Factors affecting perpendicular sighting distances on shipboard line-transect surveys for cetaceans

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ABSTRACT

Factors that affect cetacean perpendicular sighting distances are investigated using a Generalised Additive Modelling (GAM) framework to analyse 8,203 sightings of 34 cetacean species seen on 200,000km of shipboard line-transect surveys in the eastern Pacific in 1986-96. Perpendicular sighting distance is modelled as a non-linear function of the following predictor variables: species; an *a priori* species grouping; the logarithm of group size; Beaufort sea state; presence of rain or fog; sighting cue; sun glare; geographic stratum; observer; ship; year; cruise; and, in 1991-96, visibility and swell height. Based on Akaike Information Criteria (AIC), the best model for 1986-96 included all variables except rain/fog code. For the 1991-96 data, swell height anomaly was also important and replaced ship and year in the best-fit model. For independent subsets of the data, GAM coefficients were highly correlated, indicating that many of the same factors were acting in different areas and at different times. Species and sighting methods (25x binoculars vs unaided eye) had the largest effects on perpendicular sighting distances. The *a priori* species groups captured much, but not all of the among-species differences. Two other species-related factors (group size and sighting cue) were also important in all models. Factors related to search conditions (Beaufort sea state and swell height anomaly) and to the searchers themselves (individual observer) were also important. We anticipate that this information on the relative magnitudes of factors affecting perpendicular sighting distance can be used to improve both design and analysis of line-transect data.

KEYWORDS: ABUNDANCE ESTIMATE; SURVEY-VESSEL; LINE-TRANSECT; MODELLING; PACIFIC OCEAN

INTRODUCTION

The distance between a detected group of animals and a transect line is commonly referred to as the perpendicular sighting distance and its measurement is critical to the estimation of animal density using line-transect survey methods. Distributions of perpendicular sighting distances are used to estimate effective strip width (*esw*), a critical line-transect parameter (Buckland *et al.*, 1993). Many factors can potentially affect the perpendicular distance at which any particular group of cetaceans is first seen from a ship at sea. These factors can be roughly categorised as: (1) search conditions (e.g. sea state, swell height, atmospheric conditions, sun glare, visual range, vessel characteristics, search method); (2) group characteristics (e.g. species, body size, group size, activity, diving behaviour, associated animals); (3) observer characteristics (e.g. training, experience, skill, motivation); and (4) chance factors (e.g. position and movement of the group relative to the trackline, coincidence of surfacing behaviour and an observer's field of view). Typically in line-transect analysis, researchers do not attempt to quantify all of these factors; rather, they fit a curve to the pooled distribution of perpendicular distances (for a species) and depend on 'pooling robustness' to allow them to make reliable estimates of animal density (Burnham *et al.*, 1980; Buckland *et al.*, 1993). However, there are limits to pooling robustness and explicit consideration of other factors can reduce bias and improve precision (Buckland *et al.*, 1993).

A number of methods have been used to explicitly incorporate factors that affect perpendicular sighting distance. Perhaps the simplest approach is post-stratification; this approach has been used with group size, sea state, geographic stratum, cloud cover and vessel (e.g. Barlow, 1988; 1995; Buckland *et al.*, 1993). Another approach is to include factors as covariates in estimating a detection function (e.g. Drummer and McDonald, 1987; Ramsey *et al.*, 1987; Borchers *et al.*, 1998) or as terms in a linear model used to scale a detection function (Beavers and Ramsey, 1998).

The opposite of stratification is pooling which has also been used to improve precision in line-transect abundance estimates. As sample sizes become small (typically less than 30-50), the precision of line-transect estimates declines markedly. Pooling similar samples can improve precision with an acceptable increase in potential bias. For example, if too few sightings are made of one species, the detection function for that species can be estimated by pooling with sightings of another species that would, based on size, behaviour, etc, be expected to have a similar detection function (e.g. Barlow, 1995; Jefferson, 1996). The degree to which data are pooled or stratified is a tradeoff between bias and precision (Burnham and Anderson, 1998).

Despite the many examples of large-scale ship line-transect studies for cetaceans, there have been few attempts to examine which factors are most important in determining perpendicular sighting distance. For example, it is not known whether differences in sighting distances between similar species are greater or less than the differences due to sea state or group size. Most studies lack an adequate sample size to stratify simultaneously by all of the factors that might be significant. Model selection by Akaike Information Criteria (AIC) or other objective criteria can also be hampered by insufficient data.

This paper analyses cetacean line-transect data that have been collected on SWFSC (Southwest Fisheries Science Center) marine mammal surveys from 1986-96 in the eastern Pacific Ocean (Wade and Gerrodette, 1993; Barlow, 1995; 1997; Barlow and Gerrodette, 1996). These surveys have covered 200,000km of transect. The resulting 8,203 sightings include at least 34 species ranging in habitat from the tropical Fraser's dolphin *(Lagenodelphis hosei)* to the cold temperate Dall's porpoise *(Phocoenoides dalli)* and in size from the diminutive vaquita (*Phocoena sinus)* to the grand blue whale (*Balaenoptera musculus)*. A generalised additive modelling (GAM) framework is used to fit perpendicular distance data from these surveys as a function of many potentially important factors. This large sample size allows examination of more factors than can normally be studied and provides sufficient statistical power to accurately determine the relative magnitudes of these factors. The generality of the results is tested by comparison of results for two large subsets of data.

METHODS

Field methods

Survey methods remained relatively constant throughout this 11-year study period (Kinzey *et al.*, 2000). Two National Oceanic and Atmospheric Administration (NOAA) ships were used in most years: the 52m *David Starr Jordan* and the 53m *McArthur*. On both ships, the observation height from the flying bridge deck was approximately 10m above the sea surface. The primary team consisted of two observers (port and starboard) searching through pedestal-mounted 25 × 150 *Fujinon* binoculars (typically from 10° on the opposite side of the bow to 90° on their side) and one centre observer searching by unaided eyes and (occasionally) 7 × 50 handheld binoculars. The centre observer was also responsible for recording search effort and sightings data. Observers rotated among these three observation stations for two hours and then had two hours off duty to rest. The vessels surveyed pre-determined transect lines at 10 knots during daylight hours (dawn to dusk). Typically when a marine mammal was sighted, the team went 'off-effort' and directed the ship towards the animal(s) to obtain species identity and group size estimates. Immediately after making a sighting (and before turning the ship), the bearing angle from the bow to the animal (or the approximate centre of a group of animals) was measured using a protractor at the base of the 25× binoculars and the distance to the animal (or group) was measured using ocular reticules (Barlow and Lee, 1994; Lerczak and Hobbs, 1998; Kinzey and Gerrodette, 2001).

Although some changes in protocol were implemented during this time period, these are not expected to affect line-transect data collection significantly. A conditionally independent observer position was used intermittently after 1991 to measure the fraction of animals missed by the primary team; however, the person in that position did not disclose sighting information until the animal(s) had passed abeam and had been clearly missed by the primary observer team. In 1991, computer-based data entry replaced a system based on paper forms. At this time, two additional data fields were added: swell height and visibility. In 1996, approximately one third of the effort was conducted in passing mode (not turning towards or approaching cetaceans for identification or enumeration) and a new data field was recorded to indicate survey mode. Recorded variables and transformed variable used in analyses are summarised in the Appendix.

