HARBOR PORPOISE, *PHOCOENA PHOCOENA*, ABUNDANCE ESTIMATION FOR CALIFORNIA, OREGON, AND WASHINGTON: II. AERIAL SURVEYS

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ABSTRACT

We conducted aerial surveys in September 1984 and September and October 1985 to determine the abundance of harbor porpoise along the coasts of California, Oregon, and Washington. Two observers and a recorder searched along predetermined transect lines at 0.61 and 1.85 km offshore. Strip transect methods were used. A total of 366 groups of harbor porpoise were seen in the 9,500 linear kilometers that were surveyed. Apparent density was significantly affected by sea state and cloud cover. Using observations made during optimal conditions (clear skies and calm seas), apparent harbor porpoise density averaged 0.56 animals km^{-2}. Behavioral observations from shore and from a helicopter indicated that porpoise are near the surface only 23.9% of the time. To account for this, porpoise density was multiplied by a factor of 3.2, resulting in an adjusted estimate of 1.79 animals km^{-2}. Only a small percentage of the total area inhabited was surveyed under optimal sighting conditions, hence density estimates were not extrapolated to estimate total porpoise abundance. Harbor porpoise density showed similar patterns to those measured from ship surveys, and adjusted aerial estimates are approximately equal to ship estimates.

Harbor porpoise, *Phocoena phocoena*, are subject to mortality in the halibut set net fishery in central California (NMFS[4]; Diamond and Hanan[5]). To evaluate the significance of this mortality, an estimate of population size is needed. Two aerial surveys and three ship surveys were conducted from 1984 to 1986 to gather information on harbor porpoise abundance along the coasts of California, Oregon, and Washington. Observations were also made from shore-based stations and from a helicopter to provide ancillary information needed for population estimation. Results and population estimates from the ship surveys are reported by Barlow (1988). Preliminary results from the 1984 and 1985 aerial surveys were presented by Oliver and Jackson[6] and Oliver[7], respectively. Here we present population density estimates based on the aerial surveys and on shore and helicopter observations.

The aerial surveys were flown in September of 1984 and in September and October of 1985 from Point Conception, CA to Cape Flattery, WA. Surveys were coordinated by the National Marine Fisheries Service (NMFS) in collaboration with the California Department of Fish and Game, the Oregon Department of Fish and Wildlife, and the Washington Department of Wildlife. Survey design was based on information given by Dohl et al.[8] regarding harbor porpoise distribution in California. They reported that harbor porpoise were usually

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[4] NMFS. 1980. A report based on the workshop on stock assessment and incidental take of marine mammals involved in commercial fishing operations. January 1980. Available from National Marine Fisheries Service, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[5] Diamond, S. L., and D. A. Hanan. 1986. An estimate of harbor porpoise mortality in California set net fisheries: April 1, 1983 through March 31, 1984. Adm. Rep. SWR-86-15, 40 p. Available from National Marine Fisheries Service, Southwest Region, 300 S. Ferry Street, Terminal Island, CA 90731.

[6] Oliver, C. W., and T. D. Jackson. 1987. Occurrence and distribution of marine mammals at sea from aerial surveys conducted along the U.S. west coast between December 15, 1980 and December 17, 1985. Adm. Rep. LJ-87-19, 189 p. Available from National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

[7] Oliver, C. W. 1986. Trip report: 1985 harbor porpoise aerial survey, September 9 to October 15, 1985. Adm. Rep. LJ-86-21, 29 p. Available from National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

[8] Dohl, T. P., R. C. Guess, M. L. Duman, R. C. Helm. 1983. Cetaceans of central and northern California, 1980–83: status, abundance, and distribution. Report prepared for U.S. Minerals Management Service, contract #14-12-0001-29090.

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found within 0.25 nautical miles (nmi) of the shoreline. We therefore designed our aerial surveys to cover a very narrow coastal band. Subsequent information from ship surveys (Barlow 1988) has shown their distribution to extend considerably farther from the coast. Therefore, estimates of porpoise density from aerial surveys apply to a relatively small portion of harbor porpoise habitat. For this reason we do not estimate population size by extrapolating aerial density estimates to the entire area inhabited. The density estimates presented here are used to corroborate estimates based on ship surveys and to estimate density for areas that were too shallow to be surveyed by ship.

Based on previous studies of dive times (Watson and Gaskin 1983; Taylor and Dawson 1984) we expected a proportion of the harbor porpoise to be diving and therefore missed by aerial observers. Shore-based studies were conducted in September 1985 from cliffs in northern Oregon to determine average dive times for west-coast harbor porpoise. Helicopter observations were made in April and May 1986 in Monterey Bay and near Bodega Head, CA to gather dive time information and obtain a direct measure of the fraction of time that harbor porpoise groups are visible from the air. These two samples did not differ significantly from previous samples of harbor porpoise in Alaska, so all samples were pooled to adjust estimates of porpoise density from aerial surveys to account for the probability of missing submerged animals.

