Trends in harbour porpoise abundance off central California, 1986-95: evidence for interannual changes in distribution?[1]

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ABSTRACT

This paper presents an updated analysis of trends in the abundance of harbour porpoise, *Phocoena phocoena*, in central and northern California, for the period 1986-95. The most recent survey effort (1995) was comparable to previous years, and regional patterns of density were similar to those found on past surveys, with densities lowest south of Monterey Bay, intermediate from Monterey Bay to the Russian River and highest off northern California. An analysis of covariance model was constructed to test for a trend in abundance while accounting for the effects of sea state, cloud cover and area. The results are qualitatively similar to those obtained for the 1986-93 time series, but encounter rates were higher in 1995, and the estimated rate of decline over the entire time period changed from 9.4% to 5.9% per year. The decreasing trend is no longer significant at $\alpha = 0.10$ ($p = 0.149$). A power analysis based on Monte Carlo simulations revealed that power remains low to detect trends of less than 10% per year. Possible effects of oceanographic conditions, as measured by the September average sea surface temperature anomaly (SSTa), on porpoise abundance are investigated using two different techniques. Correlation tests indicate an inverse relationship between SSTa and relative porpoise abundance for the eight survey years. The correlation is greatest when considering the change between survey years (decreases in relative abundance and increases in SSTa), rather than the individual values of relative abundance and SSTa. An alternate, Poisson-based generalised additive model (GAM) of porpoise sighting rates in relation to area, sea state, cloud cover, year and SSTa indicates a significant, non-linear effect of sea surface temperature on porpoise sighting rates, with no significant year effect once SSTa is included. These results suggest that harbour porpoise may exhibit interannual movement in and out of the study area in relation to changing oceanographic conditions.

KEYWORDS: HARBOUR PORPOISE; INDEX OF ABUNDANCE; DISTRIBUTION; MOVEMENTS; NORTH PACIFIC; SURVEY-AERIAL; TRENDS; OCEANOGRAPHY

INTRODUCTION

The abundance of the harbour porpoise, *Phocoena phocoena*, in nearshore waters off central California, was recently reported to have declined between 1986 and 1993 based on aerial surveys designed to monitor the relative abundance of this species (Forney, 1995). The observed trend was statistically significant at $\alpha = 0.10$ ($p = 0.078$), but there was a large degree of uncertainty around the point estimate of a 9.4% per year decline (coefficient of variation, CV = 0.56). Several plausible explanations were presented for the observed trend, including natural and human-caused factors contributing to a true reduction in population size, and changes in the geographical distribution of harbour porpoises in this region. However, the available data were insufficient to attribute the decline to any of the possible causes.

An eighth aerial survey, conducted in 1995, has completed a 10-year time series for this population. This paper presents an updated trend analysis for 1986-95, including a power analysis to evaluate the likelihood of detecting trends in this 10-year time series. Power is similar to the values predicted in Forney *et al.* (1991), but overall it is still too low to reliably detect small changes in abundance. A Poisson-based generalised additive model (GAM) is explored as an alternative to the previously used ANCOVA model. Finally, one of the possible explanations for the observed decline in abundance - distributional shifts of this population in relation to oceanographic changes - is investigated using correlation tests and generalised additive models.

METHODS

A complete description of the field methods and the ANCOVA analysis is given in Forney *et al.* (1991), and only a brief summary is provided here.

Field methods

Aerial line transect surveys were conducted from late summer to early autumn (15 August-15 November) in 1986-91, 1993 and 1995. In each survey year, a set of 26 transects between Point Conception and the Russian River (Fig. 1a) was replicated as often as weather permitted (generally 4-8 times) to monitor the central California harbour porpoise population. Beginning in 1989, a set of 17 additional transects between the Russian River and the California-Oregon border (Fig. 1b) was surveyed 1-3 times per field season, to monitor the northern California population. The transects followed a zigzag pattern designed to survey systematically between the coast and the 92m (50 fathom) isobath, which is the depth range in which the majority of harbour porpoise are expected to be found in this region (Barlow, 1988). The only deviation from this design occurred outside of San Francisco Bay, where the 92m (50 fathom) contour is located too far offshore for safe operation of the survey aircraft; in this region, the transect lines only extended to the 55m (30 fathom) contour. Total transect length was 916km, and under good weather conditions all transects could be surveyed in two days. The survey platform was a high-wing, twin-engine *Partenavia* P-68 aircraft outfitted with two bubble windows for lateral viewing and a belly port for downward viewing. The survey team consisted of three observers (left, right and belly) and one data recorder. Line transect methods were followed, with sighting distances calculated from the declination angle to the sighting when abeam of the aircraft (obtained with a hand-held clinometer) and the aircraft's altitude. Surveys were flown at 167-185km/hr (90-100 knots) airspeed and 213m (700ft) altitude. Flights were conducted only when weather conditions were good (Beaufort sea states 0-3, with mostly clear or partly cloudy skies). Sighting information and environmental conditions were recorded and updated throughout the survey using a laptop computer connected to the aircraft's LORAN navigation system.

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[1] A version of this paper was submitted to the IWC Scientific Committee as SC/48/SM5.