Surveys were designed to cover different geographic areas in each year. The cruises in 1986-90 were designed to estimate the abundance and trends in abundance for all dolphin populations that are affected by tuna fishing in the eastern tropical Pacific. The survey in 1991 was designed to estimate the abundance of all cetaceans in waters off California. The surveys in 1992 and 1993 were designed to estimate the abundance of the central and northern stocks (respectively) of common dolphins *(Delphinus delphis*) in the eastern Pacific. The survey in 1996 was designed to estimate the abundance of all cetaceans in waters off California, Oregon and Washington. SWFSC survey efforts in 1994 and 1995 were not included in the analyses: the former because it sampled a novel environment (the foggy area south of the Aleutian Islands) that was not replicated in any other years and the latter because it was an experimental acoustic survey. Despite differing purposes, all sightings of cetaceans were recorded on all cruises. Approximately 200,000km of tracklines were searched (Fig. 1).

Analytical methods

Perpendicular sighting distance (*PDist*) was modelled in a Generalised Additive Model (GAM) framework (Hastie and Tibshirani, 1990) using SPLUS software. The full regression model can be expressed as:

$$\begin{aligned} E[1\mathrm{n}(PDist + 0.5)] = {} & d[Species] + s[Beauf,n] \\ & + s[1\mathrm{n}(TotSS),n] + d[Cue] + d[BinoCode] \\ & + d[GeoStrata] + d[Obsvr] + d[Rain\ /\ Fog] \\ & + s[SwelAnom,n] + s[Vis,n] \\ & + d[Glare] + d[Ship] + d[Year] \end{aligned}$$

where:

$E[y]$	denotes the expected value of the dependent variable y;
$d[x]$	denotes a separate parameter value for each discrete value of the variable x;
$s[x,n]$	denotes a spline fit to the continuous variable x with n degrees of freedom.

Variable names are as given in the Appendix. Residuals were modelled with a Gaussian distribution, and the identity link function was used (i.e. no link function). *PDist* (in km) was fitted as a transformed variable (*ln(PDist* + 0.5km)) to make deviations roughly symmetrical about the mean value and to construct a model of multiplicative effects on *PDist* (in exploratory analyses, values from 0.1km to 1.0km were added prior to log-transformation and the value of 0.5km was found empirically to work best). *TotSS* was log-transformed to provide greater resolution at low group sizes (where most of the data are clumped). *Beauf* is actually a ranked categorical variable, but was treated as an integer in this analysis. *SwelAnom* and *Vis* are continuous variables. All other independent variables are categorical. Sightings with more than one species were included multiple times (once for each species), but each observation was weighted by the inverse of the number of species present (weight = *1/n*, where *n* = the number of species).

Perpendicular distance models were fitted using step-wise model building based on AIC as implemented in the SPLUS procedure *step.gam*. Models of increasing complexity were built incrementally by testing the addition or deletion of each variable to the prior best model and repeating the process with the new best model. The best model was the one with the lowest AIC value, which effectively is a likelihood criterion penalised for additional parameters. Burnham and Anderson (1998) argue that model selection based on AIC results, on average, is the minimum loss of information. Continuous variables (*Beauf, SwelAnom, Vis* and *TotSS*) were smoothed using a spline-fitting algorithm with variable degrees of freedom. Once these variables were added to the model, each iteration of the step-wise model selection process tested the prior best model against versions of the model that included these variables with higher and lower degrees of smoothing. After the *step.gam* algorithm arrived at an optimal model, the procedure was restarted at that point with a new estimate of the Gaussian dispersion parameter.

Two variables (*Ship* and *Year)* are completely determined by another variable (*CruzNo*) and all could not be included in the same model. The initial stepwise fit was based on *Ship* and *Year*, and additional models were tested by substituting *CruzNo* for both variables. Similarly, *SppGroup* is determined by *Species* and both were not included in the

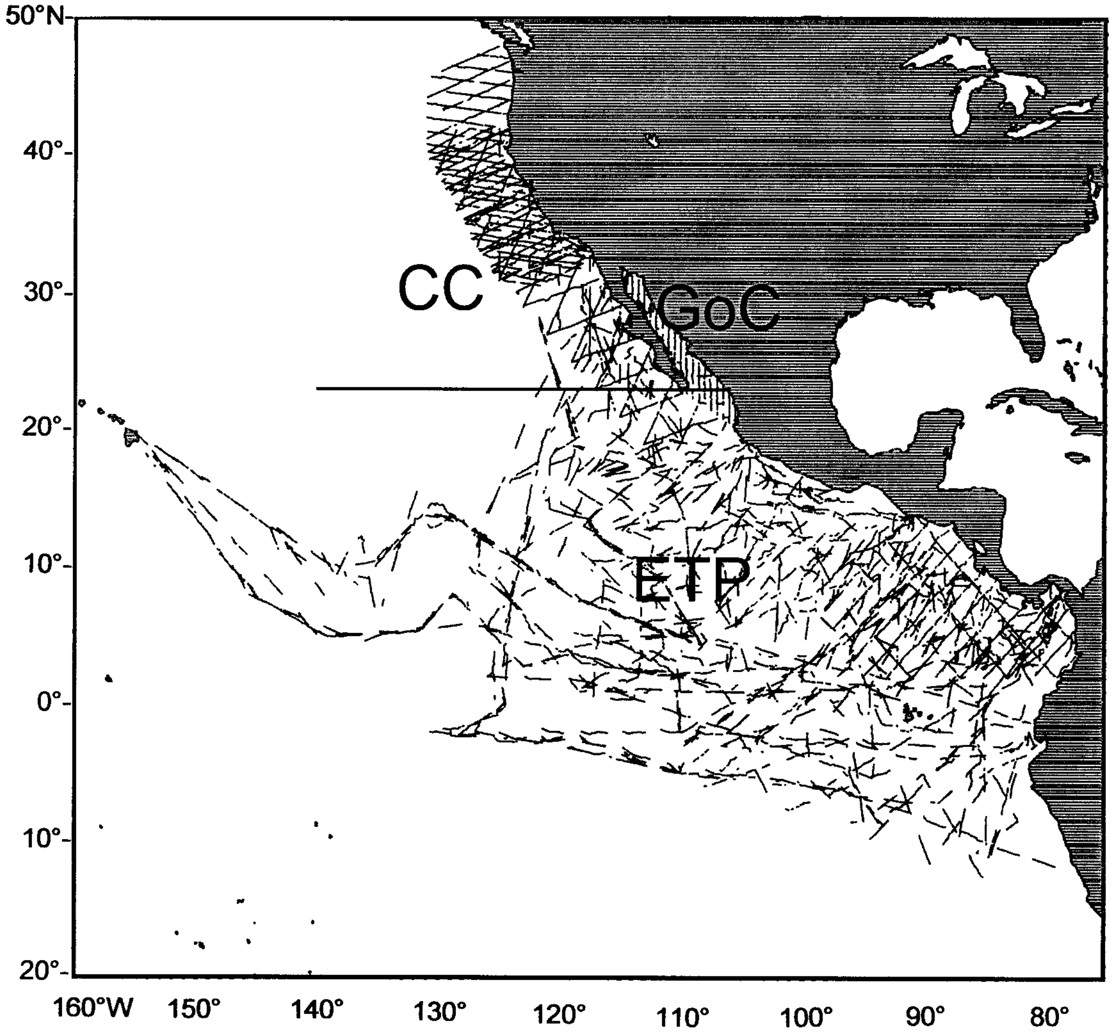

Fig. 1. Sightings used in this paper were made on approximately 200,000km of transect lines surveyed by the SWFSC from 1986-96 in the eastern Pacific Ocean. Three geographic strata are defined by the thick horizontal line at 23°N: the eastern tropical Pacific (ETP), Gulf of California (GoC) and California Current (CC).

same model. Many other strong correlations or associations are expected in the data, especially for *GeoStrata* (with *Year, Species, CruzNo*) and *Species* (with *Cue, Beauf* and *TotSS*).

