productivity level (MNPL, approximately equivalent to MSY level) between 1967 and 1980. Their conclusion is examined using models for population trends which permit a point of inflection; these are fitted globally to the time series of census estimates available up to 1987-88. A cubic and a logistic model are used. The cubic model results indicate with almost 100% confidence that the population passed through MNPL within two years of 1973-74. However, both this conclusion and that of Gerrodette and DeMaster are considered to be unreliable. This is because the curves fitted by both analyses correspond to markedly decreasing population sizes over parts of the periods to which they apply. This is inconsistent with plausible population dynamics behaviour, which is itself an underlying pre-requisite for dynamic response analysis methodology. A suggestion is made as to how applications of dynamic response analysis methodology such as that of Boveng *et al.* (1988) could be adapted to ensure the necessary respect of such constraints. Results of a parametric bootstrap procedure for confidence interval estimation applied to the logistic model indicate that the probability that the population passed through MNPL during the period of the censuses is not large. The census data are scarcely adequate to allow for reliable estimates of the curvature of the population trajectory to be made. The logistic model dynamic response analysis indicates that there is a somewhat greater likelihood that the gray whale population was below rather than above its MNPL in 1990, given the data available at the time.

KEYWORDS: ASSESSMENT; MODELLING; TRENDS; GRAY WHALE; NORTH PACIFIC

## INTRODUCTION

Dynamic response analysis (Boveng *et al.*, 1988; Gerrodette, 1988; Goodman, 1988) is an appealingly simple approach for determining whether a population is above or below its maximum net productivity level (MNPL). This is particularly so in the case of the eastern North Pacific gray whale population. The alternative method of making this determination - fitting simple population models using historic catch data - leads to inconsistencies (e.g. Cooke, 1986; Lankester and Beddington, 1986). In addition, the application of such population models requires some restrictive assumptions, such as time-invariance of carrying capacity (whose violation may perhaps be the reason for the inconsistencies that arise in the simple model fits for the gray whale population - Butterworth *et al.*, 2002). Dynamic response analysis has the advantage that such an assumption is not necessary.

Gerrodette and DeMaster (1990) point out that MNPL is not the same as MSY level (MSYL), which is a function of the sex and age-composition of the harvest. However, the difference in the case of the eastern North Pacific gray whale population is not likely to be large. The question of whether this population is above or below its MSYL has been of particular relevance in IWC Scientific Committee debates about the likely values of MSY rate (MSYR) for baleen whales. If this population is now above MSYL, then the increase rate of 3.2% per annum (IWC, 1993) evident from preceding censuses (see Table 1b), coupled with the size of the catch over that period (see Table 2), provides an estimated lower bound of some 4% for MSYR (expressed in terms of total population); however, if the population is still below MSYL, no such bound can be inferred.

Gerrodette and DeMaster (1990) present results of an application of dynamic response analysis to the eastern North Pacific gray whale population. The particular methodology they use is that of Boveng *et al.* (1988), which involves plotting a time series of the second-order coefficients of quadratics (i.e. local curvature estimates) fitted to sequences of censuses of lengths from 6-11 years. They apply this method to the annual census data from 1967-68 to 1979-80 reported in Reilly *et al.* (1983), shown in Table 1a. They go on to report that the pattern of these coefficients (although few of them are individually significantly different from zero) is indicative of a population that was below MNPL in 1967, but above MNPL by 1980.

Our particular concern is to apply dynamic response analysis to these data in a manner that allows for an easier evaluation of the statistical confidence that can be placed in the Gerrodette-DeMaster conclusion. To this end functions have been fitted which permit a point of inflection to the complete time series of censuses, instead of estimating successive local curvature values and seeing whether these pass through zero. Goodman (1988) mentions this approach, which he terms ‘global fitting’, but raises two associated problems. First, the range of the data may be inadequate for secure estimation of all the parameters of this global function - for this reason, the parameterisations used in this paper are kept as parsimonious as possible. Secondly, he cautions about possible lack of fit (model mis-specification), with attendant distortion of parameter estimates and their implications. The average of the standard deviations (SDs) of the 13 census estimates in Reilly *et al.* (1983) is 1,586 (see Table 1a); this compares with an estimated residual SD of 1,536 for an (unweighted) linear regression fitted to these data. If these data contained precise information on complex details of shape, the latter SD would be much higher than the

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[1] A version of this paper was originally presented in 1990.

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Table 1

Gray whale census estimates and SEs. See note in text concerning the SE estimates listed in (b).

| (a) Reilly *et al.* (1983) | | | (b) Buckland and Breiwick (2002)[1] | | |
|---|---|---|---|---|---|
| Year | Estimate | SE | Year | Estimate | SE |
| 1967-68 | 13,095 | 1,276 | 1967-68 | 13,012 | 879 |
| 1968-69 | 11,954 | 1,545 | 1968-69 | 12,244 | 461 |
| 1969-70 | 12,408 | 1,619 | 1969-70 | 12,777 | 502 |
| 1970-71 | 11,177 | 1,625 | 1970-71 | 11,170 | 795 |
| 1971-72 | 10,414 | 918 | 1971-72 | 9,841 | 426 |
| 1972-73 | 14,534 | 1,348 | 1972-73 | 16,962 | 629 |
| 1973-74 | 14,676 | 1,558 | 1973-74 | 14,817 | 566 |
| 1974-75 | 13,110 | 1,366 | 1974-75 | 13,134 | 516 |
| 1975-76 | 15,919 | 1,803 | 1975-76 | 14,811 | 667 |
| 1976-77 | 16,621 | 1,798 | 1976-77 | 15,950 | 489 |
| 1977-78 | 14,811 | 2,272 | 1977-78 | 17,127 | 944 |
| 1978-79 | 13,676 | 1,127 | 1978-79 | 13,300 | 476 |
| 1979-80 | 17,577 | 2,364 | 1979-80 | 16,581 | 659 |
| | | | 1984-85 | 21,942 | 960 |
| | | | 1985-86 | 20,450 | 685 |
| | | | 1987-88 | 21,113 | 641 |

[1] The values listed above, which were used for the calculations of this paper, were taken from an earlier version of Buckland and Breiwick (2002). There are minor changes to these values in the final version of that paper published in this volume, but the effect of these on the results reported in this paper is negligible.

Table 2

Annual gray whale catches during the period of censuses.
Source: C. Allison, IWC (pers. comm., 16 Jan. 1990).

| Year | Catch | Year | Catch |
|---|---|---|---|
| 1967 | 250 | 1978 | 184 |
| 1968 | 201 | 1979 | 183 |
| 1969 | 214 | 1980 | 181 |
| 1970 | 151 | 1981 | 136 |
| 1971 | 153 | 1982 | 168 |
| 1972 | 182 | 1983 | 171 |
| 1973 | 178 | 1984 | 169 |
| 1974 | 184 | 1985 | 170 |
| 1975 | 171 | 1986 | 171 |
| 1976 | 165 | 1987 | 159 |
| 1977 | 187 | 1988 | 151 |

former; their near equality suggests that model mis-specification is unlikely to be a problem for the analyses of these data that follow.

This paper considers global fits of cubic and logistic functions to the time series of gray whale census estimates up to 1987-88. Confidence intervals (CIs) relating to the year in which the population trajectory shows a point of inflection ($y^*$, corresponding to MNPL) are determined by linear model and (Monte Carlo) parametric bootstrap methods respectively for these two functions. The results are used to assess the statistical confidence which can be placed in the Gerrodette-DeMaster conclusion that dynamic response analysis indicates that the population passed through MNPL between 1967 and 1980.

## DATA AND METHODOLOGY

The gray whale census estimates used in the analyses that follow are given in Table 1. Table 1a lists the estimates reported in Reilly *et al.* (1983) for the period 1967-68 to 1979-80. These are the data that were used by Gerrodette and DeMaster (1990) in their application of dynamic response analysis. It is therefore appropriate to use this same set for the alternative analyses which follow to re-examine their conclusion. Censuses have been conducted subsequent to 1979-80, and the data from these and the earlier years have been re-analysed by Buckland and Breiwick (2002). Table 1b lists Buckland and Breiwick's 'adjusted abundance' estimates for the period 1967-68 to 1987-88; applications of the global fitting methods of this paper to this longer period have all used this more recent dataset.

Note that the standard error (SE) estimates in Table 1b differ slightly from those given in Buckland and Breiwick (2002). This is because the latter error estimates include a common contribution reflecting the variance of the multiplicative factor used by Buckland and Breiwick to convert 'relative abundance' to 'adjusted abundance' estimates. This variance contribution has not been included in the error estimates reported here. The reason is that (as discussed below) the analysis methods to be used in this paper are concerned only with population trajectory shape, not scale, so that the variance of the multiplicative factor is not relevant to the analyses which utilise the SE information.

The gray whale catches during the period of the censuses are listed in Table 2. These data were provided by C. Allison (IWC) and contain some very minor amendments to those reported in Lankester and Beddington (1986).

Strictly, dynamic response analysis involves determination of the population size corresponding to maximum production. This will not in general correspond to the size at which the population trajectory shows a point of inflection, because the annual harvest, as well as the change in population size, has to be taken into account in assessing production; equivalence occurs only if the annual harvest is constant. The annual gray whale catch over the 1967-88 period has been remarkably steady (mean 176; SD only 23). The greatest deviations of the catch from this mean are +74 and –40, which are insubstantial in the context of the SEs of the population estimates in Table 1. The analyses of this paper have thus ignored the effects of variations in the annual harvest, thereby reducing the problem to one of estimating the year in which the gray whale population trajectory shows a point of inflection. An advantage of this approach is that it requires only that the population censuses reflect relative (and comparable) indices of population size, rather than unbiased estimates of absolute abundance.

The simplest polynomial function which can show a point of inflection in the trend of relative abundance ($N$) with time/year ($y$) is the cubic:

$$N_y = a_0 + a_1 y + a_2 y^2 + a_3 y^3 \qquad (1)$$

for which this inflection occurs at time:

$$y^* = -a_2 / (3a_3) \qquad (2)$$

The particular advantage of fitting such a trend model to the census estimates is that it is linear in its parameters. The assumptions of independence and error distribution normality then allow standard linear model theory to be used to provide parameter estimates and the associated SEs. This applies both to the case when all the censuses considered are given equal weight in the fitting process and when each census is weighted by the inverse of the square of its estimated SE. The SE estimate for $y^*$ is of particular interest and is a non-linear function of the model parameters. Nevertheless, this error estimate can be readily calculated using the delta method approximation, applied using the parameter variance and covariance estimates provided by standard packages which perform linear model fits.

A disadvantage of the cubic of equation (1) is that four parameters need to be estimated, with a consequent possible loss of estimation precision. A more parsimonious approach (with one less parameter) was therefore attempted by fitting the logistic model to the census time series. To avoid problems with statistically unstable parameter estimates, Schnute's (1981) parameterisation of the logistic curve was used for this purpose:

$$N_y = \left[ N_1{}^b + (N_2{}^b - N_1{}^b)\frac{1-e^{-a(y-y_1)}}{1-e^{-a(y_2-y_1)}} \right]^{1/b} \tag{3}$$

i.e. four parameters $a$, $b$, $N_1 = \hat{N}(y=y_1)$ and $N_2 = \hat{N}(y=y_2)$, where in the special case of the logistic curve the following relations apply:

$$b=-1;\ a>[\ln(N_2/N_1)]/[y_2-y_1]$$

It then follows that:

$$y^* = y_1 + a^{-1}\ln(\beta/\alpha) \tag{4}$$

where: $\beta = [N_1{}^{-1} - N_2{}^{-1}]/[1-e^{-a(y_2-y_1)}]$

$$\alpha = N_1{}^{-1} - \beta$$

The calculations were carried out for $y_1 = 1967\text{-}68$ and $y_2$ equal to the time of the last census considered.

The choice of a logistic curve for fitting purposes is not intended to imply that the dynamics of the gray whale are governed by the associated differential equation. Rather, this curve was chosen because it is one of the simplest forms which possesses the desired general properties for the trend in abundance: plausible past and future limiting behaviour, and a point of inflection.

There is a cost in changing from the cubic to the logistic model, however. This is that the logistic model is no longer linear in its parameters, so that non-linear estimation techniques are required. A more serious problem is how to estimate an SE (or CI) for $y^*$. This could be obtained from elements of the information matrix, together with an application of the delta method. However, the non-linear nature of the problem means that the resultant CI estimates would be approximate; further, the parameter estimates for such a model fitted to relatively few data often have markedly skewed distributions, so that unless such estimates are precise, the linear approximation of the delta method is unlikely to be accurate. The likelihood ratio approach could be applied in a manner which bypasses the need for the delta method, but the resultant CI estimates would remain approximate because of the non-linearity of the model.

A bootstrap approach was, therefore, adopted to determine the precision of the logistic model $y^*$ estimate. [Note: Strictly speaking, Monte Carlo implementations of forms of what is termed a 'conditional parametric bootstrap' procedure were applied (Smith *et al.*, 1993, Table 1) - for convenience, the term 'bootstrap' is used without these qualifications in what follows.] For the case where each census estimate was given an equal weight in the fit, the bootstrap replicate datasets were generated from the fitted logistic curve ($\hat{N}_y$). Thus, for fits to the 1967-68 to 1979-80 census estimates of Table 1a for example, a re-sampled set $\{N_y{}^S : y = 67\text{-}68,\ldots,79\text{-}80\}$ where $S = 1,\ldots,S_{\max}$ was formed as follows:

$$N_y{}^S = \hat{N}_y + \epsilon_y{}^S \qquad \epsilon_y{}^S \text{ from } N(0,\sigma^2)$$

$$\hat{\sigma}^2 = \frac{1}{n-3}\sum_{y=67\text{-}68}^{79\text{-}80}(N_y - \hat{N}_y)^2, \tag{5}$$

where:

$N_y$ is the census estimate for year $y$;

$\hat{N}_y$ is the fitted logistic curve value for year $y$; and

$n$ = 13 for this example.

Note that the ($n$-3) term in the denominator of the equation for $\sigma^2$ is an *ad hoc* attempt to adjust for bias in the maximum-likelihood estimate of $\sigma^2$, by making allowance for the fact that three parameters are being estimated in the fit. This adjustment would be exact if the model being used was linear in its parameters.

For fits where the census estimates are each weighted by the inverse of their squared SEs, the bootstrap samples were generated directly from the data without reference to the fit itself:

$$N_y{}^S = N_y + \eta_y{}^S \qquad \eta_y{}^S \text{ from } N(0,\sigma_y{}^2) \tag{6}$$

where $\sigma_y$ is the estimate of the SE for census estimate $N_y$. The basis for this approach is discussed further in Appendix 1.

In either case, each time series of bootstrap censuses $\{N_y{}^S\}$ is fitted by the logistic model with the same weighting scheme as used for the associated original fit and each bootstrap fit provides a value for the year in which the curve shows a point of inflection $(y^S)^*$. The set $\{(y^S)^* : S = 1,\ldots,S_{\max}\}$ then constitutes an empirical distribution for the estimate of $y^*$; CI estimates follow straightforwardly after ordering this set. For the computations reported in this paper, $S_{\max} = 500$.

There is a philosophical difference between the two bootstrap approaches used. Equation (5), for equal weighting, tacitly assumes that the underlying population trajectory is logistic. The approach of equation (6) makes no assumption about the form of this trajectory, but generates equally likely possible time series of censuses by treating each observation as independent; in this context, the logistic curve eventually fitted is regarded only as a convenient functional form with the desired general properties (as detailed above). An advantage of the latter approach is that it avoids the need to make *ad hoc* adjustments for bias when generating the bootstrap residuals.

## RESULTS

The estimates of $y^*$ from fitting the cubic model of equation (1) to the census estimates from 1967-68 to 1979-80 and the associated delta method estimates of SE are:

Unweighted: $y^*$ = 1973-74 + 0.4 yrs SE = 0.9
Weighted: $y^*$ = 1973-74 + 0.0 yrs SE = 0.5

The fit to the data for the latter case (weighting by $1/\text{SE}^2$) is shown in Fig. 1. Gerrodette and DeMaster (1990) used an unweighted fitting procedure for the same data that have been used here (DeMaster, pers. comm.). Although, for reasons discussed in the following section, the weighted procedure is preferred here, the results are relatively insensitive to whichever procedure is chosen.

The results for fitting the logistic model of equation (3) are given in Table 3. They are given for fits to both Reilly *et al.*'s (1983) estimates for 1967-68 to 1979-80, and Buckland and Breiwick's (2002) estimates for 1967-68 to 1987-88. The weighted fits to these two series are shown in Figs 2 and 3 respectively.

A fit of the full four-parameter Schnute growth curve model (i.e. parameters $a$ and $b$ unconstrained) was carried out for both the unweighted and weighted cases, and compared to the special (three-parameter) case of the logistic model for both datasets. In all cases, a likelihood ratio test indicated that there was no statistical justification for the

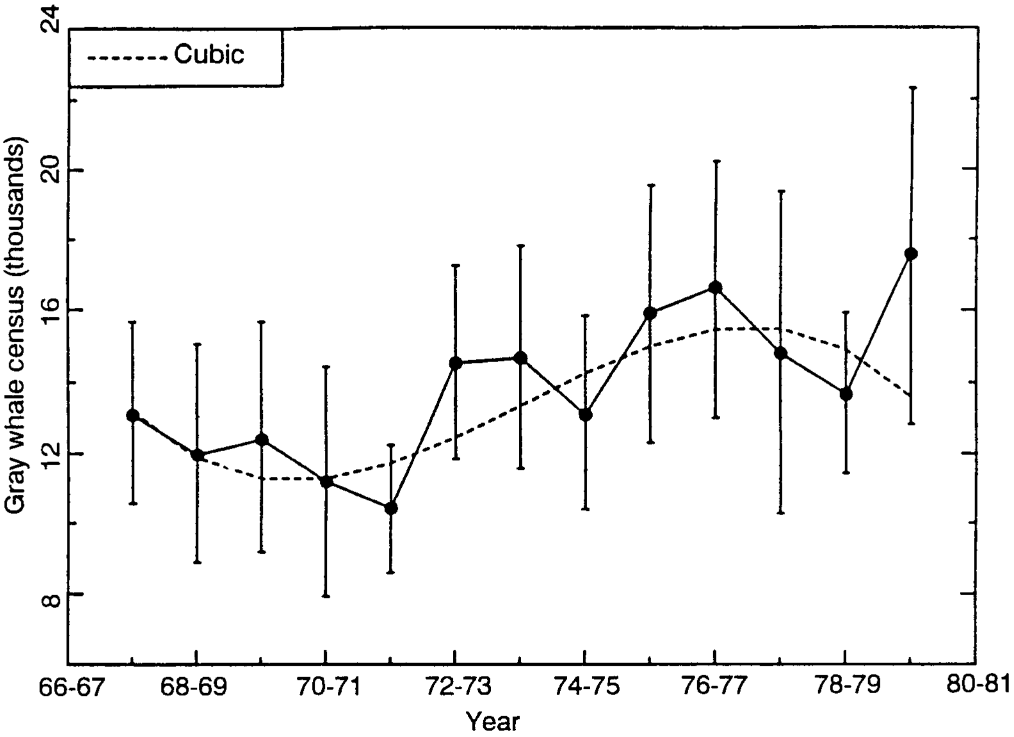

Fig. 1. The weighted cubic model fit to census estimates of Reilly *et al.* (1983) (Table 1a) from 1967-68 to 1979-80 is shown by the dashed line. The dots and associated vertical bars correspond to the actual census estimates and associated 95% CIs (taken to be ± 2 SEs).

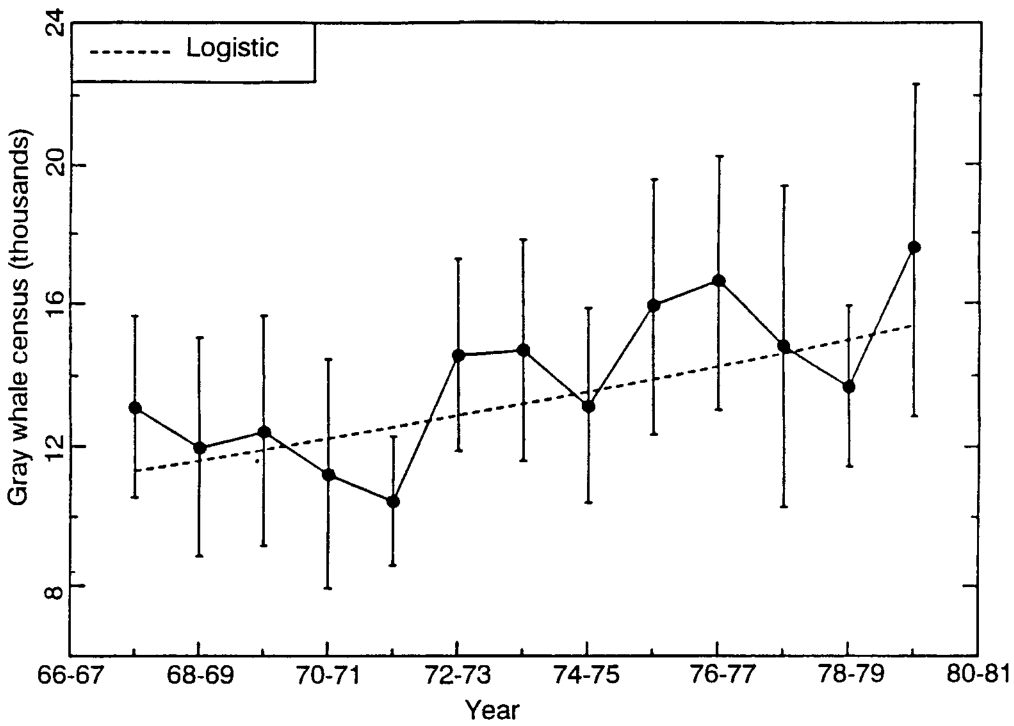

Fig. 2. As for Fig. 1, except that the dashed line corresponds to the weighted logistic model fit.

inclusion of a fourth parameter. This demonstrates that there is no evidence that the choice of the logistic form for fitting purposes is introducing any model mis-specification.

## DISCUSSION

At face value, the two approaches applied here to Reilly *et al.*'s (1983) census estimates have given startlingly different results. The cubic model suggests, with close to '100% confidence', that these estimates indicate a point of inflection in the population trajectory within two years of 1973-74. This is entirely compatible with the results shown in fig. 2 of Gerrodette and DeMaster (1990). In contrast, the corresponding results for the logistic model shown in Table 3 indicate a probability of less than 10% that the point of inflection occurs within the period of these first 13 censuses.

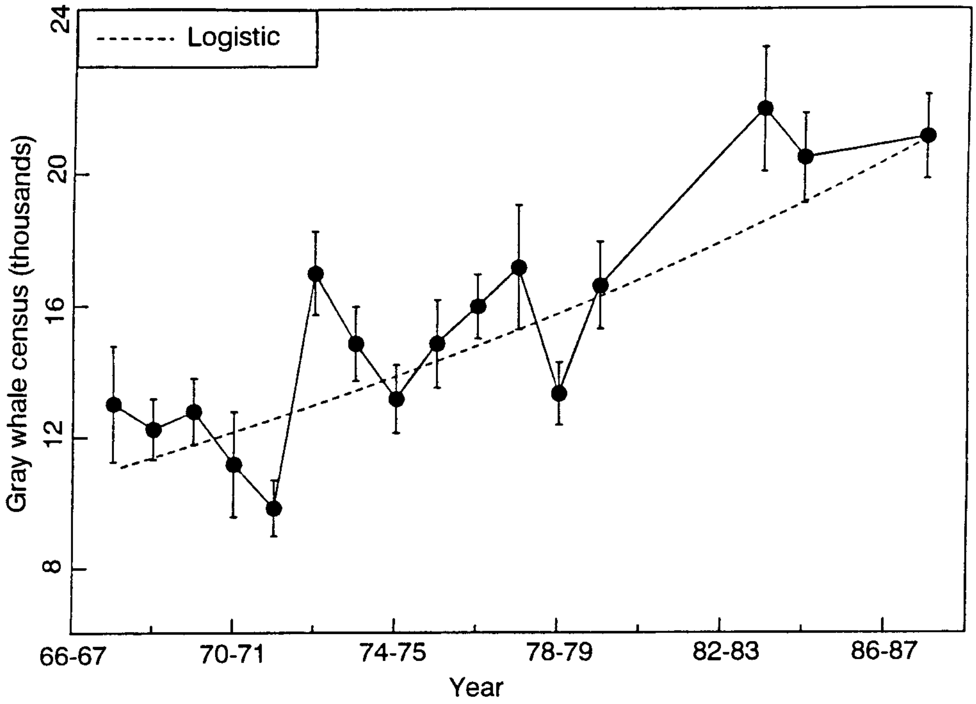

Fig. 3. As for Fig. 2 (weighted logistic model fit), except that the fit is now to the census estimates of Buckland and Breiwick (2002) (see Table 1b) for the period 1967-68 to 1987-88.