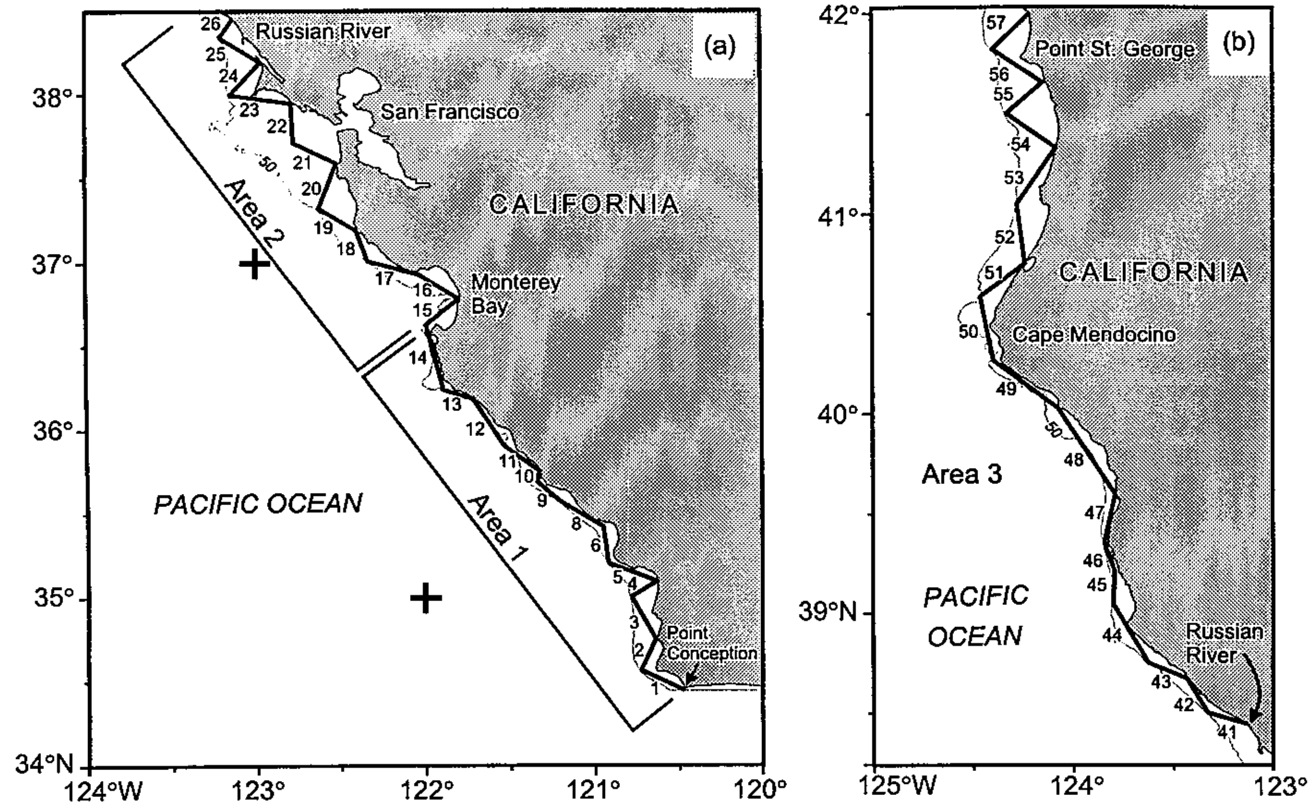

Fig. 1. Flight transects and defined areas for aerial surveys for harbour porpoise, *Phocoena phocoena*: (1a) central California (Transects 1-26, Areas 1 and 2); and (1b) northern California (Transects 41-57, Area 3). Transect 7 was combined with transect 8 after 1986 and is not shown. Crosses indicate locations for SSTa data.

The ANCOVA model

The number of harbour porpoises seen per kilometre (porpoise km^{-1}) of search effort was used as a measure of relative abundance. These data were stratified by Beaufort sea state (0-1, 2 and 3), area (transects 1-14 and 15-26 in central California, and 41-57 in northern California; see Fig. 1), and percent cloud cover (<25%; ≥25%). Data values were log-transformed, and a stepwise selection procedure was used to construct an analysis of covariance model of the form:

$$P = \mu + \beta_1 + \beta_2 + \ldots + \delta(y - \bar{y}) + \varepsilon \qquad (1)$$

where P is the log-transformed value of the number of porpoises km^{-1} + 0.001, μ is the mean value of P, the β are factors influencing apparent porpoise abundance (such as sea state), δ is the coefficient for the covariate year (y), $\bar{y}$ is the mean year and ε is a random error term. This additive model for the log-transformed data is equivalent to a multiplicative model for the actual data. (Stratification variables such as sea state are expected to change the fraction of animals observed, and thus have a multiplicative effect). Interaction terms were included in the stepwise procedure for values previously included in the model. Variability caused by unequal survey coverage in each combination of sea state, percent cloud cover and geographic area was included in the model by weighting by the number of kilometres flown. The analysis was done separately for central California alone (Transects 1-26) and for both central and northern California (Transects 1-26 and 41-57).

Simulation methods

Once the best model had been selected (see results), Monte Carlo simulations were performed as described in Forney *et al.* (1991) to determine the power of the ANCOVA to detect a given trend in porpoise abundance correctly. Only central California data were included in the simulations. Increasing and decreasing trends of 5% and 10% per year over 10 and 12 years were simulated, as well as a situation with 'no trend' to evaluate α-levels in this procedure. The random datasets were generated using the parameters and error structure obtained for the actual data from the best model. First, the expected logarithmic value of porpoises km^{-1} for each combination of conditions was calculated from the fitted parameters. A random error term for each expected value was then drawn from a normal distribution with a mean of zero and standard deviation equal to the standard error from the ANCOVA results of the best model (without year). To allow weighted analysis of the simulated data, this error term was weighted inversely, i.e., multiplied times $\sqrt{(1/w)}$, where w is the number of kilometres flown under the given conditions. For each simulation, a set of 96 values of w representing each of the 96 combinations of the predictor variables, was obtained by randomly selecting the actual numbers of kilometres flown from one of the eight survey years. Complete yearly sets were chosen rather than individual values to avoid unlikely combinations of kilometres flown.