Vis and *SwelHght* were added in 1991 and subsequent years. The stepwise model building was repeated using these variables (actually *Vis* and *SwelAnom*, see Appendix) and the 1991-96 subset of survey data.

To determine the robustness of GAM coefficients, models were fitted to two subsets of the data that did not overlap geographically: surveys in the eastern tropical Pacific stratum and surveys in the California Current stratum. Geographic stratification variables were excluded because there was no overlap. The sample size of overlapping observers was too small for meaningful comparison, so *Obsvr* was also excluded. Only those species with more than 15 sightings in each area were included. The resulting models fit to these independent subsets potentially included *Beauf, Ln(TotSS), Cue, BinoCode, Ship* and *Species*.

To evaluate various species groupings, the 1986-96 best-fit model based on all the *Species* was compared to two models with different species groups: the *a proiori* grouping (*SppGroup*) given in Table 1 and an *a posteriori* grouping which was based, in part, on the estimated GAM coefficients for each species.

RESULTS

1986-96 data

The step-wise sequence of forward model selection for the 1986-96 perpendicular distance data is given in Table 2. This ‘base model’ included *Ship* and *Year* (in place of *CruzNo*) and allowed either *Species* or *SppGroup* to be added (but not both). Based on minimising AIC, the best model included all variables except *Rain/Fog*. Of the continuous variables, *Beauf* and *Ln(TotSS)* were added as smoothed splines (df = 2 and 7, respectively). Models with AIC differences (ΔAIC) of 2.0 or less are generally considered to be worth further consideration (Burnham and Anderson, 1998) and it was found that a simpler model with almost equivalent explanatory power (ΔAIC = 0.5) could be formulated by excluding *Glare*, by including *Beauf* as a linear term and by

Table 1

Species groups, species codes, common and scientific names used in this paper, number of sightings and normalized GAM coefficients. Species group refers to a subjective classification of species (used first by Barlow, 1995) based on similarities in size, behaviour and other sighting characteristics (his category of 'cryptic species' was split into 'Porpoises' and '*Kogia* spp.'). Spotted and spinner dolphins were of special interest on the 1986-90 surveys and were typically recorded to subspecies or 'stocks'. GAM coefficients (normalised to zero mean) are from the 1986-96 best-fit model using *CruiseNo* in place of *Ship* and *Year*.

Code	Scientific name	Common name	No. sightings	GAM coefficient
Small delphinids				
02	*Stenella attenuata* (offshore)	Offshore pantropical spotted dolphin	741	-0.13
06	*Stenella attenuata graffmani*	Coastal pantropical spotted dolphin	46	0.06
90	*Stenella attenuata* (unid. subsp.)	Unidentified pantropical spotted dolphin	52	-0.01
03	*Stenella longirostris* (unid. subsp.)	Unidentified spinner dolphin	43	-0.04
10	*Stenella longirostris orientalis*	Eastern spinner dolphin	310	-0.20
11	S*tenella longirostris* hybrid	Whitebelly spinner dolphin	178	-0.17
05	*Delphinus* spp.	Unidentified common dolphin	67	-0.14
13	*Stenella coeruleoalba*	Striped dolphin	1,071	-0.03
15	*Steno bredanensis*	Rough-toothed dolphin	167	-0.22
16	D*elphinus capensis*	Long-beaked common dolphin	49	-0.25
17	*Delphinus delphis*	Short-beaked common dolphin	677	-0.14
22	L*agenorhynchus obliquidens*	Pacific white-sided dolphin	52	-0.14
26	*Lagenodelphis hosei*	Fraser's dolphin	25	-0.14
27	*Lissodelphis borealis*	Northern right whale dolphin	40	-0.17
77	Unid. delphinoid	Unidentified dolphin or porpoise	1,239	0.47
Large delphinids				
18	*Tursiops truncatus*	Bottlenose dolphin	537	-0.14
21	*Grampus griseus*	Risso's dolphin	347	-0.17
31	*Peponocephala electra*	Melon-headed whale	16	-0.06
32	*Feresa attenuata*	Pygmy killer whale	31	-0.38
33	*Pseudorca crassidens*	False killer whale	38	-0.08
34	*Globicephala* spp.	Unidentified pilot whale	86	0.04
36	*Globicephala macrorhynchus*	Short-finned pilot whale	198	0.06
37	*Orcinus orca*	Killer whale	77	0.27
Porpoises				
40	*Phocoena phocoena*	Harbour porpoise	42	-0.41
41	*Phocoena sinus*	Vaquita	14	-0.53
44	*Phocoenoides dalli*	Dall's porpoise	285	-0.18
Kogia spp.				
80	*Kogia simus/breviceps*	Dwarf or pygmy sperm whale	141	-0.34
Small whales				
49	Ziphiid whale	Unidentified beaked whale	152	0.05
51	*Mesoplodon* spp.	Unidentified Mesoplodon	148	0.15
61	*Ziphius cavirostris*	Cuvier's beaked whale	135	-0.21
71	*Balaenoptera acutorostrata*	Minke whale	18	-0.11
78	Unid. small whale	Unidentified small whale	247	0.13
Large whales				
46	*Physeter macrocephalus*	Sperm whale	285	0.46
63	*Berardius bairdii*	Baird's beaked whale	12	0.00
74	*Balaenoptera physalus*	Fin whale	129	0.25
75	*Balaenoptera musculus*	Blue whale	217	0.28
76	*Megaptera novaeangliae*	Humpback whale	98	0.37
99	*Balaenoptera borealis/edeni*	Sei or Bryde's whale	157	0.05
70	Unid. rorqual	Unidentified rorqual	234	0.61
79	Unid. large whale	Unidentified large whale	184	0.58
98	Unid. whale	Unidentified whale	157	0.50
Other				
96	Unid. cetacean	Unidentified cetacean	154	0.02

reducing the spline fit of *Ln(TotSS)* to 4 degrees of freedom. A better fitting model was obtained using *CruzNo* in place of *Ship* and *Year* (ΔAIC = –7.7, Table 2).

The magnitude of the coefficients for each of the variables in the best model is illustrated in Fig. 2 (including the version that substitutes *CruzNo* for *Ship* and *Year*). The q-q plot for this last model (the cumulative distribution of residuals versus the expected normal cumulative distribution, Fig. 3) shows that residuals are symmetrically distributed and are approximately normal within +/–1 standard error, but that the tails of the distribution are shorter than expected for a normal distribution. The q-q plots were similar for all models.