METHODS

Aerial Survey Methods

Strip transect methodology (Seber 1973) was used during the aerial surveys. This method assumes that all individuals within a transect strip are detected. Transect lines were flown parallel to the coast line at distances of 0.61 and 1.85 km (0.33 and 1.0 nmi) offshore. Transect strips of equal width were surveyed on both sides of the aircraft. The margins of the strips were denoted by tape marks or streamers on the wing struts. Strips were divided into inside and outside swaths of unequal width (Fig. 1) by a third tape mark or streamer between the other two. When porpoise were sighted within the transect strip, the pilot was directed to leave the transect line and circle over the porpoise to obtain an accurate count of the number within the original group that was sighted. If additional groups or individuals were sighted during this circling, they were excluded from density estimates. Porpoise density, x, was calculated as the number of individuals sighted within a transect, n, divided by the product of the transect width, w, times the distance, d, that was flown:

$$x = n/(W \cdot d) \qquad (1)$$

We used both single and twin-propeller, high-wing, 4-passenger aircraft in our surveys. The search team consisted of two observers seated in the right and left passenger seats. A data recorder sat in the copilot's seat and did not search. If the recorder sighted animals that were missed by the observers, these were noted but were not included in density estimates. The planes were flown at an altitude of 213 m (700 feet) and at an airspeed of 158–167 km/h (85–90 knots). The original survey plan called for all sections of the coast to be covered twice on each survey. This was accomplished in 1984, but poor weather in 1985 resulted in the Washington coast and part of the Oregon coast being covered only once. The dates flown and areas covered are given in Table 1.

TABLE 1.—Dates, areas covered, and observer teams during aerial surveys for harbor porpoise. Geographic regions refer to those shown in Figure 2. Observer team refers to a pair of individuals.

Date	Regions covered	Observer team	Distance to shore (km)
9/09/84	7,8	A	0.61
9/10/84	5,7	A	0.61
9/11/84	5,6	A	0.61
9/13/84	1,2,3,4,5	B	0.61
9/14/84	1,2,3,4,5	B	0.61
9/17/84	1,2,3,4	B	0.61
9/18/84	1,2,3,4	B	0.61
9/11/85	6,7	C	0.61
9/16/85	1,2,3	D	0.61
9/17/85	4	D	0.61
9/18/85	4,5	D	0.61,1.85
9/19/85	4,5	D	0.61,1.85
9/20/85	2,3	D	1.85
10/04/85	7,8	E	0.61
10/14/85	1,2,3	D	1.85
10/15/85	4,5	D	1.85

Data gathered on both the 1984 and 1985 surveys were similar in format. Recorded data on sighting conditions included Beaufort sea state, a measure of cloud cover, a code indicating the presence of haze or fog, sun position relative to the aircraft, and a subjective measure of the observers' ability to see into the water through turbidity, surface reflection and diffraction. The latter was called surface penetration and was recorded separately for each of the

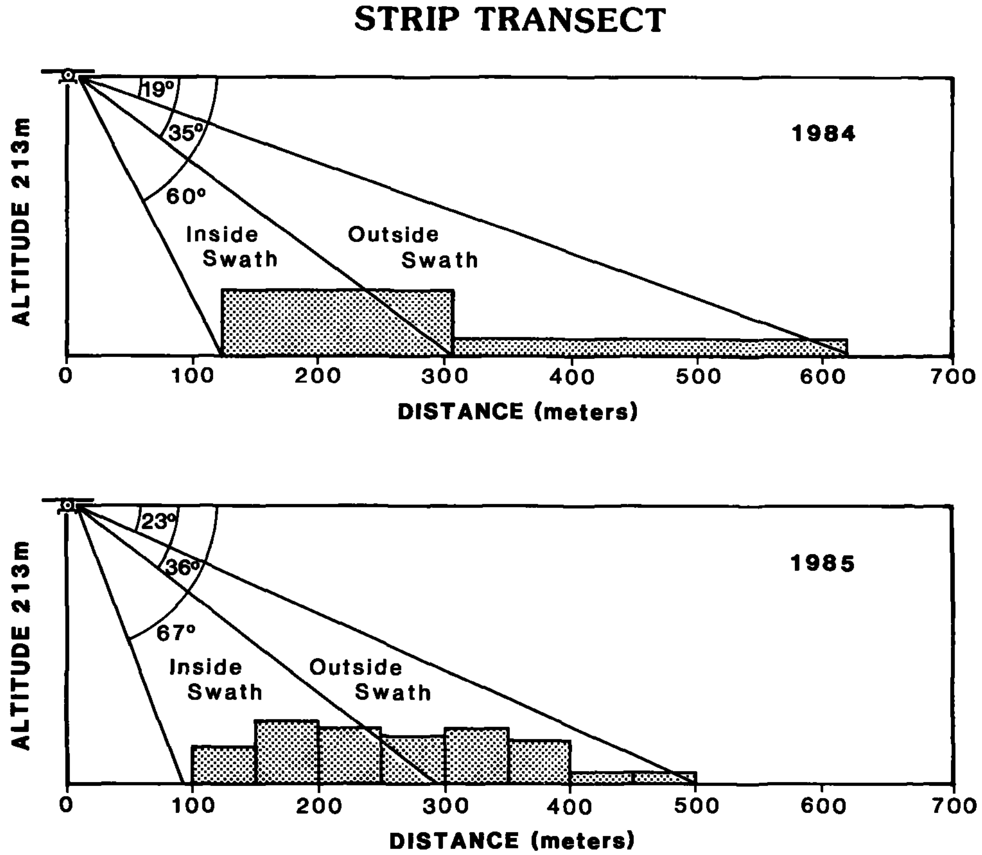

FIGURE 1.—Configuration of transect strip widths and distributions of perpendicular sighting distances for aerial surveys in 1984 and 1985. Angles are given as declinations from horizontal. Histograms indicate the relative number of porpoise seen in the given distance interval.

four swaths (inside and outside on both sides of the aircraft). In severe sun glare conditions, searching was discontinued for one or both swaths on one side of the aircraft. Additional data included individual observer numbers, date, time, and position (measured to 10ths of minutes of latitude and longitude). All of these data were recorded at the beginning and end of continuous transects and whenever conditions changed or a sighting was made. Additional data were recorded for marine mammal sightings, including a code for the species of animal seen, an estimate of the number of individuals, a code indicating on which side of the aircraft the animals were seen, and a code indicating in which of the swaths the animals were found (inside, outside, or, if the animals were not within the designated strips, neither).