Table 3

Results of fits of the logistic function to the census time series in respect of the year corresponding to the point of inflection on the curve (y*). The data in Table 1(a) were used for the fits for the 1967-68 to 1979-80 period, and those in Table 1(b) for the fits for the 1967-68 to 1987-88 period.

| | | | Probability (%) that y* occurs: | | |
|---|---|---|---|---|---|
| Period considered | Weighted (W) or unweighted (U) fit | $\hat{y}^*$ | Before period | During period | After period |
| 1967-68 to 1979-80 | U | 2,263 | 42 | 9 | 49 |
| | W | 2,241 | 28 | 4 | 68 |
| 1967-68 to 1987-88 | U | 2,150 | 7 | 31 | 62 |
| | W | 2,171 | 0 | 0 | 100 |

The method of analysis used for assessing the precision of $y^*$ for the cubic model could be questioned because it does not exclude the possibility that the point of inflection arises from a convex (viewed from above) followed by a concave curve, which would be unrealistic in a population dynamics context. However, this is a minor concern, and in any case the resolution of the apparently contradictory results from the two models is immediately evident from inspection of Fig. 1.

The rationale underlying dynamic response analysis implicitly assumes that under a constant or zero harvest, the population trajectory will be monotonically increasing. This is not the case for the fitted cubic in Fig. 1, which decreases for the period of both the first three and the last three censuses shown. This is a consequence of the decreases in the actual point estimates from the 1967-68 to 1971-72 (1969-70 excepted) and 1976-77 to 1978-79 censuses. The sizes of the CIs for the census estimates shown in Fig. 1 indicate that these drops are almost certainly stochastic fluctuations; however, the cubic model is using its available degrees of freedom to reflect these drops in the fit which it chooses. Thus, the high precision of the cubic model's estimate of $y^*$ is misleading, because it is a consequence of the model allowing unrealistic population behaviour over the early and late parts of the period considered.

For this reason, the cubic model's assessment of $y^*$ and its precision is rejected here. For exactly the same reason, the method of analysis used by Gerrodette and DeMaster (1990), which indicated that the gray whale population passed through MNPL between 1967 and 1980, is considered unreliable[2]. The drops in the census estimates between 1967-68 and 1971-72, and between 1976-77 and 1978-79, have the effect of enhancing the second order coefficients in the quadratics fitted to periods including those years, thus apparently strengthening the case for detection of a point of inflection. But the fact that the quadratics fitted over the periods indicated correspond to estimating that population size has decreased for at least parts of those periods also needs to be taken into account. Such population behaviour is inconsistent with the underlying rationale for dynamic response analysis. Future attempts to use the methodology of Boveng *et al.* (1988) when implementing dynamic response analysis should take care to constrain the parameters of the quadratics fitted to exclude such apparent behaviour. This might be achieved by fitting the logistic model (rather than a quadratic) over short time periods, and then using such fits to estimate the sign and magnitude of the curvature at the mid-point of each corresponding period. Unfortunately, of course, this approach (like any others incorporating the constraints indicated) results in the loss of the convenience and the power of a linear model analysis.

Application of the logistic model results in probabilities ranging from 0% to 31% that the gray whale population passed through MNPL for the two periods and corresponding sets of census estimates considered (Table 3). Naturally, the confidence with which conclusions can be drawn from such estimates depends on the reliability of the bootstrap methods used to provide distributions for $y^*$. Originally it had been our intention to test the procedures of equations (5) and (6) for possible bias, using simulation methods. However, the results in Table 3 are so far removed from 95% confidence that MNPL falls within the census

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[2] Our assessment of unreliability concerns their methodology when applied to this particular case; it will not necessarily hold in general.

period considered, that the bias in the bootstrap estimators of variance of $y^*$ would have to be enormous to reverse these results. This seems such an unlikely possibility that the considerable amount of computer time needed for simulation testing of these estimators for this particular dataset was not felt to be justified.

The poor discriminatory power of dynamic response analysis for the gray whale population which is indicated by the logistic model analysis above is not altogether surprising when the simulation results of Gerrodette (1988) are considered. For example, fig. 3 of Gerrodette (1988) shows the discriminatory power of fitting a quadratic to ten successive population estimates (each with $CV = 0.05$) generated from an underlying logistic model. Results are shown for different values (ranging from 0.10-0.20) of the intrinsic growth rate parameter $r$ of the logistic model. The sign of the second order coefficient of the quadratic is used to assess whether the population is above or below MNPL. This figure shows that the discriminatory power decreases as the value of $r$ drops, and for $r = 0.10$ the procedure is effectively powerless (almost equally likely to give the incorrect as the correct result) for population sizes greater than 0.4K. In comparison, for Reilly *et al.*'s (1983) gray whale data, the effective $r \approx 0.05$ and the census estimates have $CVs \simeq 0.11$, indicating a decrease in discriminatory power on both counts compared to that shown in Gerrodette's example. Admittedly, three more population estimates are available than the ten which Gerrodette considers in the figure referenced, but these can scarcely compensate for the other negative influences on discriminatory power.

The authors consider the weighted fitting procedure should be preferred to the unweighted one for the applications to Reilly *et al.*'s (1983) census estimates for 1967-68 to 1979-80. This is because the SEs of the individual census estimates (Table 1a) have very similar magnitudes to those of the residuals in the model fits to the data (note the comparison for a straight line fit discussed earlier in the paper). This suggests that 'observation errors' (in the population-model-fitting sense of this term) totally dominate any errors associated with model mis-specification, so that inverse variance weighting would seem to be the statistically preferable procedure for these data. Accordingly the weighted results were chosen for presentation in Figs 1-2.

For consistency, the weighted result is also the one plotted in Fig. 3, which shows the fit to Buckland and Breiwick's (2002) estimates for 1967-68 to 1987-88. Comparison of the error bars in Figs 2 and 3 indicates that the SE estimates in Buckland and Breiwick's case are certainly not capturing all the variability about the underlying trend (i.e. in terms of the symbols used in Appendix 1 $\tilde{\sigma}^2 < \sigma^2$). In these circumstances, the weighted procedure will give negatively biased estimates of variance, so that the unweighted results would seem to be the more reliable for these data.

All the results give point estimates of $y^*$ and probability levels which indicate a greater likelihood that the gray whale population is currently below rather than above its MNPL (see Table 3). This is more so when the latest three censuses and Buckland and Breiwick's reanalysis are taken into account, although for the reasons explained in the previous paragraph, it is considered that the weighted fit results indicate greater precision than is really the case for the data of Table 1b. The overall impression is therefore that the reliability with which population trajectory curvature can be estimated from the data available, allows a conclusion stated no more strongly than that there is a somewhat greater likelihood that the gray whale population was below rather than above its MNPL (MSYL) in 1990, given the data available at that time.

## CONCLUSIONS

Conclusions from the cubic model analysis of this paper, and from the analysis by Gerrodette and DeMaster (1990), that the gray whale population passed through MNPL ($\simeq$ MSYL) between 1967 and 1980 are unreliable. This is because the curves fitted by both analyses correspond to markedly decreasing population sizes over parts of the periods to which they apply; this is inconsistent with plausible population dynamics behaviour, which underlies the rationale for dynamic response analysis. Care should be taken to implement dynamic response analysis in a manner that respects such plausibility constraints.

The census data available up to 1987-88 are scarcely adequate to allow for reliable estimates of population trajectory curvature to be made. Fits using the logistic model indicate a somewhat greater likelihood that the gray whale population was below rather than above its MNPL in 1990.

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## Appendix 1

## A BASIS FOR THE PARAMETRIC BOOTSTRAP APPROACH OF EQUATION (6)

At first sight, it might appear that the approach of equation (6) would provide positively biased estimates of variance, because it would seem that bootstrap noise is being added to, rather than replacing the real noise about the underlying trend.

To show that this is not the case, the equivalence of the approaches of equations (5) and (6) is demonstrated for the simple case of estimating the standard error of the mean from a sample drawn from a normal distribution, i.e.:

Data: $\{y_i : i = 1,...,n\}$ where $y_i$ from $N(\mu,\sigma^2)$

Estimator: $\hat{\mu} = y = \{\sum_{i=1}^{n} y_i\} / n$ (A.1)

The requisite variance is known for this case:

$$\text{var}(\mu) = \sigma^2/n \qquad \text{(A.2)}$$

and would be estimated by:

$$\hat{\text{var}}(\mu) = \hat{\sigma}^2/n \qquad \text{(A.3)}$$

**The parametric bootstrap approach of equation (5)**

A large number ($S_{\max}$) of datasets $\{y_i^S: i=1,...,n\}$ is generated, where:

$$y_i^S = \hat{\mu} + \in_i^S$$
$$\in_i^S \text{ is from } N(0,\hat{\sigma}^2)$$
$$S = 1,....,S_{\max}$$

The estimate from the $S$th bootstrap dataset is:

$$\begin{aligned} \mu^S &= \{\sum_{i=1}^{n} y_i^S\} / n \\ &= \{\sum_{i=1}^{n} (\hat{\mu} + \in_i^S)\} / n \qquad \text{(A.4)} \\ &= \hat{\mu} + \{\sum_{i=1}^{n} \in_i^S\} / n \end{aligned}$$

and the average of these estimates is:

$$\begin{aligned} \bar{\mu} &= \{\sum_{S=1}^{S_{\max}} \mu^S\} / S_{\max} \\ &= \hat{\mu} + \{\sum_{i=1}^{n} \sum_{S=1}^{S_{\max}} \in_i^S\} / \{n\, S_{\max}\} \qquad \text{(A.5)} \\ &\to \mu \text{ for } S_{\max} \text{ large} \end{aligned}$$

Thus, for large $S_{\max}$, the bootstrap method of equation (5) provides an estimate:

$$\begin{aligned} \hat{var}_{eq(5)}(\mu) &= \{\sum_{S=1}^{S_{\max}} (\mu^S - \bar{\mu})^2\} / \{S_{\max} - 1\} \\ &\approx \{\sum_{S=1}^{S_{\max}} (\mu^S - \bar{\mu})^2\} / S_{\max} \qquad \text{(A.6)} \\ &= \{\sum_{S=1}^{S_{\max}} [\sum_{i=1}^{n} \in_i^S]^2 / n^2\} / S_{\max} \\ &= \hat{\sigma}^2 / n \text{ as cov}(\in_i^S, \in_j^S) = 0 \text{ unless } i = j \end{aligned}$$

which is the required result (see equation A.3).

**The parametric bootstrap approach of equation (6)**

In this instance, the datasets generated are $\{y_i^S : i=1,...,n\}$ where:

$$\tilde{y}_i^S = y_i + \eta_i^S$$
$$\eta_i^S \text{ is from } N(0,\tilde{\sigma}^2)$$
$$S = 1,....,S_{\max}$$

The estimate from the $S$th bootstrap dataset is:

$$\begin{aligned} \tilde{\mu}^S &= \{\sum_{i=1}^{n} \tilde{y}_i^S\} / n \\ &= \{\sum_{i=1}^{n} (y_i + \eta_i^S)\} / n \quad [\text{write } y_i = \bar{y} + (y_i - \bar{y})] \\ &= [\sum_{i=1}^{n} \bar{y} + \sum_{i=1}^{n} (y_i - \bar{y}) + \sum_{i=1}^{n} \eta_i^S] / n \qquad \text{(A.7)} \\ &= \bar{y} + 0 + \{\sum_{i=1}^{n} \eta_i^S\} / n \\ &= \hat{\mu} + \{\sum_{i=1}^{n} \eta_i^S\} / n \end{aligned}$$

Equation (A.7) has exactly the same form as equation (A.4), because the contributions from the real noise:

$$[\sum_{i=1}^{n} (y_i - \bar{y})]$$

cancel, so that under the same arguments as used above:

$$\hat{\text{var}}_{eq(6)}(\mu) \simeq \tilde{\sigma}^2/n \qquad \text{(A.8)}$$

Thus, if $\tilde{\sigma}^2$ (corresponding to the variance estimate associated with each data point) is equivalent to $\sigma^2$ (measuring the variance about the underlying trend - a constant in this illustration), the bootstrap approaches of equations (5) and (6) are identical for this case. A similar exercise demonstrates that they are also identical for the case of linear regression.

# A Bayesian stock assessment of the eastern Pacific gray whale using abundance and harvest data from 1967-1996[1]

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ABSTRACT

Abundance and harvest data since 1966/67 were used to assess the eastern Pacific stock of gray whales. A Bayesian statistical method was used to estimate probability distributions for the parameters of both a simple and an age and sex structured population dynamics model, as well as output quantities of interest. Model comparisons using the Bayes Factor provided conclusive evidence that an additional parameter should be used to account for unexplained variation in the abundance time series. Incorporating the additional variance parameter decreased the precision of the estimates of the other parameters. Point estimates of carrying capacity ranged from 24,640-31,840 for the different models, but the posterior distributions from the selected models were very broad and excluded few values. The current depletion level (population size as a fraction of carrying capacity) was estimated to be about 0.75, with a lower 2.5th percentile of 0.36. The probability that the population was still below one-half of its carrying capacity was estimated to be 0.21, with a corresponding probability of 0.28 that the population was still below its maximum sustainable yield level. Quantities from which catch limits could potentially be calculated were estimated, including current replacement yield, maximum sustainable yield and the quantity $Q_1$ (described in Wade and Givens, 1997).

KEYWORDS: GRAY WHALE; PACIFIC OCEAN; MODELLING

## INTRODUCTION

The eastern Pacific stock of gray whales (*Eschrichtius robustus*) was harvested commercially from the mid-1800s to recent times and has been harvested by aboriginals since at least the 1600s. Although the commercial harvest no longer occurs, an aboriginal harvest still exists (e.g. IWC, 1998, p.243). The gray whale is one of the best studied populations of whales. The population was surveyed on its southbound migration in 16 out of 21 years from 1966/67 to 1987/88. Three additional surveys were carried out in 1992/93 and 1993/94 (Laake *et al.*, 1994) and in 1995/96 (Hobbs *et al.*, 1996), making possible a reassessment of the stock. This paper reports the results from fitting two density-dependent models to the data. The status of the stock relative to its equilibrium population size was estimated, along with quantities of interest for setting catch limits for the harvest.

Two different population dynamics models were used: (1) generalised-logistic; and (2) density-dependent Leslie matrix. Model 1 is a simple model while model 2 is both age- and sex-structured. Bayesian statistical methods (e.g. Press, 1989) were used to estimate the model parameters by fitting the models to the abundance data. The models were compared using Bayes factors (Kass and Raftery, 1995) to evaluate which model best fitted the data.

Attempts to fit models to the available time series of gray whale abundance estimates have indicated that there is a lack of fit of the data to the model not accounted for by the estimated variance of the abundance estimates. This is readily apparent when the abundance estimates are examined, as several adjacent estimates have non-overlapping 95% confidence limits, indicating significant differences from one year to the next (Reilly, 1992). For example, the significant increase of greater than 30% from the 1992/93 estimate to the 1993/94 estimate (Table 1) is biologically implausible for gray whales and suggests that the estimated CVs do not account for all of the variance associated with the estimates of the number of southbound migrating gray whales in each year. It is unknown whether this additional variance is due to variance in components of the estimation technique that are not accounted for, or to variance in the proportion of the population that migrates past the California monitoring site. Therefore, a method was developed to account for this unexplained variance by estimating a new parameter that represents additional variance in the abundance estimates. Adding the additional variance term to each of the two models resulted in a total of four models being considered.

Table 1

Abundance estimates used in the analysis, taken from Buckland and Breiwick (2002) for 1967/68 to 1987/88, from Laake *et al.* (1994) for 1992/93 and 1993/94 and from Hobbs *et al.* (1996) for 1995/96. Standard errors (SE) and coefficients of variation (CV) are also shown.

| Year | Abundance | SE | CV |
|---|---|---|---|
| 1967/68 | 13,012 | 893 | 0.069 |
| 1968/69 | 12,244 | 484 | 0.040 |
| 1969/70 | 12,777 | 525 | 0.041 |
| 1970/71 | 11,170 | 806 | 0.072 |
| 1971/72 | 9,841 | 442 | 0.045 |
| 1972/73 | 16,962 | 660 | 0.039 |
| 1973/74 | 14,817 | 592 | 0.040 |
| 1974/75 | 13,134 | 540 | 0.041 |
| 1975/76 | 14,811 | 690 | 0.047 |
| 1976/77 | 15,950 | 524 | 0.033 |
| 1977/78 | 17,127 | 966 | 0.056 |
| 1978/79 | 13,300 | 501 | 0.038 |
| 1979/80 | 16,581 | 668 | 0.040 |
| 1984/85 | 21,942 | 994 | 0.045 |
| 1985/86 | 20,450 | 727 | 0.036 |
| 1987/88 | 21,113 | 688 | 0.033 |
| 1992/93 | 17,674 | 1,029 | 0.058 |
| 1993/94 | 23,109 | 1,262 | 0.055 |
| 1995/96 | 22,571 | 1,174 | 0.052 |

An unresolved issue regarding the eastern Pacific gray whale is that it has not been possible to reconcile the catch history from the 1800s with the recent time series of abundance data in a simple way. Several attempts have been made to project population models forwards from the 1800s

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[1] This paper was originally submitted as SC/48/AS8 to the 1996 meeting of the IWC Scientific Committee.

assuming the population was at carrying capacity prior to the start of commercial harvests in 1846, but such projections cannot produce a trend that agrees with the recent abundance estimates, which indicate the population roughly doubled between 1967 and 1988 (Reilly, 1981; Lankester and Beddington, 1986; Butterworth *et al.*, 2002). The catch history and current trend can only be reconciled through fairly dramatic assumptions, such as an increase in the carrying capacity from 1846-1988 of at least 2.5 times, an underestimation of the historic commercial catch from 1846-1900 of at least 60%, or annual aboriginal catch levels prior to 1846 of at least three times the level previously thought (Butterworth *et al.*, 2002). Although all of these scenarios are plausible, there is little concrete evidence for any of them. Any stock assessment based on projections from a pre-1900 carrying capacity would involve making an untestable assumption such as that the commercial harvest was twice the level previously thought.

A stock assessment based on data collected since 1967, while ignoring some important information regarding the catch history, will not be subject to these potential problems. Therefore, the status of the eastern Pacific stock of gray whales has been assessed here using only the harvest data collected since 1967. The analysis starts projecting the population in 1967 and does not make any assumptions about what level the population was at relative to carrying capacity at that time.

## METHODS

### Available data

Abundance surveys for the eastern Pacific stock of gray whales take place from December to February, so they are referred to by two years (e.g. a survey from December 1995 to February 1996 is called the 1995/96 survey). Abundance estimates (Table 1) for 1967/68 to 1987/88 were from Buckland and Breiwick (2002). These were the same estimates as used in Butterworth *et al.* (2002). Preliminary estimates for 1992/93 and 1993/94 were from Laake *et al.* (1994), while that for 1995/96 is from Hobbs *et al.* (1996). The catch history prior to 1993 was obtained directly from the IWC (Table 2), while that for 1994 was obtained from Blokhin (1995).

### Population dynamics models

Two different models were used:

*Generalised-Logistic*

$$N_{t+1} = N_t \left[ 1 + r_{max} \left( \frac{N_t}{N_{eq}} \right)^z \right] - H_t \qquad (1)$$

where:

| | |
|---|---|
| $N_t$ | the population size in year *t;* |
| $r_{max}$ | the maximum net recruitment rate; |
| $N_{eq}$ | the equilibrium population size (or 'carrying capacity'); |
| $z$ | the density-dependent exponent which sets the maximum sustainable yield level (the relative population size at which the maximum sustainable yield is obtained); and |
| $H_t$ | the number of animals harvested in year *t*. |

Table 2

Harvest data used in analysis, obtained directly from the IWC. The proportion of females was assumed to be 67% in 1991. The observed proportion of females in 1994 was 0.666 (Blokhin, 1995). The 1995 catch data* (Borodin, 1996) were not yet available at the time of the analysis, and thus have not been subtracted in projecting the population to 1996.

| Year | Male | Female | Total |
|---|---|---|---|
| 1966 | 123 | 97 | 220 |
| 1967 | 94 | 156 | 250 |
| 1968 | 67 | 134 | 201 |
| 1969 | 59 | 155 | 214 |
| 1970 | 26 | 125 | 151 |
| 1971 | 51 | 102 | 153 |
| 1972 | 22 | 160 | 182 |
| 1973 | 97 | 81 | 178 |
| 1974 | 94 | 90 | 184 |
| 1975 | 58 | 113 | 171 |
| 1976 | 69 | 96 | 165 |
| 1977 | 86 | 101 | 187 |
| 1978 | 94 | 90 | 184 |
| 1979 | 57 | 126 | 183 |
| 1980 | 53 | 128 | 181 |
| 1981 | 36 | 100 | 136 |
| 1982 | 56 | 112 | 168 |
| 1983 | 46 | 125 | 171 |
| 1984 | 59 | 110 | 169 |
| 1985 | 55 | 115 | 170 |
| 1986 | 46 | 125 | 171 |
| 1987 | 47 | 112 | 159 |
| 1988 | 43 | 108 | 151 |
| 1989 | 61 | 119 | 180 |
| 1990 | 67 | 96 | 163 |
| 1991 | 57 | 113 | 170 |
| 1992 | 0 | 0 | 0 |
| 1993 | 0 | 0 | 0 |
| 1994 | 15 | 29 | 44 |
| 1995 | 44* | 41* | 85* |

*Density-Dependent Leslie Matrix*

The population was projected as:

$$n_{t+1} = A_t n_t - h_t \qquad (2)$$

where:

| | |
|---|---|
| $n_t$ | vector of population size of each age class at time *t;* |
| $A_t$ | the Leslie matrix in year *t;* |
| $h_t$ | vector of age-specific harvests at time *t*. |

A simplified Leslie matrix (Leslie, 1945; 1948) was used with a total of four variable parameters. Three were elements of the matrix: (1) $s_j$, the survival rate of unrecruited age classes ('juvenile' survival rate); (2) $s$, the survival rate of recruited age classes ('adult survival rate'); (3) $f_t$, the fecundity rate at time *t* (assumed identical for all mature age classes); and (4) *ASM*, the age of sexual maturity (with the first non-zero fecundity in the subsequent age class). The maximum age was fixed at 60 years.

This model was identical to a usual Leslie matrix model, except that the fecundity term was density-dependent with a form similar to the generalised-logistic:

$$f_t = f_0 + (f_{max} - f_0) \left[ 1 - \left( \frac{N_t}{N_{eq}} \right)^z \right] \qquad (3)$$

where:

| | |
|---|---|
| $f_t$ | the realised fecundity in year *t;* |
| $f_{max}$ | the maximum fecundity rate; and |
| $f_0$ | fecundity at a net recruitment of zero, which can be solved directly from the other parameters. |

This model is thus identical to the model in Breiwick *et al.* (1984). The population growth rate ($\lambda$) associated with a Leslie matrix using a fecundity value of $f_t$ was referred to as $\lambda_t$ and the population growth rate associated with $f_t = f_{max}$ was referred to as $\lambda_{max}$. Estimates of $\lambda_{max}$ were expressed as $\lambda_{max}$-1 so they would be comparable to the parameter $r_{max}$ of the generalised-logistic model.

The harvest kills were subtracted after reproduction because in recent decades they have occurred in the summer, after the calving season in the winter. In each year, the kills were distributed to each recruited age-class according to the age distribution in that year. Recruitment was assumed to be knife-edge and to occur at age five. Each trajectory was initiated with the stable age distribution associated with that population size. In other words, the starting population size for a trajectory was used in equation (3) to find the value of $f_t$ associated with that population size and the particular values for $f_{max}$, $N_{eq}$ and $z$ used on that trajectory. Then the stable age distribution was found for the Leslie matrix composed of $s$, $s_j$, *ASM* and that value of $f_t$.

As the sex-ratio of the kill was not equal, two vectors of population size were projected, one for each sex. The same survival rates were used in the Leslie matrix to project each vector, but, obviously, the fecundity terms were set to zero when projecting the male population vector. The sex-ratio of calves was assumed to be 50:50; therefore the number of males in age-class 1 was set to be equal to the number of age-class 1 females at each time step. The population was assumed to have a 50:50 sex ratio at the beginning of 1968.

### Additional variance term

Two additional models were specified by adding a parameter, $CV_{add}$, to models 1 and 2 that represented additional variance in the abundance estimates. This was similar to the method employed by Butterworth *et al.* (1993). Here, the additional variance is thought of as the unexplained variance between annual estimates of abundance not accounted for by the estimated variance of those abundance estimates; note that the mechanism that causes the process error is unknown and is not explicitly modelled here. $CV_{add}$ was parameterised as a coefficient of variation and was considered constant across years. This implies that in any year there was the same possibility of additional variance not accounted for by the estimated variance of the abundance estimates. $CV_{add}$ was incorporated into the likelihood function in each year as an additive variance term to the abundance estimates, with the assumption that this additional variance has a Gaussian distribution. In other words, in any year, a new total CV was calculated as the square root of the sum of the squares of CV($t$) and $CV_{add}$

$$CV_{tot}(t) = \sqrt{CV^2(t) + CV_{add}^2} \tag{4}$$

where CV($t$) = $S(t)/N(t)$. The likelihood component from that year's abundance estimate was calculated as usual with the new total CV term (i.e. $S(t) = N(t)CV_{tot}(t)$).