1991-96 data

The initial stages of model building for 1991-96 (which includes two new variables: *SwelAnom* and *Vis*) was similar to the 1986-96 model (Table 3); however, *SwelAnom* and *Rain/Fog* were included and *Ship*, *Year* and *Glare* were excluded in the best-fit model. The best-fit model used spline fits for *Ln(TotSS)* and *SwelAnom* (df = 5 for both). A model with similar explanatory power (ΔAIC = 1.3) was obtained by using a spline with 4 degrees of freedom for *SwelAnom* (Table 3) and by eliminating *GeoStrata*. When *CruzNo* was added separately to the step-wise best-fit model, a modest improvement was seen in ability to model *PDist* (ΔAIC = –1.5). When *SwelAnom* was excluded from the model

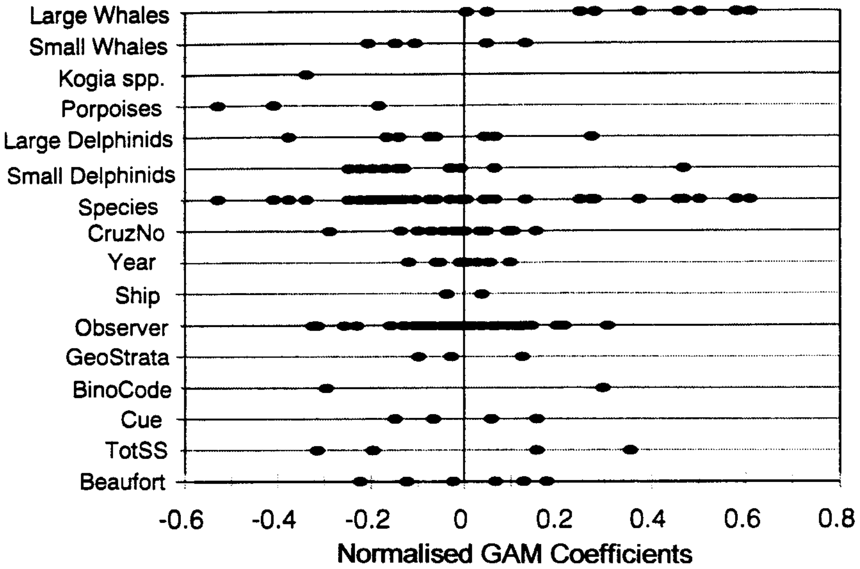

Fig. 2. GAM coefficients (normalised to a mean of zero within each factor) estimated for the best model fit to the 1986-96 sightings using *Ship* and *Year* (Table 1). GAM coefficients are also presented for the same model, substituting *CruzNo* for *Ship* and *Year*. *Species* coefficients were fit separately, but are also grouped by *SppGroup* for presentation here (these groups are not normalised). Coefficients for spline-fits to the continuous variables (*Beauf* and *TotSS*) were replaced with model fits at discrete values (Table 4).

Table 2

Sequential order in which variables were added to and/or deleted from the best GAM fit to 1986-96 data. For continuous variables, parentheses are used to indicate the degrees of freedom for spline smoothing used at that step in the model building. *SppGroup* was used as an alternate for *Species*. The dispersion parameter for modelling residuals was re-estimated and the algorithm was restarted after an optimal model had been found (dashed line); AIC values are not comparable above and below this line. The last three lines represent alternative models substituting *CruzNo* (for *Ship* and *Year*), and *a priori SppGroup* and *a posteriori SppGroup2* (for *Species*).

Model									AIC
BinoCode									4838.5
BinoCode +	*SppGroup*								4522.2
BinoCode +	*Species*								4392.6
BinoCode +	*Species* +	*Ln(TotSS)* (1)							4271.4
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1)						4196.0
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1) +	*Cue*					4143.3
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1) +	*Cue* +	*Ship*				4128.2
BinoCode +	*Species* +	*Ln(TotSS)* (2) +	*Beauf* (1) +	*Cue* +	*Ship*				4119.2
BinoCode +	*Species* +	*Ln(TotSS)* (2) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year*				4110.5
BinoCode +	*Species* +	*Ln(TotSS)* (3) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year*				4106.6
BinoCode +	*Species* +	*Ln(TotSS)* (3) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year* +	*Geostrata*			4104.9
BinoCode +	*Species* +	*Ln(TotSS)* (3) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4101.0
BinoCode +	*Species* +	*Ln(TotSS)* (4) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4099.5
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4099.0
BinoCode +	*Species* +	*Ln(TotSS)* (6) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4098.7
BinoCode +	*Species* +	*Ln(TotSS)* (6) +	*Beauf* (2) +	Cue +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4098.5
BinoCode +	*Species* +	*Ln(TotSS)* (6) +	*Beauf* (2) +	Cue +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4069.8
BinoCode +	*Species* +	*Ln(TotSS)* (7) +	*Beauf* (2) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4069.6
BinoCode +	*Species* +	*Ln(TotSS)* (7) +	*Beauf* (2) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr* +	*Glare*	4069.5
BinoCode +	*Species* +	*Ln(TotSS)* (7) +	*Beauf* (2) +	*Cue* +	*CruzNo* +	*Geostrata* +	*Obsvr* +	*Glare*	4061.8
BinoCode +	*SppGroup* +	*Ln(TotSS)* (7) +	*Beauf* (2) +	*Cue* +	*CruzNo* +	*Geostrata* +	*Obsvr* +	*Glare*	4279.0
BinoCode +	*SppGroup2* +	*Ln(TotSS)* (7) +	*Beauf* (2) +	*Cue* +	*CruzNo* +	*Geostrata* +	*Obsvr* +	*Glare*	4059.3

selection process, the resulting bestfit model did not include any different variables (ΔAIC = 10.1).

Geographic comparisons

GAM coefficients fitted to sightings data from the eastern tropical Pacific and from the California Current stratum (Table 4, Fig. 4) are correlated. The correlation is lower for coefficients associated with species-specific differences in mean perpendicular sighting distance ($r^2 = 0.49$) than for other coefficients ($r^2 = 0.83$). Correlations were calculated from the actual number of parameters estimated for each variable, which is one less than the number of normalised, dummy coefficients given in Table 4.

Species groups

The best-fit model based on all 42 *Species* (Table 1) and using *CruzNo* in place of *Ship* and *Year* (Table 2) was used as a standard for comparison to models with alternative species groupings. The *a priori* species grouping (*SppGroup*, Table 1) performed poorly relative to this