An attempt was made to gather the above information in a similar manner for both surveys. Some differences in subjective measures of sighting conditions could, however, be expected because there was no overlap in observers between years. In addition, there were some differences in design between the 1984 and 1985 surveys. In 1984, the inside and outside swaths were from 123 to 305 m and from 305 to 620 m, respectively (as measured from the midline of the transect). The margins of these swaths corresponded to declinations angles of 19°, 35°, and 60° (Fig. 1). In 1985, the swaths were 91–294 m and 294–503 m and corresponded to declination angles of 23°, 36°, and 67° (Fig. 1). In 1984, effort was concentrated on the inside swath and the outside swath was not intended for abundance estimation. The change in swath size was intended to reduce the total area being searched, thus potentially allowing the outer swath to be used for density estimation. In 1985, effort was divided equally between the two swaths. During the 1985 surveys the declination angle to marine mammals was measured when the animals were perpendicular to the aircraft using hand-held inclinometers. Declination angles were not measured during the 1984 survey.

Distance to the coast was monitored using declination angles (19° for 0.61 km and 6° for 1.85 km). On the 1984 survey, this distance was 0.61 km for the entire survey. During the 1985 survey, we surveyed at both 0.61 and 1.85 km from the coast. In 1984, the coast was taken to be the outer limit of the surf zone. In 1985, the coast was taken to be the outer limit of the surf zone or, if kelp beds were present, the outer margin of those beds.

Shore Observation Methods

Observations of harbor porpoise diving behavior were made from rocky headlands in northern Oregon (Tillamook Head, Neahkahnie Mountain, Cape Meares, and Cape Lookout) immediately before the second aerial survey (7–11 September 1985). Observers were equipped with 7×50 binoculars with compasses and ocular reticles and a single 20×120 binocular. Ventilation data were collected whenever possible and included the number of animals at the surface and the length of time spent at the surface. Observations were recited aloud by the observer and were written down by a second person or were recorded onto magnetic tape. The ventilation cycle typically consisted of a period with several surfacing rolls and breaths (which we call a surfacing series) followed by a much longer period of submergence (which we call a dive). This dive cycle corresponds to ventilation pattern B as described by Watson and Gaskin (1983) for harbor porpoise in the Bay of Fundy and the pattern described by Taylor and Dawson (1984) for porpoise in Glacier Bay.

Helicopter Observation Methods

Behavioral observations were also made by three observers in a 4-passenger, jet-turbine helicopter. Upon locating a group of harbor porpoise, a fluorescein dye marker was dropped and the helicopter hovered or circled slowly above the group at an altitude of approximately 300 m. The number of animals, the time they were visible at the surface, and the dive times were recorded, along with information on cloud cover, sea state, and water turbidity. Each behavioral session was given a subjective rating based on how well the observers could follow the group and obtain accurate dive times. Only sessions with good or excellent ratings were included in analyses.

Probability of Missing Submerged Animals

Given that a porpoise would be within the visual range of an observer, the probability that it will be at the surface during the passage of the aircraft is related to the average time it spends at the surface, s, the average time spent below the surface, d, and the window of time during which it is within the visual range of an observer, t. This probability was calculated as

$$Pr(\text{being visible}) = \frac{s+t}{s+d}. \tag{2}$$

The probability of missing a submerged animal is equal to the complement of this value.

Density Estimation

Density of harbor porpoise was estimated as the number of animals seen divided by the area searched (Equation (1)). This raw density estimate was adjusted by dividing by the probability that an animal would be visible from the air at any given instant (Equation (2)). The area searched was estimated as the swath widths times the lengths of the transects. Transect lengths were calculated as the sum of the great circle distances between successive position fixes. Densities were calculated for each of the eight statistical regions used by Barlow (1988) (Fig. 2).

The statistical difference in harbor porpoise density between different sighting conditions or different areas was tested using the raw density estimates. Density estimates for short transects were frequently zero, thus violating the parametric assumptions of normally distributed, homoscedastic error. Nonparametric tests were therefore chosen for density comparisons. In discussing statistical tests, a transect segment refers to the length of transect line between two successive position fixes and are typically <20 km. The measured variables relating to sighting conditions are constant within a segment, and because each sighting is accompanied by a new position fix, a segment will contain at most, one sighting.

Whenever applicable, the Wilcoxon paired-sample test (Wilcoxon 1945) was used to test one factor while controlling for as many other factors as possible. Ten paired measures of density were created