A yearly trend was incorporated into the simulation data by multiplying the calculated value of porpoises km^{-1} by a factor representing the desired exponential change in porpoise abundance. To make the simulated data more realistic, all values were rounded to yield only integer values of porpoises over the given number of kilometres flown. In addition, to prevent infeasible values of porpoises km^{-1}, a new error term was drawn if the original one resulted in a back-transformed value of porpoises km^{-1} that was negative or greater than 0.4. The highest value observed in central California in 1986-95 was 0.24 porpoises km^{-1}; multiplying this value by the maximum simulated increasing trend, yields an upper limit of approximately 0.4 porpoises km^{-1}. In the simulations, less than 5% of all error terms were redrawn because they failed to meet these criteria.

Tests of oceanographic correlates

No direct measurements of oceanographic conditions at the time of the surveys were available for this analysis. Therefore, the monthly mean sea surface temperature anomalies (SSTa) for September and October, estimated by the US National Weather Service (NWS) for all years from satellite, buoy and shipboard measurements of sea surface temperature[2], were obtained as an approximate indicator of oceanographic conditions off central California during the survey period. The most representative stations were located at 35°N,122°W and 37°N,123°W for Areas 1 and 2, respectively, and the average value at these stations for September and October was used as an index of oceanographic conditions for each year. [Note: Although these two stations are farther offshore than the central California study area, the NWS contour maps indicated that nearshore SSTa were identical or very similar to those at these stations.] Two different types of analyses were performed to investigate a possible environmental component to the observed patterns of abundance: correlation tests and a GAM, as described below.

Two Pearson's correlation tests were performed on SSTa and the relative abundance of harbour porpoise in central California, adjusted for the effects of sea state and cloud cover using the best-fit coefficients from the ANCOVA model. First, the values of SSTa and relative porpoise abundance were compared to investigate a potential relationship between high and low values of each variable. Second, the differences in SSTa and relative porpoise abundance between successive survey years were compared to test for a relationship between the direction and magnitude of *changes* in these two variables.

The Poisson-based generalised additive model

As an alternative to the previously used ANCOVA model, a Poisson-based GAM was explored to test for trends in harbour porpoise abundance, and to investigate possible non-linear effects of the sea surface temperature anomaly. Animal count data often follow a Poisson distribution, and therefore a Poisson model may be more appropriate for the survey data in this analysis. GAMs (Hastie and Tibshirani, 1990) differ from the more familiar generalised linear models (GLM) (McCullagh and Nelder, 1989) in that the response variable (y) is modelled as the sum of nonparametric functions of the predictor variables ($x_1, x_2, \ldots, x_n$), rather than the sum of linear relationships. A general equation describing a GAM (Hastie and Tibshirani, 1990) is:

$$y = c + \sum_{i=1}^{n} f(x_i) \tag{2}$$

In the framework of GLMs and GAMs, a Poisson process can be modelled by specifying the log-link function $\eta = \log(\mu)$ with variance $V(\mu) = \mu$ between the mean, $E(Y) = \mu$, and the sum of the predictor functions, η (McCullagh and Nelder, 1989).

In the analysis presented below, a GAM of the form:

$$s = \tau + offset(\log(km)) + \sum_{i=1}^{n} f(x_i) \tag{3}$$

was created, with the number of sightings (s) modelled as a Poisson-distributed variable predicted by an overall mean (τ), plus an offset for the number of kilometres surveyed, plus the sum of nonparametric functions of the predictor variables, x_i. The x variables included in the stepwise model selection procedure were area, sea state and cloud cover (as ordered categorical variables) and year and SSTa (as numerical variables). Because the number of kilometres surveyed under each combination of conditions varied, the logarithm of the kilometres flown was included in the model as an offset (i.e. with coefficient = 1; McCullagh and Nelder, 1989). The individual functions of the model were derived using cubic smoothing splines (Hastie and Tibshirani, 1990) and the level of smoothing was determined by specifying the degrees of freedom to use in the fitting algorithm. One degree of freedom corresponds to a linear fit, and additional degrees of freedom allow the smoothed function to track the actual data points more closely. For this analysis, the level of smoothing was set at 3 degrees of freedom to allow non-linear relationships while restricting unrealistic detail in the shape of the functions. The goodness of fit for these models is measured in terms of the residual deviance, calculated as $D = \Sigma r_D^2$ with $r_D = \mathrm{sign}(y-\hat{\mu})\ \{2(y\log(y/\hat{\mu}) - y + \hat{\mu})\}^{1/2}$, where y is each observation, $\hat{\mu}$ is the calculated mean and sign $(y - \hat{\mu})$ is either plus or minus, depending on the sign of the parenthetical expression (McCullagh and Nelder, 1989). Individual models were then compared using analysis of deviance, which is analogous to the more familiar analysis of variance used for normal distributions.

