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Inferring trackline detection probabilities, g(0), for cetaceans from apparent densities in different survey conditions

JAY BARLOW,[1] Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 8901 La Jolla Shores Drive, La Jolla, California 92037, U.S.A.

ABSTRACT

Visual line-transect surveys are commonly used to estimate cetacean abundance. A key parameter in such studies is *g*(0), the probability of detecting an animal that is directly on the transect line. This is typically considered to be constant for a species across survey conditions. A method is developed to estimate the relative values of *g*(0) in different survey conditions (Beaufort state) by comparing Beaufort-specific density estimates. The approach is based on fitting generalized additive models, with the presence of a sighting on a survey segment as the dependent variable, Beaufort state as the key explanatory variable, and year, latitude, and longitude as nuisance variables to control for real differences in density over time and space. Values of relative *g*(0) are estimated for 20 cetacean taxa using 175,000 km of line-transect survey data from the eastern and central Pacific Ocean from 1986 to 2010. Results show that *g*(0) decreases as Beaufort state increases, even for visually conspicuous species. This effect is greatest for the least conspicuous species (rough-toothed dolphins, beaked whales, minke whales, and dwarf and pygmy sperm whales). Ignoring these large effects results in a nontrivial bias in cetacean abundance estimates.

Key words: abundance, cetacean, detection probability, density, dolphin, *g*(0), line-transect, porpoise, survey, visual, whale.

Line-transect methods are often used to estimate the density and abundance of cetacean species (whales, dolphins, and porpoises) based on visual sighting surveys conducted from ships. A defined study area is surveyed with systematic or random transect lines, and cetacean density is calculated using either conventional distance sampling or multiple-covariate distance sampling methods (Buckland *et al.* 2001, 2004). One common assumption of both methods is that all animals directly on the transect line are seen or that the fraction of detected animals (the trackline detection probability or *g*(0) in distance sampling terminology) can be estimated. Cetacean species are typically seen only when some portion of their body is above the water's surface or, for larger cetaceans, when their exhalations are visible as a distinct blow. Cetaceans are typically not visible from surface vessels when diving, which would result in an underestimate of density if corrections were not applied for missed animals. This is referred to as availability bias. An additional bias,

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[1] Corresponding author (e-mail: jay.barlow@noaa.gov).

perception bias, can occur if animals surface within the visual range of observers but are not seen. This can result because the visual observers were not looking in the right direction, because the surfacing was obscured by waves, or a wide variety of other factors. Perception bias is strongly affected by weather and other conditions that affect search effectiveness, especially for inconspicuous cetacean species. The concept of perception and availability bias (as conceived by Marsh and Sinclair 1989) is helpful, but in reality the two can be convolved. Visual observers on ships typically search in a 180° arc in front of the survey vessel and out to the horizon. The probability of detecting a surfacing cetacean declines with its distance from the survey vessel, and there is no distance at which an animal suddenly becomes unavailable to being seen. At larger distances, the probability of detection becomes essentially zero, but that distance depends on sighting conditions. As noted by Laake and Borchers (2004), the distinction between availability and perception can be fuzzy, but clearly the net effect of both depends on sighting conditions. Laake and Borchers (2004) reviewed many methods that have been developed to estimate availability bias, perception bias, or the combined effect of both for line-transect surveys. This subject continues to be an area of active research as shown by several recent publications (Okamura *et al.* 2012, Borchers *et al.* 2013, Langrock *et al.* 2013).

Despite recent advances in methods to estimate availability bias, perception bias, and trackline detection probability for cetacean surveys, these quantities have not been estimated for most cetacean surveys, and available estimates often pertain to a narrow range of sighting conditions. Estimation of $g(0)$ is not robust to pooling (Buckland *et al.* 2001), and abundance estimates can be biased if the effects of sighting conditions on $g(0)$ are not explicitly considered. For inconspicuous species like beaked whales and dwarf and pygmy sperm whales (*Kogia simus* and *K. breviceps*, respectively), trackline detection probabilities may be especially dependent on sighting conditions, but values for different sea states have typically not been estimated (Barlow 1999, Okamura *et al.* 2012, Borchers *et al.* 2013). Dual-platform methods are expensive to implement and require a separate independent team of observers, which is often logistically infeasible. For long-diving whales, it is not practical to use methods that require observations from multiple surfacings. The methods developed recently by Okamura *et al.* (2012) and Borchers *et al.* (2013) require diving data to quantify intermittent availability, and these data should ideally be collected at the same time and location as the line-transect data are collected. Such data requirements are seldom met. Methods are needed that can be applied more generally to a wide variety of species to estimate trackline detection probabilities in a variety of sighting conditions.

Here I present a method to estimate trackline detection probabilities for cetacean surveys based on the simple concept that true density does not change with sighting conditions. If density is estimated for a given study area in a variety of sighting conditions, the estimates made in the best conditions will be less biased than estimates made in poorer conditions. The degree to which estimates differ in differing survey conditions can be used to infer relative difference in trackline detection probabilities. If trackline detection is certain, $g(0) = 1.0$ in the best survey conditions, absolute estimates of detection probability can be made for all other conditions from the ratio of density estimates. If some individuals are missed even in the best survey conditions, but trackline detection probabilities can be estimated for those conditions (*e.g.*, Barlow 1999), this method allows extrapolation of those estimates to poorer survey conditions. This method is intended to complement rather than replace more traditional methods of estimating *g*(0), and every effort should be made to incorporate *g*(0) estimation into the design of any cetacean survey. However, the premise of this analysis is that estimating *g*(0) for a range of species across varying sighting conditions within a single survey is almost never feasible; thus a model-based approach drawing on data from numerous surveys is useful for obtaining such estimates.

This method is applied to estimate relative *g*(0) values for 20 cetacean species groups in the eastern and central Pacific Ocean. A generalized additive model (GAM) is used to statistically tease apart the effect of sighting conditions from other factors that influence cetacean densities, such as geographical variation and temporal changes in density. A similar GAM is used to determine whether changes in group size with sighting conditions might compensate for changes in group density. Parameters for both models are fit using a large compilation of 175,000 km of cetacean line-transect survey data collected by the Southwest Fisheries Science Center (SWFSC) on ship-based surveys conducted from 1986 to 2010.

Methods

Field Methods

The SWFSC has conducted ship-based line-transect surveys for cetaceans in the eastern Pacific Ocean using consistent methods from 1986 to 2010. Survey methods are described in detail by Kinzey *et al.* (2000) and Barlow and Forney (2007). In brief, two experienced marine mammal observers searched with 25× pedestal-mounted binoculars from the flying bridge deck of 51–65 m research vessels. A third observer searched using unaided eyes and (occasionally) 7× binoculars and acted as data recorder. Survey conditions (Beaufort sea state, swell height, and visibility) were recorded every 30–40 min or whenever conditions changed. When cetaceans were seen within 3 nmi of the transect line, survey effort was typically halted, and the ship was maneuvered to approach the animals so that the observers could better determine the species present and estimate the group size. Vessels covered predetermined transect lines that representatively sampled the defined study area. Survey effort was greatest in the eastern tropical Pacific, along the U.S. West Coast, and in the central North Pacific (including waters around the Hawaiian Islands, and Palmyra and Johnston Atolls) (Table 1).