### Statistical methods

A Bayesian statistical method (e.g. Press, 1989) was used to estimate the parameters of the models and other output quantities. The same techniques were used to investigate the population dynamics of eastern tropical Pacific dolphins (Wade, 1994) and spectacled eiders (Taylor *et al.*, 1996). The method is somewhat similar in approach to Bayesian synthesis analyses of bowhead whales, *Balaena mysticetus* (Givens *et al.*, 1993; 1995; Raftery *et al.*, 1995).

Any Bayesian analysis involves integrating the product of a prior distribution for a parameter and a likelihood function that links the probability of the observed data to the specification of particular values for the parameter. The likelihood function for the parameters in a population model, given a time-series of abundance estimates, was calculated according to the methods reported in de la Mare (1986). In any single year, the likelihood of an observed abundance estimate $N(t)$ given a specified model population size $N_t$ is straight forward; it is the likelihood function defined by the assumed sampling distribution of the abundance estimate. The sampling distribution of the abundance estimates is assumed to be a Gaussian distribution with estimated mean $N(t)$ and standard error $S(t)$ and thus the likelihood is:

$$L\left(N_t \middle| N(t), S(t)\right) = \frac{1}{\sqrt{2\Pi S(t)}} e^{-\frac{1}{2}\left(\frac{N(t)-N_t}{S(t)}\right)^2} \tag{5}$$

Although $N_t$ is not an explicit parameter of the model, the model parameters uniquely determine a population trajectory $N_{68/69}, N_{69/70}, \ldots N_{95/96}$. Therefore, the total likelihood given the data is the product series of all the individual likelihoods of the $N_t$s (the model trajectory) given the $N(t)$s (the time-series of abundance estimates).

$$L\left(\theta \middle| \bar{N}(t), \bar{S}(t)\right) = \prod_{t=68/69}^{95/96} \left[ L\left(N_t \middle| N(t), S(t)\right) \right] \tag{6}$$

Note that the 1967/68 abundance estimate is not used in the likelihood calculation because it is used as a prior distribution for the population size in the beginning of 1968 (see below).

The necessary integration was approximated by using the Sampling-Importance-Resampling routine of Rubin (1988), which Smith and Gelfand (1992) advocate as a particularly useful and simple integration technique for Bayesian statistics. In this method, values for the parameters are randomly selected from their joint prior distribution to form a sample set of parameter values, called $\theta_i$. The likelihood of the data given this particular $\theta_i$ is calculated and stored. This is repeated, generating an initial sample of $n_1$ $\theta_i$s with associated likelihoods. This initial sample of $n_1$ $\theta_i$s is then re-sampled $n_2$ times with replacement with probability equal to weight $q_i$, where:

$$q_i = \frac{L(\theta_i | x)}{\sum_{j=1}^{n_1} L(\theta_j | x)} \tag{7}$$

This process forms a second sample, called the re-sample. Rubin (1988) showed that the re-sample is a random sample from the joint posterior distribution of size $n_2$. Because the initial sample is sampled with replacement, the re-sample can contain more than one occurrence of the same set of values. When properly implemented, this feature of the method improves its efficiency and makes the re-sample a better approximation of the posterior distribution than would a random sample from the joint prior distribution of similar size. However, if the initial sample is not large enough, the re-sample may be overly influenced by just a few sets of values that occur many times. Such problems can be avoided by inspecting some characteristics of the re-sample, such as the number of unique $\theta_i$s and the maximum number of occurrences of a single $\theta_i$ and increasing the size of the initial sample if necessary. In this study, values for $n_1$ were set to values large enough to avoid those problems and thus yield sufficiently smooth posterior distributions. The actual value used for $n_1$ varied in the different analyses depending upon the number and kind of parameters estimated. The value of $n_2$ was set to 5,000 for each analysis.

The surveys occurred in the beginning of each year and were assumed to apply to the 1+ population, as in previous studies such as Butterworth *et al.* (2002). The likelihood at any time-step $t$ was calculated prior to reproduction and harvest in the model (i.e. the population size at the end of year $t$-1) and therefore the model population size used in equations (1) and (2) was the sum of all males and females in all age classes.

## Prior distributions

$N_{67/68}$ was the initial population size (at the beginning of 1968) in each model. The prior distribution for $N_{67/68}$ was based on the abundance estimate in that year (1967/68) and was thus a Gaussian distribution with mean 13,012 and standard error 893 (Table 1). For the analyses with the additional variance term, the prior distribution for $N_{67/68}$ is dependent on the value of $CV_{add}$ and was thus a Gaussian with mean 13,012 and standard error of $CV_{tot}(67/68)*13,012$. In other words, for any particular set of parameter values drawn from the joint prior, a value for $CV_{add}$ would be chosen first and then that value used to draw a value from the prior for $N_{67/68}$. The resulting prior distribution for $N_{67/68}$ thus represented a combination of normal distributions with the same mean but different variances.

The prior distributions of the population growth parameters in the different models (e.g. $r_{max}$ and $\lambda_{max}$-1) were uniform distributions from 0.01 to 0.13. Preliminary trials of the analyses indicated there was little posterior probability below this range, which was confirmed in the final analyses. There was some posterior probability above

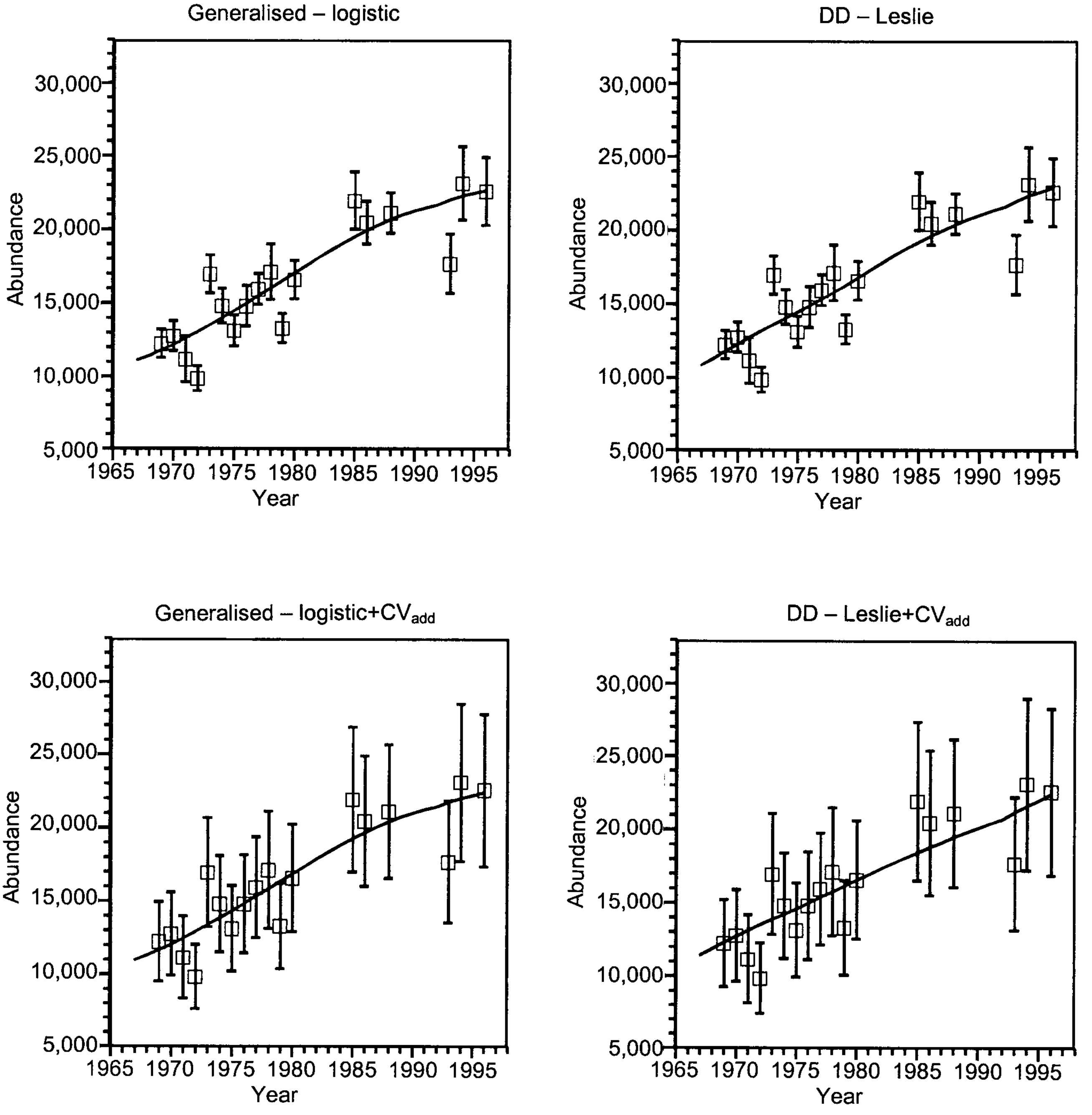

Fig. 1. Population trajectories with the greatest probability for all four model combinations. Also shown are abundance estimates with 95% confidence limits. Note that for the models with the additional variance term $CV_{add}$, the confidence limits have been re-calculated using the estimated total $CV$ for each abundance estimate.

this range for some of the models, but the prior distributions on the life history parameters of the Leslie matrix make a value of 0.13 very unlikely for $\lambda_{max}$-1 and so that value was set as the upper limit.

The ranges for the life-history parameters in the age-structured model were set to be wide enough to encompass what are thought to be reasonable values (IWC, 1993). The prior distribution for $f_{max}$ was a uniform distribution from 0.15 to 0.30 (parameterised as female calves per adult female). Age of sexual maturity (*ASM*), with the first non-zero fecundity in the next year, was a discrete uniform from 5-9 years. The adult survival rate, *s*, was a uniform distribution from 0.95 to 0.999. The only restriction on the juvenile survival rate, $s_j$, was that it be less than *s*. The prior distributions for these parameters did not remain uniform on these ranges. As mentioned above, a uniform distribution was set for $\lambda_{max}$-1. Then, values for $f_{max}$, *ASM* and *s* were drawn from the prior distributions described above. From these values, $s_j$ can be calculated (Breiwick *et al.*, 1984). If $s_j < s$, this set of values was used. If $s_j$ was $> s$, then $f_{max}$, *ASM* and *s* were re-drawn from their uniform distributions but retaining the original value for $\lambda_{max}$-1. This resulted in non-uniform realised prior distributions for these parameters, which were stored and were plotted along with the posterior distributions, but retained the uniform prior distribution for $\lambda_{max}$-1. An explicit prior was not set for $s_j$ because this would have resulted in two different prior distributions being established for $\lambda_{max}$-1 and because little information exists regarding $s_j$.

The prior distribution for $N_{eq}$ was set as uniform from 17,000 to 70,000. The lower bound was found, through preliminary analyses, to have very little probability in any of the posterior distributions. Therefore, the lower bound for the prior distribution is uninformative in the sense that any lower value could have been used instead without influencing the results (although computation time would increase because the value of $n_1$ would need to be increased). The upper bound was set to a value thought to be greater than the greatest possible value, but it was necessarily a somewhat arbitrary value. The historic catch information has been used to estimate historic population size by back-calculating from a recent abundance estimate. Between the start of commercial whaling and 1900, approximately 15,000 whales were estimated to have been harvested. Using this information, Henderson (1972) concluded that the population did not exceed 15,000-20,000 at the start of commercial whaling. However, as discussed above, Reilly (1981) and Butterworth *et al.* (2002) have shown that it is

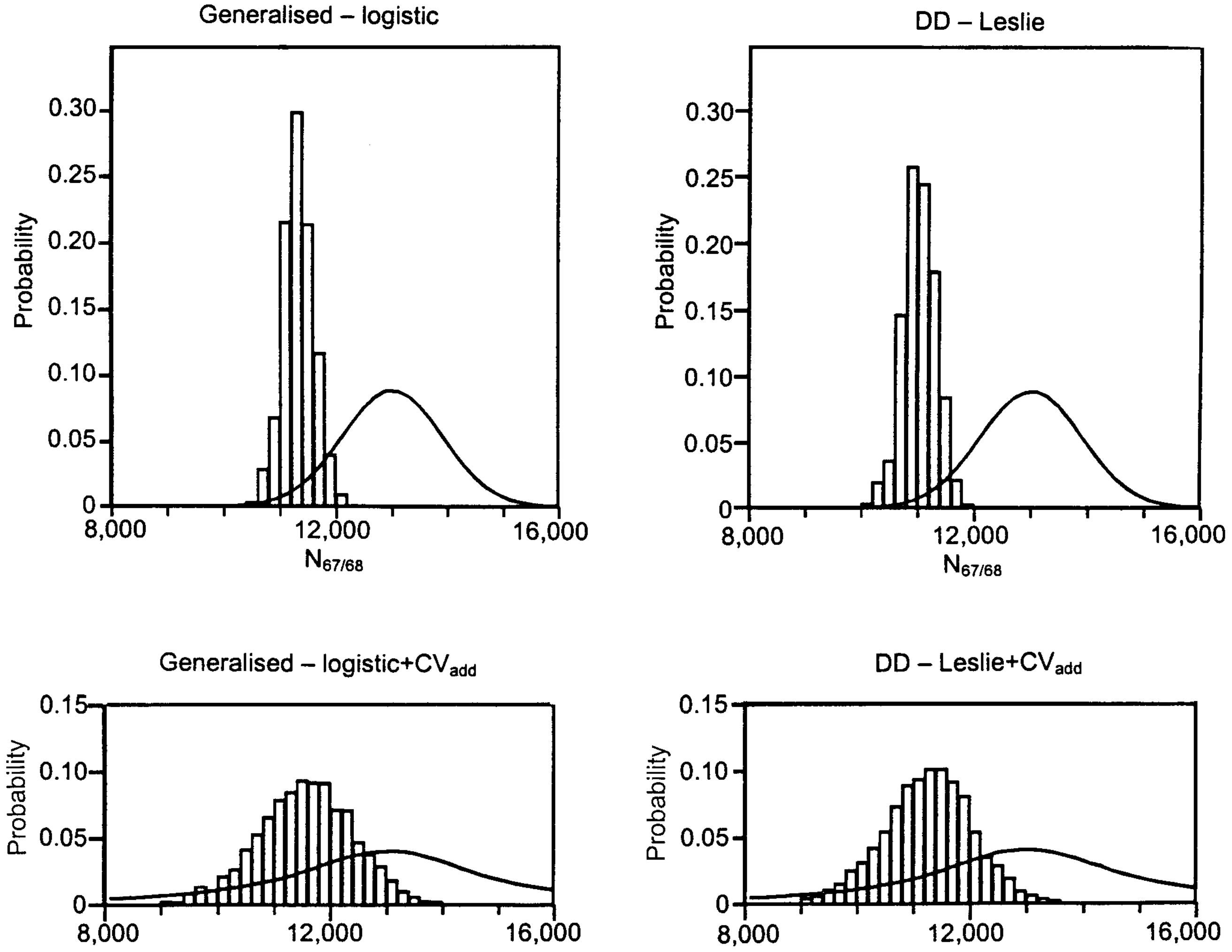

Fig. 2. Posterior probability distributions for the population size in 1967/68 ($N_{95/96}$), as approximated by the posterior sample. The prior distributions are represented as lines. For the models without the additional variance term $CV_{add}$, the prior was based on the abundance estimate from 1967/68 and was a normal distribution with a mean of 13,012 and standard error of 893. For the models with the additional variance term $CV_{add}$, the prior was a combination of normal distributions, all with a mean of 13,012 but with a variable standard error that depended upon the prior value of $CV_{add}$, that was used.

impossible to project back to a historic population size and have a trajectory consistent with the recent abundance trend without making a major untestable assumption, such as that commercial harvests were greater than estimated. Therefore, the previous estimates of historic population size may be questionable. By making certain assumptions, Reilly (1981) was able to construct some sensible population trajectories and concluded that a carrying capacity of 24,000 was in best agreement with the available information in his study. Butterworth *et al.* (2002) investigated a broader range of plausible scenarios to also construct a variety of sensible population trajectories and they found that historic population sizes greater than 30,000 were possible. However, the only simulations in their study which approach a historic population size of 60,000 either assume that commercial harvests were five times greater than estimated, or produce trajectories that do not substantially increase from 1967 to 1988. Therefore, a carrying capacity of greater than 70,000 seems unlikely.

Other lines of evidence are consistent with the idea that gray whales are currently close to their carrying capacity. For example, Stoker (1990) concluded that the recent decline of amphipods in one of the major feeding areas of the gray whale could have been caused by gray whale predation. Reilly (1992) described a recent decline in gray whale pregnancy rates in the aboriginal catch data, although he cautions that sampling bias could have produced this result because of the known differences in pregnancy rates in different areas.

The prior distribution for the maximum sustainable yield level (MSYL) was a uniform from $0.5N_{eq}$ to $0.7N_{eq}$. Values were drawn from this distribution and then transformed into the appropriate value for $z$. This creates a non-uniform prior for $z$, but MSYL was the parameter of interest and so it was most appropriate to set a uniform distribution for it.

The prior distribution for $CV_{add}$ in each model was a uniform distribution from 0.0 to 0.35. In preliminary analyses this range was found to span the region of posterior probability in all of the analyses. Again, this makes the prior for $CV_{add}$ uninformative in the sense that the specific limits of this prior distribution do not affect the results. Any value lower than 0.0 could have been used for the lower bound and any value higher than 0.35 could have been used for the upper bound without influencing the results. The value of 0.0 seems a sensible lower bound, as it represents the case where there is no additional unexplained variance. Choosing an upper bound to be a value less than 0.35 would influence the resulting posterior distribution. However, there was no *a priori* reason for choosing any particular upper bound, so there was no justifiable reason for choosing any particular upper bound lower than 0.35. Choosing an upper bound greater than 0.35 would not have changed the results, but would have increased the computation time.

### Posterior distributions

The re-sampling approach to integrating the solution makes it easy to form posterior distributions for other quantities that are functions of the model parameters. Because the

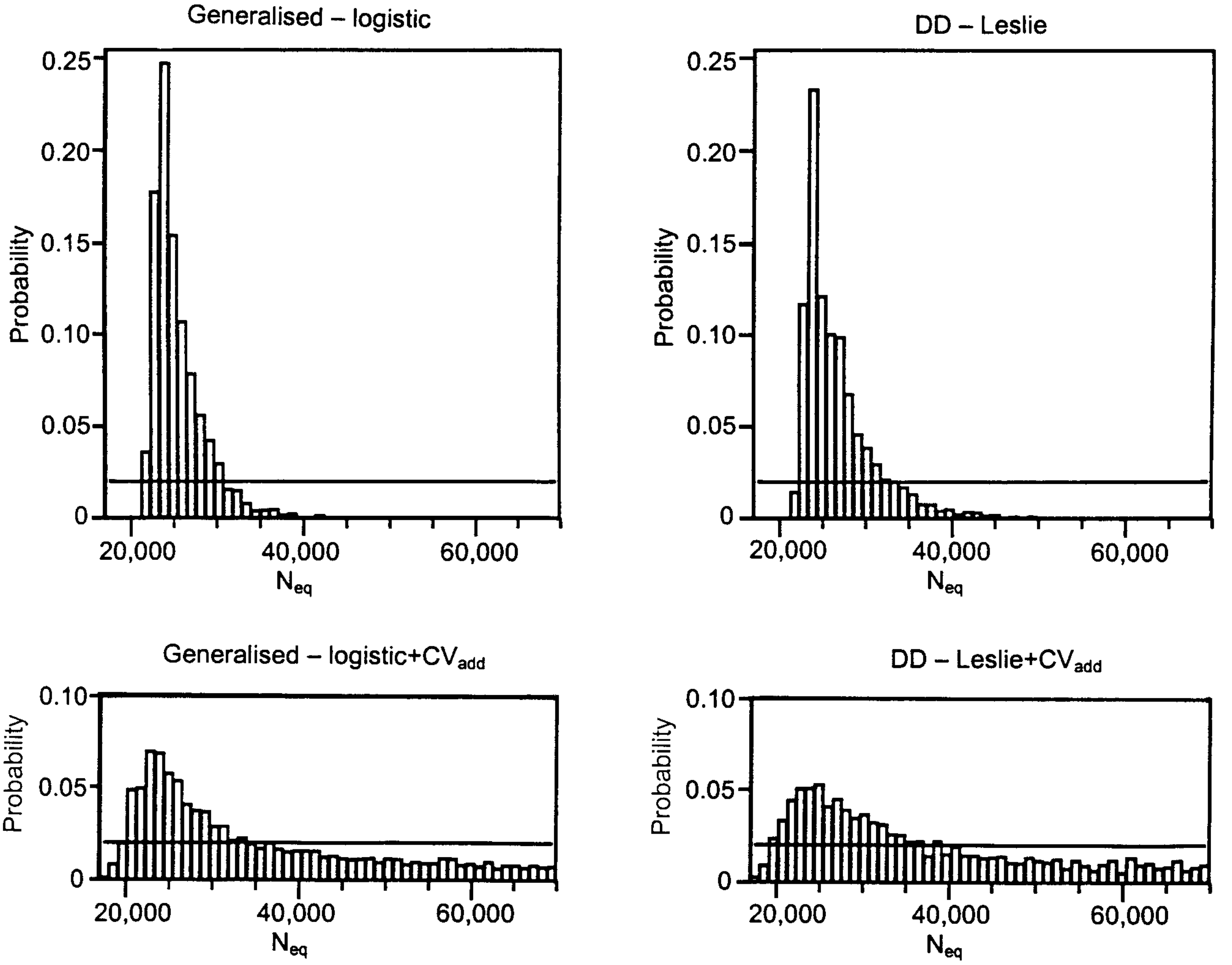

Fig. 3. Posterior probability distributions for equilibrium population size ($N_{eq}$), as approximated by the posterior sample. The prior distributions (uniform(17000,70000)) are represented as lines.

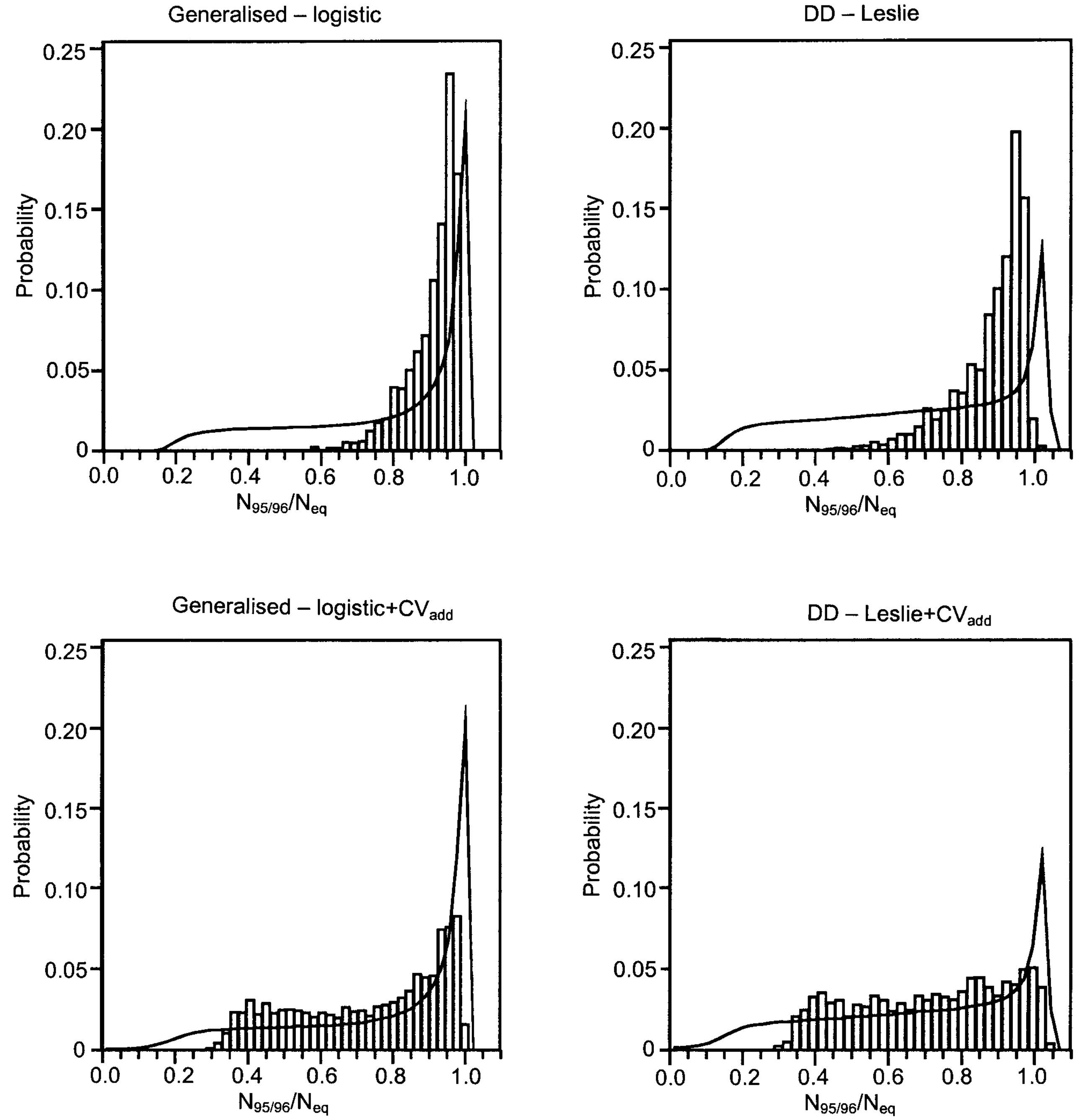

Fig. 4. Posterior probability distributions for the ratio of population size in 1996 ($N_{95/96}$) to the equilibrium population size ($N_{eq}$), as approximated by the posterior sample. The implicit prior distributions are represented as lines.

re-sample of size $n_2$ is a random sample from the joint posterior distribution, it automatically has imbedded in it any covariances between the parameter estimates. A probability distribution for any function of the parameters is easily approximated from that function calculated from the $n_2$ re-samples. Therefore, for example, it was possible to directly assess the population status by forming the posterior probability distribution for the ratio of the current population size to equilibrium population size.