The above model uses the number of sightings, rather than the number of porpoises, as the response variable, because preliminary analyses revealed that the number of porpoises was overdispersed (dispersion parameter >5) and not adequately represented by the Poisson distribution, which assumes that dispersion is about one. The number of sightings is only a valid alternate measure of relative abundance if group sizes did not vary between years. To establish this, a test was first performed using a similar GAM with group size as the response variable and area, sea state, cloud cover and year as predictor variables.

RESULTS

In central California, a total of 3,015km of survey effort was completed in 1995, which is slightly below the average for all previous years (Table 1 overleaf). However, a higher proportion (67.5%) of the survey was completed with good viewing conditions. A total of 221 porpoises were seen in 113 groups in central California. Survey effort in northern California was lower than in previous years (611km, 61.2% in good conditions), mainly because weather opportunities were more limited. A total of 192 porpoises were seen in 116 groups off northern California.

The best-fitting ANCOVA model for the 1986-95 time series, as determined by the stepwise procedure, was the same as in the previous analysis of the shorter time series (Forney, 1995), with the exception of the annual trend. Area, sea state and cloud cover categories were highly significant predictors of relative porpoise abundance, but year was not significant at $\alpha = 0.10$ ($p = 0.143$; Table 2). No interaction terms were significant. Potential inter-observer effects could not be included in the model since this would have resulted

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[2] National Oceanic and Atmospheric Administration, National Weather Service, San Francisco Forecast Office, 21 Grace Hopper Avenue, Stop 5, Monterey, California, 93143-5505.

Table 1

Summary of harbour porpoise (*Phocoena phocoena*) aerial survey data collected 1986-1995 in central and northern California. Areas 1, 2 and 3 correspond to Transects 1-14, 15-26, and 41-57, respectively (see Fig. 1). % good conditions is defined as 100 times the total km surveyed with Beaufort sea states 0-2 and <25% cloud cover, divided by the total number of km flown in all conditions. '-' indicates that no surveys were flown; SD is the standard deviation.

	1986	1987	1988	1989	1990	1991	1993	1995
Area 1								
No. of sightings	36	28	15	22	18	12	9	15
No. of porpoise	62	47	20	44	29	20	17	33
Mean group size (±SD)	1.72 (±0.91)	1.68 (±1.79)	1.33 (±0.49)	2.00 (±1.41)	1.61 (±1.04)	1.67 (±0.65)	1.89 (±0.93)	2.20 (±1.01)
Km surveyed	1,767	1,618	1,834	1,653	1,887	1,066	1,941	1,342
% good conditions	56.4%	66.7%	31.3%	32.4%	60.3%	56.5%	68.7%	68.0%
Area 2								
No. of sightings	63	44	88	60	57	43	69	98
No. of porpoise	104	76	154	134	126	76	149	188
Mean group size (±SD)	1.65 (±1.17)	1.73 (±1.11)	1.75 (±1.18)	2.23 (±1.51)	2.21 (±1.47)	1.77 (±1.11)	2.24 (±1.61)	1.92 (±1.06)
Km surveyed	1,282	1,463	2,086	1,607	1,751	669	1,919	1,673
% good conditions	55.9%	34.3%	36.0%	42.1%	32.0%	58.9%	59.9%	67.1%
Area 3								
No. of sightings	-	-	-	44	173	87	143	116
No. of porpoise	-	-	-	76	296	166	246	192
Mean group size (±SD)	-	-	-	1.73 (±1.21)	1.71 (±1.27)	1.91 (±1.02)	1.72 (±1.40)	1.66 (±0.98)
Km surveyed	-	-	-	804	1,084	612	966	611
% good conditions	-	-	-	34.1%	67.3%	77.9%	88.0%	61.2%

in a large number of missing values and over-stratification of the data. However, preliminary nonparametric tests (two-factor extension of the Kruskal-Wallis analysis of variance; Scheirer *et al.*, 1976; Zar, 1984) indicated that sighting rates (under clear skies and stratified by area to account for regional differences in porpoise density) did not differ significantly ($p > 0.50$ and $p > 0.10$ for Beaufort sea states of 0-2 and 3, respectively) for the eleven main observers in this study, defined as those who completed at least 3,000km of search effort. As in the previous analyses, visual inspection of residual values from the model in a quantile-quantile plot (Sokal and Rohlf, 1995) revealed a deviation from normality only in the extreme tails of the distribution (where $z > 2$), indicating that the log-transformation was still appropriate for inference at $\alpha \geq 0.05$. The ANCOVA results are similar for models including central and northern California combined (Table 2).

The results of the power analysis are consistent with past findings of relatively low power. For the eight surveys over ten years, this analysis would be expected to detect a decreasing trend of 10% per year about 76% of the time, or a 5% annual decrease only 32% of the time (at $\alpha = 0.10$). If α is increased to 20%, then power increases to 84% and 45%, respectively, for the 10% and 5% annual decline. Thus power remains low for this trend analysis, and the lack of significance is not surprising. The chance of obtaining a covariate representing a decline over 10 years (of any magnitude and regardless of significance; this is equivalent to $\alpha = 1.0$), if the population were in fact increasing (γ-error; Forney *et al.*, 1991) was determined to be 16% for a population increasing at 5% per year and 2% for a population increasing at 10% per year. These simulation results are illustrated in Fig. 2 for the 10-year time series. When the simulated population was stable, covariates resulting in increasing and decreasing trends were obtained with equal probability, indicating that the procedure is not biased.