Trackline detection probabilities, *g*(0) are estimated here for 20 species or mixed-species categories (Table 2). Some similar-looking species are difficult to identify at sea. If a cetacean sighting could not be identified to species with certainty, higher-level taxonomic categories were used to classify a sighting. If these higher-level categories comprised an appreciable number of sightings, these categories are used in all analyses. All beaked whales in the genus *Mesoplodon* are combined as *Mesoplodon* spp. Similarly, dwarf and pygmy sperm whales are combined as *Kogia* spp., short-beaked and long-beaked common dolphins (*Delphinus delphis* and *D. capensis*, respectively) are combined as *Delphinus* spp., and sei whales (*Balaenoptera borealis*) and Bryde's whales (*Balaenoptera edeni*) are combined as a category called Sei/Bryde's. Some subspecies of spotted dolphin (*Stenella attenuata*) and spinner dolphin (*Stenella longirostris*) are identified at sea based on external morphology, but subspecies categories are not used here.

Table 1. Areas surveyed, years surveyed, total transect length, and proportions of survey effort stratified by Beaufort state. Study area boundaries for these regions are illustrated in Barlow (2013, fig. 1).

Survey region	Survey years	Transect length (km)	Proportion of survey effort by Beaufort state							Average Beaufort state
			0	1	2	3	4	5	6	
Eastern Tropical Pacific, inner core area	1986, 1987, 1988, 1989, 1990, 1992, 1993, 1995, 1998, 1999, 2000, 2003, 2006, 2007	164,369	0.006	0.046	0.153	0.257	0.353	0.177	0.008	3.5
Eastern Tropical Pacific, western and southern areas	1986, 1987, 1988, 1989, 1990, 1992, 1993, 1995, 1998, 1999, 2000, 2003, 2006, 2007	150,873	0.002	0.015	0.057	0.015	0.453	0.306	0.020	4.0
U.S. West Coast	1991, 1993, 1996, 2001, 2005, 2008	65,476	0.005	0.038	0.119	0.196	0.394	0.237	0.012	3.7
Central North Pacific	1997, 2002, 2005, 2010	65,297	0.002	0.008	0.046	0.106	0.445	0.330	0.064	4.2
Alaska/British Columbia	1994, 2004	16,149	0.013	0.066	0.218	0.200	0.295	0.160	0.047	3.4
Gulf of California	1993, 1995	9,064	0.014	0.119	0.262	0.263	0.262	0.079	0.000	2.9
Total		471,228	0.004	0.032	0.107	0.191	0.400	0.245	0.021	3.8

Table 2. Beaufort-specific estimates of effective strip width (*ESW*) for species included in this study. The *mcds* method was used with Beaufort as the only covariate and with the indicated truncation distance. Standard errors from the jackknife method are given in italics. Note that *ESW* decreases with Beaufort for all species except three (bold).

Species	Truncation distance (km)	Beaufort state						
		0	1	2	3	4	5	6
Ziphius cavirostris	4.0	2.40	2.07	1.75	1.47	1.22	1.02	0.85
		0.25	*0.18*	*0.14*	*0.14*	*0.17*	*0.18*	*0.19*
Mesoplodon spp.	4.0	3.23	2.81	2.30	1.78	1.34	1.00	0.75
		0.35	*0.38*	*0.32*	*0.21*	*0.13*	*0.11*	*0.11*
Kogia spp.	4.0	2.13	1.89	1.66	1.46	1.28	1.12	0.98
		0.38	*0.21*	*0.09*	*0.13*	*0.22*	*0.30*	*0.35*
Balaenoptera acutorostrata	4.0	2.52	2.13	1.75	1.42	1.15	0.92	0.75
		0.89	*0.52*	*0.19*	*0.31*	*0.47*	*0.56*	*0.60*
Delphinus spp.	5.5	4.10	3.84	3.54	3.24	2.92	2.62	2.33
		0.23	*0.19*	*0.13*	*0.08*	*0.08*	*0.13*	*0.19*
Stenella coeruleoalba	5.5	3.75	3.54	3.31	3.08	2.84	2.62	2.40
		0.45	*0.30*	*0.15*	*0.06*	*0.20*	*0.36*	*0.50*
Stenella longirostris	5.5	4.14	3.98	3.81	3.63	3.44	3.25	3.06
		0.37	*0.29*	*0.19*	*0.09*	*0.10*	*0.22*	*0.34*
Stenella attenuata	5.5	3.63	3.56	3.48	3.41	3.33	3.25	3.18
		0.41	*0.30*	*0.19*	*0.09*	*0.11*	*0.21*	*0.33*
Steno bredanensis	**5.5**	**2.04**	**2.08**	**2.13**	**2.18**	**2.23**	**2.28**	**2.33**
		0.21	*0.16*	*0.12*	*0.11*	*0.14*	*0.19*	*0.26*
Lagenorhynchus obliquidens	5.5	5.13	4.64	3.73	2.55	1.60	1.00	0.63
		0.06	*0.23*	*0.79*	*1.68*	*0.46*	*0.26*	*0.22*
Tursiops truncatus	5.5	3.27	3.09	2.90	2.72	2.55	2.38	2.22
		0.12	*0.10*	*0.09*	*0.09*	*0.10*	*0.12*	*0.14*
Grampus griseus	5.5	3.60	3.14	2.68	2.26	1.89	1.58	1.31
		0.24	*0.19*	*0.14*	*0.09*	*0.08*	*0.09*	*0.10*
Globicephala macrorhynchus	5.5	4.64	4.25	3.76	3.19	2.61	2.09	1.66
		0.49	*0.48*	*0.39*	*0.21*	*0.09*	*0.21*	*0.30*
Orcinus orca	5.5	4.85	4.62	4.34	3.99	3.59	3.17	2.73
		2.57	*0.67*	*1.00*	*1.37*	*1.75*	*2.22*	*2.71*
Phocoenoides dalli	4.0	2.35	2.04	1.74	1.47	1.25	1.05	0.89
		0.16	*0.11*	*0.07*	*0.06*	*0.08*	*0.09*	*0.09*
Physeter macrocephalus	5.5	4.74	4.57	4.37	4.14	3.88	3.59	3.29
		0.54	*0.50*	*0.43*	*0.31*	*0.20*	*0.24*	*0.44*
Balaenoptera musculus	**5.5**	**2.81**	**2.88**	**2.94**	**3.01**	**3.07**	**3.14**	**3.21**
		0.38	*0.31*	*0.25*	*0.20*	*0.21*	*0.28*	*0.37*
Balaenoptera physalus	**5.5**	**3.32**	**3.36**	**3.41**	**3.45**	**3.49**	**3.54**	**3.58**
		0.38	*0.26*	*0.15*	*0.08*	*0.16*	*0.27*	*0.39*
Balaenoptera borealis/edeni	5.5	2.94	2.91	2.88	2.85	2.82	2.79	2.76
		0.40	*0.28*	*0.18*	*0.10*	*0.13*	*0.23*	*0.33*
Megaptera novaeangliae	5.5	4.57	4.38	4.17	3.94	3.68	3.41	3.13
		3.19	*1.93*	*1.66*	*1.41*	*1.37*	*1.58*	*1.95*

