Abstract.–Boat surveys along randomly placed line transects were conducted from June to August 1991 and June to October 1992 to determine distribution and abundance of and habitat use by harbor porpoise (*Phocoena phocoena*) off the northern San Juan Islands, Washington. There were 301 sightings (average 4.4 sightings/h) of 526 harbor porpoise during 73 random boat surveys, with group sizes of 1 to 8 individuals (mean=1.87, SE=0.06, n=278). An estimated 299 harbor porpoise (1.26 porpoise/km^2, SE=0.20) were distributed in an aggregated pattern within a 237 km^2 area (10% of Washington Sound), indicating that a large proportion (30%) of harbor porpoise in Washington Sound occur in the northern San Juan Islands. Harbor porpoise were distributed over a depth range from 20.1 to 235.0 m (mean= 141.6 m, SE=2.43, n=275) and were observed more than expected ($P<0.05$) in depths greater than 125 m and over shallow slopes (<10%) and observed less than expected ($P<0.05$) in depths less than 75 m. Porpoise occurred at sea surface temperatures of 10.1° to 16.3°C and were sighted more frequently than expected ($P<0.05$) in water temperatures of 11° to 12°C. Boat surveys along fixed location transects indicated distribution was similar between 1991 and 1992. The occurrence of harbor porpoise in deep water, at cooler sea surface temperatures, over shallow sloping seafloor, and in tidally mixed regions (owing to currents and tide rips) within our study area may, collectively, affect prey distribution and associated harbor porpoise distribution.

Distribution and abundance of and habitat use by harbor porpoise, *Phocoena phocoena,* off the northern San Juan Islands, Washington

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Harbor porpoise (*Phocoena phocoena*) are present year-round off the coast and inland waters of Washington State. Historically, harbor porpoise have been present throughout the Strait of Juan de Fuca, Washington Sound (San Juan Island archipelago), and south in Puget Sound. Once considered the most common cetacean in southern Puget Sound (Scheffer and Slipp, 1948), harbor porpoise sightings are now rare (Everitt et al., 1980; Calambokidis et al., 1984, 1985). Although harbor porpoise have not been sighted off the central San Juan Islands in recent years (Flaherty and Stark[1]; Calambokidis et al.[2]), sightings off the northern San Juan Islands have been common (Flaherty and Stark[1]; Calambokidis et al.[2]). Reasons for the disappearance of harbor porpoise from South Puget Sound are unclear but may be due to reduced availability of prey (because of changes in environmental conditions), fishing pressure, disturbance, net entanglement, or pollution.

Many biological (e.g. prey) and physical oceanographic factors (e.g. depth, seafloor relief, tidal currents, and sea surface temperature) affect the distribution of cetaceans. Increased availability of prey in deep waters may be a factor affecting the distribution of harbor porpoise. Smith and Gaskin (1983) found a significant positive correlation between abundance of mother-and-calf pairs and bottom depth and copepod (*Calanus* spp.) density. Abundance of harbor porpoise also was positively correlated with depth and physiographic features that concentrated Atlantic herring (*Clupea harengus*) in near-surface waters (Watts and Gaskin, 1985). In Fish Harbor, New Brunswick, Canada, harbor porpoise were associated with reduced sea surface temperatures that coincided with a large influx of juvenile herring in the region (Gaskin and Watson, 1985). Tidal state affected movements of harbor porpoise in the Bay of Fundy; har-

[1] Flaherty, C., and S. Stark. 1982. Harbor porpoise (*Phocoena phocoena*) assessment in "Washington Sound." Final report for subcontract 80-ABA-3584. National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA, 84 p.