Based on the parameters of the ANCOVA, the number of porpoises km^{-1} of search effort was adjusted for the effects of sea state and cloud cover to produce a plot of relative porpoise abundance through time (Fig. 3). There is a large degree of variability in the point estimates, corresponding to the low power. Despite this variability, an inverse relationship between relative abundance and the mean September/October sea surface temperature (measured in terms of the anomaly from the long-term mean) is nonetheless apparent (Fig. 4 overleaf). The Pearson's correlation tests revealed a weak correlation between sea surface temperature and relative abundance (Pearson's $r = -0.567, p = 0.1426$) and a stronger correlation that borders

Table 2

Results of the analysis of covariance for central California and combined central and northern California aerial survey data. The dependent variable is the log-transformed number of porpoise per km, and the independent variables tested are area, sea state, cloud cover and year. df = degrees of freedom; F = F-ratio; p = probability value; R-squared = proportion of variance explained by model.

	Central California			Central and Northern California		
Source	df	F	p	df	F	p
Model	5	19.73	0.0001	6	28.34	0.0001
Area	1	62.48	0.0001	2	58.40	0.0001
Sea state	2	14.34	0.0001	2	18.23	0.0001
Cloud cover	1	18.28	0.0001	1	19.83	0.0001
Year	1	2.12	0.1489	1	1.88	0.1730
Error	84			102		
R-Squared		0.540			0.625	
Year coefficient (standard error)		-0.060 (0.041)			-0.050 (0.037)	
Annual rate of change		-5.9%			-5.0%	

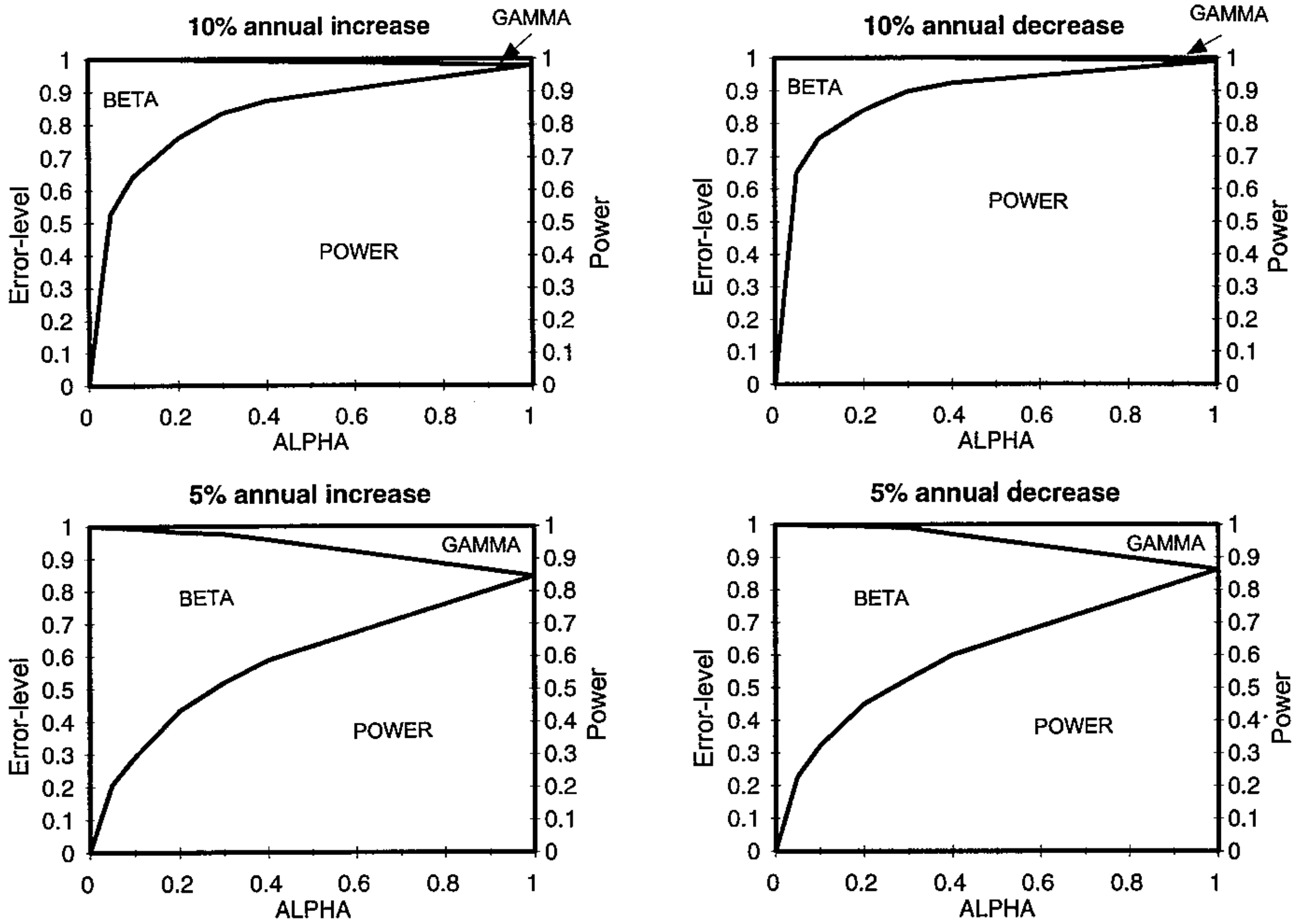

Fig. 2. Graphical representation of the results of the power simulations for the trend analysis of the 1986-95 harbour porpoise aerial surveys for rates of change of ±5% and ±10% per year. Areas represent probability levels as follows: ALPHA is the chosen α-error (the probability of detecting a significant trend when in fact none is present), BETA is the resulting β-error (the probability of not detecting a trend that is present) and GAMMA is the resulting γ-error (Forney *et al.*, 1991: the probability of detecting a trend in the wrong direction). POWER to detect trends correctly is 1-(BETA + GAMMA).