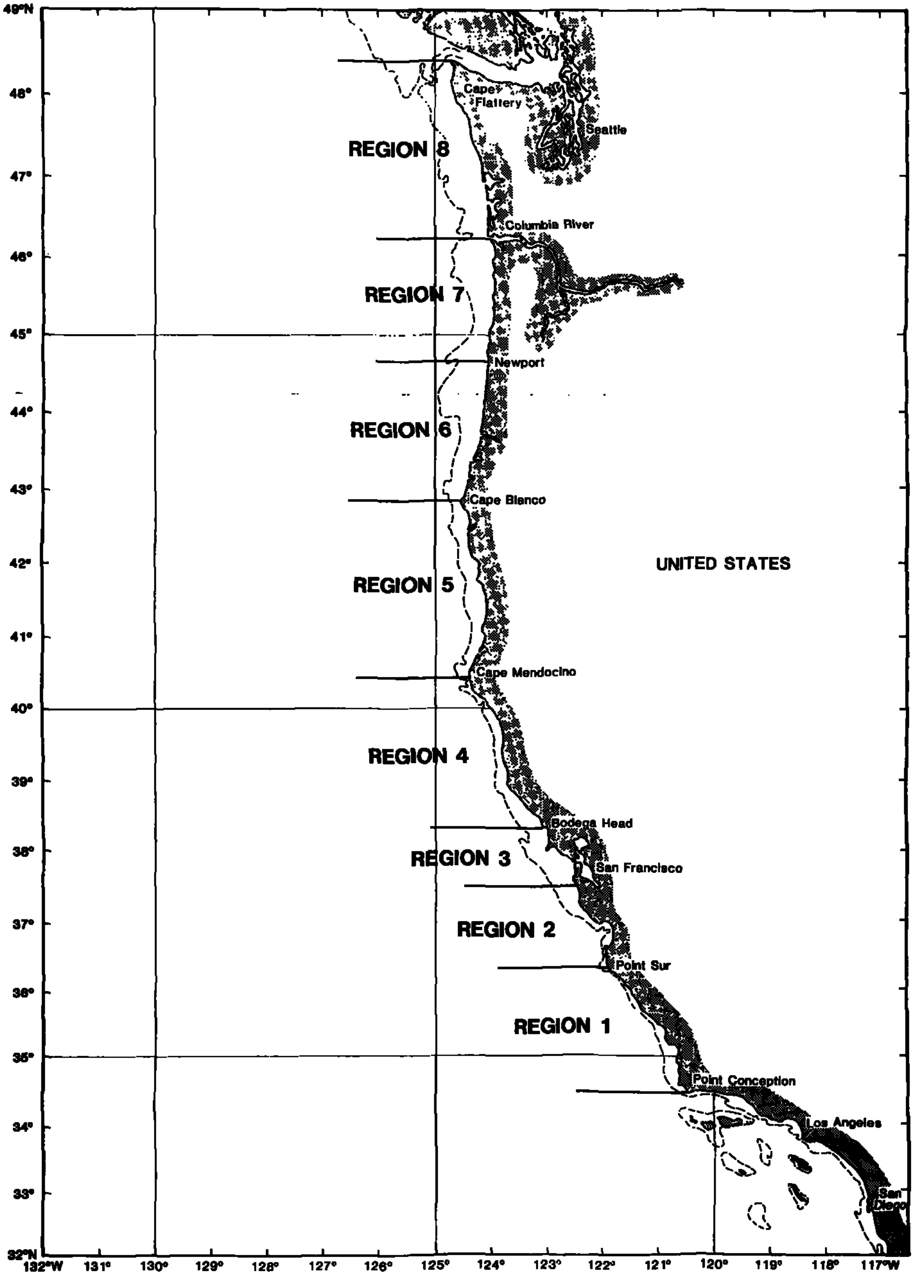

FIGURE 2.—Geographic regions used as strata in density estimation.

by adding all appropriate transect segments to a linear array and dividing that array into 10 equal parts.

When paired tests were not applicable, nonparametric ANOVA models were used. For simple comparisons, the Kruskal-Wallis single-factor analysis of variance was used (Kruskal and Wallis 1952). For two-way comparisons, we used a two-factor extension of the Kruskal-Wallis test (Scheirer et al. 1976). For both tests, three replicate measures of density were created for each cell by randomly assigning transect segments as replicate 1, 2, or 3.

A principal assumption of strip transect methods is that all individuals within the designated strip are counted. Assuming that the fraction of diving animals does not vary with sighting conditions, any effect of sighting conditions on apparent density is likely due to missed animals. In any instance where we show that poorer sighting conditions result in a significant decrease in apparent density (one-tailed for paired tests, two-tailed for ANOVA tests), we eliminate the category of sighting conditions which resulted in that lower estimate. If it is not possible to predict which category would be worse a priori in paired tests (e.g., right swath vs. left), two-tailed probabilities are used. Although we cannot be sure of eliminating all biases using these methods, this pattern of data paring should avoid much of the bias due to missed animals.

RESULTS

In 1984, 247 groups of harbor porpoise (680 individuals) were seen within transect strips which covered a linear distance of 5,763 km. In 1985, we saw 119 groups (384 individuals) in surveys of 3,715 km. Mean group sizes were 2.75 and 3.23 individuals, respectively, for 1984 and 1985. For 1984, the relative frequencies of individuals seen within the inside and outside swaths are illustrated in Figure 1. For 1985, the perpendicular distances from the trackline to the animals were calculated from declination angles, and the relative distribution of sightings is shown in Figure 1 as a function of perpendicular distance.

Inside vs. Outside Swath

For 1984 data, only the inside swaths were used, but for 1985 both inside and outside swaths were considered for density estimation. For 1985, we tested whether the density in the inside swaths was greater than the density of the outside swaths. We only considered cases when the water surface penetration codes were equal in both the inside and outside swaths. Data for inside and outside were thus paired, with all other sighting factors equal. For 1985, the density in the inside was greater (0.09 vs. 0.06 porpoise/km^2), but this difference was not significant ($P > 0.10$).