[2] Calambokidis, J., J. C. Cubbage, J. R. Evenson, S. J. Jeffries, and R. F. Brown. 1993. Abundance estimates of harbor porpoise in Washington and Oregon waters. Final Report to National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA, 55 p.
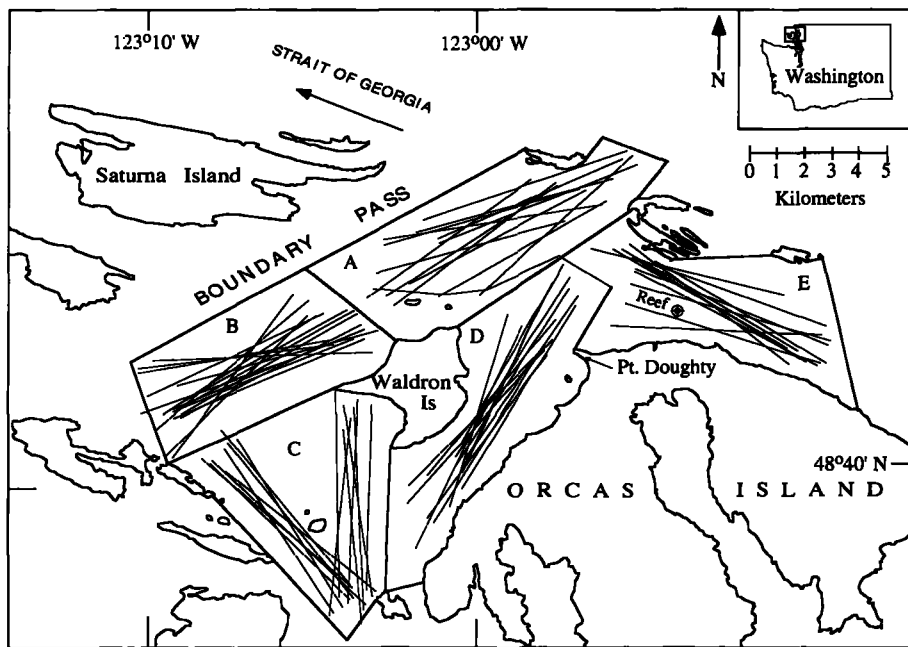
Figure 1

Random boat transects (*n*=73) completed from June to October 1992 within five stratified sections (A, B, C, D, E), northern San Juan Islands, Washington.

bor porpoise were observed more often during flood tide than ebb tide (Watson, 1976) and moved inshore during flood tides and offshore during ebb tides (Gaskin and Watson, 1985).

Harbor porpoise in northern Puget Sound are vulnerable to some of the same detrimental effects (disturbance, net entanglement, and pollution) that may have caused the disappearance of harbor porpoise in southern Puget Sound. It is important, therefore, to determine the abundance of harbor porpoise and identify habitat variables that may influence their distribution in northern Puget Sound. The main objectives of this study were to determine 1) the spatial and temporal distribution, density, and abundance of harbor porpoise occurring off the northern San Juan Islands and 2) the relation of harbor porpoise to depth and percentage slope of the seafloor, sea surface temperature (SST), tidal state, and time of day.

Methods

Study area

Washington Sound is located in the northwest corner of Washington State (48°15' to 48°50'N and 122°27' to 123°13'W), between the southern portion of Vancouver Island and the mainland, from Fidalgo Island to north of Vancouver, including the Ameri-

can and Canadian islands of the San Juan Archipelago (Kozloff, 1973). Mean diurnal tide heights are between 1.3 and 2.9 m (NOAA, 1991). Northern Washington Sound (northern San Juan Islands) has numerous islands and reefs with deep channels, strong currents, and tide rips. The study area off the northern San Juan Islands (Fig. 1) was selected on the basis of preliminary boat surveys conducted in 1991 to determine areas of harbor porpoise occurrence. Additionally, information was obtained from local residents and The Whale Museum, Friday Harbor, Washington.

Random boat surveys

Randomly located boat transects (*n*=73; Fig. 1) were conducted from 27 June to 2 October 1992 within a study area composed of five strata (lettered A–E; Fig. 1) to determine harbor porpoise distribution, density, abundance, and habitat use. Eight-km transects were located within each approximately equal (42 to 50 km²) stratum by using random starting points and random compass bearings. Strata were originally chosen so that transects would adequately cover the entire study area. Because placement of straight 8-km transects was constrained by the boundaries of strata and islands or reefs within strata, however, some regions of each strata were not adequately sampled. When sea conditions permitted, the five

strata, hereafter referred to as sections, were surveyed on the same day. Sections were chosen in a random starting order and every attempt was made to complete all sections before surveying the same sections again.