Analytical Methods

Assuming that the true density of whales does not vary with sighting conditions, the ratio of density estimates for poorer survey conditions to those for good conditions provides an estimate of the proportional differences in $g(0)$ values (given that a constant $g(0)$ value was used initially to obtain the estimates for all conditions). If $g(0) = 1.0$ in excellent conditions, these relative estimates of $g(0)$ are also absolute estimates. If $g(0) < 1.0$ in excellent conditions but can be estimated (*e.g.*, Barlow 1999), absolute $g(0)$ for other conditions can be scaled using the relative estimates. Beaufort state is a subjective measure of wind speed as perceived by visual appraisal of the effect of wind on the water's surface and is the most frequently used measure of sighting conditions on visual line-transect surveys for cetaceans. Previous analyses of the SWFSC cetacean survey data have shown a measurable effect of Beaufort state on mean perpendicular sighting distances (Barlow *et al.* 2001) and on effective strip widths (Barlow *et al.* 2011) for all species, so Beaufort state is used here as a general measure of sighting conditions. Averaged values for Beaufort state vary geographically within the study area (Fig. 1), but calm and rough seas have been observed in all parts of the study area (Table 1).

The density, D_i, of groups of whales (number of groups per square kilometer) of species group i can be estimated using a conventional line-transect approach (Buckland *et al.* 2001):

$$D_i = \frac{n_i \cdot f_i(0)}{2 \cdot L \cdot g_i(0)}, \tag{1}$$

where L = the length of "on-effort" transect lines, $f_i(0)$ = the probability density of the detection function evaluated at zero perpendicular distance, $g_i(0)$ = the trackline detection probability, and n_i = the number of sightings.

Density D is expected to vary spatially and temporally, whereas $f(0)$ and $g(0)$ are expected to vary with sighting conditions. A statistical approach is used to differentiate between real differences in density and "apparent" differences caused by the effect of sighting conditions and to quantify the effect of sighting conditions on $g(0)$.

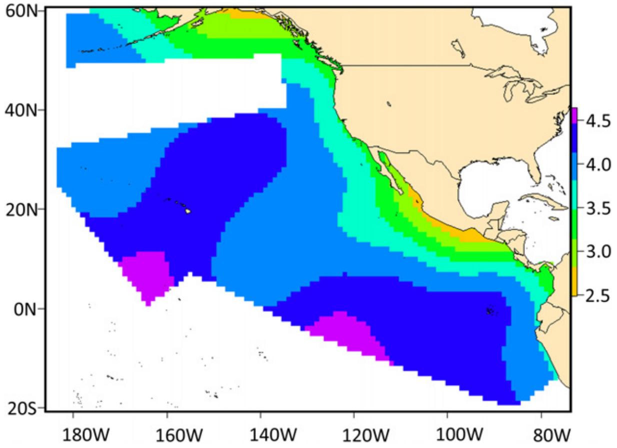

Figure 1. Smoothed contours of average Beaufort state in the eastern and central Pacific study area for the cetacean survey data used in this paper. Beaufort states are smoothed using a 2-D thin-plate spline regression model with a Gaussian link function. Gridded values are displayed on a 1° × 1° scale using *predict.gam* in R package *mgcv*. Unsurveyed areas are masked.

Substituting effective strip width (ESW_i) for $1/f_i(0)$ and rearranging the terms, Equation 1 can be expressed as

$$n_i = D_i \cdot g_i(0) \cdot (2 \cdot L \cdot ESW_i). \tag{2}$$

Beaufort conditions change frequently, often several times within a single survey day, so density is modeled using short segments of search effort (~10 km) with relatively constant survey conditions. The majority of these short segments contain at most a single sighting of a single species. Therefore, we can model group density as presence/absence on a survey segment. Statistically, the probability of seeing a species on a survey segment is modeled as continuous smoothed functions of space (latitude and longitude), time (year), and sighting conditions (Beaufort state) (all treated as fixed effects) using a general additive model (GAM) with a logit link function (Wood 2006) in R 12.2.0 (R Development Core Team 2010). The logit-probability of detecting a group on a survey segment is assumed to be proportionate to the area effectively searched ($2•L•ESW$), so this effective search area (ESA) is used as an offset in the GAM. Beaufort-specific values of ESW are estimated using the multiple-covariate distance-sampling (*mcds*) model (Thomas *et al.* 2010) in the R package *mrds*. Penalized thin-plate regression spline functions, s, (Wood 2003) as implemented in the program *gam* in the R package *mgcv* are used for the smoothed terms. The observation of a species, p, on a survey segment is modeled as a Bernoulli-distributed variate using the following GAM model specification:

$$\text{Logit}(p) \sim s(\text{Beaufort}) + s(\text{Latitude} \times \text{Longitude}) + s(\text{Year}) + \ \text{offset}(ESA). \tag{3}$$

To prevent model over-fitting, the maximum degrees of freedom for the univariate terms (year and Beaufort) is limited (*mgcv* parameter $k = 4$) and the overall penalty for model complexity is inflated (*mgcv* parameter $gamma = 1.4$) (Kim and Gu 2004, Wood 2006).

To fit this statistical model, survey effort was subdivided into sequential segments of at least 10 km. A new segment was created when a recorded location indicated that 10 km had been surveyed since the last segment was created. Because positions are not recorded continuously, actual segments were typically greater than 10 km (mean = 11.8 km, 1st and 3rd quartiles = 10.58 and 12.38 km). Shorter segments (<10 km) were generated at the end of each survey day and when a ship passed from one geographic stratum to another. When survey effort stopped during a day (due to weather or a sighting), an incomplete survey segment was continued when survey effort resumed that day, so survey effort within a segment is not necessarily continuous. Overall, 26% of effort segments include one or more cetacean sightings.