Surface Penetration

Observers used a subjective coding system to describe their ability to see through the sea surface. Cloud cover, haze, and water turbidity contributed to poor surface penetration. In 1984, observers used codes to indicate good and poor conditions; in 1985, observers used codes for excellent, good, and poor. There were frequent cases when observers recorded different codes for the inside swaths on opposite sides of the plane; hence, paired tests were again appropriate. For 1984, we tested whether density in the "good" category was higher than density in the "poor" category. When surface penetration was different in the inside swaths on opposite sides of the plane, mean density in the "good" category was higher than in the "poor" category (0.16 vs. 0.12 porpoise/km^2), but this difference was not significant ($P > 0.25$). For 1985, no tests were necessary because the mean density in "excellent" category was lower than in the "good" category, and likewise, density in the "good" was lower than in the "poor" category. All categories of water surface penetration were included in subsequent analyses.

Effects Due to Observers and Side of the Plane

Sightings were classified based on which observer made the sighting and on whether the sighting was on the inshore or offshore side of the aircraft. In fact, these two classifications were confounded in 1985 because the two principal observers were situated on the same sides of the aircraft for most of this survey. Effects of these classifications on density estimation were considered together. Survey teams were defined as pairs of observers who worked together. There were two such teams for 1984 and three for 1985 (Table 1). Only one of the teams in 1985 had sufficient numbers of sightings to be considered here. Statistical tests were based on paired cases during which both members of the sighting team were searching.

For 1984, porpoise density on the offshore side of the airplanes was greater than on the inshore side for both team A and team B (Table 2). The difference in density estimates between observers was less than the difference between inshore and off-

TABLE 2.—Relative harbor porpoise densities (km^{-2}) for teams of observers. Density estimates are stratified by inshore and offshore sides of the aircraft and by individual observers.

Observer team	Inshore	Offshore	Observer 1	Observer 2
A	0.275	0.425	0.320	0.380
B	0.168	0.244	0.232	0.179
D	0.281	0.164	0.300	0.146

shore (Table 2), and neither was statistically significant. For 1985, the opposite was seen; the density on the inshore side was greater than on the offshore side and this difference was less than the difference between observers (Table 2), but again, neither difference was statistically significant. In 1984, both observers had previous experience doing aerial surveys, but in 1985, the observer with the lower density estimates had no previous experience in cetacean surveys. Experience may be a factor in density estimates from strip transects, but since the inexperienced observer was always on the same side of the plane, it was not possible to test this with a factorial design.

Area and Sea State

Analysis of research vessel data (Barlow 1988) indicated two geographic regions in California with low porpoise density (regions 1 and 3 in Figure 2). We tested whether density observed from aircraft are also lower in these areas. Because observation conditions may have differed in the two areas, we included sea state as a second factor in a two-way ANOVA. Mean values are presented in Table 3. For 1984, three categories of sea state were used: Beaufort 0 & 1, Beaufort 2, and Beaufort 3 and greater. The effect due to area was significant ($P < 0.001$), with the area that showed low density in the ship surveys also showing lower density in the aerial survey. For 1985, only the first two categories of sea state were used due to insufficient data at Beaufort 3 and greater. Again the effect of area was significant ($P < 0.025$), and the same trends were seen. In neither case were the effects of sea state or the interaction effects significant. To eliminate area effects from confounding statistical results, only data for the larger, high-density area were included in subsequent tests. The low-density area was included in later estimates of overall harbor porpoise density.

TABLE 3.—Uncorrected harbor porpoise densities (km^{-2}) for the two-way comparison of area and sea state. Low-density areas refer to two regions in California that were found to have much lower than average density in previous ship surveys (see text). High-density areas include all other regions. Only inside swaths were included. Numbers in parentheses refer to area (km^2) surveyed under the given condition. Densities in brackets were excluded from two-way comparisons due to the small area covered in one cell.

	1984 survey		1985 survey	
Beaufort sea state	Low-density area	High-density area	Low-density area	High-density area
0 & 1	0.027 (183)	0.579 (264)	0.089 (124)	0.762 (126)
2	0.081 (308)	0.312 (1012)	0.089 (214)	0.183 (425)
3+	0.102 (79)	0.191 (252)	[0.000] (28)	[0.049] (566)

Sea State and Cloud Cover

Both sea state and cloud cover can affect sighting conditions. Because both are affected by local weather, the effects of these are likely to be confounded. These two factors were therefore tested simultaneously in a two-way ANOVA. We considered only the inside swath and excluded the two low-density regions. We used the same sea state categories as above. The sky was categorized as clear if cloud cover was <25% and cloudy if >25%. Mean porpoise densities for each category are given in Table 4. It was necessary to exclude the Beaufort 0 & 1 category for 1985 because only 52 km were surveyed in cloudy conditions for these sea states. The effect due to cloud cover was significant for 1984 ($P < 0.025$) and 1985 ($P < 0.05$). The effect of sea state and the interaction effect of sea state and cloud cover were not significant for either survey ($P > 0.10$). Transect segments with >25% cloud cover were excluded from subsequent analyses.

TABLE 4.—Uncorrected harbor porpoise densities (km^{-2}) for the two-way comparison of sea state and cloud cover. Clear refers to <25% cloud cover, and cloudy refers to >25%. Data include only inside swaths in high-density areas. Numbers in parentheses refer to area (km^2) surveyed under the given condition. Densities in brackets were excluded from two-way comparisons due to the small area covered in one cell.

	1984 survey		1985 survey	
Beaufort sea state	Clear	Cloudy	Clear	Cloudy
0 & 1	1.340 (81)	0.240 (183)	[0.832] (115)	[0.000] (11)
2	0.371 (572)	0.236 (440)	0.271 (232)	0.078 (193)
3+	0.266 (162)	0.056 (90)	0.088 (272)	0.014 (294)

Sea State

The effect of sea state was tested alone using only the transect segments which occurred under clear skies (<25% cloud cover) and within the high-density areas. For 1984, only the inside swath was included.