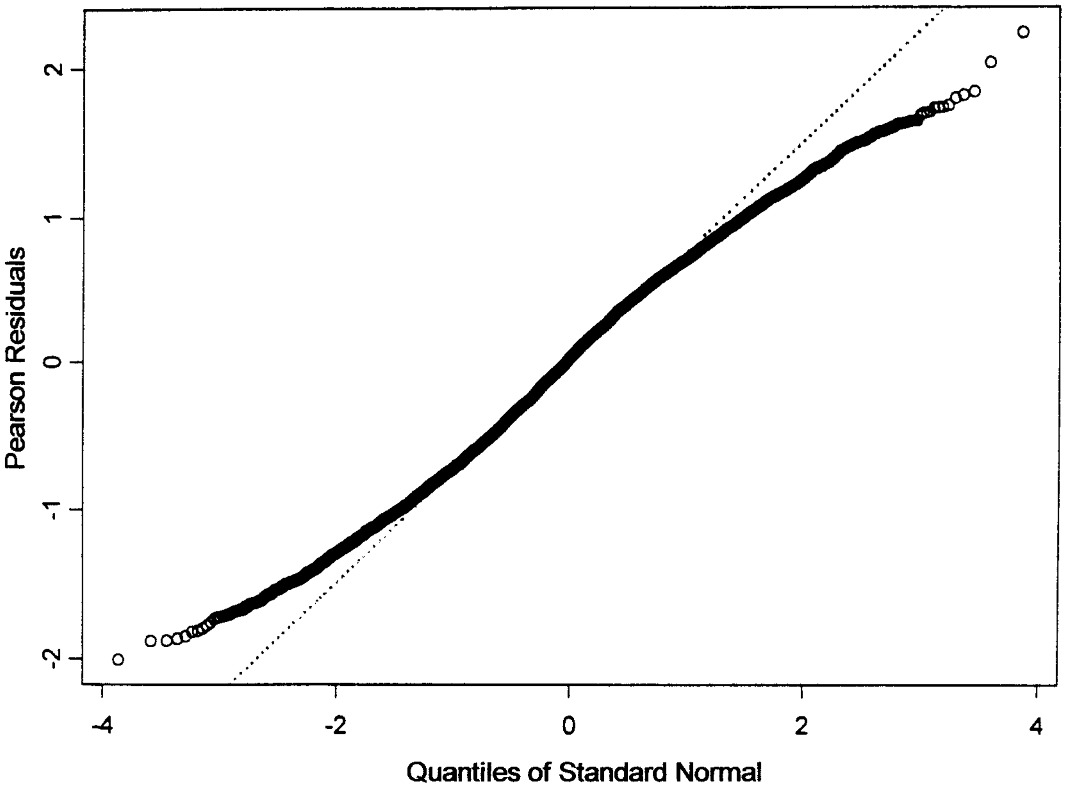

Fig. 3. A quantile (q-q) plot of residuals from one of the models developed here (open circles) compared to the expected quantiles from a standard normal distribution (dotted line). The model fits shown here are from the third to the last in Table 2, but q-q plots from all models were similar.

Table 3

Sequential order in which variables were added to and/or deleted from the best-fit GAM fit to 1991-96 data. For continuous variables, parentheses are used to indicate the order of spline smoothing used at that step in the model building. *SppGroup* was used as an alternate for *Species*. The dispersion parameter was re-estimated and the algorithm was restarted after an optimal model had been found (dashed line); AIC values are not comparable above and below this line.

Model									AIC
BinoCode									1828.6
BinoCode +	*SppGroup*								1696.5
BinoCode +	*SppGroup* +	*Ln(TotSS)* (1)							1665.3
BinoCode +	*Species* +	*Ln(TotSS)* (1)							1590.3
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1)						1575.8
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1) +	*Cue*					1557.7
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (1)				1544.6
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (1) +	*Rain/Fog*			1539.2
BinoCode +	*Species* +	*Ln(TotSS)* (2) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (1) +	*Rain/Fog*			1536.1
BinoCode +	*Species* +	*Ln(TotSS)* (3) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (1) +	*Rain/Fog*			1533.1
BinoCode +	*Species* +	*Ln(TotSS)* (4) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (1) +	*Rain/Fog*			1531.9
BinoCode +	*Species* +	*Ln(TotSS)* (4) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (2) +	*Rain/Fog*			1530.8
BinoCode +	*Species* +	*Ln(TotSS)* (4) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (3) +	*Rain/Fog*			1529.5
BinoCode +	*Species* +	*Ln(TotSS)* (4) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (4) +	*Rain/Fog*			1529.1
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (4) +	*Rain/Fog*			1529.0
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	Cue +	*SwelAnom* (4) +	*Rain/Fog*			1512.3
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (4) +	*Rain/Fog* +	*Obsvr*		1511.2
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (4) +	*Rain/Fog* +	*Obsvr* +	*GeoStrata*	1510.0
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (5) +	*Rain/Fog* +	*Obsvr* +	*GeoStrata*	1509.9

best-fit model (ΔAIC = 217.2, Table 2). Inspection of the GAM coefficients for *Species* (Table 1) indicated that the largest outliers within a *SppGroup* were the sightings that could not be assigned to a species with certainty (unidentified dolphin or porpoise, unidentified beaked whale, unidentified small whale, unidentified rorqual, unidentified large whale, unidentified whale and unidentified cetacean). A new, *a posteriori* species grouping (called *SppGroup2*) was created from the *a priori SppGroup* by keeping these unidentified categories separate (but combining unidentified rorquals and unidentified large whales because of similarities in their GAM coefficients). The identified categories of small delphinids and large delphinids were also combined based on similarities in their GAM coefficients. Based on GAM coefficients, Dall's porpoises were an outlier among the porpoise group, and sperm whales were an outlier among the large whales, so these species were given separate categories. Killer whales were an outlier among the large delphinids, so they were combined with large whales which had similar GAM

Table 4

Comparison of GAM coefficients (normalised to zero mean) estimated by fitting a model of perpendicular sighting distance to sighting data from two non-overlapping geographic strata: the eastern tropical Pacific (ETP) and the California Current (CC). Coefficients for spline-fits to the continuous variables (*Beauf* (d.f.=5) and *LnTotSS* (d.f.=4)) were replaced with model fits at discrete values representing the spread of typical values (*Beauf* = 1, 2, 3, 4 and 5 and *TotSS* = 1, 10, 100 and 1000). Because normalised, dummy coefficients are presented, the actual number of coefficients listed is one greater than the number of parameters estimated for each variable.

		GAM Coefficients	
Factors	Codes	ETP	CC
Intercept		0.456	0.565
Beauf	1	0.150	0.230
	2	0.120	0.170
	3	0.010	0.070
	4	- 0.070	- 0.120
	5	- 0.190	- 0.210
TotSS	1	- 0.130	- 0.320
	10	- 0.080	- 0.080
	100	0.200	0.380
	1000	0.490	0.500
Cue	Bird	0.180	- 0.030
	Splash	- 0.067	0.026
	Mammal	- 0.140	- 0.122
	Blow	0.026	0.126
BinoCode	25x	0.344	0.228
	eye/7x	- 0.344	- 0.228
Ship	DSJ	0.051	- 0.010
	MAC	- 0.051	0.010
Species	Striped dolphin	- 0.017	- 0.382
	Short-beaked common dolphin	- 0.080	- 0.449
	Bottlenose dolphin	- 0.193	- 0.169
	Risso's dolphin	- 0.233	- 0.233
	Killer whale	0.248	0.194
	Sperm whale	0.433	0.371
	Ziphiid whale	- 0.079	0.195
	Mesoplodon spp.	- 0.213	0.049
	Cuvier's beaked whale	- 0.256	- 0.299
	Blue whale	0.291	0.142
	Unidentified dolphin	0.443	0.156
	Unidentified small whale	0.033	0.144
	Unidentified large whale	0.526	0.514
	Kogia spp.	- 0.485	- 0.081

coefficients. Baird's beaked whales and sei/Bryde's whales shared similar GAM coefficients and were separated from the other large whales into a new category of medium sized whales. The resulting *a posteriori* species groups contained 13 categories (Table 5). A model based on this *a posteriori* species group was slightly better than the previous best-fit model using all *Species* (ΔAIC = –2.5, Table 2).

DISCUSSION

'All models are wrong, but some are useful' (Box, 1976).

The analyses presented here are based on perpendicular sightings distance although factors that affect effective strip width (*esw*), a line-transect parameter, are ultimately of greater interest. Mean perpendicular sighting distance is used here as a surrogate for *esw* in order to gain the power and versatility of the Generalised Additive Modelling framework. However, it should be noted that mean perpendicular distance is a sufficient surrogate for *esw* only for the simplest 1-parameter line-transect models (such as the half-normal or negative exponential). Nonetheless, *esw* will be closely related to mean perpendicular distance for any family of line-transect models. It seems probable that any factor that affects mean perpendicular sighting distance will also affect *esw*.

The modelling of perpendicular sighting distance was motivated by a desire to identify the most important factors to be included in future line-transect analyses. The best model for the 1986-96 data included most of the potential variables. This result is not entirely surprising given that the variables were recorded because they were thought to potentially affect the distance at which cetaceans can be seen. Nonetheless, no approach to modelling can guarantee that all of the included variables are truly important. Some of the factors that were included in the best model may just be correlated with causal factors (either other factors in the model or factors that were not recorded).