Posterior distributions were calculated for several output quantities of interest that were functions of the other parameters. The maximum sustainable yield rate (MSYR) was calculated as the $\lambda_t$-1 value associated with the MSYL, defined in terms of the 1+ population. The maximum sustainable yield (MSY) was calculated as the product of MSYR, MSYL and $N_{eq}$ (because MSYL was parameterised as a fraction of $N_{eq}$). Current replacement yield (RY) was calculated directly as the model population size in 1996 minus the model population size in 1995. Another catch statistic was calculated, based on the catch control law quantity $Q_1$ described by Wade and Givens (1997) that was designed to meet the intent of aboriginal whaling management objectives. $Q_1$ was calculated as 0.9MSY for populations above the MSYL, as the minimum of 0.9MSY and the product $N_t$*MSYR for populations below the MSYL and as zero for populations below $P_{min}$, the population size below which no aboriginal catches are allowed. $P_{min}$ was assumed to be $0.1*N_{eq}$.

Prior distributions were also calculated for the output quantities of interest. They were simply the distributions of these parameters in the initial sample $n_1$. They represent the implied prior distributions for these parameters that result from the prior distributions specified for the parameters of the population dynamics models.

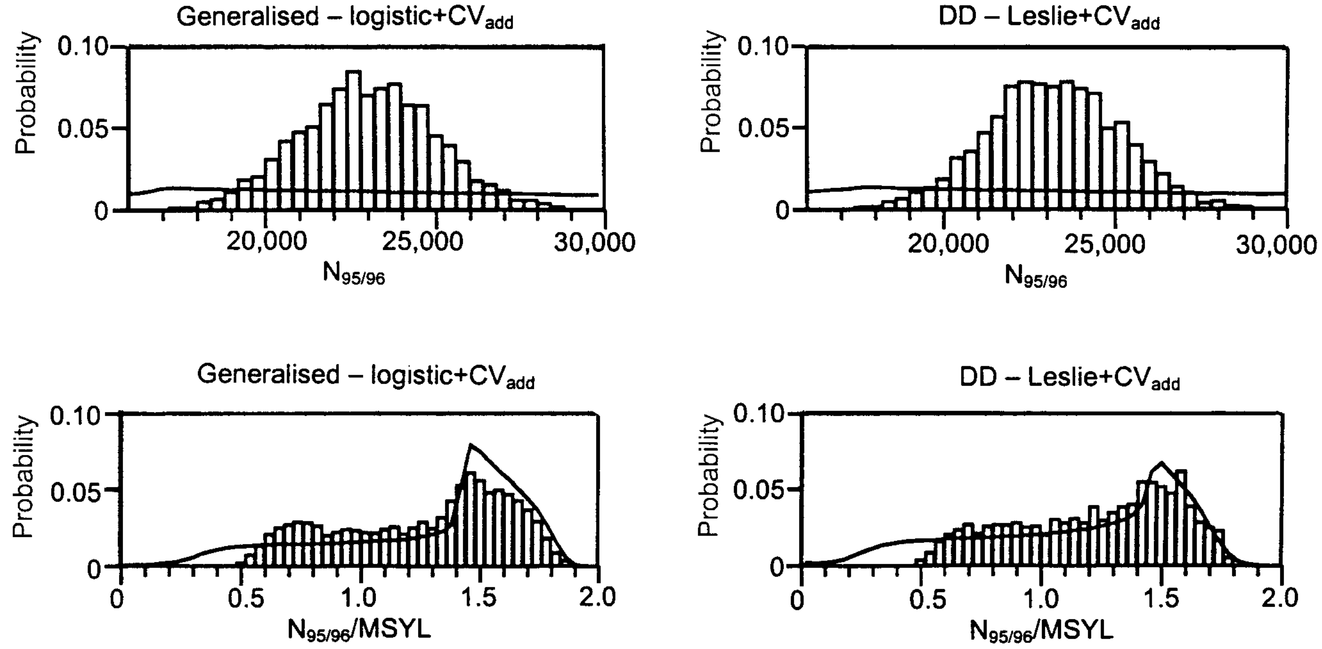

Fig. 5. Upper panel: posterior probability distributions for the population size in 1995/96 ($N_{95/96}$), as approximated by the posterior sample. Note that although there was an abundance estimate in 1995/96, these posterior distributions are different because they are conditioned on the full time series of abundance estimates. Lower panel: posterior probability distributions for the ratio of population size in 1996 ($N_{95/96}$) to the maximum sustainable yield level (MSYL), as approximated by the posterior sample. The implicit prior distributions are represented as lines.

### Model comparison

The models were compared through the use of the Bayes factor (Kass and Raftery, 1995). The Bayes factor is defined as the ratio of the probability of the data given by one hypothesis to the probability of the data given by a second hypothesis:

$$B_{12} = \frac{pr(D|H_1)}{pr(D|H_2)} \tag{8}$$

This has the form of the ratio of two likelihood functions, but the densities in equation (8) are obtained by integrating, not maximising, across the parameter space and so the Bayes factor is not equivalent to a likelihood ratio test unless there are no unknown parameters. In comparing models, the different hypotheses represent different models and so the Bayes factor is the ratio of the probability of the data given one model to the probability of the data given a different model. The Bayes factor is only dependent upon the evidence provided by the data and is thus not influenced by the prior probability of the hypotheses. When the different hypotheses are given equal prior probability, the Bayes factor is equal to the posterior odds, or the posterior probability of $H_1$, $pr(H_1|D)$, divided by 1-$pr(H_1|D)$.

The Bayes factor is found by calculating the probability of the data given a hypothesis, $H$:

$$pr(D|H) = \int pr(D|\theta, H)\, pr(\theta|H)\, d\theta \tag{9}$$

Under a Monte Carlo numerical integration method, such as Sampling-Importance-Resampling, this is estimated as:

$$\hat{pr}(D|H) = \frac{1}{n_1}\sum_{i=1}^{n_1} pr(D|\theta_i^{(H)}) \tag{10}$$

where the $\theta_i^{(H)}$s are the $n_1$ initial samples from the prior distribution. This represents the average likelihood of the sampled parameter values (Kass and Raftery, 1995).

## RESULTS

Initial samples in the numerical integration technique ranged from 250,000 to 4,000,000 (Table 3). A re-sample of 5,000 points was drawn in each case from the initial sample, resulting in from 1,275 to 3,905 unique points in the re-sample. The models which did not include the additional variance term required a relatively greater number of iterations because the posterior distributions from those analyses were narrower and thus a random point from the joint prior distribution was less likely to be a point that had any significant probability in the posterior distribution. The initial sample sizes used for the age structured models were large enough to result in sufficiently well determined posterior distributions. Sample sizes larger than necessary were used for the generalised-logistic models because the computational speed of the simpler model allowed it.

The use of the additional variance term was decisively supported by the Bayes factor comparisons (Table 4). A visual explanation for this can be seen in that only one of the confidence limits re-calculated with $CV_{add}$ lies outside the model trajectory (in 1972), while without the use of $CV_{add}$ from 6 to 7 of the confidence limits on the abundance estimate lie outside the model trajectory (Fig. 1). The comparison between the simple model and the age-and-sex-structured model without $CV_{add}$ resulted in

Table 3

Sample sizes and other information from the integration method, the Sampling-Importance-Re-sampling routine. '$n_1$' is the size of the initial sample, '$n_2$' is the size of the re-sample, 'Unique' is the number of unique values in the re-sample and 'Max' is the maximum number of occurrences of a unique value in the re-sample.

| | $n_1$ | $n_2$ | Unique | Max |
|---|---|---|---|---|
| Generalised-logistic | 4,000,000 | 5,000 | 1,810 | 47 |
| Generalised-logistic+$CV_{add}$ | 1,000,000 | 5,000 | 3,905 | 6 |
| Density-dependent Leslie | 2,000,000 | 5,000 | 1,275 | 172 |
| Density-dependent Leslie+CV | 500,000 | 5,000 | 3,386 | 8 |

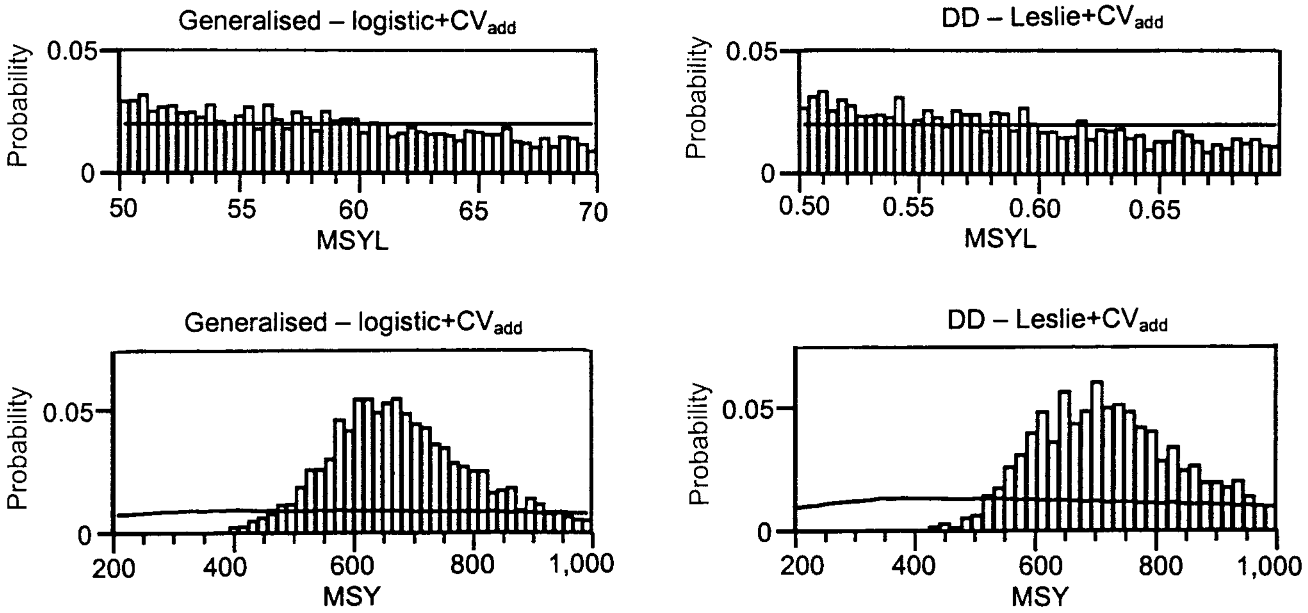

Fig. 6. Upper panel: posterior probability distributions for MSYL, the maximum sustainable yield level, as approximated by the posterior sample. The prior distributions (uniform(0.50,0.70)) are represented by lines. Lower panel: posterior probability distributions for MSY, the maximum sustainable yield, as approximated by the posterior sample. The implicit prior distributions are represented as lines.

Table 4

Calculated Bayes factors for pair-wise model comparisons. Evidence categories are modifications of the original categories of Jeffreys (1961), as presented in Kass and Raftery (1995): >150 is decisive evidence, 12-150 is strong evidence, 3-12 is positive evidence and 1-3 is evidence not worth more than a bare mention.

| | | |
|---|---|---|
| Generalised-logistic with $CV_{add}$ *vs* w/out | $0.504\times10^{23}$ | Decisive |
| DD-Leslie with $CV_{add}$ *vs* w/out | $0.186\times10^{24}$ | Decisive |
| DD-Leslie *vs* Generalised-logistic | 3.72 | Positive |
| DD-Leslie with $CV_{add}$ *vs* Generalised-logistic with $CV_{add}$ | 1.01 | Not worth more than a bare mention |

marginal evidence in favour of the simple model (Table 4). However, when $CV_{add}$ was used, there was no difference between the fit of the simple and age-structured models, as the Bayes factor was close to 1.0.

One of the effects of the additional variance term can be seen in the prior distribution for $N_{67/68}$, which was much broader and flatter with $CV_{add}$ than without (Fig. 2). The posterior distribution was broader also, which gave an indication of how much less certain the trajectory of the population was when $CV_{add}$ was used.

Both analyses without $CV_{add}$ estimate $N_{eq}$ to be within the range 22,000-39,000 and it can be seen that the posterior distribution falls off to zero probability quickly outside this range (Fig. 3). However, the analyses with $CV_{add}$ provide a lower bound for $N_{eq}$ but not an upper bound. The posterior distributions still have some posterior probability even at the highest value specified in the prior, 70,000. In spite of this large difference in the width of the posterior distributions, the values of $N_{eq}$ with the highest probability (the modes of the distributions) are all fairly similar, in the neighbourhood of 23,000 (Fig. 3). Even the point estimates do not differ too greatly, as the posterior medians of approximately 25,000 increase to about 30,000-32,000 (Table 5).

The point estimates of current depletion level ($N_{95/96}/N_{eq}$) were all greater than 70% of equilibrium population size, indicating the population is close to its equilibrium level (Table 5b). However, the lower tail of the posterior distribution extends as low as 30% of $N_{eq}$ when $CV_{add}$ was used in the model (Fig. 4), so there is still some probability that the population is not yet above 50% of $N_{eq}$ (e.g. 0.21 for the density-dependent Leslie matrix model). The specified models do not allow for the model populations to 'overshoot' the equilibrium value by very much given the specified parameter values, which explains the peak at a value of 1.0.

The 2.5th percentiles for the posterior distributions for $N_{95/96}$ ranged from about 19,000-27,000 with $CV_{add}$ (Table 5b, Fig. 5). This range was narrower than the re-calculated confidence limits (approximately 17,000-29,000) on the abundance estimate for 1995/96 (Fig. 1), meaning that conditioning on the entire time-series improved the estimate of current abundance, but not by a large amount.

Without $CV_{add}$ there was a probability of 1.0 that the population was above MSYL, but under the models using $CV_{add}$ there was substantial probability that the population was still below MSYL (Fig. 5). For example, the probability that the population was still below its maximum sustainable yield level was estimated to be 0.28 for the density-dependent Leslie matrix model. As in the previous plot, there was a peak in each distribution around the values representing the ratio of population sizes close to $N_{eq}$ to MSYL.

The posterior distribution for MSYL was nearly identical to the prior distribution (Fig. 6). The posterior distributions for the quantities MSY (Fig. 6) and $Q_1$ (Fig. 7) were similar and fairly normally distributed, with point estimates ranging from 592-728 (Table 5c). In each case, the distributions were much broader and dispersed for the models with $CV_{add}$. The 2.5th percentiles of the posterior distributions were 407-564 for $Q_1$ and 468-627 for MSY (Table 5).

The widest posterior distributions for RY range from about 50 to about 1,000 animals (Fig. 7). The low numbers were a result of trajectories that closely approach equilibrium, as the population growth rate approaches zero at this level and thus RY approaches zero. The high numbers represent trajectories far from equilibrium that thus have growth rates on the order of 3-4% applied to a current population size (e.g. 0.35*23,000 = 805).

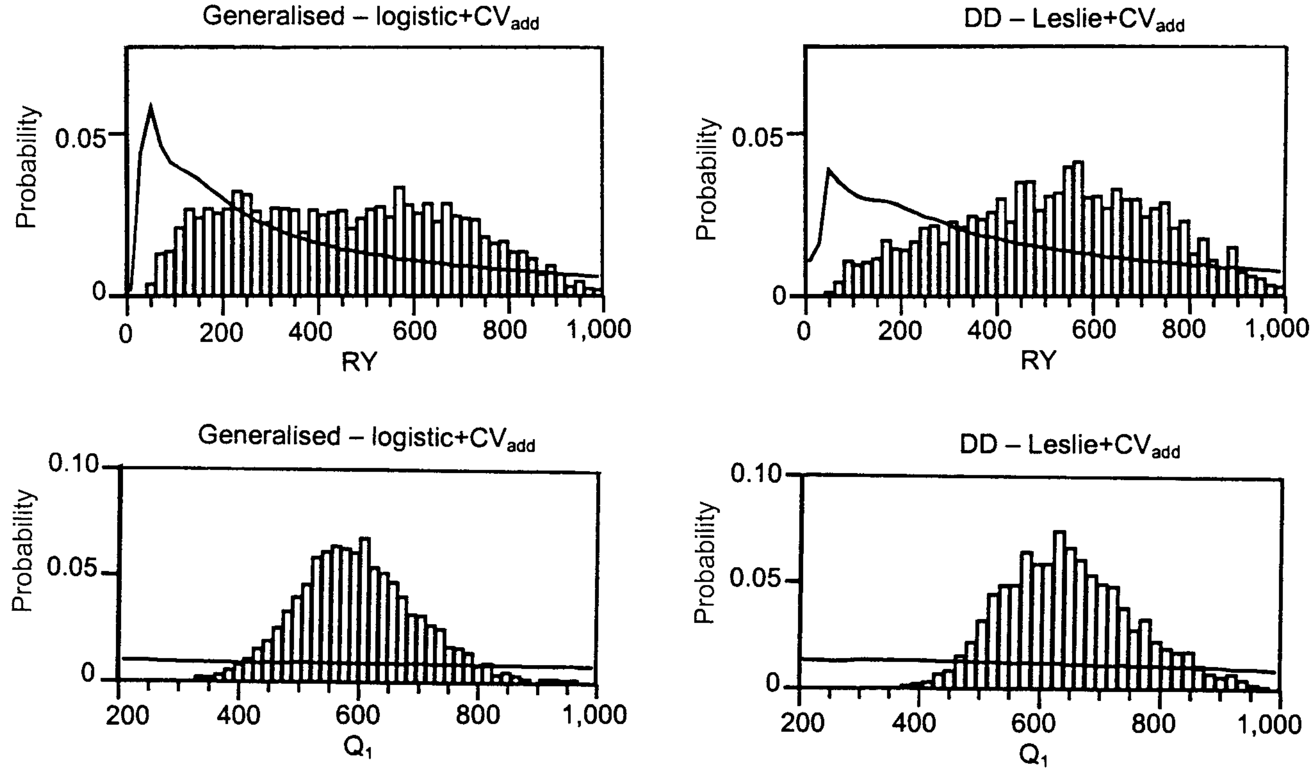

Fig. 7. Upper panel: posterior probability distributions for RY, the current replacement yield, as approximated by the posterior sample. Lower panel: posterior probability distributions for $Q_1$, as defined in Wade and Givens (1997), as approximated by the posterior sample. The implicit prior distributions are represented as lines.

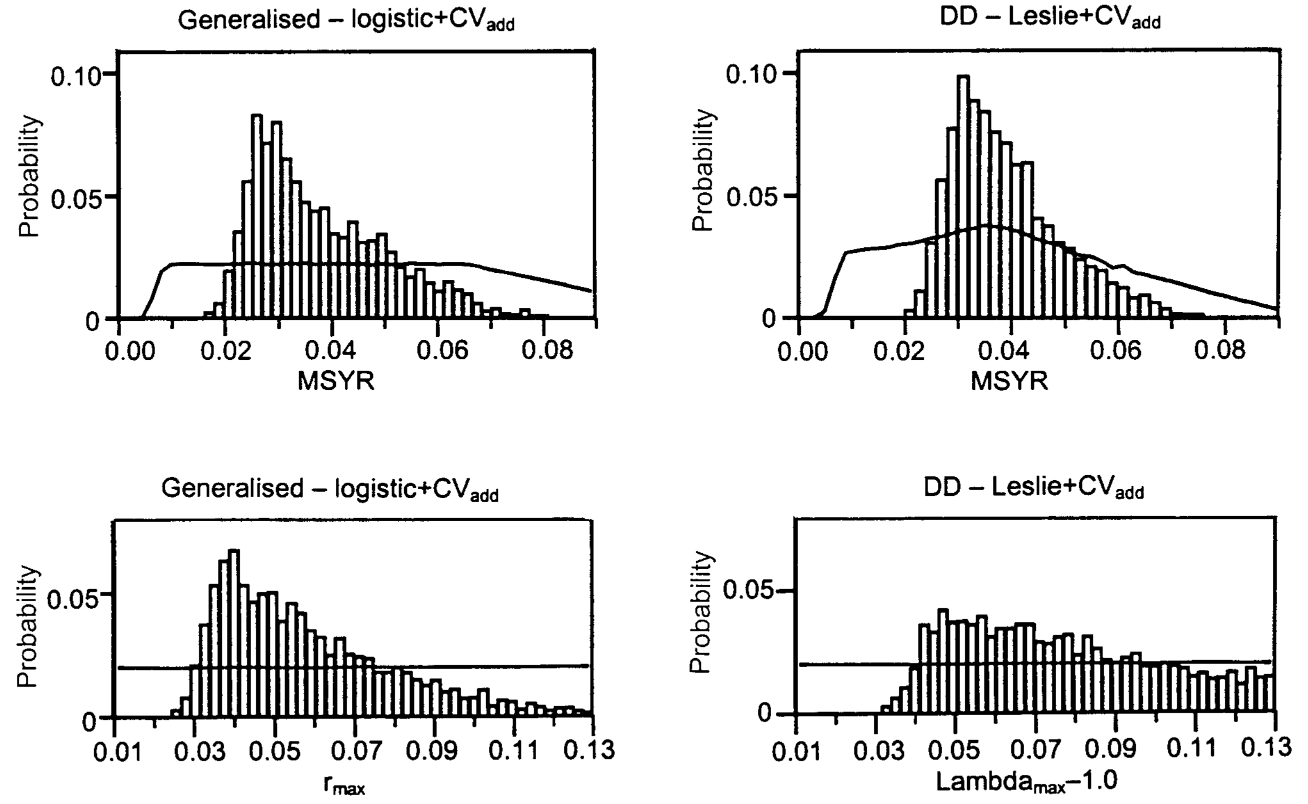

Fig. 8. Upper panel: posterior probability distribution for MSYR, the maximum sustainable yield rate, as approximated by the posterior sample. The implicit prior distributions are represented as lines. Lower panel: posterior probability distribution for $r_{max}$ and $\lambda_{max}$-1, the population growth parameters, as approximated by the posterior sample. The prior distributions (uniform(0.01,0.13)) are represented as lines.