For 1985, both inside and outside swaths were included. As in previous stratifications, apparent density clearly decreased with increasing sea state (Table 5). This effect was significant for surveys in both 1984 ($P < 0.05$) and 1985 ($P < 0.005$). Transect segments surveyed during sea states of 2 or greater were excluded in subsequent analyses.

TABLE 5.—Uncorrected harbor porpoise densities (km^{-2}) for the stratification based on sea state. Data include only high-density areas surveyed when cloud cover was <25%. Data for 1984 include inside swaths only; data for 1985 include inside and outside swaths. Numbers in parentheses refer to area (km^2) surveyed under the given condition.

Beaufort sea state	1984 survey	1985 survey
0 & 1	1.340 (81)	0.807 (234)
2	0.371 (572)	0.193 (471)
3+	0.266 (162)	0.058 (553)

Between Survey Differences

We considered the 1984 survey and the 1985 surveys at 0.61 km and 1.85 km from shore as three independent estimates of harbor porpoise density. Because apparent density was shown to vary greatly with sighting conditions and because sighting conditions varied between surveys, it was necessary to compare these three under similar conditions.

The highest (and presumably least biased) densities were obtained when sea state was Beaufort 0 & 1 and when cloud cover was <25%. Between survey comparisons under these conditions are given in Table 6 for the eight geographic regions given in Figure 2. For 1985, there were no transect segments at 0.61 km from shore under the conditions Beaufort 0 & 1 and clear skies. For 1984, only three regions contained more than 10 km^2 of searching effort at 0.61 km from shore. For 1985, only four areas had any searching effort at 1.85 km from shore. The only direct density comparisons with reasonable sample sizes are for region 1 (0.000 vs. 0.048 porpoise/km^2) and region 3 (0.111 vs. 0.110 porpoise/km^2) (respectively for 1984 and 1985). The densities for all regions pooled (0.671 and 0.510 porpoise/km^2) are similar, but because of the small sample size and geographic variation in sampling, a statistical test of this difference is meaningless.

In comparing surveys, sample size and regional coverage improved slightly when Beaufort 2 was considered (still allowing a maximum of 25% cloud cover) (Table 7). For 1984, coverage was relatively complete in all regions. For 1985, coverage at 0.61 km from shore was limited to regions 2–4, and coverage at 1.85 km was limited to regions 1–5. Comparing the two surveys in 1985, distance from shore made little difference in overall density for all regions combined, and neither survey had consistently higher values than the other. Comparing the 1984 survey to the two 1985 surveys, the former had a higher overall density for all regions combined, but again this difference was not consistent among regions. Sample size and regional coverage were again too poor for meaningful statistical tests.

TABLE 6.—Uncorrected harbor porpoise densities (km^{-2}) in eight geographic regions surveyed during Beaufort 0 & 1 conditions. Data for 1984 are based on inside swaths of transects flown 0.61 km from the coast. Data for 1985 are based on inside and outside swaths of transects flown at 0.61 and 1.85 km from the coast. Only those segments surveyed when cloud cover was <25% are included. Numbers in parentheses refer to area (km^2) surveyed under the given condition.

Geographic region	1984 survey density 0.61 km	1985 survey density 0.61 km	1985 survey density 1.85 km
1	0.000 (43)	— (0)	0.048 (103)
2	0.000 (1)	— (0)	0.609 (51)
3	0.111 (45)	— (0)	0.110 (55)
4	0.953 (6)	— (0)	0.862 (183)
5	1.120 (9)	— (0)	— (0)
6	1.374 (64)	— (0)	— (0)
7	5.745 (1)	— (0)	— (0)
8	— (0)	— (0)	— (0)
All regions	0.671 (170)	— (0)	0.510 (392)

Ventilation Patterns

Harbor porpoise did not appear to react to the helicopter during aerial observations; they were visible throughout a surfacing series and were not visible during dives. Knowing this, we were able to use data on surfacing series and dive times to determine the fraction of time harbor porpoise would be visible from the air. Data on ventilation patterns were available from the helicopter study in California (13 groups were observed, mean group size was 2.7), the Oregon shore observations (11 groups, mean group size was 4.2), and a previous shore study in Glacier Bay, AK (28 solitary individuals). The mean times spent in surfacing series were 34.2, 24.6, and 30.0 seconds (respectively for the three studies). The corresponding mean dive times did not differ significantly between study sites ($P > 0.05$ using pairwise t-tests). Using the pooled data set ($n = 52$), the mean time spent in a surfacing series was 30.02 seconds (SE = 1.95) and the mean time spent in a dive was 95.81 seconds (SE = 5.32). The percentage of time spent at the surface is 23.9%.

Average and Adjusted Density Estimates

Harbor porpoise densities under optimal conditions (Beaufort 0 & 1 and <25% cloud cover) were averaged for the two surveys, weighting by transect length (Table 8). Given an average survey speed of 160 km/h and assuming that the window for harbor porpoise observation is 400 m long, the time window during which a point would be visible is 9.0 seconds. Using this estimate and the surface and dive times estimated above, the probability that a porpoise will be seen is estimated as 0.310 from Equation (2). An instantaneous count would therefore underestimate porpoise abundance by a factor of 3.2. Average values were therefore multiplied by this factor (Table 8).

TABLE 7.—Uncorrected harbor porpoise densities (km^{-2}) in eight geographic regions surveyed during Beaufort 2 conditions. Data for 1984 are based on inside swaths of transects flown 0.61 km from the coast. Data for 1985 are based on inside and outside swaths of transects flown at 0.61 and 1.85 km from the coast. Only those segments surveyed when cloud cover was <25% are included. Numbers in parentheses refer to area (km^2) surveyed under the given condition.