Harbor porpoise were surveyed from a 7.3-m aluminum marine patrol vessel during Beaufort sea state 0 (wind speed=0–1.8 km/h), 1 (wind speed=1.8–5.6 km/h), or rarely Beaufort 2 (wind speed=7.4–11 km/h). Each transect was completed in approximately 52 min, at an average boat speed of 9 km/h. Date, time, and tidal phase (flood or ebb) were recorded before each transect was surveyed. At the beginning and end of each transect, Secchi disk readings were recorded to the nearest 0.1 m and SST was recorded (by a calibrated thermometer located on the transducer of the survey vessel) to the nearest 0.1°C. During surveys, two observers divided the field of view across the forward 180° of the transect path. Observations were made from the roof of the vessel (height above the waterline=2.68 m, measured to the observers' eyes in surveying position) with unaided eyes and with Fujinon 7 × 50 reticle and compass binoculars. When an individual or group of harbor porpoise was located, an observer recorded time; group size and composition; compass bearing to the porpoise; ocular reticle marks from the horizon to the porpoise; Beaufort sea state; number of boats, birds, and marine mammals within 1 km of vessel; and direction of harbor porpoise travel. A group of harbor porpoise was defined as two or more porpoise visible at the water's surface within three body lengths (5 m) of each other, having nearly synchronous diving patterns (<15 seconds between sightings of each individual). Observers were trained and tested in the use of reticle binocompasses and in calibrating their readings on buoys and points of land and comparing distance accuracy to National Oceanic and Atmospheric Administration (NOAA) navigational charts and vessel's radar. Compasses on binoculars were also tested and were found not to be significantly affected by metal on the survey vessel. Although not common, the horizon was sometimes obscured by land in the observers' viewing area. To compensate for this, we estimated the number of reticles from the land-water interface (directly beyond the porpoise) to the porpoise sighting, then carefully rotated the binoculars from the land to the horizon. We then determined the number of reticles the horizon was beyond the land and added this amount to the reticle reading of the harbor porpoise sighting. Loran coordinates, Beaufort sea state, visibility, SST, and number of boats within 1 km of the vessel were recorded every ten minutes during surveys and for each harbor porpoise sighting. Depth and seafloor slope

(at each harbor porpoise sighting) were determined from NOAA navigational charts and bathymetric charts.

Locations of harbor porpoise were determined with the aid of Fujinon 7 × 50 reticle (one reticle=17 min or 0.283°) and compass binoculars. Vertical angle was calculated as the angle between the horizon and the harbor porpoise. Distance to harbor porpoise was calculated as

$$D_r = \frac{H}{\tan(\alpha)},$$

where D_r = the radial distance from the vessel to the porpoise;

H = the eyeheight of observers; and

α = the vertical angle between the horizon and porpoise.

Locations were plotted on NOAA navigational charts by using Loran (latitude and longitude) coordinates of the vessel at the time harbor porpoise were sighted, and distance and bearing to the sighting.

Perpendicular distance from the trackline to harbor porpoise was determined by using

$$D_p = D_r \times \sin(\alpha),$$

where D_p = perpendicular distance;

D_r = the radial distance to the harbor porpoise; and

α = the angle off the trackline (the difference between the trackline heading and the bearing to porpoise).

Seafloor depth and slope were determined by using a NOAA navigational chart and bathymetric map. Percentage slope was calculated as

$$\% slope = \frac{dz}{ds} \times 100\%,$$

where dz = the difference between the two closest depths (m) printed on the chart on either side of a harbor porpoise location (with contour lines drawn among depths); and

ds = the distance (m) between those two depths.

Bathymetric charts with contour intervals of 10 m were used to verify angle of slope between depths.

To determine if harbor porpoise occurred over depths and slopes in proportion to available depths

and slopes in the study area, eight random points were plotted within a 2-km strip along the length of each 8-km transect (n=73 transects, 584 points) and depth and slope were determined for each point. The number of random points chosen was determined by plotting precision (standard deviation/mean) against sample size until there was little variability in this measure (i.e. a plateau and subsequent leveling of the curve).