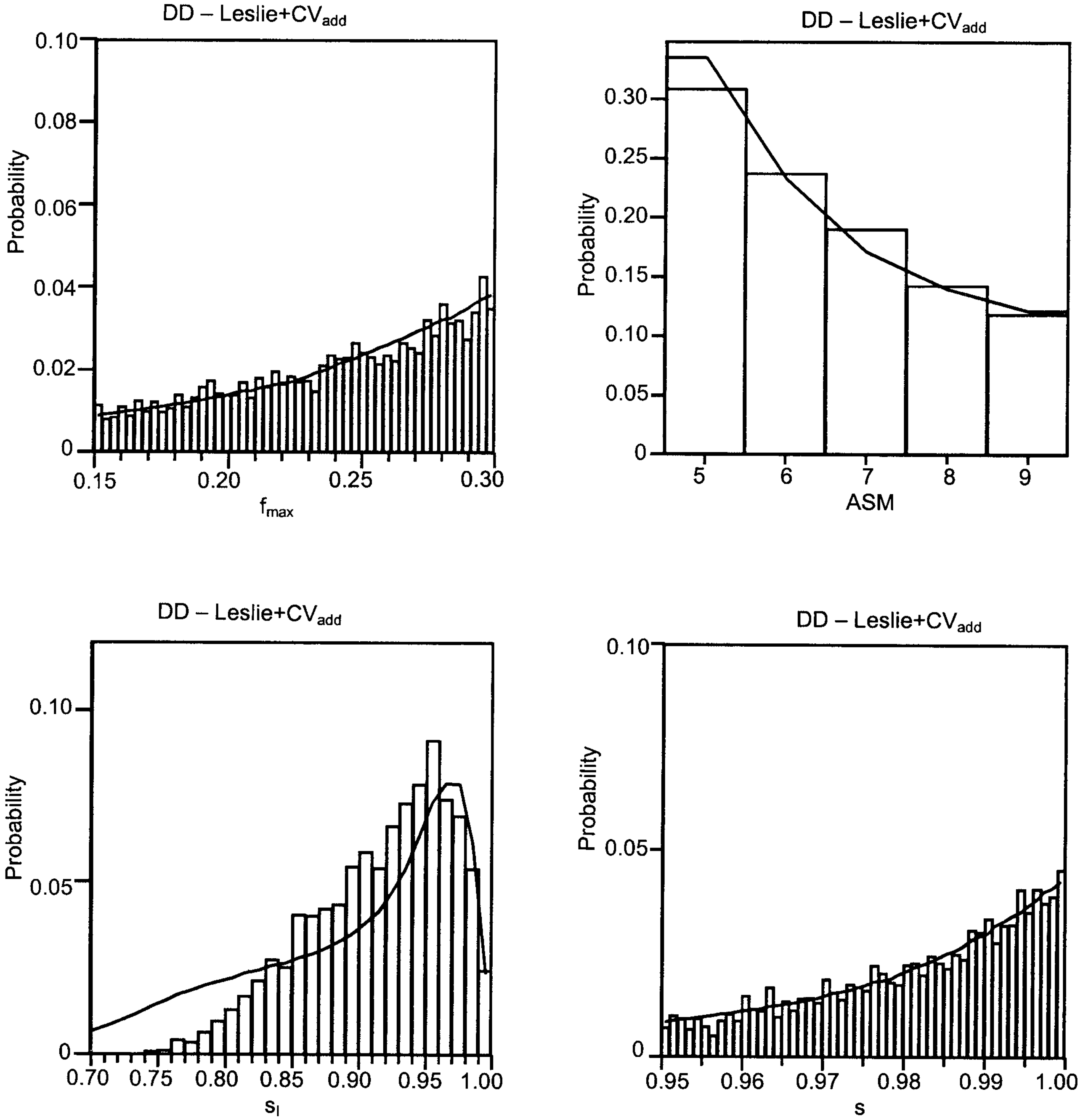

Fig. 9. Posterior probability distributions for four of the parameters of the density-dependent Leslie matrix model with the additional variance term $CV_{add}$. $f_{max}$ is the maximum fecundity, *ASM* is the age of sexual maturity, $s_j$ is the juvenile survival rate and *s* is the adult survival rate. The prior distributions for $f_{max}$, *ASM* and *s* were initially set to uniform distributions over the ranges shown, while the only prior restriction put on $s_j$ was that it be less than *s*. The lines represent the prior distributions that resulted from forcing the Leslie matrix parameters to be consistent with a uniform prior from 0.1 to 0.13 for $\lambda_{max}$-1.

The posterior distributions for MSYR were all greater than 0.02 (Fig. 8), with point estimates ranging from 0.035 to 0.047 (Table 5). This resulted because of the increase in population size over the last 28 years in combination with the low probability that the population is at a small fraction of its equilibrium population size. The point estimate for $r_{max}$ was 0.053 and for $\lambda_{max}$-1 was 0.072 (Table 5), with 2.5th percentiles of 0.031 and 0.039 respectively. The posterior distributions for $r_{max}$ and $\lambda_{max}$-1 both had long tails on the right (Fig. 8), which caused the median values to be greater than values of the modes of the distributions.

The posterior distributions for the four life-history parameters were virtually identical to their prior distributions. The sloped prior distributions with higher probability at values that lead to higher growth rates were due to the fact that $\lambda_{max}$-1 itself was forced to have a uniform prior distribution.

## DISCUSSION

The model comparisons through use of the Bayes factor led to the conclusion that an additional variance term should be included in population dynamics models fitted to the gray whale abundance data. In other words, it is clear that not all of the variance associated with the abundance estimate has

Table 5

A summary of the posterior distributions of the output quantities, including the posterior median and the 2.5th and 97.5th percentiles of the posterior sample.

(a) Population model parameters. $CV_{add}$ is the additional variance term, $r_{max}$ and $\lambda_{max}$ are the maximum net recruitment rates, MSYR is the net recruitment rate at the maximum sustained yield level, $f_{max}$ is the maximum fecundity rate, ASM is the age of sexual maturity, $s$ is the adult survival rate, $s_j$ is the juvenile survival rate. All quantities are for the 1+ population.

| Model | Parameter | Posterior median | 2.5th percentile | 97.5th percentile |
|---|---|---|---|---|
| Generalised-logistic+$CV_{add}$ | $CV_{add}$ | 0.140 | 0.095 | 0.217 |
| Density-dependent Leslie+$CV_{add}$ | $CV_{add}$ | 0.142 | 0.098 | 0.214 |
| Generalised-logistic | $r_{max}$ | 0.055 | 0.045 | 0.087 |
| Generalised-logistic+$CV_{add}$ | $r_{max}$ | 0.053 | 0.031 | 0.113 |
| Density-dependent Leslie | $\lambda_{max-1}$ | 0.072 | 0.053 | 0.128 |
| Density-dependent Leslie+$CV_{add}$ | $\lambda_{max-1}$ | 0.072 | 0.039 | 0.126 |
| Generalised-logistic | MSYR | 0.042 | 0.033 | 0.050 |
| Density-dependent Leslie | MSYR | 0.045 | 0.033 | 0.054 |
| Generalised-logistic+$CV_{add}$ | MSYR | 0.035 | 0.021 | 0.068 |
| Density-dependent Leslie+$CV_{add}$ | MSYR | 0.037 | 0.025 | 0.066 |
| Density-dependent Leslie | $f_{max}$ | 0.244 | 0.155 | 0.297 |
| Density-dependent Leslie+$CV_{add}$ | $f_{max}$ | 0.248 | 0.158 | 0.298 |
| Density-dependent Leslie | *ASM* | 6 | 5 | 9 |
| Density-dependent Leslie+$CV_{add}$ | *ASM* | 6 | 5 | 9 |
| Density-dependent Leslie | $s$ | 0.982 | 0.952 | 0.999 |
| Density-dependent Leslie+$CV_{add}$ | $s$ | 0.985 | 0.953 | 0.999 |
| Density-dependent Leslie | $s_j$ | 0.950 | 0.845 | 0.992 |
| Density-dependent Leslie+$CV_{add}$ | $s_j$ | 0.925 | 0.800 | 0.990 |

(b) Population size and depletion level. $N_{95/96}$ is the population size in the beginning of 1996, $N_{eq}$ is the equilibrium population size, $N_{95/96}/N_{eq}$ is the population size in 1996 relative to the equilibrium population size, $N_{95\text{-}96}$/MSYL is the population size in 1996 relative to the maximum sustained yield level. All quantities are for the 1+ population.

| Model | Parameter | Posterior median | 2.5th percentile | 97.5th percentile |
|---|---|---|---|---|
| Generalised-logistic | $N_{95/96}$ | 22,950 | 21,560 | 24,730 |
| Density-dependent Leslie | $N_{95/96}$ | 23,290 | 21,870 | 24,990 |
| Generalised-logistic+$CV_{add}$ | $N_{95/96}$ | 22,990 | 19,080 | 27,070 |
| Density-dependent Leslie+$CV_{add}$ | $N_{95/96}$ | 23,200 | 19,280 | 27,090 |
| Generalised-logistic | $N_{eq}$ | 24,640 | 22,160 | 34,250 |
| Density-dependent Leslie | $N_{eq}$ | 25,590 | 22,630 | 41,140 |
| Generalised-logistic+$CV_{add}$ | $N_{eq}$ | 29,880 | 19,980 | 66,720 |
| Density-dependent Leslie+$CV_{add}$ | $N_{eq}$ | 31,840 | 19,890 | 66,840 |
| Generalised-logistic | $N_{95/96}/N_{eq}$ | 0.933 | 0.711 | 0.981 |
| Density-dependent Leslie | $N_{95/96}/N_{eq}$ | 0.912 | 0.606 | 0.980 |
| Generalised-logistic+$CV_{add}$ | $N_{95/96}/N_{eq}$ | 0.781 | 0.359 | 0.988 |
| Density-dependent Leslie+$CV_{add}$ | $N_{95/96}/N_{eq}$ | 0.734 | 0.356 | 1.018 |
| Generalised-logistic | $N_{95\text{-}96}$/MSYL | 1.437 | 1.291 | 1.660 |
| Density-dependent Leslie | $N_{95\text{-}96}$/MSYL | 1.434 | 1.122 | 1.706 |
| Generalised-logistic+$CV_{add}$ | $N_{95\text{-}96}$/MSYL | 1.361 | 0.599 | 1.776 |
| Density-dependent Leslie+$CV_{add}$ | $N_{95\text{-}96}$/MSYL | 1.293 | 0.600 | 1.725 |

(c) Catch limit quantities and related information. $Q_1$, is defined in Wade and Givens (1997), RY is the replacement yield in 1996 and MSY is the maximum sustained yield. All quantities are for the 1+ population.

| Model | Parameter | Posterior median | 2.5th percentile | 97.5th percentile |
|---|---|---|---|---|
| Generalised-logistic | $Q_1$ | 592 | 532 | 660 |
| Density-dependent Leslie | $Q_1$ | 647 | 563 | 732 |
| Generalised-logistic+$CV_{add}$ | $Q_1$ | 593 | 407 | 841 |
| Density-dependent Leslie+$CV_{add}$ | $Q_1$ | 637 | 460 | 907 |
| Generalised-logistic | RY | 285 | 136 | 567 |
| Density-dependent Leslie | RY | 391 | 219 | 671 |
| Generalised-logistic+$CV_{add}$ | RY | 461 | 91 | 910 |
| Density-dependent Leslie+$CV_{add}$ | RY | 533 | 118 | 947 |
| Generalised-logistic | MSY | 658 | 591 | 733 |
| Density-dependent Leslie | MSY | 719 | 626 | 813 |
| Generalised-logistic+$CV_{add}$ | MSY | 678 | 468 | 1,122 |
| Density-dependent Leslie+$CV_{add}$ | MSY | 728 | 524 | 1,284 |

been included in previous estimates. A similar conclusion was reached by the IWC Scientific Committee in 1994, where it was noted that 'sampling variability was either under-estimated or was not the only source of variation in the estimates' (IWC, 1995). Results are reported here for all four combinations of population model and use or not of $CV_{add}$, but the model comparisons clearly indicate that the two models that incorporate the additional variance term, $CV_{add}$, provide a better fit to the data. A robust management strategy should therefore be based on a model assessment including this term. Including the term $CV_{add}$, has a large influence on the results, as without it the evidence is very strong that the population is at a large fraction of its equilibrium and is no longer depleted. In general the same conclusion is suggested from the analyses with $CV_{add}$, but those analyses leave some possibility that the population is still currently depleted.

The lower percentiles of $Q_1$ were lower in the analyses including $CV_{add}$, but these lower values were clearly supported by the data and thus represent the preferred quantities on which to base management. It can be seen that the estimated distributions for $Q_1$ were very close to what a distribution of 0.9MSY would be. This resulted because of the high probability that the population was above MSYL, with the only difference due to the small fraction of trajectories which were still below MSY in 1996. $Q_1$ represents a harvest level that would allow a depleted population to increase and allows it to increase faster the more depleted it is (Wade and Givens, 1997). An estimate of about 600 is thus consistent with the evidence that the population has increased substantially under a harvest of approximately 174 per year. Note that because there is no probability that the current depletion level is less than 0.25 (Fig. 4), a value for $P_{min}$ as high as 0.25 could have been used without changing the estimates of $Q_1$.

Another way of putting a potential harvest of 600 animals into context is to consider the available time-series of abundance estimates, which indicates that the population increased by approximately 3% per year from 1967/68 to 1987/88 (Reilly, 1992) while an annual harvest of approximately 174 whales took place. If the population was at approximately 10,000 animals in 1968 and increased at 3% per year for 20 years, it would have increased by an average of about 400 animals per year. Given that the harvest was about 174 per year, this indicates that the population, on average, produced about 575 more whales each year than would die from natural mortality. This can give some indication of what the population could currently sustain given the evidence of the last 28 years.

It should be noted that a harvest level of MSY (or even 0.9MSY) will cause a population well above MSYL (such as one close to carrying capacity) to decline. Because the gray whale is estimated to be well above MSYL, this suggests that a current harvest as high as the point estimates for $Q_1$ (593-646 using $CV_{add}$) would cause the population to decline. If continued, in theory such a harvest would cause the population to decline to a level just above the MSYL. Such a decline would be consistent with the specified aboriginal management principles.

When the gray whale population was clearly thought to be increasing (such as from 1968-1988), RY was a useful quantity to represent the maximum harvest that the population might currently sustain. Now that the recent abundance estimates indicate there is some likelihood that the population growth rate is slowing as the population approaches its equilibrium, the quantity RY becomes less useful for management. Obviously, if the population stabilises, RY will go to zero. Therefore, it now becomes important to use other quantities when assessing whether a specified harvest level would meet the requirement of aboriginal subsistence management.

As suggested in Kass and Raftery (1995), the posterior distributions for the quantities of interest could be combined across models, using the probability of each model as a weight for each posterior distribution. In the case here, this would probably change the results little, as such a combined distribution would be dominated by the models including $CV_{add}$, which give fairly similar results. The nearly equal probability of the generalised-logistic+ $CV_{add}$, model and the density-dependent Leslie matrix+ $CV_{add}$, model indicates that a combined posterior would be approximately an equal mixture of those two posterior distributions.

In conclusion, this method for accounting for additional variance results in an analysis that reconciles the contradiction inherent in sequential abundance estimates that differ more than expected according to their estimated variances. The evidence, as expressed by the Bayes factor, supports the use of a parameter representing unexplained variance for a robust stock assessment of the eastern Pacific gray whale population.

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# An examination of certain of the assumptions made in the Bayesian approach used to assess the eastern North Pacific stock of gray whales (*Eschrichtius robustus*)[1]

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ABSTRACT

An assessment of the eastern North Pacific stock of gray whales (*Eschrichtius robustus*) is conducted using a variant of the Bayesian stock assessment method of Wade (2002). This variant is based on the BALEEN II population dynamics model and uses parameters whose values are more familiar to members of the International Whaling Commission's Scientific Committee. The sensitivity of the results to changes to some of the specifications used in the assessment is examined. The results are shown to be relatively insensitive to the first year considered in the analysis and the year for which a prior on absolute abundance is specified. An alternative Bayesian assessment method which involves projecting the population forward from pre-exploitation equilibrium in 1600 is also considered. As expected from previous assessments, results from this method are unable to mimic the recent trends in absolute abundance obtained from shore counts and are inconsistent with the fact that the fishery was commercially extinct by the end of the 19th Century. Allowing for underestimation of historical commercial and aboriginal catches provides improved consistency with recent trends in abundance but does not resolve these problems completely. The impact of process error (in the form of temporally correlated fluctuations in calf survival) on the dynamics of the population is found to be largely inconsequential in terms of resolving the inconsistency between historical catches and recent estimates of abundance.

KEYWORDS: GRAY WHALE; PACIFIC OCEAN; MODELLING; ABUNDANCE ESTIMATE

## INTRODUCTION

Assessments of the eastern North Pacific stock of gray whales based on the assumption that the population was at its pre-exploitation equilibrium level in 1846 are unable to mimic the virtual doubling in abundance inferred from the survey estimates from 1967-1994. Various authors (e.g. Reilly, 1981; Cooke, 1986; Lankester and Beddington, 1986; Mathews, 1986; Butterworth *et al.*, 2002) have examined hypotheses related to why the fits of population models to the abundance data are poor. These include changes in environmental carrying capacity, the disruptive influence of intensive whaling on the breeding rate, underestimated historical commercial catches, an overestimate of the recent rate of population growth and inadequate allowance for historical aboriginal catches. However, none of these explanations in isolation seem particularly likely because the magnitude of the required difference from the 'conventional wisdom' of no such 'errors' is large. For example, Butterworth *et al.* (2002) found that only if the environmental carrying capacity was currently 250% (or more) than that in 1846 (and $MSYR_{\text{exp}}$ $\geq$4%, where 5+ animals constitute the exploitable component of the population) is it possible to reconcile the catch history with the abundance data. They also showed that the requisite magnitude of the factors that they considered became smaller if more than one applied. Wade (2002) and Wade and DeMaster (1996) assessed the stock, but made no attempt to fit a population model to the entire period of exploitation, relying instead on the assumption of a stable age-structure at the start of 1968.

The assessments of Wade (2002) and Wade and DeMaster (1996) are based on the population model used by Breiwick *et al.* (1984) to assess the Bering-Chukchi-Beaufort Seas (B-C-B) stock of bowhead whales. This paper instead uses the BALEEN II population dynamics model (Punt, 1999). This population model has been used extensively in recent assessments of the bowhead stock (e.g. Givens *et al.*, 1993; Butterworth and Punt, 1995) and is parameterised in terms of MSYR and MSYL, parameters with whose values most members of the Scientific Committee are rather more familiar than those of the Breiwick *et al.* (1984) model ($\lambda$ and $z$).

This paper first outlines the method used by Wade (2002) as applied here using the BALEEN II model (the base-case analysis). It then contrasts the results of this analysis with those of Wade (2002). The primary intent of the paper, however, is to consider the sensitivity of the results of this base-case analysis to variations in its specifications. In particular, sensitivity is examined to changing the year in which the population is assumed to have had a stable age-structure, changing the year for which a prior distribution for the (1+) population size is specified, allowing for underestimation of historical commercial and aboriginal catches, and incorporating 'process error' in the form of a stochastic term in the annual calf survival rate.

## DATA AND METHODS

### The base-case assessment

The philosophy underlying the Bayesian assessments of Wade (2002) and Wade and DeMaster (1996) is to place a prior distribution on the abundance in a particular year (1968 in those assessments) and to assume that the population had a stable age-structure at the start of that year. The population is then projected forwards from 1968 to 1996 and the likelihood for the projection is calculated. The only data included in the likelihood function are the estimates of abundance (Table 1). The catch data (commercial and

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aboriginal) used when projecting the population forwards over this period are listed in Tables 2 and 3. The posterior distributions for the quantities of interest to management are computed using the SIR algorithm (Rubin, 1987; Gelman *et al.*, 1995). A total of 500,000 iterations of this algorithm are used for the calculations of this paper to ensure that adequate numerical representations of the posterior distributions of interest are achieved.

A disadvantage, when working with an age-structured population model (such as BALEEN II), of initiating population trajectories in a year (here 1968) subsequent to the onset of exploitation is that it is then no longer possible to generate the starting age-structure under the assumption of unharvested equilibrium. Instead it becomes necessary to assume a stable age structure, which in turn involves specifying the effective 'rate of increase' ($\gamma$) that applies to each age-class. There are two components contributing to $\gamma$, one relating to the overall population rate of increase ($\gamma^+$)

Table 1

Estimates of absolute abundance with associated standard errors (SE) for the eastern North Pacific stock of gray whales based on shore counts (source: Wade, 2002).

| Year | Estimate | SE |
|---|---|---|
| 1967/68 | 13,012 | 893 |
| 1968/69 | 12,244 | 484 |
| 1969/70 | 12,777 | 525 |
| 1970/71 | 11,170 | 806 |
| 1971/72 | 9,841 | 442 |
| 1972/73 | 16,962 | 660 |
| 1973/74 | 14,817 | 592 |
| 1974/75 | 13,134 | 540 |
| 1975/76 | 14,811 | 690 |
| 1976/77 | 15,950 | 524 |
| 1977/78 | 17,127 | 966 |
| 1978/79 | 13,300 | 501 |
| 1979/80 | 16,581 | 668 |
| 1984/85 | 21,942 | 994 |
| 1985/86 | 20,450 | 727 |
| 1987/88 | 21,113 | 688 |
| 1992/93 | 17,674 | 1,029 |
| 1993/94 | 23,109 | 1,262 |
| 1995/96 | 22,571 | 1,174 |

Table 3

Historical (pre-1944) aboriginal catches from the eastern North Pacific stock of gray whales. The sex ratio of these catches is assumed to be 1:1 (source: IWC 1993).

| Years | Annual catch (both sexes) |
|---|---|
| 1600 - 1750 | 160 |
| 1871 - 1850 | 260 |
| 1851 - 1860 | 190 |
| 1861 - 1880 | 90 |
| 1881 - 1891 | 80 |
| 1892 - 1900 | 40 |
| 1901 - 1915 | 30 |
| 1916 - 1930 | 20 |
| 1931 - 1939 | 10 |
| 1940 - 1943 | 20 |

Table 2

Commercial and recent aboriginal (post 1943) catches from the eastern North Pacific stock of gray whales. Sources: 1846 -1854: IWC (1993); 1855-1961: Lankester and Beddington (1986); 1962-1991: C. Allison, pers. comm.; 1994: Blokhin (1995); 1995: Borodin (1996).

| Year | Male | Female | Year | Male | Female | Year | Male | Female | Year | Male | Female |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1846 | 23 | 45 | 1884 | 23 | 45 | 1922 | 2 | 3 | 1960 | 58 | 115 |
| 1847 | 23 | 45 | 1885 | 21 | 41 | 1923 | 5 | 11 | 1961 | 71 | 141 |
| 1848 | 23 | 45 | 1886 | 17 | 33 | 1924 | 5 | 11 | 1962 | 49 | 98 |
| 1849 | 23 | 45 | 1887 | 7 | 13 | 1925 | 50 | 99 | 1963 | 60 | 120 |
| 1850 | 23 | 45 | 1888 | 7 | 13 | 1926 | 19 | 38 | 1964 | 70 | 140 |
| 1851 | 23 | 45 | 1889 | 7 | 13 | 1927 | 16 | 32 | 1965 | 68 | 108 |
| 1852 | 23 | 45 | 1890 | 7 | 13 | 1928 | 9 | 18 | 1966 | 123 | 97 |
| 1853 | 23 | 45 | 1891 | 7 | 13 | 1929 | 6 | 12 | 1967 | 94 | 156 |
| 1854 | 23 | 45 | 1892 | 7 | 13 | 1930 | 5 | 10 | 1968 | 67 | 134 |
| 1855 | 162 | 324 | 1893 | 0 | 0 | 1931 | 5 | 11 | 1969 | 59 | 155 |
| 1856 | 162 | 324 | 1894 | 0 | 0 | 1932 | 5 | 10 | 1970 | 26 | 125 |
| 1857 | 162 | 324 | 1895 | 0 | 0 | 1933 | 3 | 7 | 1971 | 51 | 102 |
| 1858 | 162 | 324 | 1896 | 0 | 0 | 1934 | 18 | 36 | 1972 | 22 | 160 |
| 1859 | 162 | 324 | 1897 | 0 | 0 | 1935 | 11 | 23 | 1973 | 97 | 81 |
| 1860 | 162 | 324 | 1898 | 0 | 0 | 1936 | 34 | 68 | 1974 | 94 | 90 |
| 1861 | 162 | 324 | 1899 | 0 | 0 | 1937 | 5 | 9 | 1975 | 58 | 113 |
| 1862 | 162 | 324 | 1900 | 0 | 0 | 1938 | 18 | 36 | 1976 | 69 | 96 |
| 1863 | 162 | 324 | 1901 | 0 | 0 | 1939 | 10 | 19 | 1977 | 86 | 101 |
| 1864 | 162 | 324 | 1902 | 0 | 0 | 1940 | 35 | 70 | 1978 | 94 | 90 |
| 1865 | 162 | 324 | 1903 | 0 | 0 | 1941 | 19 | 38 | 1979 | 57 | 126 |
| 1866 | 79 | 159 | 1904 | 0 | 0 | 1942 | 34 | 67 | 1980 | 53 | 128 |
| 1867 | 79 | 159 | 1905 | 0 | 0 | 1943 | 33 | 66 | 1981 | 36 | 100 |
| 1868 | 79 | 159 | 1906 | 0 | 0 | 1944 | 0 | 0 | 1982 | 56 | 112 |
| 1869 | 79 | 159 | 1907 | 0 | 0 | 1945 | 10 | 20 | 1983 | 46 | 125 |
| 1870 | 79 | 159 | 1908 | 0 | 0 | 1946 | 7 | 15 | 1984 | 59 | 110 |
| 1871 | 79 | 159 | 1909 | 0 | 0 | 1947 | 3 | 6 | 1985 | 55 | 115 |
| 1872 | 79 | 159 | 1910 | 0 | 0 | 1948 | 6 | 13 | 1986 | 46 | 125 |
| 1873 | 79 | 159 | 1911 | 0 | 0 | 1949 | 9 | 17 | 1987 | 47 | 112 |
| 1874 | 79 | 159 | 1912 | 0 | 0 | 1950 | 4 | 7 | 1988 | 43 | 108 |
| 1875 | 17 | 33 | 1913 | 0 | 1 | 1951 | 4 | 9 | 1989 | 61 | 119 |
| 1876 | 17 | 33 | 1914 | 6 | 13 | 1952 | 15 | 29 | 1990 | 67 | 96 |
| 1877 | 17 | 33 | 1915 | 0 | 0 | 1953 | 13 | 25 | 1991 | 57 | 113 |
| 1878 | 17 | 33 | 1916 | 0 | 0 | 1954 | 13 | 26 | 1992 | 0 | 0 |
| 1879 | 21 | 42 | 1917 | 0 | 0 | 1955 | 20 | 39 | 1993 | 0 | 0 |
| 1880 | 17 | 34 | 1918 | 3 | 5 | 1956 | 41 | 81 | 1994 | 15 | 29 |
| 1881 | 17 | 33 | 1919 | 1 | 1 | 1957 | 33 | 65 | 1995 | 44 | 41 |
| 1882 | 17 | 33 | 1920 | 1 | 1 | 1958 | 49 | 99 | | | |
| 1883 | 19 | 39 | 1921 | 1 | 1 | 1959 | 65 | 131 | | | |

and the other to the exploitation rate. Under the assumption in this paper of knife-edge recruitment to the fishery at age five, only the $\gamma^+$ component applies to ages $a$ of 4 or less. The number of animals of age $a$ at the start of 1968 relative to the number of calves at that time, $N^*_{1968,a}$, is therefore given by the equation:

$$N^*_{1968,a} = \begin{cases} 1 & \text{if } a = 0 \\ N^*_{1968,a-1}\, s_{a-1}(1-\gamma^+) & \text{if } a \le 5 \\ N^*_{1968,a-1}\, s_{a-1}(1-\gamma) & \text{if } 5 < a < x \\ N^*_{1968,x-1}\, s_{x-1}(1-\gamma)/(1-s_x(1-\gamma)) & \text{if } a = x \end{cases} \tag{1}$$

where:

$s_a$ is the survival rate of animals of age $a$ (assumed to be independent of sex);

$N_0$ is the number of calves in 1968[2]:

$$N_0 = \left(1-\left[1/(P_{\text{mat}}\, fec)-1\right]/A\right)^{1/z}\frac{\tilde{K}_{\text{mat}}}{P_{\text{mat}}} \tag{2}$$

$P_{\text{mat}}$ is the number of mature animals per calf in 1968:

$$P_{\text{mat}} = \sum_{a=a_m+1}^{x} N^*_{1968,a} \tag{3}$$

$A$ is the resilience parameter;

$z$ is the degree of compensation;

$a_m$ is the age-at-maturity (note that the summation in Equation (3) commences from age $a_m$+1 to allow for a one year gestation period);

$\tilde{K}_{\text{mat}}$ is the number of mature animals at the projected equilibrium in the absence of future catches[3];

$fec$ reflects fecundity (the annual number of births per mature animal) at pre-exploitation equilibrium; and

$x$ is the maximum age considered.