In interpreting the results of the statistical model, we assume that true variations in cetacean densities are effectively modeled by year, latitude and longitude, and that the residual modeled by Beaufort state represents differences in apparent density due to the effect of sighting conditions on $g(0)$. Values of $g(0)$ at Beaufort states 1–6 are estimated relative to its value at Beaufort state 0 (excellent sighting conditions) as the ratio of predicted probabilities from the GAM. Because there are no interaction terms in the above model, the Beaufort effect estimated by the model is the same for every position in space and every point in time; therefore, there is no need to average results over space or time to estimate the Beaufort effect on $g(0)$. The R routine *predict.gam* is used to predict the probability of a sighting per unit area searched, p_b, for

Beaufort states, b, ranging from 0 to 6 at a single fixed point in time (year) and space (latitude and longitude). Relative $g(0)$ values, ${}_{R}g_b(0)$, are thus given by:

$$ {}_{R}g_b(0) = \frac{p_b}{p_0}. \tag{4} $$

Coefficients of variation (CVs) for estimates of ${}_{R}g(0)$ were calculated using a jackknife procedure (Efron and Gong 1983). The GAM was fit to 10 subsets of the original data, each leaving out a sequential 10% of the survey segments. Standard errors (SEs) and CVs are calculated from the jackknife subsamples using standard methods (Efron and Gong 1983). Because *ESW* was estimated for each of the jackknife samples, variation in this component of the overall $g(0)$ estimation is accounted for in the overall CV for ${}_{R}g(0)$. $g(0)$ is expected to decrease with poorer survey conditions, but in some preliminary analyses, estimates of $g(0)$ increased slightly between Beaufort 0 and Beaufort 1. Since $g(0)$ values are relative to the best survey conditions, this resulted in implausible $g(0)$ values that were >1. Only 0.4% of survey effort was in Beaufort 0 and 3.2% in Beaufort 1, and this unusual increase in $g(0)$ with Beaufort was likely due to random chance and very small sample of sightings in low Beaufort conditions. Monotonicity constraints were applied by pooling data from the lower Beaufort states as needed to achieve a monotonic decline in $g(0)$ values. This approach generally resulted in lower AIC values as well.

Absolute $g(0)$ values for Beaufort 0–2 (excellent to good sighting conditions) were previously estimated for *Ziphius*, *Mesoplodon*, and *Kogia* using a model that accounts for both perception and availability bias (Barlow 1999). The model requires a large sample of sightings and therefore cannot be applied to estimate $g(0)$ for rougher Beaufort states, for which there are few sightings. The same model is fit here to the larger set of 1986–2010 data for the single Beaufort state with the greatest number of sightings (Beaufort 0 for *Kogia* spp. and Beaufort 1 for the beaked whales). These new estimates of absolute $g_i(0)$ for a single Beaufort state b are scaled by the relative values estimated here (Eq. 4) to yield absolute $g(0)$ values for other Beaufort states. For example, absolute $g_b(0)$ values for other sea states are estimated from estimates in Beaufort 1, $g_1(0)$, as:

$$ g_b(0) = g_1(0)\ {}_{R}g_b(0)/{}_{R}g_1(0). \tag{5} $$

Group sizes are also modeled as functions of sighting conditions (Beaufort state) to evaluate whether differences in group size estimates might be the cause for differences in group density estimates. If a species forms larger groups in rougher conditions, this could explain an apparent decrease in group density with Beaufort state. Mean group sizes of each species for each survey segment is used as the dependent variable, and GAMs are fit to mean group size with a log-normal link function using the *mgcv* package in R. Again, location (latitude × longitude) and time (year) are included as explanatory variables to control for real differences in group size that might be correlated with sighting conditions. Again, the risk of over-fitting is reduced by limiting the degrees of freedom for the univariate terms (*mgcv* parameter $k = 4$) and the overall penalty for model complexity is inflated (*mgcv* parameter $gamma = 1.4$) (Kim and Gu 2004, Wood 2006).

RESULTS

Estimates of effective strip widths generally decrease with increasing Beaufort states for most species (Table 2), as is expected if the animals are harder to see when sighting conditions are worse. Similarly, estimated $g(0)$ values generally decline with increasing Beaufort sea states (Fig. 2, Table 3). The Beaufort term was significant ($P < 0.05$, 2-tailed) in the GAM regressions for all species except humpback whales (*Megaptera novaeangliae*). The decline in modeled probability with Beaufort is greatest for less conspicuous species such as small whales (Fig 2C). For *Kogia* spp., the trackline detection probability is close to zero, $g(0) < 0.03$ in Beaufort state 3 and above (Table 3). Even for the most conspicuous species (*e.g.*, blue whales, *Balaenoptera musculus*), the estimates of $g(0)$ for Beaufort 6 is less than half that for Beaufort zero (Table 3).

Modeled detection probability also varies significantly ($P < 0.05$) with the geographic component (latitude × longitude) of the GAM regression model (Fig. 3) for all species except minke whales (*Balaenoptera acutorostrata*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) (Table 4). The year effect is significant ($P < 0.05$, two-tailed) for 12 of 20 species categories, and significant increases in abundance were indicated for 10 of these 12 (Table 4).

Results of the group size GAM (Table 5) show significant effects of Beaufort state for 10 of 20 species categories, and estimated group size decreases with increasing Beaufort state in 8 of these 10 of these cases. A significant trend in group size over time is seen for 11 species categories, with 6 showing a decreasing trend and five showing an increasing trend. Significant spatial variation in group size is seen for 9 species categories.

Absolute $g(0)$ values for *Kogia*, *Mesoplodon*, and *Ziphius* are estimated by fitting a model (Barlow 1999) to 1986–2010 survey data for a single Beaufort state, and these values are extrapolated to other Beaufort states by scaling by relative $g(0)$ values (Table 6). Results show that the $g(0)$ values for Beaufort 0 range from 0.5 to 0.81 for these species, showing that the assumption of $g(0) = 1.0$ does not hold even in the best survey conditions.

DISCUSSION

In analyses of cetacean survey data, trackline detection probability, $g(0)$, is often assumed to be 1.0 in all sighting conditions (Gunnlaugsson and Sigurjónsson 1990, Wade and Gerrodette 1993, Fulling *et al.* 2003, Mullin and Fulling 2004, Kaschner *et al.* 2012) if only because estimates of true $g(0)$ are often not available. It is widely recognized that this assumption is violated for surveys of species that are either hard to see or that dive for long periods of time (Barlow 1999, Hammond *et al.* 2002), but the assumption that all groups on the trackline are seen has often been considered reasonable for conspicuous species like dolphins that occur in large groups or baleen whales with large blows. Hammond *et al.* (2002) found that detection probability was not significantly affected by Beaufort state in ship surveys for minke whales and white-beaked dolphins (*Lagenorhynchus albirostris*), but the Beaufort effect was significant for harbor porpoises (*Phocoena phocoena*), which are smaller and occur singly or in small groups. Barlow (1995) presented evidence that $g(0)$ equals 1.0 for larger groups of delphinids (>20 individuals) and for larger groups of large whales (>3 individuals), but not for smaller groups of those species. Based on a much larger sample size than any of these previous studies, the current results