Density and abundance estimates were calculated by using the line transect method as described by Burnham et al. (1980) and the computer program DISTANCE (Laake et al., 1993). Each transect was considered a replicate. Density and variance estimates of harbor porpoise sightings (n=250) were calculated by replicate for each section (n=12 to 15 transects) and by replicate for all sections combined (n=70 transects). Transects with Beaufort sea state of 2 (n=3) were deleted from analyses because sighting rates of harbor porpoise in Beaufort 2 are less than Beaufort 0 or 1 (Barlow, 1988). Density was calculated as

$$D = \frac{n \times f(0) \times s}{2L},$$

where n = number of individual harbor porpoise sightings;

$f(0)$ = the probability density function of distances from the trackline evaluated at zero distance;

s = average group size of harbor porpoise sightings, and

L = total length of the trackline.

Abundance was calculated as density multiplied by area of each section (A–E) and all sections (237 km²). The parameter $f(0)$ is essentially a measure of sighting efficiency and should not vary with porpoise abundance as long as sighting conditions (e.g. Beaufort sea state, visibility) remain the same. Because we surveyed only during optimal sighting conditions (Beaufort ≤1, no rain or fog) within all sections and because relatively large sample sizes are required to estimate $f(0)$ accurately, values of $f(0)$ for each section were estimated by pooling all sightings in all sections. Effective strip width is defined as $1/f(0)$, which equals one-half the transect width, such that as many objects are detected outside the strip as remain undetected within it (Buckland et al., 1993). Because group size was independent of distance from the trackline (determined through size-bias regression analysis with DISTANCE software), average group size was used to calculate density. Average

group size was estimated by section and for all sightings combined.

Uniform, half-normal (hermite), hazard rate, and negative exponential models were compared with the frequency distributions of perpendicular sighting distance of harbor porpoise to trackline with DISTANCE. Several groupings and truncation points were investigated to achieve the best model fit. Buckland et al. (1993) recommend truncating 5 to 10% of objects detected at the greatest distances from the trackline. The half-normal (hermite) model, grouped into 50 m intervals and truncated at 750 m (deleting 5% of sightings), was chosen on the basis of lowest Akaike Information Criterion (AIC; Buckland et al., 1993) score for all sections combined.

The probability of detection at zero perpendicular distance, $g(0)$, was assumed to be one (all harbor porpoise on the trackline were assumed to be seen) because we were unable to estimate perception bias (bias resulting from animals available to be seen but that were not; Marsh and Sinclair, 1989). We did not have an independent observer to watch the trackline for porpoise that were missed by our two observers, therefore, a correction was not applied to $g(0)$. It is likely $g(0)$ was less than one but it is probably high (slow boat speed and excellent sighting conditions). Because $g(0)$ was constant over the survey time period, the habitat correlations are valid; however, the abundance estimate is underestimated by an unknown amount.

Seafloor depth and slope available in the study area in relation to areas of harbor porpoise occurrence were compared by using chi-square goodness-of-fit analyses. To test whether the frequency of occurrence of harbor porpoise was independent of frequency of tidal currents and surface temperature, we also used chi-square goodness-of-fit analyses. More surveys were conducted during flood tide (n=52) than during ebb tide (n=17); therefore, the number of harbor porpoise observed per minute during flood or ebb tide was used to standardize the data. A Mann-Whitney U, nonparametric two-sample test was conducted to examine differences in number of harbor porpoise observed per minute for each transect (n=73) during flood and ebb tides.

Power analyses (Cohen, 1988) were conducted on nonsignificant categories of chi-square goodness-of-fit analyses. Randomization statistics with the program Resampling Stats (Resampling Stats, 1995) were performed to assess the probability of detecting a difference between flood and ebb tides when the difference was determined to be nonsignificant. Additionally, power analyses were used to estimate the probability of detecting trends in abundance over time (Gerrodette, 1987).

Not all times of day were sampled equally; therefore, abundance of harbor porpoise in relation to time of day was compared by using number of porpoise observed per minute to standardize the data. Mean number of harbor porpoise observed per minute for each hour of daylight was compared with Kruskal-Wallis nonparametric analysis of variance and Kolmogorov-Smirnov goodness-of-fit analyses (Zar, 1984). Nonparametric statistics were used for data with non-normal distributions or unequal variances.