on statistical significance between the direction and magnitude of the change in these two variables between successive survey years ($r = -0.744$, $p = 0.055$). Given that only a rough measure of average oceanographic conditions was available for these analyses, these correlations are surprisingly high. The results suggest that although sea surface temperature itself may not be strongly correlated with harbour porpoise abundance, changes in sea surface temperature do appear to correlate negatively with changes in porpoise abundance between successive years.

The results of the GAMs (Table 3) provide further insights into the possible nature of the observed decline in abundance and the potential relationship between relative porpoise abundance and oceanographic conditions. The test of group size as a function of area, sea state, cloud cover and year, indicated that group size did not vary significantly between years ($p = 0.254$), confirming that sighting rates are a suitable proxy for relative abundance in this analysis. The model of porpoise sighting rates including area, sea state, cloud cover and year as predictors (but excluding the SSTa) resulted in a year effect of similar significance to that of the ANCOVA model ($p = 0.119$). The pattern of relative abundance by year (Fig. 5b) is also qualitatively similar to that derived from the ANCOVA model (Fig. 3), with a decreasing trend between 1986 and 1993, and a subsequent increase in 1995. However, in the GAM, the SSTa was more significant ($p = 0.022$) and was included in the stepwise selection procedure instead of year. After the inclusion of the SSTa, the year pattern is less pronounced (Fig. 5c) and the level of statistical significance decreases considerably ($p = 0.570$). The non-linear function of porpoise sightings in relation to the SSTa (Fig. 5) indicates that sighting rates are greatest in the coolest years, decrease slowly as temperatures

Table 3

Results of the Poisson generalised additive model for central California aerial survey data. The dependent variable is the number of porpoise sightings, and the independent variables tested are area, sea state, cloud cover, year and sea-surface-temperature anomaly. The number of km flown is included in the model as an offset. df = degrees of freedom, F = F-ratio, p = probability value.

Source	df	Deviance	F	p
Best Model				
Model	7	900.80	55.25	<0.0001
Area	1	76.93	33.03	<0.0001
Sea state	2	130.86	27.68	<0.0001
Cloud cover	1	62.74	26.83	<0.0001
SST anomaly	3	23.54	3.36	0.022
Residual	82	186.95		
Best Model plusYear				
Model	10	905.54	38.69	<0.0001
Area	1	73.07	31.23	<0.0001
Sea state	2	127.95	26.96	<0.0001
Cloud cover	1	59.45	25.31	<0.0001
SST anomaly	3	13.90	1.98	0.124
Year	3	4.74	0.68	0.570
Residual	79	182.20		

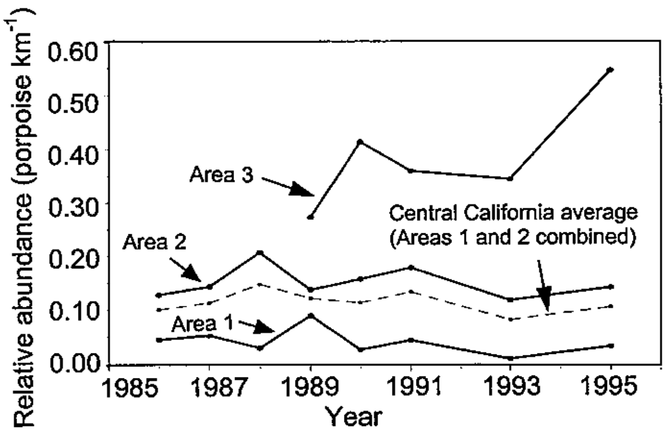

Fig. 3. Relative abundance of harbour porpoise for the period 1986-95. Relative abundance is defined as the number of porpoise observed per kilometre surveyed, adjusted for the effects of sea state and cloud cover on sighting rates. Areas correspond to those shown in Fig. 1. The combined relative abundance for central California was calculated as the average of the adjusted values of porpoise km^{-1} for Areas 1 and 2, weighted by the proportion of the 6,951km^{2} central California study area encompassed by each (33.6% for Area 1, 66.4% for Area 2).

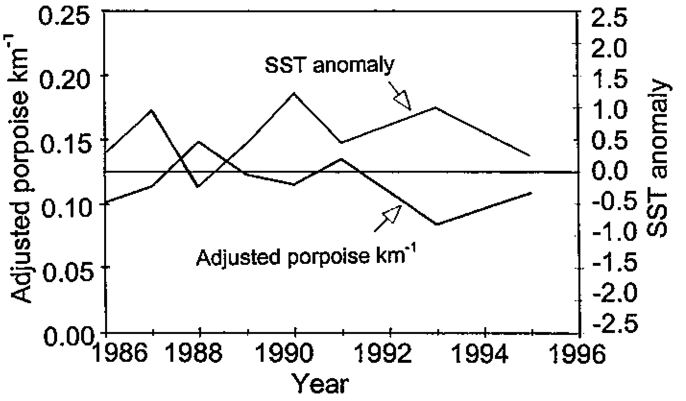

Fig. 4. Relative abundance of harbour porpoise in central California (thick line; calculated as for Fig. 3) and mean sea surface temperature anomaly (thin line; averaged for September and October at two stations along the central California coast) for 1986-95.

increase to about the mean climatological values and drop off rapidly as the anomaly exceeds about +1.0°C (Fig. 5). These combined results support the hypothesis that oceanographic changes may be responsible for the observed interannual trend.