Geographic region	1984 survey density 0.61 km	1985 survey density 0.61 km	1985 survey density 1.85 km
1	0.000 (107)	— (0)	0.184 (103)
2	0.092 (109)	0.102 (59)	0.103 (68)
3	0.196 (117)	0.062 (48)	0.287 (52)
4	0.562 (180)	0.282 (110)	0.070 (57)
5	0.489 (119)	0.459 (6)	0.234 (171)
6	0.439 (57)	— (0)	— (0)
7	0.114 (70)	— (0)	— (0)
8	0.268 (37)	— (0)	— (0)
All regions	0.295 (796)	0.192 (224)	0.188 (452)

DISCUSSION

Results indicate that sighting conditions must be very good in order to estimate harbor porpoise abundance from aerial strip transects. Both sea state and cloud cover had very large and significant effects on apparent density. Limiting observations to the best categories of sea state (Beaufort 0 & 1) and cloud cover (<25%) can be used to minimize the bias due to missed animals. These conditions are, however, rare and only occurred during 5.3% and 10.3% of the transects in 1984 and 1985. The actual occurrence of these conditions is even more rare if one considers flights that were cancelled due to bad weather.

The effects on sea state and cloud cover on sighting conditions were predicted by observers before analysis of survey data was begun. Most harbor porpoise were first seen when submerged a small distance below the surface. Surfacings were relatively inconspicuous to aerial observers and were not an important cue in sighting porpoise. Both sea state and cloud cover affect the ability of observers to see through the water's surface and to spot submerged animals. Increasing sea state causes more refraction of light at the water's surface, increases glit-

TABLE 8.—Harbor porpoise densities (km^{-2}) in eight geographic regions from a) a weighted average of uncorrected estimates from 1984 and 1985 aerial surveys, b) the same average adjusted by a factor of 3.2 to account for submerged porpoise that were missed by aerial observers, and c) a weighted average for the 1984 and 1985 ship surveys. Aerial estimates are based on observations made under conditions of Beaufort 0 & 1 and with <25% cloud cover. Ship estimates include Beaufort sea states of 0, 1, and 2.

Geographic region	Area surveyed (km^2)	Aerial estimates		Research vessel estimates
		Uncorrected a	Corrected b	c
1	146	0.03	0.10	0.05
2	1	—	—	0.66
3	100	0.11	0.35	0.04
4	189	0.86	2.75	3.68
5	9	1.12	3.58	1.18
6	64	1.37	4.38	2.88
7	1	—	—	3.43
8	0	—	—	1.42
All regions	562	0.559	1.79	1.73

tery reflection of sunlight, and causes whitecaps which obscure subsurface observation. Cloud cover decreases penetration of sunlight into the sea and causes its surface to appear dark and glazed. It is therefore not surprising that calm seas and clear skies result in higher apparent densities.

It is more surprising that apparent density did not vary with observer's subjective appraisal of surface penetration. This may have been because surface penetration was only tested in paired cases for which sea state and cloud cover were identical. In these cases, differences in surface penetration may have been due primarily to subjective differences in the way individual observers were coding it. If all cases are considered, surface penetration is very highly correlated with sea state and cloud cover and probably could be used as an alternative measure of sighting conditions. We prefer, however, to use sea state and cloud cover because their measure is less subjective than surface penetration and could more easily be used by other researchers.

Missed Animals

A principal assumption of strip transect methods is that all individuals within the strip are counted. We cannot necessarily meet this assumption just by eliminating the categories of sighting conditions with significantly lower density. In fact, it is possible that this method of selectively eliminating data could overestimate density by eliminating a category of sighting conditions which (by random chance) had a significantly lower density. We do not believe that this is likely in the cases of sea state or cloud cover because the trends were the same for both surveys and because the categories that were eliminated were judged a priori as being poorer sighting conditions. We believe that porpoise density is more likely underestimated due to missed animals. Kraus et al. (1983) found that observers in aircraft saw only 14% of the harbor porpoise groups known to be present based on shore-based observations. Missed animals may include some individuals that were near the surface and visible but were not seen, as well as others that were diving and were too deep to be seen.

We infer that some near-surface animals were missed based on three reasons. First, apparent density decreased with increasing sea state and cloud cover, hence near-surface animals must be missed in (at least) the poorer conditions. (An alternative explanation is that porpoise spend less time near the surface when sighting conditions are poor.) Second, of the two principal observers in 1985, the less experienced observer may have missed more porpoise. Third, in five instances in 1984 and one instance in 1985, the data recorder saw harbor porpoise in the inside swath that were missed by the observer. In three of these cases, conditions were Beaufort 1 with <25% cloud cover. Recorders searched only occasionally as conditions permitted, so it is not possible to use these data to quantify how many near-surface animals were missed under good conditions.

Based on behavioral observations, we can also be certain that some harbor porpoise are missed because they are too deep to be seen. Water visibility was typically only 2–5 m during the surveys. Aerial observers have seen harbor porpoise dive out of view during the passing of the plane or while circling. Harbor porpoise were not visible from the helicopter during dives, even in very calm water. Some fraction of porpoise must be missed because they are too deep to be seen.

We have tried to account for the fraction of diving animals by dividing density estimates by the fraction of time harbor porpoise are known to be near the surface (i.e., within surfacing series). Uncorrected estimates of harbor porpoise density are based on the assumption that porpoise are never too deep to be seen; this undoubtedly results in an underestimate of porpoise density. Our method of adjusted estimates of porpoise density assumes that, when diving, porpoise are always too deep to be seen; this has been corroborated by helicopter observations. The latter estimate should therefore be closer to the true value of porpoise density (if biases due to other factors have been eliminated).