Based on reductions in AIC, the most important factors affecting mean perpendicular distance were, in order, method of searching (*BinoCode*), differences among species *(Species or SppGroup)*, group size (*ln(TotSS)*), sea state (*Beauf)*, and the cue that lead to the sighting *(Cue*) (Table 2). These factors are intuitive and have long been suspected to be the most important factors affecting *esw*, but this study represents the first empirical demonstration of their importance based on field data.

Species

Species-specific factors are clearly important in determining the perpendicular distance at which cetaceans can be seen. The range of GAM coefficients for different species is greater than the range for any other single factor (Fig. 2). *Species* entered the models second, after *BinoCode*. The *a priori* species groupings captured some, but not all of the among-species differences. Killer whales appear to be an outlier among large delphinids and are seen at greater perpendicular distances. Dall's porpoises are seen at greater distances than the other two species of porpoises. Sperm whales are seen at greater distances and both Bryde's and sei whales are seen at lesser distances than other members of the large whale group. The grouping of species to estimate line-transect detection functions is a valuable tool when dealing with small sample sizes and mixed-species aggregations (Barlow, 1995). Relatively minor adjustments to the species groups (e.g. including killer whales with large whales, combining the other large delphinids with small delphinids, separating Dall's porpoise from the other porpoises and creating new groups for the unidentified categories) resulted in a lower AIC value and hence a better fitting model of perpendicular sighting distance than the model which included all species. The success of these *a posteriori* groupings is somewhat artificial because the groupings were based, in part, on knowledge of GAM coefficients. Nonetheless, use of *a posteriori* species groupings from a GAM analysis may improve precision when estimating *esw* and abundance by line-transect methods.

The 'unidentified' species categories (e.g. unidentified dolphin, unidentified large whale, etc.) were clearly outliers in the species groups and were, on average, seen at greater perpendicular distances than the categories that could be identified to species. This result was not unexpected because animals that are seen further from the ship are less likely to be identified. Indeed, this dependence between the 'apparent' distribution of unidentified groups and distance from the trackline violates one of the primary assumptions of

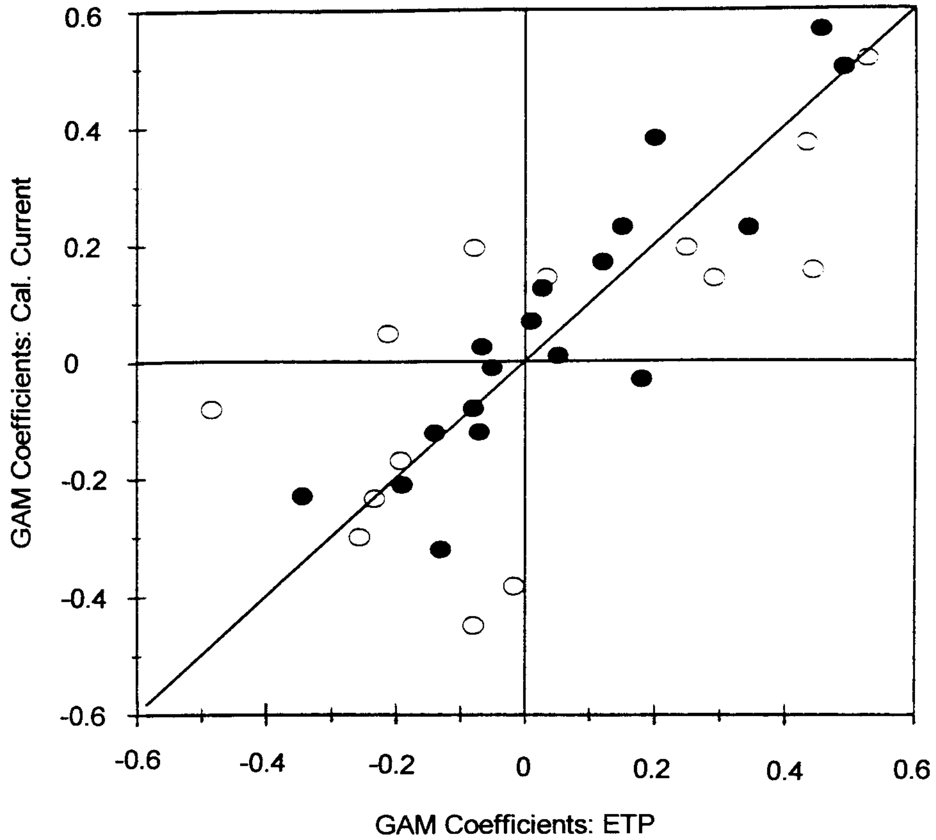

Fig. 4. Comparison of GAM coefficients (normalised to zero mean) estimated by fitting a model of perpendicular sighting distance to sighting data from two non-overlapping geographic strata: the eastern tropical Pacific (ETP) and the California Current. Coefficients for spline-fits to the continuous variables (*Beauf* with 5 degrees of freedom and *TotSS* with 4 degrees of freedom) were replaced with model fits at discrete values (Table 4). Species coefficients are given as open circles, and all others as closed circles. Diagonal lines represents 1:1 parity line. Because normalised, dummy coefficients are presented, the actual number of points plotted is one greater than the number of parameters estimated for each variable.

line-transect abundance estimation. Additional work is needed on appropriate methods for estimating the abundance of groups that cannot be identified to species.

Comparison of the species coefficients for the two non-overlapping data subsets (Table 4) shows two clear outliers: short-beaked common dolphins and striped dolphins. Both of these species were seen closer to the trackline in the California Current than in the eastern tropical Pacific. This difference could be related to behavioural differences between these areas. Common dolphins are much more likely to bow-ride and thus be attracted to ships off California compared to the eastern tropical Pacific. Striped dolphins seldom bow-ride but are frequently associated with bow-riding common dolphins off California; whereas, in the tropics, striped dolphins are wary of ships and are seldom associated with any other species.

Two of the other factors that most affect perpendicular sighting distance (*TotSS* and *Cue*) are also related to species. For fin whale and blue whales, group sizes are typically less than two, whereas for some of the small delphinids, group size may be in the hundreds or even thousands. The relationship between perpendicular sighting distance and the logarithm of total school size is a complicated non-linear function (Fig. 5) but shows a general increase in sighting distances with group size. *Cue* also varies between species, with the *cue* of ‘blow’ being most common for large whales and some large delphinids and the *cue* of ‘splash’ being seldom associated with vaquita or harbour porpoise. The *cues* of ‘bird’ and ‘blow’ are usually above the horizon and are conspicuous even when sighting conditions are poor; these two *cues* were seen at the greatest perpendicular distances (Fig. 5).

Other factors

Several factors other than species are important in determining perpendicular sighting distances in a predictable manner. *BinoCode* was added first to all models and perpendicular distances are obviously greater when observers search with 25x binoculars compared to naked eye and 7x binoculars (Table 4, Fig. 5). Beaufort sea state was also important and was negatively (and very nearly linearly) related to mean perpendicular distance (the only deviation from linearity appeared between the (rarely observed) Beaufort 0 and Beaufort 1) as seen in Fig. 5. This linear relationship implies that at each higher sea state, mean perpendicular distance (and hence sighting rate) is reduced by a constant proportional amount, as assumed by Beavers and Ramsey (1998).