DISCUSSION

The updated trend analysis for harbour porpoise abundance off central California in 1986-95 shows a reduced magnitude compared to the previously documented downward trend (Forney, 1995), and this trend is no longer significant at $\alpha = 0.10$. Inclusion of data for northern California yields similar results (5.0% per year decline, $p = 0.1730$; Table 2). [Note: Although the 1995 index of relative abundance of harbour porpoise in northern California was very high (Fig. 3), this point has a large uncertainty because of low survey effort.] The implications of this decreasing trend are not clear, but a potential link to oceanographic conditions (Forney, 1995) is suggested by the correlation between SSTa and porpoise abundance, and by the results of the GAM. The correlation is strongest when considering the direction of change in the two measurements: when the SSTa became more positive (i.e. water temperature increased from one survey year to the next), the relative abundance of harbour porpoise tended to decrease, and *vice versa*. In contrast, the actual value of the SSTa was less well correlated with the relative abundance of harbour porpoise. In part, this lack of correlation may be due to the presence of non-linear effects, as determined by the GAM: porpoise sighting rates appear to decline rapidly in warmer than average conditions, but exhibit only a slight decreasing trend in cold to average years (Fig. 5). These results underscore the importance of investigating non-linear effects of environmental variables in models of species abundance.

A caveat to the above relates to the nature of the measure of oceanographic conditions used in this analysis, the mean SSTa averaged for the months of September and October at two stations off central California (for the northern and southern parts of the study area, respectively). This rough measure of general sea surface temperature was used because no detailed oceanographic information was available on a scale comparable to the aerial survey data. Depending on the likely response time of harbour porpoise in relation to oceanographic changes, a two month average may not be the most appropriate choice. The choice of September and October was based on the timing of the surveys (15 August to 15 November, with most effort in September and October) and the documented summer/autumn increase in harbour porpoise densities in Monterey Bay (Sekiguchi, 1995). Although this choice seems reasonable, it is arbitrary. Thus the interpretation of these data is limited by our lack of understanding about temporal and geographic scales of movement of harbour porpoise.

Pollutant studies have revealed differences in pollutant ratios in harbour porpoises from central California and Oregon/Washington, suggesting that north-south movement is limited (Calambokidis and Barlow, 1991); however, no samples from northern California were available for that study. Insufficient data are available to establish whether harbour porpoises may use deeper waters outside the central California study area to a variable extent during different years, because systematic surveys have only been conducted in nearshore waters. In recent years, harbour porpoises have occasionally been observed in deeper waters off California during the summer/autumn period (J. Calambokidis, pers. comm.; J. Barlow, pers. comm.), but such observations have been rare despite considerable search effort for other cetaceans in these offshore areas.

The potential influence of variability in oceanographic conditions on the measured abundance of harbour porpoises is an important consideration when evaluating the status of this species. The central California population probably was depleted during the 1970s and 1980s when incidental mortality in coastal set gillnet fisheries was high (Barlow and Hanan, 1995). After a substantial reduction in fishery mortality beginning in the late 1980s, the population was expected to recover. The subsequent decline documented for the period 1986-93 (Forney, 1995) was therefore surprising. The analysis presented here provides some support for one of the potential explanations: that the observed patterns may reflect distributional changes resulting from interannual variability in oceanographic conditions, rather than a true decline in abundance. However, the evidence at this point is far from conclusive and targeted studies will be necessary to confirm or reject this possibility.

Indices of oceanographic conditions (such as SSTa or measures of productivity) may provide additional explanatory power, but they should be collected in conjunction with the sighting data in order to be more meaningful. For this reason, shipboard surveys on which