Offshore Distribution of Harbor Porpoise

In 1985, aerial transects were flown at 0.61 and 1.85 km from the shore. The latter value was chosen to correspond approximately to the ship transects along the 10-fathom (18.3 m) isobath. The intent was to directly compare aerial estimates of density to estimates made from ships at the same distance from shore (considered below) and to provide a means to extrapolate ship estimates to regions that were too shallow to survey by ship. In regard to the latter, we wish to know whether harbor porpoise density at 0.61 km from shore is different from that at 1.85 km.

In 1985, surveys at 0.61 km were never flown under good sighting conditions (Beaufort 0 & 1 and <25% cloud cover), so direct comparisons between 0.61 and 1.85 km are not possible. Considering only the best category of sighting conditions, it is possible to compare 1985 transects at 1.85 km with 1984 transects at 0.61 km in geographic regions 1 and 3 (Table 6). Sample sizes are very small, but densities are roughly comparable (0.070 vs. 0.057, respectively for 1.85 and 0.61 km from shore). Sample sizes in 1985 can be increased if Beaufort 2 is considered instead of Beaufort 0 & 1 (still with <25% cloud cover). Based on geographic regions 1 through 5, porpoise densities are virtually identical at 1.85 and 0.61 km from shore (0.188 vs. 0.192, respectively, Table 7).

In a preliminary model of harbor porpoise depth distribution, Barlow (1988) hypothesized that harbor porpoise density is constant from the shore to the 75 m isobath. Ship data did not, however, include any transects inshore of 18.3 m depth. In this shallow area, the model was not based on any data. Although sparse, data from aerial surveys show that densities are similar in areas that were surveyed by ship (1.85 km from shore) and in areas that were too shallow to be surveyed by ship (0.61 km from shore). These data are consistent with the model proposed by Barlow.

Comparison of Ship and Aerial Density Estimates

Estimates of harbor porpoise density from 1984 to 1985 ship surveys (Barlow 1988) can be compared with adjusted and unadjusted estimates from the aerial surveys (Table 8). The overall density for all regions is higher for the ship surveys than for the unadjusted aerial. Adjusted estimates from the aerial surveys are very close to the overall estimates from ship surveys.

Previous comparisons have been made of sighting efficiency from aerial and surface vessel platforms (Kraus et al. 1983). They found that observers on boats saw 52% of the harbor porpoise groups seen by shore-based observers, whereas aerial observers saw only 14%. Based on this, density from aerial surveys might be expected to be only 27% of that from ship surveys. In the present study, unadjusted density based on aerial surveys is 32% of the density from ship surveys. The two studies are not directly comparable, however. Weather conditions are not reported by Kraus et al. (1983) and may have included less than optimal sighting conditions. It should be noted that the fraction of harbor porpoise groups seen by aerial observers in their study (14%) is even lower than the fraction of harbor porpoise we assumed would be in surfacing series and hence near the surface (23.9%). It is possible that behavioral differences between harbor porpoise from the two coasts (such as travelling or behavior mode "A" noted by Watson and Gaskin (1983)) could account for some of the differences noted above.

Estimates based on ship surveys cannot, of course, be considered the true density of harbor porpoise. The overall estimate based on ship surveys is relatively imprecise (C.V. = 49%) and may be biased (Barlow 1988). The ship survey estimate is, however, superior to current estimates from aircraft for several reasons. Line transect methods were used on the ship surveys, and the principal assumption of this method (that 100% of the animals in the immediate vicinity of the trackline are seen) is more easily met than the comparable strip transect assumption (that 100% of the animals within a strip are seen). Acceptable sighting conditions for ship surveys included Beaufort 0 & 1, and 2 and were not restricted by cloud cover (Barlow 1988). This allowed more complete geographic coverage than did aerial surveys. Also, the ship travelled much slower than the aircraft (10 knots vs. 80–90 knots), thus the probability of missing a diving individual was much less. Barlow (1988) calculated that diving animals located near the trackline would be missed by observers on ships only if dive times exceeded 2 minutes. Finally, estimates of the correction factor to account for submerged animals is relatively imprecise. Additional observations on ventilation patterns may allow further refinements in density estimates based on aerial surveys.

RECOMMENDATIONS

The design of future surveys for harbor porpoise could be improved based on the results obtained from our aerial surveys. We found that sighting conditions deteriorated rapidly with both increasing cloud cover and rougher sea states. To the extent that is possible, aerial surveys for harbor porpoise should only occur on clear days with little wind. Observations made by the data recorders indicate that some harbor porpoise will be missed even in good sighting conditions. If strip transects are used, experiments with two independent teams of observers searching at the same time could be used to quantify the fraction of animals that are missed by using just one team. Given that fewer harbor porpoise were seen between 400 and 500 m of the track line, we also suggest that, when surveying at 213 m altitude, the strip widths should be decreased to only include the area between 100 and 400 m.

We believe, however, that the problem of missing harbor porpoise could be reduced if line transect methods were used in place of strip transects. Line transect methods assume that 100% of all animals are seen directly along the trackline and use statistical techniques to estimate the number of animals that are missed as a function of the distance from this trackline. Line transects would require use of an aircraft with unobstructed downward visibility through a belly window and use of a third observer who could view animals directly under the aircraft.

Harbor porpoise are now known to occur further from the shoreline than was believed at the beginning of this study (Barlow 1988). In future surveys, transect lines should be placed so as to cover a greater fraction of the harbor porpoise habitat.

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