Differences in sighting distances between individual observers were large and potentially very important. These differences are not unexpected, because sighting distances should be inversely related to sighting rates, and sighting rates sometimes differed among individuals by a factor of two (cf. Hill and Barlow, 1992; Table 5). Individual differences in sighting distances or sighting rates are, however, difficult to interpret because observers work in teams of three with a region of overlap in their search patterns. Groups are unavailable to one observer if they have

Table 5

A posteriori species groups. GAM coefficients (normalised to zero mean) are from Table 1.

Species group and common name	GAM coefficient	Species group and common name	GAM coefficient
Delphinids		**Dwarf and pygmy sperm whales**	
Offshore pantropical spotted dolphin	-0.13	Dwarf or pygmy sperm whale	-0.34
Coastal pantropical spotted dolphin	0.06		
Unid. pantropical spotted dolphin	-0.01	**Small whales**	
Unid. spinner dolphin	-0.04	Unid. Mesoplodon	-0.15
Eastern spinner dolphin	-0.20	Cuvier's beaked whale	-0.21
Whitebelly spinner dolphin	-0.17	Minke whale	-0.11
Unid. common dolphin	-0.14		
Striped dolphin	-0.03	**Unid. small whales**	
Rough-toothed dolphin	-0.22	Unid. beaked whale	0.05
Long-beaked common dolphin	-0.25	Unid. small whale	0.13
Short-beaked common dolphin	-0.14		
Pacific white-sided dolphin	-0.14	**Sperm whales**	
Fraser's dolphin	-0.14	Sperm whale	0.46
Northern right whale dolphin	-0.17		
Bottlenose dolphin	-0.14	**Large whales**	
Risso's dolphin	-0.17	Killer whale	0.27
Melon-headed whale	-0.06	Fin whale	0.25
Pygmy killer whale	-0.38	Blue whale	0.28
False killer whale	-0.08	Humpback whale	0.37
Unid. pilot whale	0.04		
Short-finned pilot whale	0.06	**Medium whales**	
		Baird's beaked whale	0.00
Unid. Delphinoid		Sei or Bryde's whale	0.05
Unid. dolphin or porpoise	0.47		
		Unid. large whales	
Harbour Porpoises		Unid. rorqual	0.61
Harbour porpoise	-0.41	Unid. large whale	0.58
Vaquita	- 0.53	Unid. whale	0.50
Dall's Porpoises		**Unid. cetacean**	
Dall's porpoise	-0.18	Unid. cetacean	0.02

been already seen by another observer. Given the methods, it would be difficult to adjust for individual differences between observers in line-transect abundance estimation. Early in the study, from 1986 to 1990, two teams of three observers were generally constant throughout a cruise, thus it would be possible to consider a line-transect analysis stratified by team. However, since 1991, an open rotation system was adopted and six teams could be defined for each cruise.

The least important factors in determining perpendicular sighting distances in these data are *Ship*, *Year* and *GeoStrata* (in that order, Fig. 2), which provides *post hoc* justification for pooling over these factors in past analyses (Wade and Gerrodette, 1993; Barlow and Gerrodette, 1996).

Interaction effects

Exploration of interaction effects between factors that affect perpendicular sightings distance have been deliberately avoided in this study. Given the large number of important factors, the number of potential interaction effects is enormous and some are certainly important. This exclusion of interaction effects is not intended to downplay their importance. However, the primary aim of the paper is to identify and concentrate on the first-order effects.

The most important interaction effects are probably those that include *Species* and other sighting conditions. Sea conditions (Beaufort and swell height) are more likely to obscure a small *Species* or one producing an inconspicuous *Cue*. *Glare* makes it more difficult to see animals, but backlighting makes blows easier to see. Group sizes span four orders of magnitude and often the ranges do not overlap between species. The effect of group size on perpendicular sighting distance is almost certainly different for different species. There are, however, so many *Species* that interaction effects will be difficult to tease out. Clearly from this analysis, species can be clustered in groups with similar sighting characteristics and these similarities are evident in the similarities between GAM coefficients of *species* within our *a priori* groups. The use of species groups is one possible approach to reduce the dimensionality of the problem and to allow future analyses of interaction effects.

Covariation and colinearity

Some variables included as linear terms were co-linear (i.e. correlated to one another). For example, *CruzNo* determined *Ship* and *Year* effects. In the best model, *Species* & *Cue* and *GeoStrat* & *CruzNo* were pairs of linear terms that would be expected to be correlated. A strong co-linearity may affect the ability to correctly estimate model parameters (Legendre and Legendre, 1998), which may be the ultimate use of the GAM analysis. If model parameters are to be directly used (such as in the Beavers and Ramsey (1998) approach to scaling detection functions), every effort should be made to minimise co-linearities. One useful approach (used here for Beaufort sea state and swell height) may be to express one variable as deviations from expected values based on the other.

Recommendations for design and analysis

The results presented here have implications for both the design and analysis of cetacean line-transect surveys. It is clear that there may be many factors that significantly affect perpendicular sighting distance. In designing surveys, researchers should ensure the accurate recording of as many of these variables as possible so that the information will be