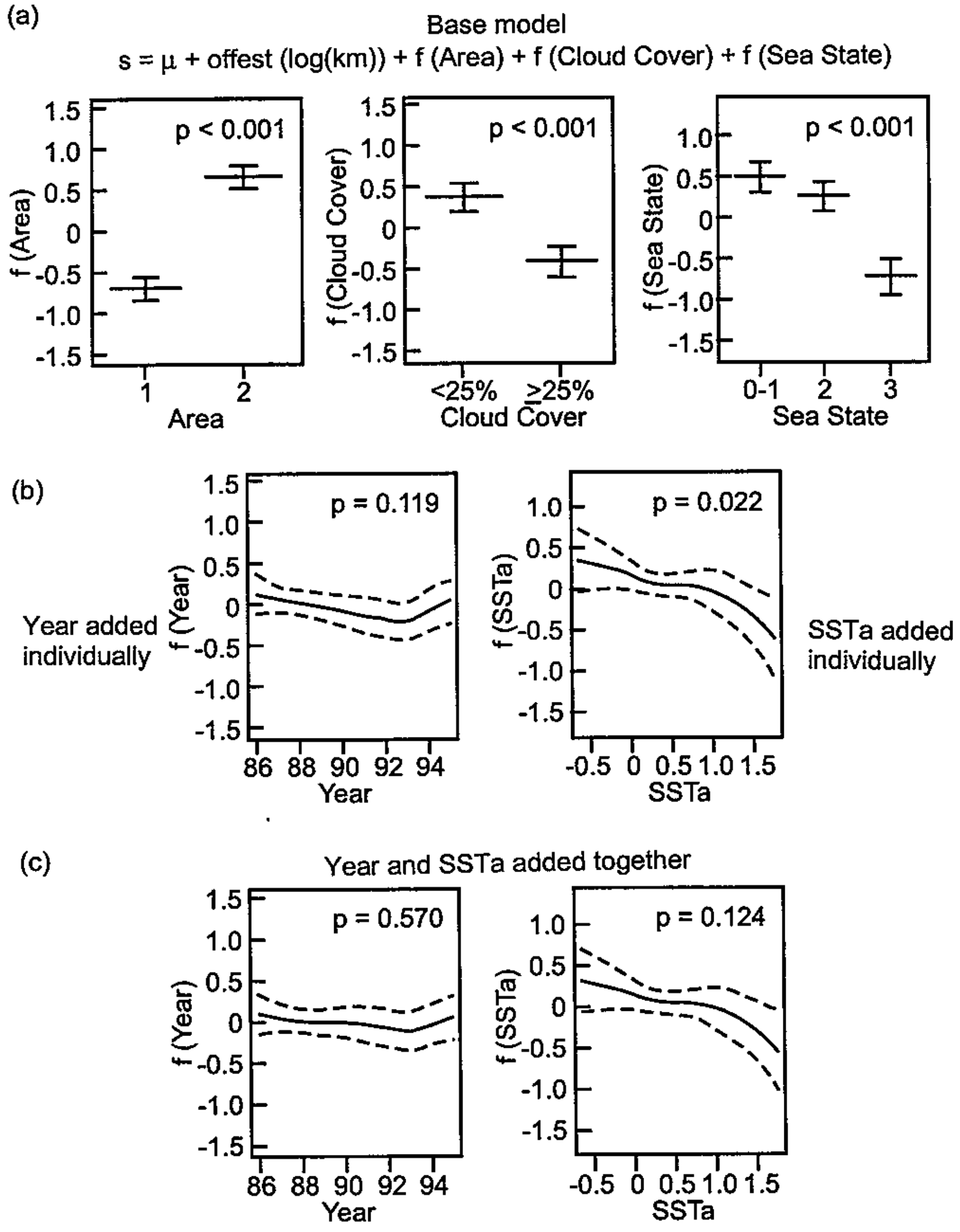

Fig. 5. Graphical results and probability values for variables included in the Poisson generalised additive model of the number of porpoise sightings for central California: (a) 'Base model', including effects of area, sea state and cloud cover; (b) effects of year and SSTa when added individually to the base model; and (c) effects of year and SSTa when both are included in the model. Dashed lines are 2× standard error bands for the fitted functions with three degrees of freedom.

oceanographic data are collected along with the sighting data would be more effective than aerial surveys. Future studies should also attempt to address movement patterns and possible changes in depth distribution of California harbour porpoises, but until suitable methods of capturing and radio-tagging free swimming harbour porpoises in this region have been perfected, this goal may remain elusive.

The continued low power of the ANCOVA analysis and the large amount of unexplained variability that remains in the data will continue to make the detection of trends very difficult. GAMs may provide greater power to detect trends in the future because of their greater flexibility to include non-linear relationships. The Poisson model using the number of sightings as a response variable yielded similar results to the previous ANCOVA model that used the logarithm of the number of porpoise km^{-1}. However, these models are not entirely comparable because one implicitly includes group size information and the other assumes group sizes to be constant across years. The present analysis revealed that the Poisson distribution does not adequately model trends in total harbour porpoise abundance, because the number of porpoises is overdispersed. More sophisticated GAMs, such as those using a negative binomial distribution family (Chambers and Hastie, 1992), may be required in the future to allow individual-based trend analyses.

ACKNOWLEDGEMENTS

Financial support and personnel were provided by the National Marine Fisheries Service (Southwest Regional Office and Southwest Fisheries Science Center) and the California Department of Fish and Game (CDFG). The observers and data recorders were J. Barlow, M. Beeson, J. Carretta, D. DeMaster, S. Diamond, T. Farley, D. Fink, T. Gallegos, D. Hanan, A. Hudoff, L. Jones, E. Konno, S. Kruse, M. Larson, J. Lecky, T. Lee, M. Lowry, R. Pitman, J. Scholl, J. Sisson, B. Taylor (and the author). Aircraft were chartered from *Aspen Helicopters, Inc.* and contracted from *CDFG.* Pilots were B. Cheney, B. Cole, J. Drust, B. Hansen, D. Hansen, L. Heitz, K. Lankard, E. Schutze, J. Turner, R. Riediger, R. Throckmorton and R. Van Benthuysen. The computer data acquisition software was written by J. Cubbage and modified by J. Barlow. Aerial surveys were conducted under Marine Mammal Protection Act Permit No. 748 and NOAA Sanctuary permits GFNMS/MBNMS-03-93, MBNMS-11-93 and GFNMS/MBNMS/CINMS-09-94. I thank J. Barlow, J. Bradbury, R. Brownell Jr., J. Carretta, D. Checkley, J. Cooke, D. DeMaster, J. Enright, P. Smith, B. Taylor, C. Winant and an anonymous reviewer for their helpful comments and suggestions on earlier drafts of this manuscript.

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