Fixed boat surveys

To determine temporal changes in harbor porpoise distribution between 1991 and 1992, six 8-km transect lines (hereafter called fixed transects; Fig. 2), placed in areas of harbor porpoise occurrence (preliminary harbor porpoise surveys and information from Orca Hotline, The Whale Museum, Friday Harbor, Washington), were surveyed regularly from 27 July to 26 August 1991 and from 24 July to 28 August 1992. In 1991, there was only one observer per survey; therefore, only one half the transect (bow out to 90° port or starboard) was completed during each survey. To be consistent in 1992, one observer surveyed from bow to 90° port while the other surveyed from bow to 90° starboard so that one half of each transect could randomly be compared to 1991 transects.
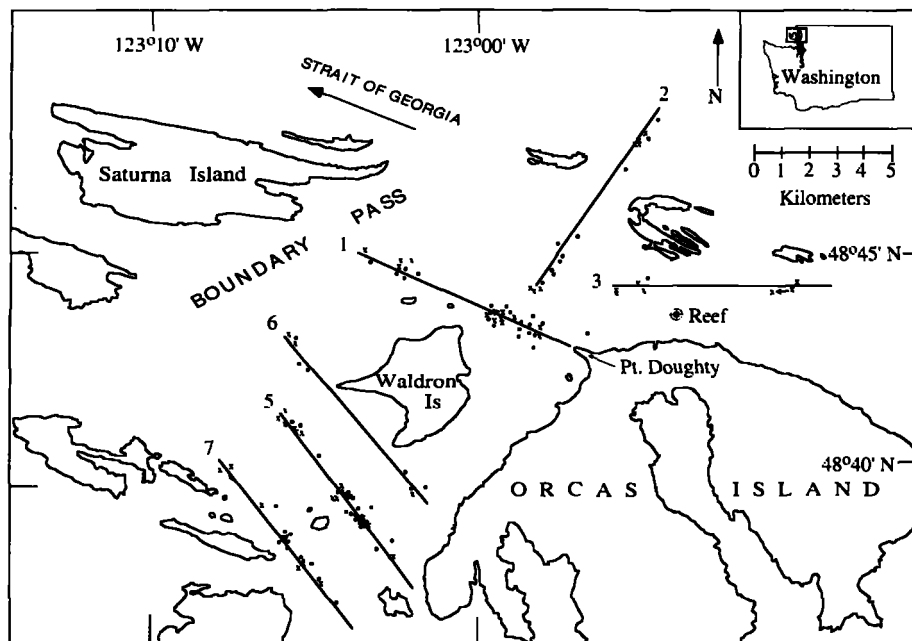
Harbor porpoise were counted from the same 7.3-m vessel as in random surveys during a Beaufort sea state of 0 or 1. Each fixed transect survey was conducted at an average speed of 11 km/h and completed in 40 to 45 minutes. This vessel speed was chosen in 1991, and to be consistent, 1992 fixed transect surveys were conducted at the same speed (instead of 9 km/h as in random boat surveys). Harbor porpoise locations were calculated as in random boat survey methods.

Mean number of sightings of harbor porpoise per survey between 1991 and 1992 was compared by using a t-test. Because both sides of the vessel were observed during a single survey in 1992, each side could not be considered an independent sample. Therefore, one side of the vessel was randomly chosen from each survey in 1992 to compare with 1991. Power tests (Cohen, 1988) were performed when results were not significant.

Results

Random boat surveys

There were 301 sightings of 526 harbor porpoise (Fig. 3) during random boat surveys. Of these, 20 sightings (39 porpoise) were possible resightings (i.e. observer believed the porpoise had already been seen during that survey, given the location and direction of travel of porpoise), therefore, these possible resightings were not used in analyses. An average of 4.4 harbor porpoise sightings were recorded per hour (8.1 harbor porpoise per hour), with group sizes of 1 to 8 (mean=1.87, SE=0.06, n=278) individuals. Thirteen cow and calf pairs were observed between June and September. Harbor porpoise were sighted during 75% of surveys at a mean perpendicular distance of 237 m (SE=13.89, n=250, range: 0 to 1060 m) from the trackline. The half-normal (hermite) model, truncated at 750 m, best fitted the frequency distribution of perpendicular distance of harbor porpoise sighted from the trackline (Fig. 4). Using harbor porpoise sightings (n=250) for all sec-

Figure 2

Harbor porpoise locations along fixed boat transects (1, 2, 3, 5, 6, 7) in 1991 and 1992 off the northern San Juan Islands, Washington. The "x" denotes locations of harbor porpoise sighted in 1991; the "•" denotes locations in 1992.

tions combined, we estimated that the effective half-strip width (ESW) was 337 m (95% CI=307–371 m; coefficient of variation, CV=0.048), with an $f(0)$ of 2.96/km (SE=0.14, CI=2.70–3.25, CV=0.048).