The value of $x$ (the age at which the numbers-at-age are accumulated in a plus-group) is set equal to 15 for the analyses of this paper. This choice is based on computational convenience; given the assumptions of uniform selectivity harvesting above age five and a maximum age-at-first parturition of 10, any choice for $x$ of 10 or larger would lead to identical results.

Given a specification for the relationship between $\gamma$ and $\gamma^+$, and if $N^g_{1968}$ is a value generated from the prior for the total (1+) abundance in 1968, the following equation is then solved for the 'rate of increase' effective in 1968, $\gamma$:

$$N^g_{1968} = N_0 \sum_{a=1}^{x} N^*_{1968,a} \tag{4}$$

The value of $\gamma$ is restricted to lie between 0 and 1. This implies that the 1+ abundance at the start of 1968 is restricted to be smaller than the projected equilibrium level, $\tilde{K}_{1+}$. Any draws from the prior distribution for which it is not possible to satisfy Equation (4) are rejected and assigned zero likelihood. Given an increasing population, it follows that $0 < \gamma^+ < \gamma$, but it is not immediately clear how a prior distribution for the ratio $\gamma^+/\gamma$ might be specified. One option would be to assign an 'uninformative' U[0, 1] prior. The approach taken in this paper is to set $\gamma^+ = 0$, i.e. equal to one of the extremes of its possible range. This choice was made primarily for computational convenience. Sensitivity of the results to the assumption of the other extreme ($\gamma^+ = \gamma$) is examined later in the paper.

The assumption of a stable age-structure at the start of 1968 is defensible only if the population was increasing geometrically at that time. If this is true, the value of $\gamma$ obtained from solving Equation (4) should be consistent with the population increase and exploitation rates for the trajectory in question. This can be checked by comparing the posterior distribution for $\gamma$ with the posterior distribution for the effective 'rate of increase' ($\gamma^*$) estimated directly from the population estimates generated by the population model. This effective 'rate of increase' is again defined as the sum of the actual rate of increase of the population and the exploitation rate:

$$\gamma^* = \gamma_1 + \gamma_2 \tag{5}$$

where:

$\gamma_1$ is the average annual increase of the exploitable (5+) population from 1968 to 1972 as estimated from a linear regression fit to the logarithms of the model estimates of (5+) population size over this period;

$\gamma_2$ is the exploitation rate over the period 1959-1968:

$$\gamma_2 = \sum_{y=1959}^{1968} C_y \bigg/ \sum_{y=1959}^{1968} N^{\text{exp}}_{1968}(1-\gamma_1)^{1968-y} \tag{6}$$

$C_y$ is the catch during year $y$; and

$N^{\text{exp}}_{\text{y}}$ is the exploitable (5+) population size for year $y$.

The estimate of the exploitation rate is based on the years 1959-1968, and assumes that the population rate of increase from 1959-1968 is the same as that from 1968-1972. A period prior to 1968 is chosen because the age-structure of the population in 1968 would depend particularly on the size of the catches in the years immediately preceding. In principle, $\gamma_1$ should have been calculated for the same years as the exploitation rate. However, this is not possible because the population projections start only in 1968.

Fig. 1 presents the posterior distributions for $\gamma$ and $\gamma^*$ as well as the posterior distribution for the difference between $\gamma$ and $\gamma^*$. The results in this Figure suggest little difference and hence that the assumption of a stable age-structure at the start of 1968 is not violated to any substantial extent.

The prior distributions assumed for the analyses are listed in Table 4. The distributions for the non-calf natural survival rate ($s$) which is assumed to be independent of age, the age-at-maturity ($a_m$), the projected equilibrium level ($\tilde{K}_{1+}$), and the maximum pregnancy rate ($\rho_{\text{max}}$) are taken from Wade (2002). The prior distribution for $MSYL_{\text{mat}}$ is selected (by analogy) as that used in the 1994 assessment of the B-C-B bowhead stock by the Scientific Committee (IWC, 1995). The prior distribution for $MSYR_{\text{mat}}$ is also not based on the choices made by Wade (2002), but is instead expanded to capture the whole range of values considered by Butterworth *et al.* (2002). The selection of uniform prior distributions is intended to reflect a lack of information about the parameters in question.

The analysis does not incorporate a prior distribution for the survival rate of calves ($s_c$) explicitly. Instead, following Wade (2002), an implicit prior distribution for this parameter is calculated from the priors for the five parameters $s$, $a_m$, $\rho_{\text{max}}$, $MSYL_{\text{mat}}$ and $MSYR_{\text{mat}}$. For any specific draw from the prior distributions for these five parameters, the value for $s_c$ is selected so that the relationships imposed by the

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[2] Equation (2) follows directly from the definition of fecundity (see Punt, 1999 for further details).

[3] Unlike the norm for baleen whale assessments, $\tilde{K}$ is not necessarily equal to the pre-exploitation size of the resource (hence the ~ notation), because (for example) this analysis does not preclude a change over time in the environmental carrying capacity. For this reason, we will refer to $\tilde{K}$, which corresponds to the *current* environmental carrying capacity, as the 'projected equilibrium level' for the remainder of this paper.

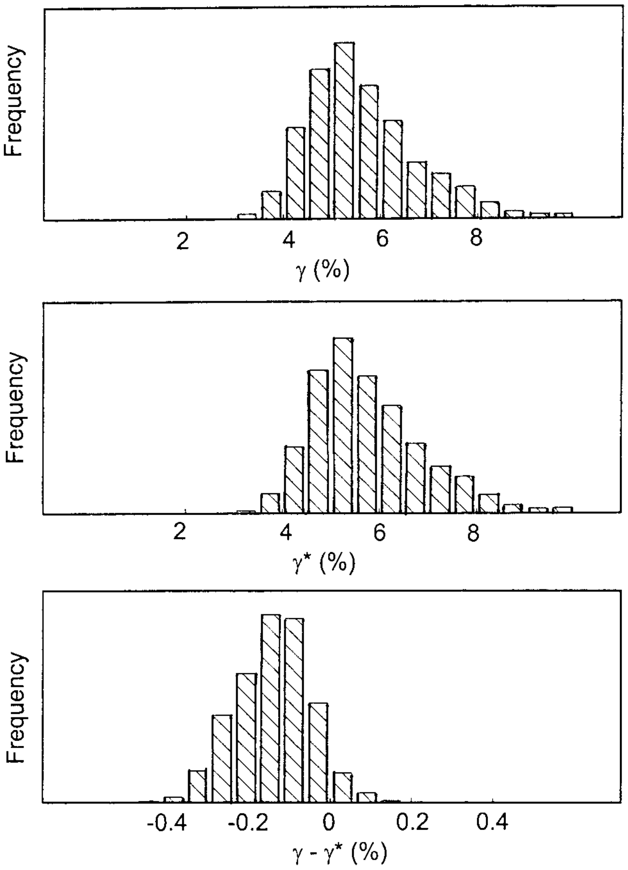

Fig. 1. Posterior distributions for $\gamma$, $\gamma^*$ and $\gamma - \gamma^*$ for the base-case analysis (see text for definitions).

Table 4

The prior distributions used in this assessment of the eastern North Pacific stock of gray whales.

| Parameter | Prior distribution |
|---|---|
| Non-calf survival rate, $s$ | U[0.95; 0.999] |
| Age-at-maturity, $a_m$ | U[5; 9] |
| $\tilde{K}_{1+}$ | U[0; 70,000] |
| $MSYL_{\mathrm{mat}}$ | U[0.4; 0.8] |
| $MSYR_{\mathrm{mat}}$ (%) | U[0; 10] |
| Maximum pregnancy rate, $\rho_{\max}$ | U[0.3; 0.6] |
| Additional variation, $CV_{\mathrm{add}}$ | U[0; 0.35] |

population model among the six parameters are satisfied. If the resulting value for $s_c$ is less than zero or greater than that of $s$, the values for $s$, $a_m$, $\rho_{\max}$ and $MSYL_{\mathrm{mat}}$ are drawn again. Thus, the prior for $s_c$ is forced to conform to the intuitive notion that the survival rate of calves must be lower than that for older animals (and must be larger than zero). The process introduces a correlation between survival rate and age-at-maturity, i.e. it updates these priors to some extent (Punt and Butterworth, 1999). However, the redrawing procedure deliberately leaves the original draw for $MSYR_{\mathrm{mat}}$ unchanged, so that the associated uninformative prior is (intentionally) not updated until information on population trends is taken into account via the likelihood. A prior distribution for the age-at-recruitment is not specified. Instead, all of the analyses of this paper assume knife-edged recruitment at age five (IWC, 1993; Butterworth *et al.*, 2002). This assumption has little impact on the results, which hardly change if a value of four or six is used instead.

It is conventional to denote the shore-count-based estimates of abundance for these gray whales by the seasons during which the counts were conducted (e.g. 1968/69). However, in this paper, the estimates are labelled by the latter of the two years and they are assumed to be indices of the numbers at the start of that year – specifically 1+ abundance because the fraction of cow-calf pairs observed is very small (Shelden *et al.*, 1997). Following the example of Wade (2002), the 19 estimates in Table 1 are assumed to be independent estimates of absolute abundance. This treatment of the data differs from that of Butterworth *et al.* (2002), who assumed that the estimate of 21,113 for 1988 (Breiwick *et al.*, 1988) provided an estimate of absolute abundance while the remaining abundance estimates were indices of relative abundance.

Wade (2002) highlights the point that the coefficients of variation for the shore-count-based estimates of abundance are clearly negatively biased, although the reason for this is not fully understood. To account for this, Wade (2002) followed the example of Butterworth *et al.* (1993) by introducing an extra parameter to account for 'additional variation'. This practice is followed here so that the likelihood function (excluding multiplicative constants) is therefore[4]:

$$L = \prod_y \frac{1}{\sqrt{\sigma_y^2 + CV_{\mathrm{add}}^2}} \exp\left( -\frac{(\ell n N_y^{obs} - \ell n \hat{N}_y)^2}{2(\sigma_y^2 + CV_{\mathrm{add}}^2)} \right) \qquad (7)$$

where:

$N_y^{obs}$ is the shore-count-based estimate of the (1+) abundance at the start of year $y$;

$\hat{N}_y$ is the model-estimate of the (1+) abundance at the start of year $y$;

$\sigma_y$ is the standard deviation of the logarithm of $N_y^{obs}$ (approximated here by its coefficient of variation); and

$CV_{\mathrm{add}}^2$ is the additional variation.

Following the example of Wade (2002), a U[0, 0.35] prior for $CV_{\mathrm{add}}$ is assumed for the analyses of this paper.

The prior distribution for the (1+) abundance at the start of 1968 is taken to be the same as the sampling distribution for the survey estimate for 1967/68[5] (Wade, 2002) and this estimate is consequently omitted from Equation (7). This is equivalent to including all of the shore-count-based estimates of abundance in the likelihood function and placing a U[0, ∞) prior on the (1+) abundance at the start of 1968 (Punt and Butterworth, 1999).

## Sensitivity tests: underestimation of historical commercial and aboriginal catches

IWC (1993) examines the implications of the possibilities that the early (1846-1900) commercial catches and the historical aboriginal catches may have been underestimated. The latter possibility is handled in this paper by multiplying the values in Table 3 by a quantity $\mu_A$, and similarly the possibility that the commercial catches prior to 1901 are underestimated by multiplying them by a quantity $\mu_C$.

The bulk of the analyses ignore the possibility that the historical catches are underestimated (i.e. $\mu_C = \mu_A = 1$).

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[4] The assumption of a log-normal distribution for the observation errors is based on the suggestion of Buckland (1992).

[5] The $CV$ for the prior distribution for this abundance estimate includes a contribution from the additional variation.

However, five sensitivity tests examine the implications of placing prior distributions on $\mu_C$ and $\mu_A$:

(a) $\mu_C \sim U[1,2]$ and $\mu_A \sim U[1,2]$
(b) $\mu_C = 1$ and $\mu_A \sim U[1,3]$
(c) $\mu_C \sim U[1,3]$ and $\mu_A = 1$
(d) $\mu_C = 1$ and $\mu_A \sim U[1,5]$
(e) $\mu_C \sim U[1,5]$ and $\mu_A = 1$

The basis for the prior distributions for the first sensitivity test is the selection of values considered by IWC (1993), while the other four sets of prior distributions examine the impact of uncertainty in one of these contributions to the historical catches only. The upper bounds of the priors are larger for these sensitivity tests and were chosen to incorporate the values identified by Butterworth *et al.* (2002) as being sufficient to allow the population model to fit the observed abundance estimates adequately, and to check sensitivity to the choice of the value for this bound.

The population projections for these sensitivity tests start in 1600 and assume that the population was at its pre-exploitation equilibrium level ($K$) at that time. An analysis which is based on the assumption that the population was at its pre-exploitation equilibrium level at the start of 1600 but assumes that $\mu_C = \mu_A = 1$ (abbreviation 'original') was conducted to assess the extent to which underestimation of historical catches can improve the fit to the abundance data.

### Sensitivity tests: initial conditions

The base-case analysis involves projecting the population forwards from the start of 1968 and placing a prior distribution on the abundance in that year. The choice of the year 1968 by Wade (2002) is based on computational convenience. The sensitivity of the results to alternative choices for the year for which a prior distribution on (1+) abundance is specified, $y_{\text{prior}}$, and the first year considered in the analysis, $y_1$[6], can be explored as follows.

(a) The 1+ abundance at the start of year $y_{\text{prior}}$ is generated from its prior distribution. If $y_{\text{prior}}$ is one of the years for which a shore-count-based estimate of abundance is available, this prior distribution is taken to be the sampling distribution for the survey in that year and the corresponding abundance estimate is omitted from the likelihood function.
(b) The abundance at the start of year $y_1$ is chosen so that if the population model is projected from year $y_1$ to year $y_{\text{prior}}$, the 1+ abundance in year $y_{\text{prior}}$ is equal to the value generated at step (a).

Two sets of sensitivity tests are conducted to explore the impact of different choices for the years $y_1$ and $y_{\text{prior}}$. The first set involves fixing $y_1$ to the base-case choice of 1968 and examining the implications of different choices for $y_{\text{prior}}$ in the range [1968, 1996][7]. The abbreviations for these sensitivity tests are '$y_{\text{prior}} = 19??$'. The second set of sensitivity tests involves fixing $y_{\text{prior}}$ at 1968 and examining the implications of different choices for $y_1$ (abbreviation '$y_1 = 19??$').

### Sensitivity tests: process error

The base-case analysis assumes that the population dynamics are deterministic. To examine whether the inability to fit the abundance data is caused by periods of better/worse calf survival (the population parameter considered most likely to be impacted by process error, S. Reilly, pers. comm.), sensitivity tests are conducted in which the annual number of calves is multiplied by the factor $e^{\varepsilon_y - \sigma_r^2/2}$ where $\varepsilon_y \sim N(0;\sigma_r^2)$. To mimic extended periods of better/worse calf survival, the same multiplicative factor is applied to the births during each decade of the projection[8]. The sensitivity of the results to the choice of the parameter $\sigma_r$ is examined by considering values of 0 (base-case), 0.05, 0.1 and 0.2.

## RESULTS AND DISCUSSION

### Management-related quantities

The results are summarised by the values of nine management-related quantities:

(a) $MSYR_{\text{mat}}$: the Maximum Sustainable Yield Rate (in terms of harvesting of the mature component of the population) expressed as a percentage;
(b) $\tilde{K}_{1+}$: the projected equilibrium level for the 1+ component of the population;
(c) $N^f_{96} / \tilde{K}_{\text{mat}}$: the number of mature females at the start of 1996 expressed as a fraction of that corresponding to the projected equilibrium level;
(d) $N^f_{96} / MSYL_{\text{mat}}$: the number of mature females at the start of 1996 expressed as a fraction of that at which *MSY* is achieved;
(e) *Slope*: the average annual increase of the total (1+) population from 1968-1996 as estimated from a linear regression fit to the logarithms of the model estimates of (1+) population size over this period;
(f) *RY* (1996): the 1996 replacement yield;
(g) *RY** (1996):

$$RY^*(1996) = \begin{cases} RY(1996) & \text{if } N_{96} / MSYL_{\text{mat}} < 1 \\ MSY & \text{otherwise} \end{cases} \tag{8}$$

where *MSY* is defined in terms of harvesting of the exploitable component of the population, and *N* is the number of mature animals of both sexes;
(h) $CV_{\text{add}}$: the additional variation expressed as a coefficient of variation; and
(i) $N^f_{00} / \tilde{K}_{\text{mat}}$: the number of mature females at the start of 1900 expressed as a fraction of that corresponding to the projected equilibrium level[9].

The depletion of the mature female component of the population at the start of 1900 is used to assess the extent of consistency with the perception (Reilly, 1981) that the population was commercially extinct by the end of the 19th century.

### The base-case analysis

Table 5 contrasts the post-model-pre-data and posterior distributions for base-case analysis. In addition to quantities (a)-(h) above, results are presented for the calf and non-calf survival rates ($s_c$ and $s$ respectively), the maximum pregnancy rate, $\rho_{\max}$, $MSYL_{\text{mat}}$, *MSYR* for harvesting on the exploitable component of the population, $MSYR_{\text{exp}}$, and the ratios of the 1996 1+ abundance to $\tilde{K}_{1+}$ and to $MSYL_{1+}$. Where possible, the estimates obtained by Wade (2002) are

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[6] Although these years need not be the same, year $y_1$ must, of course, be earlier than year $y_{\text{prior}}$. The age-structure at the start of year $y_1$ is assumed to be stable.

[7] If $y_{\text{prior}}$ is set equal to 1996, the analysis is analogous to the 'backwards' method of Butterworth and Punt (1995).

[8] These multiplicative process error terms are also applied to the age-structure for the first year of the projection, with different values applying to the cohorts from each decade.

[9] Computed only for those analyses for which $y_1 \leq 1900$.

included in this table. Table 5 also provides the posterior distribution for the 'original' analysis that involves projecting the population from pre-exploitation equilibrium in 1600 and ignores any possible underestimation of historical catches.

Table 5 gives results for the base-case assumption that $\gamma^+ = 0$ (see Equation (2) and following discussion), and also for the other extreme of the possible range for an increasing population: $\gamma^+ = \gamma$. The two sets of results are virtually identical. This strongly suggests that the assumption $\gamma^+ = 0$ made for this paper (rather than making allowance for the fact that its value actually lies between 0 and $\gamma$) does not introduce a bias of any quantitative consequence for the results presented.

Of the fourteen quantities in Table 5, only four (*Slope*, *RY* (1996), *RY** (1996) and $CV_{\rm add}$) are updated markedly by the data (Fig. 2). Of the remaining eleven, the lower 2.5 percentiles of the distributions for $N^f_{96} / \tilde{K}_{\rm mat}$, $N^f_{96} / MSYL_{\rm mat}$, $MSYR_{\rm mat}$, $N^{1+}_{96} / \tilde{K}_{1+}$, $N^{1+}_{96} / MSYL_{1+}$, $MSYR_{\rm exp}$ and $\tilde{K}_{1+}$ are increased by including the abundance estimates in the analysis. The probability that the mature population size is larger than $MSYL_{\rm mat}$ is slightly above 50% at 0.53. However, the posterior distribution for this quantity is very wide (Fig. 3). The status of the resource relative to its projected equilibrium level is also very uncertain (Fig. 3). There is a 0.15 probability that the resource has reached this level in terms of the mature component of the population. The negative value of the lower 2.5 percentile for *RY**(1996) for the post-model-pre-data distribution is a consequence of transient age-structure effects.

Fig. 4 shows the fits achieved by the base-case and 'original' analyses to the abundance estimates. The slope of a linear regression of the logarithms of the abundance estimates against time where each data point is weighted by the inverse of its (sampling) variance is 0.0253 $\text{yr}^{-1}$, but this drops to 0.0241 when additional variation with a *CV* of 0.14 (the median of the base-case posterior for $CV_{\rm add}$) is taken into account. The median of the posterior distribution for the '*slope*' statistic for the base-case analysis is 0.0242 which is almost the same as the latter figure. The median of the posterior for the '*slope*' statistic for the 'original' analysis (0.0177) is much smaller than either of these values.

It is not straightforward to compare the base-case results with those of Wade (2002) because the two sets of analyses are based on different population models, use different sets of parameters and make different assumptions regarding prior distributions. The posterior distribution for the calf survival rate ($s_c$) differs the most between the two sets of analyses (Table 5). The reason for this is that Wade (2002) defined $s_c$ differently – as the geometric average survival rate from birth to maturity rather than the survival rate in the first year of life.