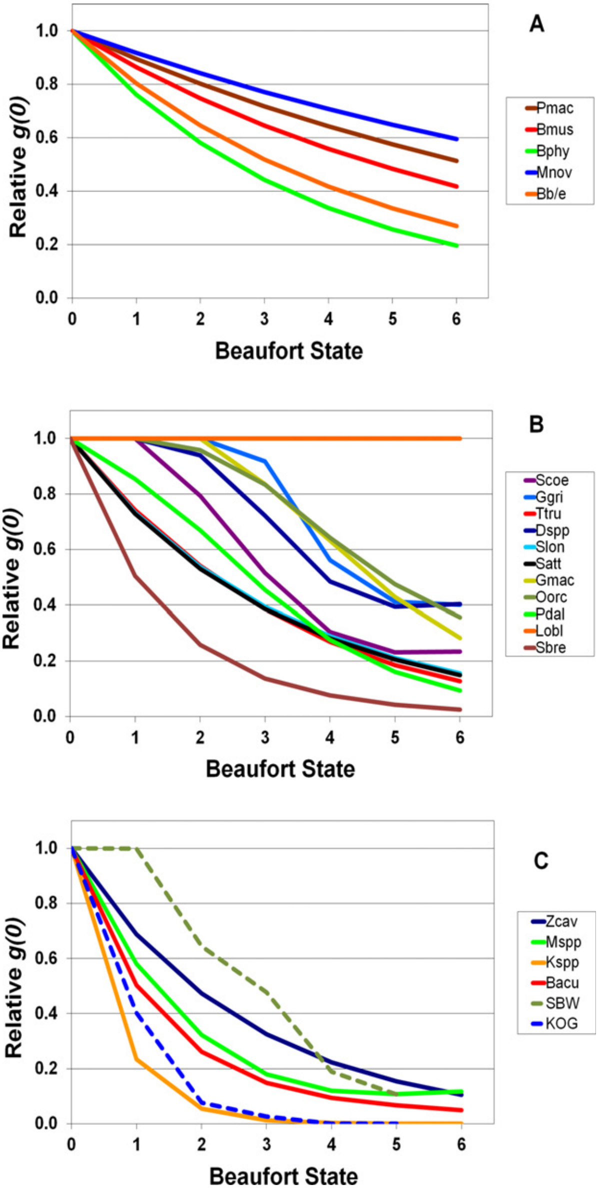

Figure 2. Estimated values of $g(0)$ in Beaufort states 1–6 relative to Beaufort zero for (A) large whales, (B) delphinoids (dolphins and porpoises), and (C) small whales. KOG (*Kogia*) and SBW (small beaked whale) estimates are from Barlow (2013). Other abbreviations are based on the first letter of the genus name and the first three letters of the species name (or "spp" to indicate all species in that genus).

show that the estimated number of cetacean groups per unit area declines in rougher sea conditions and that mean group sizes do not increase to compensate (in fact, group size estimates were more likely to decrease in rougher seas). Therefore, the

Table 3. Estimated values of $g(0)$ for sightings conditions in Beaufort states 1–6 relative to Beaufort zero and total number of sightings used for these estimates. Coefficients of variation (CV) from jackknife method are in italics, and $g(0)$ values significantly different from 1.0 (z-test) are in bold.

Species	Number of sightings	Beaufort state						
		0	1	2	3	4	5	6
Ziphius cavirostris	262	1	**0.688**	**0.473**	**0.325**	**0.224**	**0.154**	**0.106**
			0.10	*0.19*	*0.26*	*0.30*	*0.34*	*0.37*
Mesoplodon spp.	322	1	**0.581**	**0.323**	**0.179**	**0.120**	**0.108**	**0.118**
			0.14	*0.21*	*0.25*	*0.29*	*0.39*	*0.66*
Kogia spp.	249	1	**0.234**	**0.055**	**0.013**	**0.003**	**0.001**	**0.0002**
			0.08	*0.16*	*0.25*	*0.33*	*0.41*	*0.49*
Balaenoptera acutorostrata	43	1	**0.503**	**0.262**	**0.148**	**0.094**	**0.067**	**0.050**
			0.36	*0.70*	*0.88*	*0.82*	*0.71*	*0.91*
Delphinus spp.	1,247	1	1	0.940	0.722	**0.485**	**0.394**	**0.404**
				0.25	*0.25*	*0.14*	*0.20*	*0.50*
Stenella coeruleoalba	1,621	1	1	**0.794**	**0.516**	**0.303**	**0.231**	**0.234**
				0.11	*0.14*	*0.11*	*0.16*	*0.31*
Stenella longirostris	969	1	**0.733**	**0.537**	**0.394**	**0.289**	**0.212**	**0.155**
			0.03	*0.06*	*0.09*	*0.13*	*0.16*	*0.19*
Stenella attenuata	1,653	1	**0.728**	**0.531**	**0.386**	**0.282**	**0.205**	**0.149**
			0.03	*0.06*	*0.09*	*0.12*	*0.15*	*0.18*
Steno bredanensis	379	1	**0.505**	**0.259**	**0.137**	**0.076**	**0.043**	**0.024**
			0.18	*0.33*	*0.41*	*0.43*	*0.41*	*0.41*
Lagenorhynchus obliquidens	78	1	1	1	1	1	1	1
Tursiops truncatus	1,076	1	**0.742**	**0.542**	**0.386**	**0.269**	**0.185**	**0.127**
			0.16	*0.27*	*0.30*	*0.26*	*0.24*	*0.26*
Grampus griseus	616	1	1	1	0.917	**0.561**	**0.412**	**0.401**
					0.14	*0.09*	*0.20*	*0.48*
Globicephala macrorhynchus	494	1	1	1	**0.835**	**0.631**	**0.430**	**0.283**
					0.08	*0.15*	*0.24*	*0.35*
Orcinus orca	190	1	1	0.958	0.834	0.642	**0.475**	**0.356**
				0.35	*0.48*	*0.44*	*0.48*	*0.63*
Phocoenoides dalli	314	1	0.854	0.670	**0.455**	**0.276**	**0.161**	**0.094**
			0.32	*0.54*	*0.59*	*0.56*	*0.55*	*0.58*
Physeter macrocephalus	367	1	0.896	0.802	0.718	0.643	**0.575**	0.514
			0.11	*0.20*	*0.26*	*0.31*	*0.38*	*0.50*
Balaenoptera musculus	171	1	0.865	0.748	0.646	**0.559**	**0.483**	**0.418**
			0.10	0.19	0.28	0.36	0.44	0.51
Balaenoptera physalus	200	1	**0.762**	**0.581**	**0.442**	**0.337**	**0.257**	**0.196**
			0.08	0.16	0.23	0.30	0.35	0.40
Balaenoptera borealis/edeni	431	1	**0.804**	**0.646**	**0.520**	**0.418**	**0.336**	**0.270**
			0.05	*0.10*	*0.15*	*0.20*	*0.25*	*0.30*
Megaptera novaeangliae	116	1	0.917	0.841	0.772	0.708	0.649	0.595
			0.09	0.17	0.25	0.32	0.39	0.45

density of all cetaceans is likely underestimated for rough sea conditions (high Beaufort states) unless $g(0)$ corrections are used.