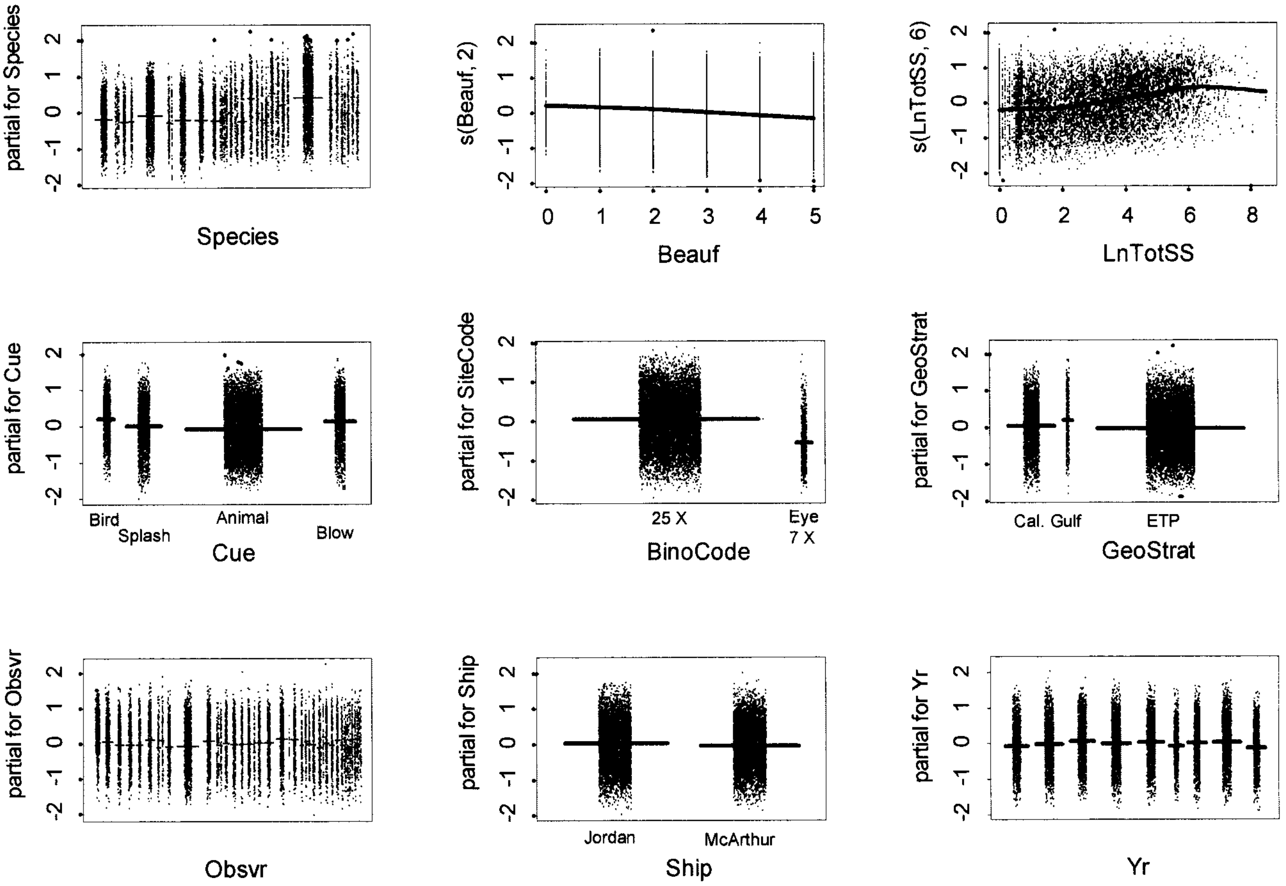

Fig. 5. Partial residuals for significant factors affecting perpendicular sighting distance on 1986-96 surveys based on a generalised additive model. Y-axes represent residual deviations from a model that include all factors other than the one represented on the x-axis. Positive residuals represent greater perpendicular distances from the trackline.

available for analysis. Most notably, Beaufort sea state is not a sufficient descriptor of sea surface conditions and additional important information is contained in swell height.

One encouraging finding, from the perspective of data analysis, is that the species that are similar in size and behaviour have similar mean perpendicular sighting distances (after accounting for other variables such as sighting conditions and group size). This is significant because it greatly increases the ability to estimate the abundance of rare species which might not, by themselves, be seen frequently enough to estimate a detection function. Abundance of these rare species can be estimated by pooling them with other more abundant species; however, this approach would require that other variables that affect perpendicular sighting distance, such as group size, are included as covariates or stratification criteria if the distributions of these variables differ among species.

Another important finding is the relative lack of differences in perpendicular sighting distances among years or between similar vessels (again, after controlling for other variables that do affect perpendicular sighting distance). This is significant because it justifies the pooling of sightings made on different surveys for the purpose of estimating a detection function. This approach is likely to greatly increase the precision of line-transect abundance estimates.

The analyses and results presented here represent a first step in uncovering the factors that most affect *esw* in cetacean line-transect surveys. Mean perpendicular sighting distance was used as a convenient surrogate for *esw* in order to gain the power and flexibility of GAM analysis. However, additional research is needed to extend these analyses to direct estimates of *esw*. Such work is ongoing at our laboratory.

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APPENDIX

Recorded effort variables

Effort variables were recorded at the start of search effort and whenever sighting conditions changed. In addition to time, date, latitude and longitude, these include:

Beauf	Beaufort sea state is a categorical variable that is representative of wind speed as judged by eye based on the characteristics of the ocean's surface (Bowditch, 1975).
Rain/Fog	Rain/fog code is used to indicate the presence of rain, fog, haze, or both rain and fog within the primary search area (typically defined as within 3 n.miles from the ship in the two forward quadrants).
SwelHght	Swell height is an estimate of the height of the dominant swell in feet.
Vis	Visibility is the observers' estimate of the distance (in n.miles) at which a conspicuous cue could be seen if present.
CruzNo	Cruise number is a unique number assigned to each marine mammal survey cruise from the SWFSC. Each year's effort on each ship is given a different cruise number.

Recorded sighting variables

Sighting variables are recorded whenever a cetacean sighting is made. In addition to time, date, latitude and longitude, these include:

RDist	Radial (or line-of-sight) sighting distance is the estimated distance (in n.miles) between the ship and the cetacean(s). *RDist* was typically estimated using reticles in the oculars of the 7x or 25x binoculars but was occasionally estimated 'by eye' for sightings that were made without binoculars or were very close to the ship.
Angle	Sighting angle is the angular deviation of the group from the trackline.
Species	Species codes (Table 1) represent the lowest taxonomic group into which an animal could be classified based on observed field characteristics. For pantropical spotted dolphins and spinner dolphins, sightings were often classified into sub-species or distinct stocks (Perrin *et al.*, 1991; 1994). Some sightings could not be identified to species, in which case the species code represented the lowest taxonomic category for which identification was certain (e.g. *Kogia* spp., or unidentified rorqual). When more than one category of '*Species*' was present within a group, all appropriate species codes were listed with an estimate from each observer of the proportion of that species present in the group. Because a large fraction of *Kogia* spp. and *Mesoplodon* spp. sightings were identified only to genus, these genus categories were used in the analyses.
TotSS	Total school size was estimated as the weighted geometric mean of calibrated group size estimates (Barlow *et al.*, 1988) from all observers who made an estimate. Direct calibration factors for individual observers were

based on aerial photographic counts of actual school size (Barlow *et al.*, 1998). Indirect calibration factors are based on comparisons with other, directly calibrated observers (Barlow, 1995).

Cue	Cue code represents the aspect of the sighting that first drew the observer's attention to the likely presence of a cetacean. These primarily included bird flocks, splashes, blows and the body of the animal itself.
BinoCode	Sighting code represents the method used by the observer who made the sighting: either 25x binoculars or naked eye/7x binoculars.
Obsvr	Each observer is assigned a unique number. Observer numbers have been assigned sequentially to each new observer and have been used consistently whenever this individual worked on our surveys.
VSun/HSun	Vertical and horizontal sun angles relative to the ship's bow were recorded to provide a measure of the potential effect of sun glare. Horizontal sun angle was recorded in integer bearings from 1 to 12 (based on a clock's face, with 12 o'clock being straight ahead, 3 o'clock being abeam on the starboard side, etc.). Vertical sun angle was recorded in 4 categories: 12 o'clock (directly overhead) to 3 o'clock (on the horizon).

Derived variables

GeoStrata	Geographic stratum represents one of three general areas where surveys were conducted (Fig. 1) and was derived from the recorded latitude and longitude. The areas included the Eastern Tropical Pacific (south of 23°N), the Gulf of California (north of 23°N and east of Baja California) and California Current (north of 23°N and west of Baja California).
SppGroup	Species group is a subjective *a priori* assignment of species into one of seven groups (small delphinids, large delphinids, small whales, large whales, porpoises, *Kogia* spp. and 'other'; Table 1) which are expected to have similar sighting characteristics.
Glare	Sun glare is a binary variable created from the vertical and horizontal sun positions and is used to indicate the presence of glare on the trackline. Based on at-sea experience, sun glare was assumed to be a potential problem if the horizontal sun angle was 11, 12 or 1 o'clock and the vertical sun angle was 2 or 3 o'clock or if the horizontal sun angle was 12 o'clock and the vertical sun angle was 1 o'clock.
PDist	Perpendicular sighting distance is the primary dependent variable in this analysis and was estimated from the radial sighting distance (*RDist*) and the angular deviation of the group from the trackline (*Angle*): $\mathit{PDist} = \mathit{RDist} * \sin(\mathit{Angle})$.
SwelAnom	Swell height is correlated with Beaufort sea state ($r^2 = 0.166$), so the swell anomaly (the deviation of the swell height from that expected for a given Beaufort sea state) was used calculated from regression: $\mathit{SwelAnom} = \mathit{SwelHght} - 1.90 - (0.465 * \mathit{Beauf})$.