Table 5

Posterior and post-model-pre-data distributions for 15 management-related quantities for the eastern North Pacific stock of gray whales. The point estimates given are distribution medians, followed by distribution means in round parentheses. 95% credibility intervals are given in square parentheses. Results are shown for the base-case analysis, the analysis conducted by Wade (2002), and an analysis that considers the entire period 1600-1995 and assumes no underestimation of historic commercial and aboriginal catches ('Original').

| | Base-case | | | Wade (2002) | Original |
|---|---|---|---|---|---|
| Quantity | Posterior distribution, $\gamma^+=0$ | Posterior distribution, $\gamma^+=\gamma$ | Post-model-pre-data distribution | Posterior distribution | Posterior distribution |
| $MSYR_{\rm mat}$ (%) | 5.2 (5.4)<br>[2.9; 9.1] | 5.2 (5.4)<br>[3.0; 9.0] | 4.9 (4.9)<br>[0.3; 9.7] | | 7.9 (7.9)<br>[5.5; 9.8] |
| $\tilde{K}_{1+}$ * | 31,327 (35,427)<br>[16,240; 67,722] | 31,199 (35,392)<br>[16,207; 67,768] | 39,815 (40,273)<br>[13,384; 68,460] | 31,840<br>[19,890; 67,220] | 14,684 (14,354)<br>[10,685; 16,397] |
| $N^f_{96} / \tilde{K}_{\rm mat}$ * | 0.58 (0.64)<br>[0.26; 1.18] | 0.59 (0.64)<br>[0.26; 1.17] | 0.52 (0.56)<br>[0.12; 1.15] | | 1.16 (1.17)<br>[0.98; 1.35] |
| $N^f_{96} / MSYL_{\rm mat}$ | 1.04 (1.09)<br>[0.43; 1.90] | 1.05 (1.09)<br>[0.42; 1.90] | 0.91 (0.96)<br>[0.22; 1.89] | | 1.59 (1.60)<br>[1.30; 1.92] |
| *Slope* (%) | 2.42 (2.42)<br>[1.63; 3.24] | 2.42 (2.42)<br>[1.62; 3.23] | 1.99 (1.94)<br>[-1.69; 5.56] | | 1.77 (1.75)<br>[0.96; 2.67] |
| *RY* (1996) | 545 (497)<br>[-183; 852] | 544 (496)<br>[-186; 855] | 390 (619)<br>[-273; 2,435] | 533<br>[118; 940] | -126 (-94)<br>[-668; 474] |
| *RY** (1996) | 651 (662)<br>[446; 935] | 650 (661)<br>[447; 934] | 609 (813)<br>[-17; 2,715] | | 654 (658)<br>[476; 847] |
| $CV_{\rm add}$ | 0.14 (0.14)<br>[0.09; 0.21] | 0.13 (0.14)<br>[0.09; 0.21] | 0.17 (0.17)<br>[0.01; 0.34] | 0.14<br>[0.10; 0.22] | 0.15 (0.15)<br>[0.09; 0.23] |
| $s_{\rm c}$ | 0.607 (0.626)<br>[0.380; 0.944] | 0.607 (0.625)<br>[0.381; 0.940] | 0.561 (0.593)<br>[0.376; 0.930] | 0.927<br>[0.802; 0.989] | 0.688 (0.699)<br>[0.421; 0.938] |
| $s$ | 0.973 (0.973)<br>[0.952; 0.997] | 0.973 (0.973)<br>[0.952; 0.997] | 0.969 (0.971)<br>[0.951; 0.997] | 0.984<br>[0.952; 0.999] | 0.973 (0.972)<br>[0.950; 0.997] |
| $\rho_{\rm max}$ | 0.453 (0.451)<br>[0.308; 0.591] | 0.455 (0.453)<br>[0.309; 0.597] | 0.438 (0.440)<br>[0.306; 0.590] | 0.494<br>[0.316; 0.596] | 0.462 (0.448)<br>[0.307; 0.579] |
| $MSYL_{\rm mat}$ | 0.578 (0.585)<br>[0.421; 0.772] | 0.581(0.588)<br>[0.424; 0.776] | 0.589 (0.588)<br>[0.411; 0.774] | | 0.744 (0.732)<br>[0.609; 0.797] |
| $MSYR_{\rm exp}$ (%) | 4.2 (4.4)<br>[2.6; 6.9] | 4.2 (4.4)<br>[2.6; 7.0] | 4.0 (4.0)<br>[0.2; 8.1] | 3.7<br>[2.4; 6.5] | 5.4 (5.4)<br>[3.9; 6.8] |
| $N^{1+}_{96} / \tilde{K}_{1+}$ * | 0.76 (0.79)<br>[0.35; 1.28] | 0.77 (0.79)<br>[0.35; 1.28] | 0.69 (0.70)<br>[0.15; 1.29] | 0.73<br>[0.36; 1.01] | 1.27 (1.29)<br>[1.10; 1.75] |
| $N^{1+}_{96} / MSYL_{1+}$ | 1.08 (1.04)<br>[0.47; 1.56] | 1.09 (1.04)<br>[0.46; 1.56] | 0.96 (0.93)<br>[0.26; 1.54] | 1.29<br>[0.60; 1.73] | 1.19 (1.19)<br>[1.00; 1.47] |

* $K$ replaces $\tilde{K}$ for results under 'Original'.

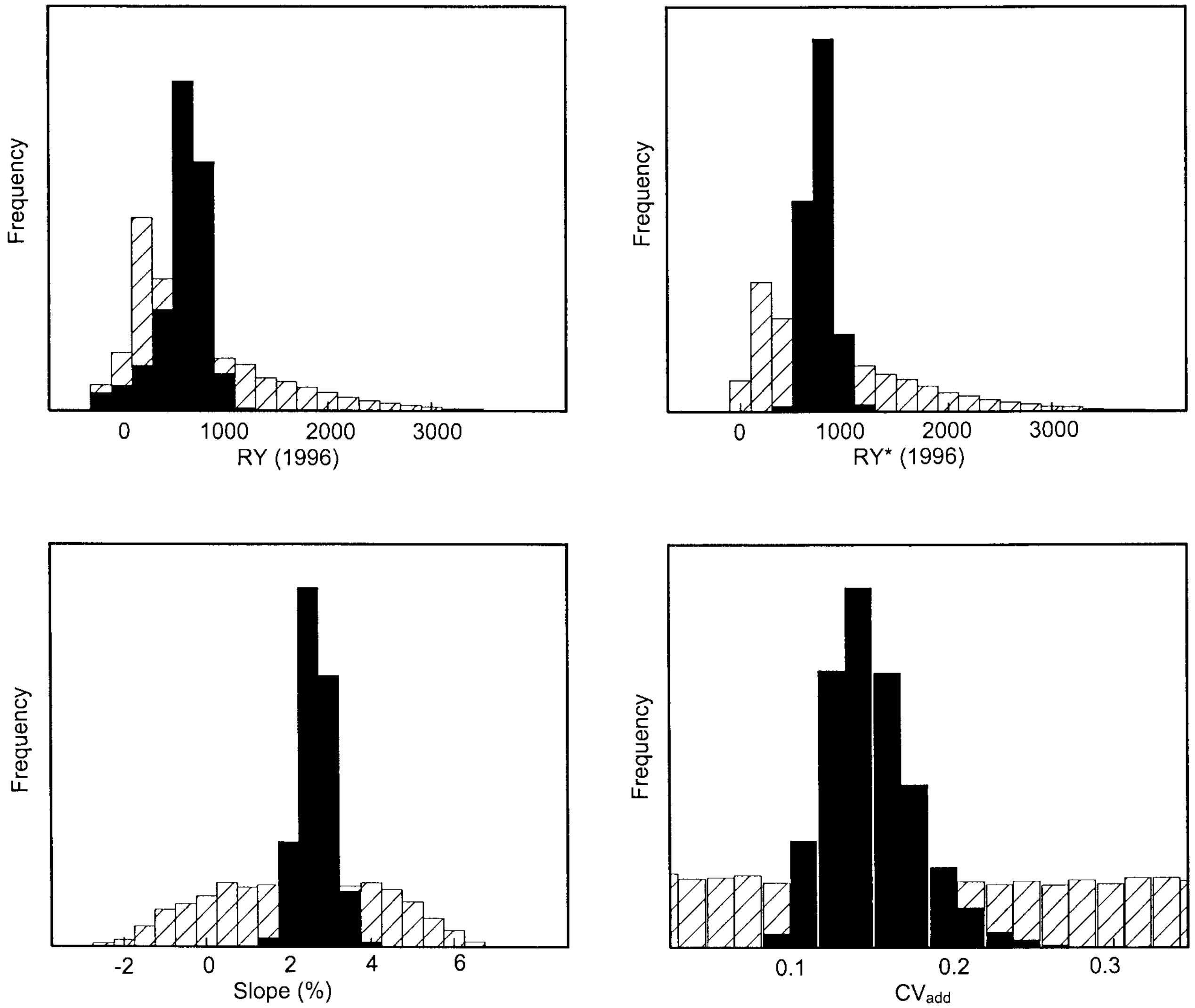

Fig. 2. Post-model-pre-data and posterior distributions (hashed and solid bars respectively) for the base-case analysis for four quantities of interest to management.

Qualitatively, the results for the 'original' analysis differ markedly from those for the base-case analysis in that the resource is assessed to have a much lower pre-exploitation equilibrium level ($K$) than the projected equilibrium level ($\tilde{K}$) for the other analyses, and to be currently above $K$ with high probability (Table 5). The 1996 replacement yield is consequently assessed to be negative with high probability. One unrealistic feature of the results for the 'original' analysis is that the population size is assessed to have been fairly large at the start of the 20th century (Table 6); this would seem to be contradicted by the fact (Reilly, 1981) that the gray whale population was extinct in terms of commercial fishing potential at this time. Although the base-case and 'original' analyses differ in terms of assessments of current status, the posterior distributions for *RY** (1996) are fairly similar.

### Sensitivity tests: underestimation of historical commercial and aboriginal catches

Allowance for underestimation of historical catches (Table 6) improves the fit to the abundance estimates (see '*slope*' posterior statistics). Of the five analyses which consider such underestimation, those which allow for underestimation of commercial catches alone lead to the most realistic results in terms of the size of the population in 1900, though only the analysis in which the prior for $\mu_C$ is U[1, 5] results in what might be considered to be commercial extinction at that time. The posterior distribution for $N^f_{00} / \tilde{K}_{\text{mat}}$ for this $\mu_C \sim$ U[1, 5] analysis is very skew. The median is 0.07 but the probability that $N^f_{00} / \tilde{K}_{\text{mat}} > 1$ exceeds 30%, so that the mean of this distribution (0.49) is much larger than the median. The posterior distributions for the '*slope*' statistic remain markedly different from that for the base-case analysis. Therefore, the introduction of priors for the extent of underestimation of historical catches as considered in this paper is insufficient to allow the population model to mimic the observed trend in the indices of absolute abundance.

### Sensitivity tests: initial conditions

The fits to the abundance estimates (as measured by the median of the posterior distribution for the '*slope*' statistic) for the analyses which involve changing the value of $y_{\text{prior}}$, the year for which a prior on absolute abundance is specified, from its base-case choice of 1968 are generally as good as that for the base-case analysis (Table 7a). Some of the management-related quantities are sensitive to the choice of $y_{\text{prior}}$. For example, the assessments based on choices of 1972, 1993, 1994 and 1996 suggest a rather lower probability that the stock has recovered to its *MSY* level in terms of the mature component of the population and there is a decreasing trend in $MSYR_{\text{mat}}$ estimates with increasing $y_{\text{prior}}$. In contrast to the results for $N^f_{96}$ / $MSYL_{\text{mat}}$ and *RY*

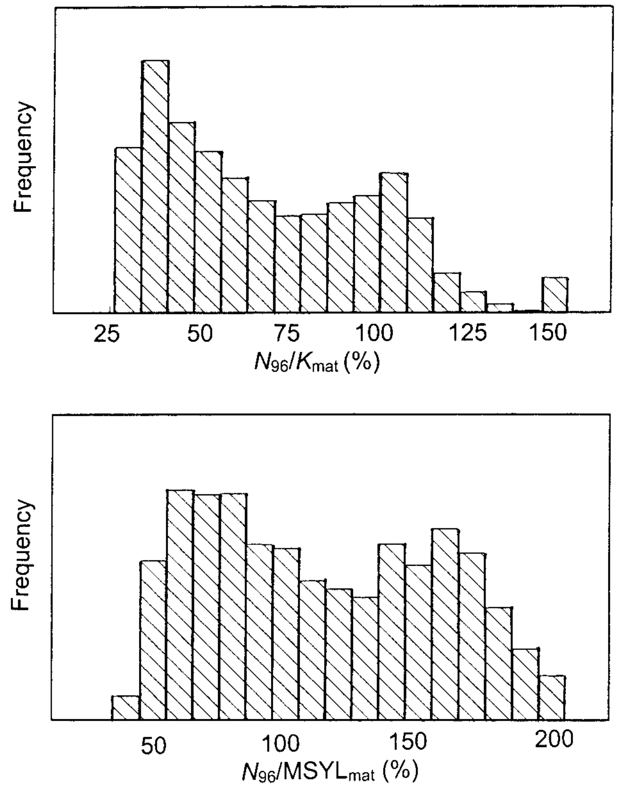

Fig. 3. Posterior distributions for $N^f_{96} / \tilde{K}_{mat}$ and $N^f_{96} / MSYL_{mat}$ from the base-case analysis.

(1996), the posterior distribution for *RY** (1996) is not particularly sensitive to the choice of $y_{prior}$. The reasons for the sensitivity to the choice of $y_{prior}$ are unclear, but are likely not related to the data used for assessment purposes because

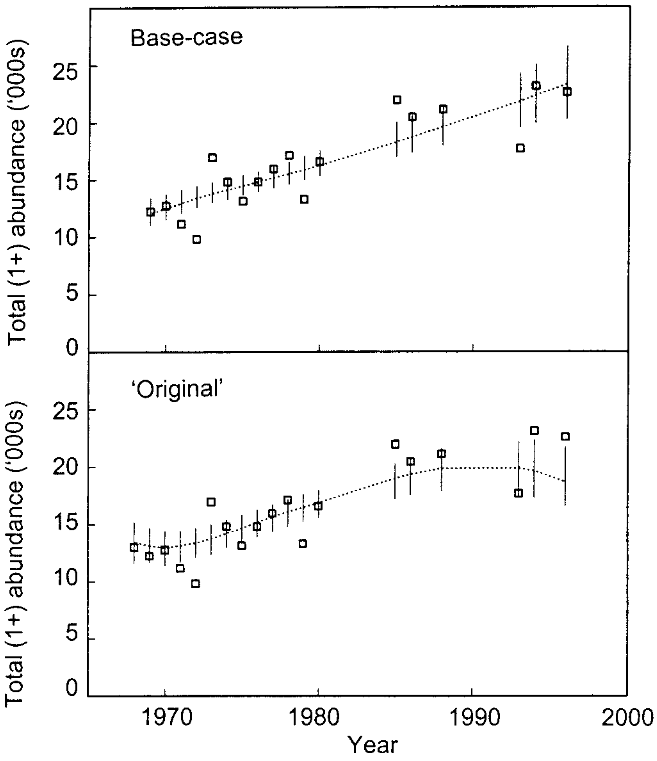

Fig. 4. Shore-count-based estimates of 1+ abundance for the eastern north Pacific stock of gray whales (open squares) along with posterior distributions of 1+ population size for the base-case and 'original' analyses. The dotted line joins the posterior medians and the bars represent posterior 95% credibility limits.

some of the patterns evident in Table 7a (for example, that for $N^f_{96} / MSYL_{mat}$) are also evident in statistics of the post-model-pre-data distributions (Table 7b).

Table 6

Estimates of eleven management-related quantities for the eastern North Pacific stock of gray whales. The point estimates given are posterior medians, followed by posterior means in round parentheses. Posterior 95% credibility intervals are given in square parentheses. Results are shown for analyses that place prior distributions on the extent of under-reporting of historical catches.

| | Base-case | Original | Priors for $\mu_A$ and $\mu_C$ | | | | |
|---|---|---|---|---|---|---|---|
| Quantity | Posterior distribution | Posterior distribution | $\mu_A \sim U[1, 2]$<br>$\mu_C \sim U[1, 2]$ | $\mu_A = 1$<br>$\mu_C \sim U[1, 3]$ | $\mu_A \sim U[1,3]$<br>$\mu_C = 1$ | $\mu_A = 1$<br>$\mu_C \sim U[1, 5]$ | $\mu_A \sim U[1,5]$<br>$\mu_C = 1$ |
| $MSYR_{mat}$ (%) | 5.2 (5.4)<br>[2.9; 9.1] | 7.9 (7.9)<br>[5.5; 9.8] | 8.4 (8.1)<br>[4.8; 9.9] | 7.8 (7.5)<br>[4.1; 9.8] | 8.1 (8.0)<br>[5.2; 9.9] | 6.4 (6.5)<br>[3.9; 9.8] | 7.9 (7.9)<br>[4.6; 9.9] |
| $\tilde{K}_{1+}$ * | 31,327 (35,427)<br>[16,240; 67,722] | 14,684 (14,354)<br>[10,685; 16,397] | 15,613 (15,652)<br>[11,088; 19,253] | 15,553 (16,549)<br>[10,611; 27,957] | 15,286 (15,330)<br>[11,452; 21,401] | 18,525 (24,103)<br>[12,971; 46,594] | 15,301 (15,724)<br>[11,280; 32,687] |
| $N^f_{96} / \tilde{K}_{mat}$ * | 0.58 (0.64)<br>[0.26; 1.18] | 1.16 (1.17)<br>[0.98; 1.35] | 1.11 (1.12)<br>[0.80; 1.36] | 1.10 (1.06)<br>[0.58; 1.38] | 1.12 (1.13)<br>[0.77; 1.37] | 0.87 (0.84)<br>[0.37; 1.30] | 1.11 (1.11)<br>[0.55; 1.38] |
| $N^f_{96} / MSYL_{mat}$ | 1.04 (1.09)<br>[0.43; 1.90] | 1.59 (1.60)<br>[1.30; 1.92] | 1.60 (1.59)<br>[1.22; 1.89] | 1.53 (1.49)<br>[0.96; 1.89] | 1.62 (1.60)<br>[1.21; 1.91] | 1.31 (1.25)<br>[0.58; 1.77] | 1.55 (1.56)<br>[0.92; 1.91] |
| *Slope* (%) | 2.42 (2.42)<br>[1.63; 3.24] | 1.77 (1.75)<br>[0.96; 2.67] | 1.94 (1.91)<br>[1.13; 2.52] | 1.91 (1.87)<br>[1.01; 2.55] | 1.86 (1.83)<br>[1.11; 2.38] | 1.99 (1.99)<br>[1.22; 2.81] | 1.91 (1.87)<br>[1.08; 2.45] |
| *RY* (1996) | 545 (497)<br>[-183; 852] | -126 (-94)<br>[-668; 474] | 46 (-1)<br>[-611; 510] | 75 (57)<br>[-590; 718] | -0 (-22)<br>[-660; 469] | 377 (254)<br>[-574; 795] | 35 (14)<br>[-518; 532] |
| *RY** (1996) | 651 (662)<br>[446; 935] | 654 (658)<br>[476; 847] | 674 (676)<br>[469; 842] | 678 (662)<br>[437; 838] | 648 (658)<br>[490; 844] | 641 (636)<br>[420; 865] | 645 (657)<br>[498; 846] |
| $N^f_{00} / \tilde{K}_{mat}$ * | N/A | 1.11 (1.06)<br>[0.35; 1.35] | 1.04 (0.79)<br>[0.03; 1.32] | 0.58 (0.65)<br>[0.03; 1.37] | 1.15 (1.08)<br>[0.11; 1.31] | 0.07 (0.49)<br>[0.02; 1.36] | 1.16 (1.06)<br>[0.09; 1.40] |
| $CV_{add}$ | 0.14 (0.14)<br>[0.09; 0.21] | 0.15 (0.15)<br>[0.09; 0.23] | 0.14 (0.15)<br>[0.10; 0.22] | 0.14 (0.15)<br>[0.10; 0.23] | 0.14 (0.14)<br>[0.10; 0.22] | 0.14 (0.14)<br>[0.09; 0.22] | 0.14 (0.14)<br>[0.10; 0.23] |
| $\mu_C$ | 1 | 1 | 1.33 (1.39)<br>[1.02; 1.92] | 1.46 (1.61)<br>[1.04; 2.80] | 1 | 1.94 (2.39)<br>[1.06; 4.69] | 1 |
| $\mu_A$ | 1 | 1 | 1.51 (1.49)<br>[1.01; 1.96] | 1 | 1.82 (1.82)<br>[1.08; 2.71] | 1 | 1.87 (1.87)<br>[1.05; 3.22] |

* *K* replaces $\tilde{K}$ for results under 'Original' and 'Priors for $\mu_A$ and $\mu_C$'.

Table 7

Estimates of eight management-related quantities for the eastern North Pacific stock of gray whales. The point estimates given are posterior medians, followed by posterior means in round parentheses. Posterior 95% credibility intervals are given in square parentheses. Results are shown for analyses that vary $y_{\text{prior}}$, the year for which a prior distribution on 1+ abundance is specified.