The primary assumption of the method used here to estimate relative $g(0)$ is that true group densities do not vary with Beaufort state. The most likely violation of this

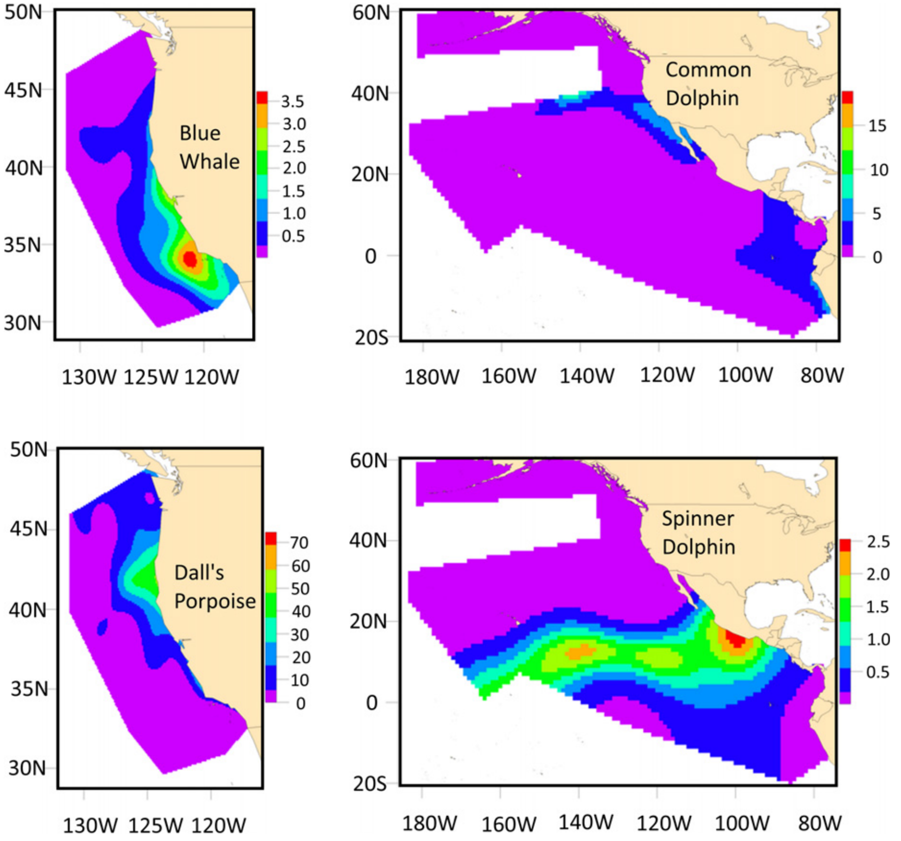

Figure 3. Geographic components of group encounter rate models that also included Beaufort sea state and year as covariates in a GAM framework for several example species (see Fig. S1 for all species). The geographic effect was modeled with latitude and longitude as a 2-D thin-plate spline in the R package *mgcv*. Predicted group densities (groups per 1,000 km^2) were obtained with *predict.gam* for Beaufort 0 and a mid-point year (1998). Gridded values are displayed on a 1° × 1° scale for the entire Pacific and on a 0.1° × 0.1° scale for species that were modeled using only U.S. West Coast data. Unsurveyed areas are masked.

assumption would occur if all cetacean species in our study were more likely to occur in windy or calm areas. Primary production is correlated with wind-driven upwelling in some oceanographic areas, and cetacean abundance can be correlated with primary production (Jaquet *et al.* 1996). Different study areas have different distributions of Beaufort state (Table 1). The broad-scale correlation between Beaufort state and cetacean density should, however, be captured with the geographic term in the GAM analysis. Although average Beaufort varies geographically, daily values in all areas vary from very calm to very rough with daily changes in weather. There should, therefore, be sufficient contrast within these data to tease apart geographic and Beaufort state variations in apparent cetacean density. Moreover, not all species would be expected to be similarly distributed with respect to sea conditions; some species could be more likely to occur in calmer areas (*e.g.*, near-coast species) while others could be

Table 4. Summary of general additive models of probability of detecting a group on a segment of survey effort as functions of Beaufort state, year, and location (latitude × longitude). The effective degrees of freedom and approximate significance levels (from *mgcv* package) are given for each predictor in the GAM model. All Beaufort trends showed a decrease with increasing Beaufort except for *L. obliquidens*. The year trend (increase or decrease) is given for models with a significant year term based on whether the final estimate is greater or less than the initial. Significance levels are coded as $P < 0.05$ (*), $P < 0.01$ (**), and $P < 0.001$ (***).

		GAM model terms						
		Beaufort state		Year		Latitude × longitude		
Species group	Species/genus name	e.d.f.	sig.	e.d.f.	sig.	e.d.f.	sig.	Year trend
Small whales								
	Ziphius cavirostris	1.0	***	1.0		18.1	***	
	Mesoplodon spp.	2.5	***	2.4		18.8	***	
	Kogia spp.	1.0	***	1.0		23.3	***	
	Balaenoptera acutorostrata	1.4	***	1.0		19.6		
Delphinoids								
	Delphinus spp.	2.7	***	2.7	***	28.8	***	increase
	Stenella coeruleoalba	2.9	***	1.0	*	27.6	***	increase
	Stenella longirostris	1.0	***	1.0	**	22.4	***	increase
	Stenella attenuata	1.0	***	1.4	***	21.7	***	increase
	Steno bredanensis	1.4	***	1.0	***	19.5	***	increase
	Lagenorhynchus obliquidens	1.0	*	2.4		9.8		
	Tursiops truncatus	1.4	***	1.6	***	23.1	***	increase
	Grampus griseus	2.4	***	1.0		18.7	***	
	Globicephala macrorhynchus	2.0	***	1.7	***	26.3	***	increase
	Orcinus orca	1.7	**	1.0		10.7	***	
	Phocoenoides dalli	1.8	***	1.0		28.6	***	
Large whales								
	Physeter macrocephalus	1.0	*	2.1	***	19.6	***	decrease
	Balaenoptera musculus	1.0	*	1.0	**	19.0	***	decrease
	Balaenoptera physalus	1.0	***	1.0	***	19.6	***	increase
	Balaenoptera borealis/edeni	1.0	***	1.4	***	25.3	***	increase
	Megaptera novaeangliae	1.0		1.4	***	12.7	***	increase

more likely to occur in rougher areas (*e.g.*, offshore deepwater species). The nearly ubiquitous pattern in our analysis of lower density estimates in rougher sea conditions seems to provide additional evidence that the effect of sighting conditions on $g(0)$ is not merely an artifact of a geographic bias in the data.

Differences in relative $g(0)$ values estimated here for different Beaufort states may not be due entirely to difference in trackline detection probabilities near the vessel. Estimates of cetacean density can be biased by undetected movement of animals

Table 5. Summary of general additive models of group sizes as functions of Beaufort state, year, and location (latitude × longitude). The effective degrees of freedom (e.d.f.) and approximate significance levels (from *mgcv* package) are given for each predictor in the GAM model. The Beaufort and year trends (increase or decrease) is given for models with a significant year term based on whether the final estimate is greater or less than the initial. Significance levels are coded as $P < 0.05$ (*), $P < 0.01$ (**), and $P < 0.001$ (***).