No significant correlation (r=0.097, n=250, P=0.938) was detected between harbor porpoise group size and perpendicular distance from the trackline. For surveys conducted during Beaufort ≤1 (n=70) in all sections (A–E), the mean group size was 1.91 harbor porpoise (SE=0.07, n=250; Table 1) and mean density was 1.26 harbor porpoise/km² (SE=0.20; Table 1). Harbor porpoise densities were least in section A (0.60 porpoise/km², SE=0.21) and greatest in section D (2.3 porpoise/km², SE=0.74; Table 1). There were an estimated 299 harbor porpoise (CI=219–409) in all sections (Table 1), ranging from 30 harbor porpoise (CI= 5–60) in section A to 116 harbor porpoise (CI=62–221) in section D (Table 1). The pooled estimate of harbor porpoise abundance (299 porpoise) for all sections yielded the same abundance estimate as adding the estimates for each individual strata (A–E; Table 1).

If the present surveys were conducted annually with a similar sampling regime that produced an equally low CV (0.159), there would be sufficient power (80%) to detect a 14% annual change (α=0.05; 12% change for α=0.10) after five years.

Mean number of harbor porpoise per survey was greatest in section D and least in section E (Fig. 5A). Mean depth throughout the study area was 108.1 m (SE=21.68, n=584); section D had the greatest mean depth and section E the least (Fig. 5B). Harbor porpoise were distributed over a depth range of 20.1 to 235.0 m (mean=141.6 m, SE=2.43, n=275), with 83% of harbor porpoise sightings occurring over depths greater than 100 m. Significantly (P<0.05) fewer than expected harbor porpoise occurred in depths less than 75 m and sig-
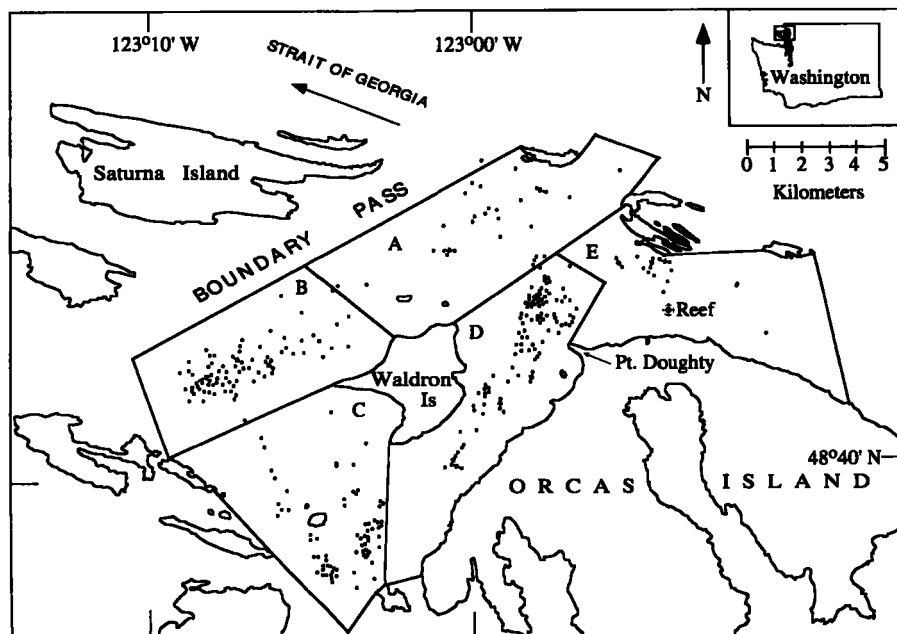