| $y_{\text{prior}}$ | $MSYR_{\text{mat}}$ | $\tilde{K}_{1+}$ | $N^f_{96} / \tilde{K}_{\text{mat}}$ | $N^f_{96} / MSYL_{\text{mat}}$ | *Slope* (%) | $RY$ (1996) | $RY$* (1996) | $CV_{\text{add}}$ |
|---|---|---|---|---|---|---|---|---|
| **(a) Posterior distributions** | | | | | | | | |
| 1968 | 5.2 (5.4) | 31,327 (35,427) | 0.58 (0.64) | 1.04 (1.09) | 2.42 (2.42) | 545 (497) | 651 (662) | 0.14 (0.14) |
| (Base-case) | [2.9; 9.1] | [16,240; 67,722] | [0.26; 1.18] | [0.43; 1.90] | [1.63; 3.24] | [-183; 852] | [446; 935] | [0.09; 0.21] |
| 1969 | 5.2 (5.4) | 30,317 (35,046) | 0.61 (0.65) | 1.07 (1.11) | 2.42 (2.42) | 543 (491) | 654 (664) | 0.14 (0.14) |
| | [3.0; 9.1] | [16,267; 67,704] | [0.26; 1.17] | [0.42; 1.92] | [1.59; 3.24] | [-223; 848] | [442; 935] | [0.09; 0.21] |
| 1970 | 5.2 (5.4) | 30,187 (35,236) | 0.61 (0.64) | 1.06 (1.10) | 2.43 (2.42) | 544 (492) | 655 (665) | 0.14 (0.14) |
| | [2.9; 9.1] | [16,374; 67,753] | [0.26; 1.17] | [0.42; 1.91] | [1.60; 3.24] | [-251; 858] | [446; 942] | [0.09; 0.21] |
| 1971 | 5.2 (5.4) | 32,189 (35,903) | 0.57 (0.63) | 1.01 (1.07) | 2.41 (2.42) | 548 (499) | 653 (661) | 0.13 (0.14) |
| | [3.0; 9.1] | [16,001; 67,540] | [0.26; 1.18] | [0.42; 1.89] | [1.61; 3.22] | [-226; 844] | [443; 934] | [0.09; 0.21] |
| 1972 | 5.1 (5.3) | 37,939 (39,332) | 0.48 (0.57) | 0.76 (0.93) | 2.33 (2.34) | 562 (521) | 637 (644) | 0.13 (0.13) |
| | [3.0; 8.8] | [16,395; 68,339] | [0.26; 1.13] | [0.38; 1.89] | [1.60; 3.18] | [-231; 843] | [437; 917] | [0.08; 0.20] |
| 1973 | 5.0 (5.3) | 33,034 (36,410) | 0.55 (0.62) | 0.98 (1.06) | 2.39 (2.41) | 551 (502) | 642 (657) | 0.13 (0.14) |
| | [3.0; 8.9] | [15,987; 67,812] | [0.26; 1.16] | [0.43; 1.88] | [1.63; 3.24] | [-186; 860] | [449; 940] | [0.09; 0.21] |
| 1974 | 5.2 (5.4) | 31,327 (35,672) | 0.58 (0.63) | 1.03 (1.08) | 2.42 (2.42) | 552 (501) | 653 (662) | 0.14 (0.14) |
| | [3.0; 9.0] | [16,272; 67,536] | [0.26; 1.17] | [0.42; 1.91] | [1.61; 3.22] | [-202; 851] | [444; 935] | [0.09; 0.21] |
| 1975 | 5.2 (5.4) | 31,807 (35,884) | 0.57 (0.63) | 1.00 (1.07) | 2.43 (2.43) | 549 (497) | 656 (665) | 0.14 (0.14) |
| | [3.0; 9.1] | [16,001; 67,901] | [0.26; 1.19] | [0.41; 1.89] | [1.61; 3.23] | [-223; 854] | [437; 941] | [0.09; 0.21] |
| 1976 | 5.2 (5.4) | 31,897 (35,815) | 0.57 (0.63) | 1.01 (1.08) | 2.42 (2.43) | 550 (496) | 653 (665) | 0.14 (0.14) |
| | [2.9; 9.1] | [16,115; 67,624] | [0.26; 1.19] | [0.42; 1.87] | [1.63; 3.24] | [-251; 852] | [444; 947] | [0.09; 0.21] |
| 1977 | 5.1 (5.3) | 32,529 (36,222) | 0.56 (0.62) | 0.99 (1.06) | 2.42 (2.42) | 551 (506) | 650 (660) | 0.14 (0.14) |
| | [2.9; 8.9] | [16,349; 67,695] | [0.26 1.17] | [0.42; 1.86] | [1.60; 3.23] | [-201; 859] | [445; 938] | [0.09; 0.21] |
| 1978 | 5.1 (5.4) | 31,883 (35,991) | 0.57 (0.63) | 1.01 (1.06) | 2.44 (2.43) | 557 (507) | 655 (665) | 0.14 (0.14) |
| | [3.0; 9.0] | [16,350; 67,877] | [0.26; 1.17] | [0.42; 1.87] | [1.64; 3.23] | [-201; 861] | [446; 938] | [0.09; 0.21] |
| 1979 | 5.0 (5.3) | 34,781 (37,218) | 0.53 (0.60) | 0.94 (1.03) | 2.41 (2.41) | 562 (520) | 648 (660) | 0.13 (0.14) |
| | [3.0; 8.9] | [16,329; 67,701] | [0.26; 1.18] | [0.42; 1.88] | [1.60; 3.23] | [-180; 866] | [441; 946] | [0.09; 0.21] |
| 1980 | 5.1 (5.3) | 32,842 (36,546) | 0.55 (0.62) | 0.97 (1.04) | 2.42 (2.42) | 559 (511) | 654 (663) | 0.14 (0.14) |
| | [2.9; 8.8] | [16,265; 67,753] | [0.26; 1.18] | [0.42; 1.85] | [1.62; 3.22] | [-211; 854] | [441; 937] | [0.09; 0.21] |
| 1985 | 4.9 (5.1) | 35,741 (38,150) | 0.51 (0.58) | 0.90 (0.99) | 2.42 (2.42) | 573 (533) | 643 (654) | 0.14 (0.14) |
| | [2.9; 8.6] | [16,719; 67,889] | [0.26; 1.15] | [0.42; 1.80] | [1.60; 3.20] | [-115; 857] | [435; 921] | [0.09; 0.21] |
| 1986 | 5.0 (5.2) | 35,973 (38,249) | 0.51 (0.58) | 0.90 (0.98) | 2.43 (2.43) | 574 (547) | 648 (656) | 0.14 (0.14) |
| | [2.9; 8.4] | [16,880; 68,055] | [0.26; 1.14] | [0.42; 1.80] | [1.62; 3.23] | [-60; 864] | [436; 917] | [0.09; 0.21] |
| 1988 | 4.9 (5.0) | 37,394 (39,426) | 0.49 (0.55) | 0.86 (0.94) | 2.42 (2.42) | 582 (572) | 642 (648) | 0.14 (0.14) |
| | [2.9; 8.0] | [17,577; 68,372] | [0.26; 1.07] | [0.41; 1.74] | [1.61; 3.23] | [190; 873] | [435; 910] | [0.09; 0.21] |
| 1993 | 4.7 (4.8) | 42,763 (43,716) | 0.43 (0.47) | 0.72 (0.80) | 2.43 (2.43) | 610 (625) | 637 (651) | 0.14 (0.14) |
| | [2.9; 7.3] | [20,742; 68,308] | [0.25; 0.87] | [0.39; 1.55] | [1.58; 3.29] | [377; 934] | [425; 949] | [0.09; 0.21] |
| 1994 | 4.6 (4.7) | 43,007 (43,528) | 0.42 (0.48) | 0.75 (0.83) | 2.38 (2.39) | 595 (604) | 627 (635) | 0.14 (0.14) |
| | [2.9; 6.9] | [19,827; 68,510] | [0.25; 0.91] | [0.40; 1.58] | [1.58; 3.20] | [377; 872] | [425; 888] | [0.09; 0.21] |
| 1996 | 4.6 (4.7) | 43,807 (44,378) | 0.42 (0.46) | 0.72 (0.80) | 2.40 (2.40) | 609 (615) | 631 (639) | 0.14 (0.14) |
| | [2.8; 7.0] | [21,376; 68,682] | [0.25; 0.85] | [0.40; 1.53] | [1.57; 3.24] | [382; 890] | [424; 901] | [0.09; 0.21] |
| **(b) Post-model-pre-data distributions** | | | | | | | | |
| 1968 | 4.9 (4.9) | 39,815 (40,273) | 0.52 (0.56) | 0.91 (0.96) | 1.99 (1.94) | 390 (619) | 609 (813) | 0.17 (0.17) |
| (Base-case) | [0.3; 9.7] | [13,384; 68,460] | [0.12; 1.15] | [0.22; 1.89] | [-1.69; 5.56] | [-273; 2,435] | [-17; 2,715] | [0.01; 0.34] |
| 1969 | 4.8 (4.9) | 39,206 (39,648) | 0.49 (0.54) | 0.84 (0.91) | 1.98 (1.93) | 402 (629) | 570 (783) | 0.17 (0.17) |
| | [0.2; 9.7] | [12,157; 68,291] | [0.12; 1.14] | [0.21; 1.84] | [-1.85; 5.65] | [-205; 2,443] | [-19; 2,707] | [0.01; 0.34] |
| 1970 | 5.0 (5.0) | 39,026 (39,529) | 0.51 (0.55) | 0.88 (0.93) | 2.02 (1.98) | 412 (633) | 595 (793) | 0.18 (0.17) |
| | [0.2; 9.7] | [12,122; 68,259] | [0.13; 1.15] | [0.22; 1.84] | [-1.73; 5.61] | [-225; 2,415] | [-18; 2,636] | [0.01; 0.34] |
| 1971 | 4.9 (4.9) | 38,607 (39,048) | 0.42 (0.48) | 0.73 (0.81) | 2.00 (1.90) | 391 (596) | 503 (696) | 0.17 (0.17) |
| | [0.3; 9.7] | [11,838; 68,192] | [0.10; 1.11] | [0.17; 1.76] | [-2.03; 5.70] | [-41; 2,268] | [-21; 2,474] | [0.01; 0.34] |
| 1972 | 4.9 (4.9) | 38,154 (38,856) | 0.35 (0.42) | 0.61 (0.71) | 1.97 (1.81) | 372 (553) | 447 (615) | 0.17 (0.17) |
| | [0.2; 9.7] | [11,498; 68,303] | [0.08; 1.08] | [0.14; 1.68] | [-2.35; 5.60] | [-31; 2,049] | [-24; 2,180] | [0.01; 0.34] |
| 1973 | 5.0 (5.0) | 40,181 (40,436) | 0.60 (0.63) | 1.04 (1.07) | 2.00 (2.03) | 425 (659) | 682 (878) | 0.17 (0.17) |
| | [0.3; 9.7] | [12,477; 68,465] | [0.20; 1.18] | [0.35; 1.87] | [-1.16; 5.58] | [-357; 2,534] | [-7; 2,793] | [0.01; 0.34] |
| 1974 | 4.9 (4.9) | 39,583 (40,155) | 0.52 (0.57) | 0.90 (0.96) | 2.09 (2.08) | 438 (660) | 621 (804) | 0.17 (0.17) |
| | [0.3; 9.7] | [12,593; 68,428] | [0.17; 1.14] | [0.29; 1.82] | [-1.35; 5.70] | [-183; 2,432] | [-11; 2,613] | [0.01; 0.34] |
| 1975 | 5.0 (4.9) | 39,518 (39,926) | 0.45 (0.50) | 0.78 (0.86) | 2.16 (2.07) | 453 (636) | 568 (730) | 0.17 (0.17) |
| | [0.2; 9.7] | [11,994; 68,363] | [0.14; 1.10] | [0.24; 1.75] | [-1.54; 5.71] | [-40; 2,222] | [-17; 2,355] | [0.01; 0.34] |
| 1976 | 4.9 (5.0) | 39,733 (40,027) | 0.50 (0.55) | 0.87 (0.93) | 2.15 (2.13) | 468 (655) | 604 (770) | 0.17 (0.17) |
| | [0.3; 9.7] | [12,489; 68,385] | [0.17; 1.12] | [0.29; 1.77] | [-1.29; 5.70] | [-122; 2,294] | [-10; 2,450] | [0.01; 0.34] |
| 1977 | 4.9 (4.9) | 39,751 (40,336) | 0.51 (0.56) | 0.89 (0.95) | 2.14 (2.13) | 471 (670) | 626 (790) | 0.17 (0.17) |
| | [0.3; 9.7] | [12,496; 68,365] | [0.19; 1.13] | [0.32; 1.78] | [-1.20; 5.74] | [-122; 2,344] | [-7; 2,489] | [0.01; 0.34] |
| 1978 | 4.9 (5.0) | 40,391 (40,657) | 0.53 (0.58) | 0.93 (0.98) | 2.18 (2.18) | 486 (679) | 649 (817) | 0.17 (0.17) |
| | [0.3; 9.8] | [12,401; 68,290] | [0.20; 1.14] | [0.34; 1.80] | [-1.09; 5.73] | [-169; 2,332] | [-4; 2,534] | [0.01; 0.34] |
| 1979 | 4.8 (4.9) | 39,292 (39,687) | 0.41 (0.47) | 0.71 (0.80) | 2.07 (2.04) | 429 (592) | 509 (659) | 0.17 (0.17) |
| | [0.3; 9.7] | [12,073; 68,289] | [0.15; 1.09] | [0.25; 1.69] | [-1.41; 5.66] | [-29; 2,041] | [-12; 2,174] | [0.01; 0.34] |
| 1980 | 4.9 (4.9) | 40,573 (40,797) | 0.48 (0.54) | 0.84 (0.92) | 2.22 (2.15) | 495 (653) | 609 (750) | 0.17 (0.17) |
| | [0.3; 9.7] | [12,847; 68,290] | [0.19; 1.11] | [0.33; 1.77] | [-1.12; 5.66] | [-32; 2,182] | [-5; 2,317] | [0.01; 0.34] |
| 1985 | 5.1 (5.2) | 41,812 (41,548) | 0.55 (0.59) | 0.94 (1.00) | 2.39 (2.33) | 606 (747) | 722 (852) | 0.17 (0.17) |
| | [0.4; 9.7] | [12,254; 68,472] | [0.25; 1.09] | [0.42; 1.78] | [-0.94; 5.77] | [-18; 2,229] | [21; 2,368] | [0.01; 0.34] |

cont...

Table 7 continued.

| $y_{\text{prior}}$ | $MSYR_{\text{mat}}$ | $\tilde{K}_{1+}$ | $N^f_{96}/\tilde{K}_{\text{mat}}$ | $N^f_{96}/MSYL_{\text{mat}}$ | *Slope* (%) | *RY* (1996) | *RY** (1996) | $CV_{\text{add}}$ |
|---|---|---|---|---|---|---|---|---|
| **(b) Post-model-pre-data distributions (continued)** | | | | | | | | |
| 1986 | 5.0 (5.0) | 41,187 (41,252) | 0.50 (0.55) | 0.87 (0.94) | 2.37 (2.27) | 576 (701) | 666 (786) | 0.17 (0.17) |
| | [0.3; 9.7] | [12,439; 68,492] | [0.23; 1.07] | [0.38; 1.76] | [-0.95; 5.72] | [-15; 2,085] | [12; 2,246] | [0.01; 0.34] |
| 1988 | 5.1 (5.1) | 41,600 (41,589) | 0.49 (0.54) | 0.84 (0.92) | 2.43 (2.32) | 603 (704) | 683 (784) | 0.17 (0.17) |
| | [0.4; 9.7] | [12,440; 68,583] | [0.23; 1.02] | [0.38; 1.73] | [-0.91; 5.70] | [-6; 1,996] | [23; 2,180] | [0.01; 0.34] |
| 1993 | 4.8 (4.9) | 41,132 (41,195) | 0.37 (0.43) | 0.64 (0.74) | 2.07 (2.02) | 468 (538) | 499 (578) | 0.17 (0.17) |
| | [0.3; 9.7] | [12,666; 68,505] | [0.16; 0.95] | [0.27; 1.61] | [-0.97; 5.23] | [-12; 1,657] | [3; 1,845] | [0.01; 0.34] |
| 1994 | 5.2 (5.3) | 42,031 (41,908) | 0.45 (0.50) | 0.77 (0.85) | 2.43 (2.32) | 604 (665) | 663 (733) | 0.18 (0.18) |
| | [0.6; 9.7] | [12,220; 68,524] | [0.20; 1.00] | [0.34; 1.71] | [-0.89; 5.48] | [-7; 1,857] | [39; 2,009] | [0.01; 0.34] |
| 1996 | 5.1 (5.2) | 42,318 (42,128) | 0.41 (0.47) | 0.70 (0.80) | 2.32 (2.20) | 557 (603) | 610 (670) | 0.17 (0.17) |
| | [0.6; 9.7] | [12,388; 68,549] | [0.18; 1.00] | [0.31; 1.71] | [-0.91; 5.25] | [-6; 1,723] | [38; 1,905] | [0.01; 0.34] |

The results for the analyses that involve changing the first year considered in the projection ($y_1$) are given in Table 8. The assumption of a stable age-structure at the start of year $y_1$ becomes less defensible as $y_1$ is reduced. However, the influence of violations of this assumption on the dynamics of the population during the period for which abundance estimates are available also decreases as $y_1$ is reduced. Butterworth *et al.* (1995) assessed the Cape fur seal population off southern Africa using an approach similar to that applied here, and selected $y_1$ so that the impact of transient age-structure effects on the period for which abundance estimates are available is slight.

The fits to the abundance data (as measured by the median of the posterior distribution for the '*slope*' statistic) are worst for $y_1 = 1900$ and $y_1 = 1890$, although the median of the posterior for '*slope*' is nevertheless closer to the base-case value than for the 'original' analysis. The posterior distributions for the depletion of the mature population in 1900 for the three analyses which set $y_1$ to 1900 or earlier are much more consistent with perceptions of a stock highly depleted at that time. For example, the posterior for $N^f_{00}/\tilde{K}_{\text{mat}}$ for the $y_1 = 1880$ analysis has a median of 0.03 and 95% credibility interval [0.01, 0.07].

The results are generally insensitive to decreasing $y_1$ from 1968 to any year after 1930. For a choice of $y_1$ between 1890 and 1910, the assessment becomes slightly more pessimistic than the base-case analysis (lower $MSYR_{\text{mat}}$, lower *RY** (1996) and a more depleted resource). However, the results for $y_1 = 1880$ are closer to those for $y_1 = 1920$ than to those for $y_1 = 1890$.

The results in Tables 7 and 8 indicate that although the base-case choices for $y_1$ and $y_{\text{prior}}$ were selected primarily for computational convenience, the results of the assessment are not markedly sensitive to them. This conclusion applies particularly to the posterior for *RY** (1996), the median of which varies within a narrow range for all of the choices for $y_1$ and $y_{\text{prior}}$ examined.

### Sensitivity tests: process error

Table 9 lists the results for the analyses which allow for process error. Results are shown for variants of the base-case and the 'original' analyses. For the analyses based on $y_1 = y_{\text{prior}} = 1968$, the posterior distributions for '*slope*' and $CV_{\text{add}}$ are relatively insensitive to the value assumed for $\sigma_r$. However, the results in terms of the other quantities generally become a little less optimistic and more variable as the value of $\sigma_r$ is increased from 0 to 0.2. The increase in variability is most notable for *RY* (1996) and *RY** (1996). For the computations based on the 'original' analysis with $y_1 = 1600$, the results frequently become more optimistic (in terms of resource productivity levels and population increase rates) and variable as $\sigma_r$ is increased. Despite some

Table 8

Estimates of eight management-related quantities for the eastern North Pacific stock of gray whales. The point estimates given are posterior medians, followed by posterior means in round parentheses. Posterior 95% credibility intervals are given in square parentheses. Results are shown for analyses that vary $y_1$, the first year considered in the analysis.

| $y_1$ | $MSYR_{\text{mat}}$ | $\tilde{K}_{1+}$ | $N^f_{96}/\tilde{K}_{\text{mat}}$ | $N^f_{96}/MSYL_{\text{mat}}$ | *Slope* (%) | *RY* (1996) | *RY** (1996) | $CV_{\text{add}}$ |
|---|---|---|---|---|---|---|---|---|
| 1968 | 5.2 (5.4) | 31,327 (35,427) | 0.58 (0.64) | 1.04 (1.09) | 2.42 (2.42) | 545 (497) | 651 (662) | 0.14 (0.14) |
| (Base-case) | [2.9; 9.1] | [16,240; 67,722] | [0.26; 1.18] | [0.43; 1.90] | [1.63; 3.24] | [-183; 852] | [446; 935] | [0.09; 0.21] |
| 1960 | 5.3 (5.5) | 30,234 (34,951) | 0.60 (0.64) | 1.07 (1.10) | 2.41 (2.41) | 548 (496) | 660 (669) | 0.14 (0.14) |
| | [3.0; 9.2] | [15,836; 67,490] | [0.26; 1.18] | [0.43; 1.89] | [1.60; 3.24] | [-222; 862] | [449; 944] | [0.09; 0.21] |
| 1950 | 5.3 (5.6) | 29,504 (34,411) | 0.61 (0.65) | 1.11 (1.12) | 2.42 (2.41) | 546 (499) | 665 (670) | 0.14 (0.14) |
| | [3.1; 9.3] | [15,728; 67,551] | [0.26; 1.16] | [0.43; 1.92] | [1.60; 3.21] | [-165; 850] | [454; 919] | [0.09; 0.21] |
| 1940 | 5.3 (5.6) | 29,706 (34,364) | 0.60 (0.64) | 1.11 (1.14) | 2.40 (2.40) | 544 (499) | 661 (665) | 0.13 (0.14) |
| | [3.1; 9.2] | [15,935; 67,378] | [0.25; 1.15] | [0.45; 1.92] | [1.58; 3.19] | [-148; 847] | [450; 913] | [0.09; 0.21] |
| 1930 | 5.2 (5.5) | 30,392 (34,924) | 0.59 (0.63) | 1.10 (1.12) | 2.39 (2.38) | 545 (507) | 654 (658) | 0.14 (0.14) |
| | [3.0; 9.2] | [16,191; 67,640] | [0.25; 1.11] | [0.46; 1.88] | [1.57; 3.19] | [-77; 836] | [446; 896] | [0.09; 0.21] |
| 1920 | 5.1 (5.3) | 32,871 (36,267) | 0.54 (0.60) | 1.03 (1.07) | 2.38 (2.38) | 560 (531) | 648 (653) | 0.13 (0.14) |
| | [3.0; 8.7] | [16,116; 67,865] | [0.25; 1.09] | [0.45; 1.77] | [1.57; 3.17] | [28; 851] | [449; 884] | [0.09; 0.21] |
| 1910 | 4.7 (4.8) | 38,836 (40,293) | 0.46 (0.52) | 0.85 (0.92) | 2.31 (2.30) | 575 (569) | 624 (629) | 0.14 (0.14) |
| | [2.8; 7.3] | [17,341; 68,243] | [0.24; 1.02] | [0.45; 1.61] | [1.53; 3.02] | [238; 836] | [430; 857] | [0.09; 0.21] |
| 1900 | 4.3 (4.4) | 44,872 (44,544) | 0.38 (0.44) | 0.71 (0.78) | 2.19 (2.17) | 564 (566) | 591 (594) | 0.14 (0.14) |
| | [2.7; 6.3] | [19,654; 69,026] | [0.24; 0.87] | [0.43; 1.39] | [1.37; 2.81] | [331; 798] | [395; 805] | [0.09; 0.21] |
| 1890 | 4.3 (4.4) | 45,853 (45,136) | 0.38 (0.44) | 0.69 (0.76) | 2.17 (2.14) | 563 (562) | 586 (588) | 0.14 (0.14) |
| | [2.7; 6.3] | [19,333; 68,999] | [0.24; 0.88] | [0.43; 1.38] | [1.39; 2.75] | [328; 778] | [399; 793] | [0.09; 0.21] |
| 1880 | 5.1 (5.3) | 32,712 (36,384) | 0.54 (0.60) | 1.04 (1.08) | 2.38 (2.38) | 554 (526) | 648 (653) | 0.13 (0.14) |
| | [2.9; 9.1] | [16,116; 68,099] | [0.25; 1.09] | [0.46; 1.83] | [1.56; 3.18] | [-2; 855] | [446; 891] | [0.09; 0.21] |

Table 9

Estimates of eight management-related quantities for the eastern North Pacific stock of gray whales. The point estimates given are posterior medians, followed by posterior means in round parentheses. Posterior 95% credibility intervals are given in square parentheses. Results are shown for analyses that allow for process error in calf survival rate.

| Specification | $MSYR_{\text{mat}}$ | $\tilde{K}_{1+}$ | $N_{96}^{f} / \tilde{K}_{\text{mat}}$ | $N_{96}^{f} / MSYL_{\text{mat}}$ | *Slope* (%) | *RY* (1996) | *RY** (1996) | $CV_{\text{add}}$ |
|---|---|---|---|---|---|---|---|---|
| $y_1$=$y_{\text{prior}}$=1968 | | | | | | | | |
| Base-case | 5.2 (5.4) | 31,327 (35,427) | 0.58 (0.64) | 1.04 (1.09) | 2.42 (2.42) | 545 (497) | 651 (662) | 0.14 (0.14) |
| | [2.9; 9.1] | [16,240; 67,722] | [0.26; 1.18] | [0.43; 1.90] | [1.63; 3.24] | [-183; 852] | [446; 935] | [0.09; 0.21] |
| $\sigma_r$=0.05 | 5.2 (5.4) | 31,299 (35,589) | 0.59 (0.64) | 1.04 (1.09) | 2.42 (2.42) | 537 (496) | 651 (659) | 0.14 (0.14) |
| | [2.9; 9.1] | [16,247; 67,697] | [0.26; 1.16] | [0.43; 1.90] | [1.62; 3.24] | [-201; 888] | [419; 953] | [0.09; 0.21] |
| $\sigma_r$=0.1 | 5.2 (5.4) | 31,213 (35,489) | 0.59 (0.64) | 1.05 (1.09) | 2.41 (2.42) | 516 (486) | 647 (653) | 0.13 (0.14) |
| | [2.8; 9.2] | [16,074; 67,247] | [0.26; 1.18] | [0.43; 1.90] | [1.60; 3.25] | [-193; 929] | [346; 984] | [0.09; 0.21] |
| $\sigma_r$=0.2 | 5.0 (5.2) | 34,285 (36,950) | 0.54 (0.61) | 0.96 (1.05) | 2.41 (2.41) | 464 (458) | 613 (621) | 0.13 (0.14) |
| | [2.6; 9.3] | [16,276; 67,729] | [0.26; 1.19] | [0.42; 1.95] | [1.59; 3.22] | [-214; 1,041] | [172; 1,068] | [0.09; 0.21] |
| $y_1$=1600 | | | | | | | | |
| Original | 7.9 (7.9) | 14,684 (14,354) | 1.16 (1.17) | 1.59 (1.60) | 1.77 (1.75) | -126 (-94) | 654 (658) | 0.15 (0.15) |
| | [5.5; 9.8] | [10,685; 16,397] | [0.98; 1.35] | [1.30; 1.92] | [0.96; 2.67] | [-668; 474] | [476; 847] | [0.09; 0.23] |
| $\sigma_r$=0.05 | 7.8 (8.0) | 14,942 (14,800) | 1.13 (1.16) | 1.62 (1.62) | 1.77 (1.78) | -34 (-66) | 666 (664) | 0.13 (0.14) |
| | [5.6; 9.8] | [11,186; 17,448] | [0.99; 1.36] | [1.30; 1.96] | [1.05; 2.37] | [-539; 434] | [490; 826] | [0.10; 0.22] |
| $\sigma_r$=0.1 | 8.2 (8.1) | 15,103 (14,871) | 1.12 (1.16) | 1.63 (1.63) | 2.02 (2.00) | 78 (34) | 665 (669) | 0.13 (0.14) |
| | [5.6; 9.8] | [11,322; 17,128] | [1.01; 1.42] | [1.36; 1.95] | [1.22; 2.63] | [-612; 525] | [490; 849] | [0.09; 0.21] |
| $\sigma_r$=0.2 | 8.0 (7.7) | 14,848 (14,906) | 1.21 (1.18) | 1.67 (1.68) | 1.95 (1.96) | -242 (-157) | 631 (636) | 0.14 (0.14) |
| | [3.8; 9.7] | [11,495; 17,627] | [0.90; 1.42] | [1.26; 2.11] | [1.06; 2.59] | [-656; 502] | [326; 849] | [0.09; 0.22] |

improvement, these analyses nevertheless remain unable to fit the shore-count-based abundance estimates adequately. This indicates that process error effects alone are not sufficient to resolve the discrepancy between the historical catches and the trend in the abundance estimates.

## CONCLUDING REMARKS

The results of this paper confirm previous analyses that suggested that population models based on the assumption that the eastern North Pacific stock of gray whales was at pre-exploitation equilibrium in 1600 (or 1846) cannot mimic the size of and trends in recent shore-count-based estimates of abundance. The method proposed by Wade (2002) sidesteps this problem by starting the population projection from a stable age-structure in 1968. This paper indicates that the results of such an assessment approach are not sensitive to the choice of 1968 either as the year for which a prior for abundance is specified, or that from which projections commence. *RY** is among the most robust quantities that can be estimated from the data; the median of the posterior distribution for this quantity varies within a relatively narrow range for most of the analyses of this paper.

The 95% credibility intervals for the additional CV parameter ($CV_{\text{add}}$) have lower 2.5 percentiles well in excess of zero and therefore confirm that the inclusion of the term in Equation (7) for additional variance is justified. Wade and DeMaster (1996) showed using Bayes factors that models that included the possibility of additional variance provided more satisfactory fits to the abundance data.

Neither allowing for underestimation of historical commercial and aboriginal catches nor including the possibility of decade-long deviations from expectancy in pregnancy rate permit the model to mimic the observed data adequately. This result differs from the conclusions of Butterworth *et al.* (2002) who found that making allowance for under-estimation of historical removals could resolve this problem. This discrepancy is probably a consequence of the fact that the current assessment is based on a Bayesian rather than a maximum-likelihood estimation approach conditional on certain choices for the values of the biological parameters (i.e. some choices for these parameters do allow the model to fit the abundance data, but the bulk of them do not).

It is noteworthy that the posterior distributions for some of the model outputs (e.g. *MSYL*) are not notably different from their priors. This suggests that even this dataset (arguably one of the best for any marine mammal population) is unable to provide much information about some of the quantities of interest to management. The posterior distributions for $N_{96}^{f}$ / $\tilde{K}_{\text{mat}}$ and $N_{96}^{f}$ / $MSYL_{\text{mat}}$ are relatively imprecise. This is somewhat unexpected from the results of other Bayesian assessments (e.g. those for a standard approach for the Bering-Chukchi-Beaufort Seas stock of bowhead whales (Punt and Butterworth, 1999)). It seems likely that this imprecision is a consequence of dropping the assumption that the population was at its pre-exploitation equilibrium level at the start of the population projections.

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