		GAM model terms							
		Beaufort state		Year		Latitude × longitude			
Species group	Species/genus name	e.d.f.	sig.	e.d.f.	sig.	e.d.f.	sig.	Beaufort trend	Year trend
Small whales									
	Ziphius cavirostris	1.7		1.0		3.5			
	Mesoplodon spp.	1.0	***	1.9	*	6.2		decrease	decrease
	Kogia spp.	1.0		1.4		2.0			
	Balaenoptera acutorostrata	1.4		1.0		2.0			
Delphinoids									
	Delphinus spp.	1.6		1.8	*	18.4	***		decrease
	Stenella coeruleoalba	1.7		2.9	*	21.8	***		increase
	Stenella longirostris	2.3	***	2.9	***	28.6	***	increase	increase
	Stenella attenuata	2.9	***	2.8	*	16.4	***	decrease	decrease
	Steno bredanensis	2.9	***	3.0	***	15.1	***	decrease	decrease
	Lagenorhynchus obliquidens	1.0	*	1.0	***	19.5	***	decrease	increase
	Tursiops truncatus	2.8	**	1.0		28.9	***	increase	
	Grampus griseus	1.3	**	2.9	*	10.7		decrease	decrease
	Globicephala macrorhynchus	1.0	**	1.0	***	16.4		decrease	increase
	Orcinus orca	3.0	***	1.0		17.5		decrease	
	Phocoenoides dalli	1.4		1.0		2.0			
Large whales									
	Physeter macrocephalus	1.8		1.0		8.5			
	Balaenoptera musculus	1.0		2.6	**	2.1	**		increase
	Balaenoptera physalus	1.0		1.0		2.0			
	Balaenoptera borealis/edeni	3.0	***	1.0	***	19.5	***	decrease	decrease
	Megaptera novaeangliae	1.0		2.4		14.2			

Table 6. Absolute values of $g(0)$ for *Ziphius, Mesoplodon*, and *Kogia* estimated using a model (Barlow 1999) fitted to the 1986–2010 survey data for the single Beaufort state with the greatest number of observations (Beaufort 0 for *Kogia*, and Beaufort 1 for the beaked whales). Absolute estimates are scaled by the relative estimates from Table 3 to give absolute values for Beaufort states 0–6.

Genus/species	Beaufort state	Absolute $g(0)$ estimates	Relative $g(0)$ estimates	Scaled absolute $g(0)$ estimates
Ziphius cavirostris	0		1.000	0.584
	1	0.402	0.688	0.402
	2		0.473	0.276
	3		0.325	0.190
	4		0.224	0.131
	5		0.154	0.090
	6		0.106	0.062
Mesoplodon spp.	0		1.000	0.813
	1	0.472	0.581	0.472
	2		0.323	0.262
	3		0.179	0.146
	4		0.120	0.097
	5		0.108	0.088
	6		0.118	0.096
Kogia spp.	0	0.495	1.000	0.495
	1		0.234	0.116
	2		0.055	0.027
	3		0.013	0.006
	4		0.003	0.001
	5		0.001	0.000
	6		0.000	0.000

either towards or away from the transect line in response to the ship (Buckland *et al.* 2001). Because animals can be detected at greater distances in good conditions, this bias is likely to depend on survey conditions. The methods used here cannot truly distinguish between bias due to differences in trackline detection probability and bias caused by responsive movement. The relative values of $g(0)$ presented here should be considered general factors that can be used to account for a variety of factors that might bias estimates of cetacean group density as functions of Beaufort state. It should be noted, however, that the pattern of declining relative $g(0)$ values with Beaufort state is seen both for species that avoid vessels (*e.g.*, the *Stenella* spp.) and species that are attracted to vessels (*e.g.*, *T. truncatus*) within the study area.

The observed decreases in estimates of group density with increasing Beaufort state would not necessarily lead to decreased estimates of animal density if it were caused by a real increase in characteristic group sizes. Here we show that estimated group sizes actually decrease with increasing Beaufort state for most species with a significant Beaufort term in their group size model. This could result in an additional negative bias in estimates of individual density. The general pattern of decreasing group sizes with Beaufort may, however, be perceptual. Group size is certainly more difficult to estimate in rougher seas and group sizes are likely to be underestimated if fewer individuals can be seen at the surface. Additional research is needed to determine whether real group sizes change with Beaufort or whether the observed decline is only due to estimation error. Additional corrections may be needed for the effect of Beaufort state on group size estimation and hence on cetacean density estimation.

A nearly exponential decline in detection probability with Beaufort state is seen for most species (Fig. 2), which resulted from a nearly linear fit of log-transformed values (e.d.f. < 1.5, Table 4). Overall, less than 4% of survey effort was conducted in Beaufort 0 and 1 (Table 1), and the fraction of sightings in these calm conditions is very low for some species. Because there is so little data in calm conditions, there is some danger of extrapolating the trend seen for apparent densities in other sea states to values at Beaufort 0 and 1. When relative *g*(0) values were estimated for small beaked whales using a stratified density approach instead of a model-based approach (SBW in Fig. 2C), values for relative densities in Beaufort 0 and 1 were similar (Barlow 2013). If trackline detection probability in Beaufort 0 is really not greater than in Beaufort 1, all values of relative *g*(0) could be biased downward.

The expectation of monotonically decreasing *g*(0) values with increasing Beaufort states was achieved by pooling lower Beaufort states (which had low sample sizes) for six species (all delphinids). This could be done more elegantly using shape constrained additive models such as implemented the R package *scam* (Pya and Wood 2014). In practice, that approach was not favored by AIC model selection, as it required many more parameters (knots) and resulted in greater decreases in *g*(0) with Beaufort than were supported by the data.

Small Whales

The grouping of small whales (Table 4) includes species which typically occur in small groups and which are difficult to see because they typically do not have a visual blow and do not splash or leap when they surface. This group includes small beaked whales and *Kogia* spp., which have relatively long dive times (Barlow 1999). It has long been recognized that the density of these species is likely underestimated even in calm conditions (Barlow 1999) due to availability bias. Sightings of these species are so rare in higher sea states that density is often estimated only from survey data collected in calm seas (Mullin *et al.* 2004, Barlow and Forney 2007). It is not surprising then that the relative *g*(0) values for this group of small whales show the greatest decline with Beaufort state (Table 3, Fig. 2B). The rate of decline is nearly exponential and is greatest for *Kogia* spp.

Relative *g*(0) values in different Beaufort states have been estimated previously using a slightly different method (Barlow 2013) and were used in an analysis of trends in beaked whale abundance (Moore and Barlow 2013). Barlow (2013) estimated density of small beaked whales (the genera *Ziphius* and *Mesoplodon*) and of *Kogia* spp. in two nonoverlapping study areas in the eastern tropical Pacific, stratified by Beaufort state. The study areas were defined to include relatively uniform distributions of average Beaufort state so as to reduce the confounding effect of different densities and Beaufort states. The 1986–2008 survey data in that study were largely overlapping with data used in the current study. Resulting estimates of relative *g*(0) from that study (for Beaufort states 0–6, respectively, averaged for the two study areas) were 1.00, 1.00, 0.64, 0.48, 0.19, 0.11 for small beaked whales and 1.00, 0.40, 0.08, 0.03, 0.00, 0.00 for *Kogia* spp. (Barlow 2013). These values are very similar to estimates from the statistical approach used here for *Kogia* spp., and estimates for small beaked whales are very similar to estimates for *Z. cavirostris* in Beaufort 4 and 5 conditions (Fig. 2C). Relative *g*(0) values for small beaked whales are higher in that study for Beaufort states 1–3. The methods used in this paper are likely to be more reliable than those in Barlow (2013) because they are based on a larger sample size and use a more robust estimation procedure.