Figure 3

Location of 301 harbor porpoise sightings made during 73 random boat surveys completed from June to October 1992 within five stratified sections (A, B, C, D, E).
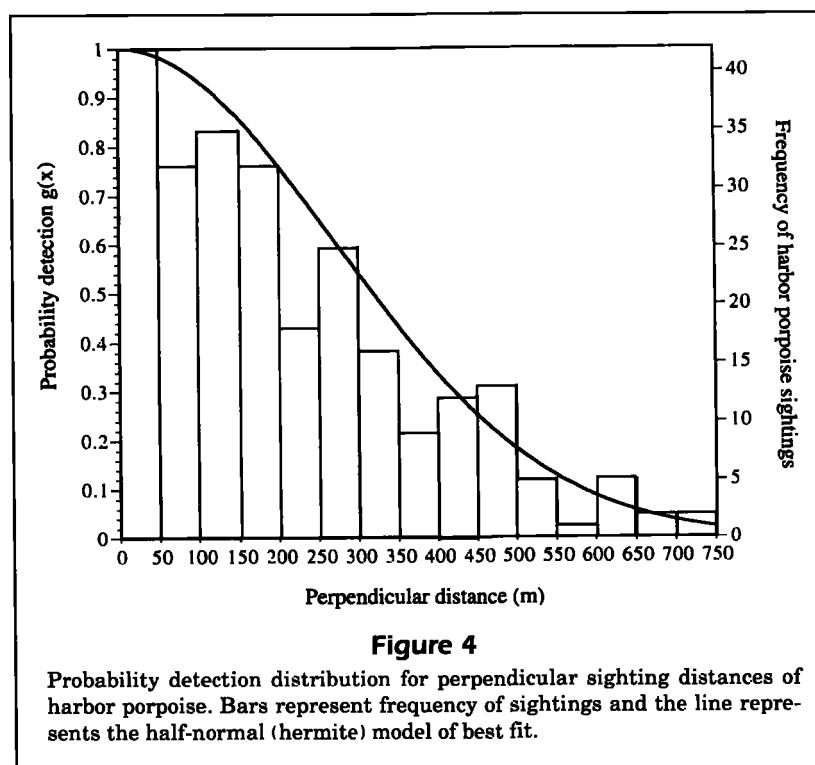

Figure 4

Probability detection distribution for perpendicular sighting distances of harbor porpoise. Bars represent frequency of sightings and the line represents the half-normal (hermite) model of best fit.

nificantly (P<0.05) more than expected in depth categories greater than 100 m (Fig. 6). The effect size (degree to which depths differed among categories) was small and the power to detect a difference was

Table 1

Survey effort, line transect model parameters, density, and abundance estimates of harbor porpoise for each section (A–E) and all sections combined surveyed within the northern San Juan Islands, Washington, from June to October 1992.

Parameter	Section A	Section B	Section C	Section D	Section E	All sections
Area (km²)	50.26	43.12	50.40	50.47	42.43	237
Effort (km)	112	120	120	112	96	560
Transect lines	14	15	15	14	12	70
Truncation width (m)	750	750	750	750	750	750
Probability density $f(0)$/km	2.96	2.96	2.96	2.96	2.96	2.96
Sightings of harbor porpoise	26	62	67	80	15	250
Mean group size	2.19	1.94	1.81	1.90	1.80	1.91
Standard error (SE) of group size	0.32	0.15	0.11	0.11	0.26	0.07
Density (porpoise/km²)	0.60	1.03	1.55	2.33	0.76	1.26
95% confidence intervals (porpoise/km²)	0.30–1.21	0.60–1.75	0.77–3.10	1.24–4.4	0.35–1.66	0.92–1.73
SE of density	0.21	0.27	0.52	0.74	0.30	0.20
% coefficient of variation (CV) of density	35.09	26.00	33.86	31.55	39.16	15.86
Abundance	30	44	77	116	32	299
95% confidence interval (abundance)	15–60	26–75	39–155	62–221	15–70	217–406
SE of abundance	10.53	11.43	26.07	36.91	12.53	47.0

low (37%) for categories that were not significantly different (Fig. 6). Given the small effect size, a power of 80% would require 358 locations of harbor porpoise in these three depth categories (there were 122 in this study). It is, therefore, unlikely that harbor porpoise occur in depths within these nonsignificant categories in different proportions than those available.