Absolute $g(0)$ values have been previously estimated for the genera *Ziphius, Mesoplodon,* and *Kogia* in a pooled category of Beaufort 0–2 (Barlow 1999). These values (0.23 for *Ziphius*, 0.45 for *Mesoplodon*, and 0.35 for *Kogia*) correct density estimates for both availability bias and perception bias. When this method is applied to estimated absolute $g(0)$ for a single Beaufort state category, relative $g(0)$ values can be used to scale this value to give absolute $g(0)$ estimates for other Beaufort states. Results show that $g(0)$ is appreciably less than 1.0 for these species even in the calmest seas and that values decrease rapidly with Beaufort state (Table 6), which emphasizes the need to collect dive data to allow $g(0)$ estimation for these species using one of the other estimation methods.

Delphinoids

Estimates of $g(0)$ decrease with Beaufort state and are <0.5 at Beaufort 6 for all delphinoid species except *L. obliquidens* (Fig 2B). Previously, Brandon *et al.* (2002) and Gerrodette and Forcada (2005) suggested that the assumption of $g(0) = 1.0$ is generally valid for large groups of dolphins. Data from independent observers generally have supported this assumption, at least for large groups (Barlow *et al.* 1995, Hammond *et al.* 2002). Although many porpoise species occur in small groups and surface without conspicuous splashes, the delphinids are typically very conspicuous, and it is hard to conceive of missing a large group on the transect line, even in rough conditions. Data presented here appear to contradict this commonly held perception.

Beaufort trends in $g(0)$ for *L. obliquidens* and *S. bredanensis* appear as contrasting outliers among the other dolphins (Table 3, Fig. 2). For *L. obliquidens*, $g(0)$ estimates increased with Beaufort and the decreasing monotonicity constraint resulted in values of 1.0 for all conditions. This is likely because ESW decreased with Beaufort much more rapidly for this species than for any other dolphin, possibly an artifact of the small sample size for this species (n = 78). *S. bredanensis* occurs in small groups and is difficult to see, which may help explain why $g(0)$ decreases with Beaufort conditions much more rapidly for this species than for other dolphins. This does not help explain why ESW increases slightly with Beaufort state for *S. bredanensis* (Table 2).

Many delphinoids are attracted to bow ride on research vessels, including some of the species studied here. Buckland and Turnock (1992) analyzed the effect of vessel attraction on estimates of Dall's porpoise (*Phocoenoides dalli*) abundance and concluded that abundance can be overestimated by a factor of 4. The reactive movement (attraction or avoidance) will affect density estimation if it occurs before the group is seen, and this is most likely to occur in poor sighting conditions. This suggests that $g(0)$, as estimated here, could either decrease or increase with Beaufort state depending on whether animals either avoid or are attracted towards the survey platform. It is surprising then, that apparent $g(0)$ decreases with Beaufort state for virtually all delphinoid species, including ones that are strongly attracted to ships. Vessel attraction could, however, help explain the unusual results seen for *L. obliquidens*.

Large Whales

The blows of large whales are relatively conspicuous, even in rough seas. It is not surprising that the decline in $g(0)$ with Beaufort state is smallest for these species (Fig. 2A). Nonetheless, $g(0)$ decreases to below 0.6 in Beaufort 6 conditions for all species. Barlow and Forney (2007) estimated *g*(0) for large whales in the U.S. West Coast study area to be approximately 0.92 (CV = 0.02) using a conditionally independent observer method developed by Barlow (1995) and applied to Beaufort sea states 0–5. That method assumes that all whales are available to be seen and thus only corrects for perception bias. To compare the current estimates for individual Beaufort state to this earlier estimate for pooled Beaufort states, average *g*(0) values are calculated for each species weighted by the proportion of survey time at each Beaufort state for the U.S. West Coast (Table 1). Weighted average values are 0.67, 0.59, 0.39, 0.46, and 0.73 respectively for sperm whales, blue whales, fin whales, sei and Bryde's whales, and humpback whales. All weighted averages are considerably less than the *g* (0) value of 0.92 that was calculated by Barlow and Forney (2007) based on perception bias alone.

Relative *g*(0) values can be used as absolute *g*(0) estimates if all trackline whales are seen in the calmest sea states. Typical dive times for large whales range from several minutes (for Bryde's whales) to over an hour (for sperm whales). Availability bias in calm conditions is likely to vary considerably among these large whale species. Additional research is needed to determine absolute *g*(0) values in calm conditions. When this is done, these values can be scaled to other sea states using the relative *g*(0) values estimated here. Until then, however, relative *g*(0) values are minimum estimates and should be used in place of estimates that only include perception bias.

Future Directions

The approach presented here uses Beaufort state as the sole measure of sighting conditions. On most cetacean surveys, other measures of sighting conditions are often recorded, including swell height and the presence of rain, snow, fog, or haze. All of these might affect trackline detection probability for cetaceans. Additional covariates could be added in future analyses to obtain better estimates of relative *g*(0). This might improve precision by explaining more of the variation in apparent density but also might reduce bias by ensuring that absolute *g*(0) is closer to 1.0 for the best survey conditions. Additional research is needed to more effectively implement a monotonically decreasing constraint in estimating *g*(0) as a function of sighting conditions.

The empirical approach used here to estimate *g*(0) values relative to the best survey conditions could be integrated with more theoretical approaches that estimate absolute values for *g*(0). The application of other approaches to estimate Beaufort-specific estimates of *g*(0) are typically limited by sample size, especially for hard-to-see species in poor conditions. But a failure to explicitly consider sighting conditions can result in bias because pooling robustness does not generally apply to *g*(0) estimation. The relative approach used here uses additional information (apparent density in different conditions) to help inform the pattern of change in *g*(0) with Beaufort state.

The approach presented here, using a Cartesian spatial model of variation in cetacean densities, could be easily extended to spatial models of cetacean density based habitat metrics instead of or in addition to latitude and longitude (Redfern *et al.* 2006). Beaufort state is often included in such habitat-based spatial models to account for non-habitat variation in apparent density, but predicted densities are typically based on average Beaufort conditions (Forney *et al.* 2012). Relative *g*(0) estimation can easily be extended to habitat-based spatial models if, instead, predictions are made for the best-case survey conditions (Beaufort 0) or (better yet) for the conditions for which absolute $g(0)$ has been previously estimated. In this way, the effect of Beaufort on $g(0)$ would implicit in the predicted density estimates.

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SUPPORTING INFORMATION

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Figure S1. Geographic components of group encounter rate models that also included Beaufort sea state and year as covariates in a GAM framework for all species. The geographic effect was modeled with latitude and longitude as a 2-D thin-plate spline in the R package *mgcv*. Predicted group densities (groups per 1,000 km^2) were obtained with *predict.gam* for Beaufort 0 and a mid-point year (1998). Gridded values are displayed on a 1° × 1° scale for the entire Pacific and on a 0.1° × 0.1° scale for species that were modeled using only U.S. West Coast data. Unsurveyed areas are masked.