Mean seafloor slope for all sections combined was 9.85% (SE=0.656, n=584). Section B had the least slope and section C the greatest (Fig. 7). Harbor porpoise were sighted over a mean slope of 6.90% (SE=0.51, n=275, range: 0.37% to 45.75%). The greatest number of harbor porpoise sightings (79%) occurred over shallow slopes (<10%). There were significantly (P<0.05) greater numbers of harbor porpoise sightings than expected in category 0 to 2% slope, and significantly (P<0.05) fewer numbers of harbor porpoise than expected in categories 6 to 8%, 18 to 20%, and >26% slope (Fig. 8). The power to detect a difference was fairly high (69%) for categories that were not significantly different (Fig. 8). To increase power to 80%, we would need 151 samples within these ten categories (we had 126 samples).

Mean sea surface temperature (SST) recorded during all transects was 12.6°C (SE=0.081, n=427, range: 10.1° to 17.5°C). Little variability was found among the five sections. Section E had the greatest mean SST (mean=13.5°C, SE=0.22, n=69) and section B the least (mean=12.3°C, SE=0.14, n=97). Mean SST recorded during harbor porpoise sightings was 12.1°C (SE=0.09, n=267, range: 10.1° to 16.3°C). Harbor porpoise were sighted more frequently than expected (P<0.05) in water temperatures of 11° to 12°C and

less frequently than expected (P<0.05) in water temperatures >16° C (Fig. 9). The power to detect a difference was moderate (50%) for categories that were not significantly different (Fig. 9). To increase power to 80%, we would need 180 samples within these ten categories (we had 171 samples).

There was no significant difference between number of harbor porpoise observed per minute during flood and ebb tides (U=315.5, n=69, P=0.076, α=0.05). Bootstrap estimates (resampling statistics; 10,000 iterations) indicated an 86% chance of correctly rejecting the null hypothesis that mean number of sightings was equal between flood and ebb tides. Fifty samples in each tide stage (we sampled 52 in flood and 17 in ebb tide) were required to reject the null hypothesis at α = 0.05.

Mean Secchi reading for all harbor porpoise sightings was 9.3 m (SE=0.09, n=275, range: 5.7 to 11.9 m).

Greatest numbers of harbor porpoise were observed in mid-morning (1000 h) and afternoon (1400 to 1500 h) throughout the study area (Fig. 10). Fewer harbor porpoise were observed at midday (1100 to 1300 h; Fig. 10), although there was no significant difference (H=10.99, n=274, P=0.276) among mean number of harbor porpoise observed per minute and each hour of daylight surveyed (0900 to 1800 h).

Density estimates were calculated over all four months of the survey period rather than by month, which would have yielded too low of a sample size. If abundance estimates of porpoise had varied greatly among months during our survey period, we should have observed a higher CV (ours was relatively low: 0.159).

Fixed boat surveys

Fifty-six sightings of 92 harbor porpoise were recorded during 33 surveys (port or starboard) in 1991, and 69 sightings of 118 harbor porpoise during 24 surveys (both sides of vessel surveyed) in 1992 (Fig. 2). Harbor porpoise were sighted during 79% of surveys in 1991 and 75% in 1992. Mean group size was 1.6 harbor porpoise (SE=0.09, n=56) in 1991 and 1.7 harbor porpoise (SE=0.127, n=69) in 1992. Distribution of harbor porpoise was patchy but similar between 1991 and 1992 (Fig. 2).

The greatest number of harbor porpoise sightings recorded per survey were along transects 1, 2, and 5 in 1991 and transects 1 and 5 in 1992 (Table 2; Fig. 2). The least number of sightings were recorded for transects 3 and 6 in 1991 and 1992 (Table 2; Fig. 2). Mean number of harbor porpoise sightings per survey was not significantly different (P>0.05) between 1991 and 1992 for any of the fixed transects (Table 2). Sample sizes for all transects were low because of the limited survey period (July to August). Given our low sample size (Cohen, 1988, requires a sample size of eight or more), we were unable to determine power. If eight samples of each fixed transect line had been taken, power to detect a difference in density between 1991 and 1992 would still have been low (power<27% for all fixed transects except transect three which had<6% power).

Figure 5

Mean number of harbor porpoise (A) and mean water depth (B) of each section (A–E) determined during random boat surveys (June–October 1992). Vertical lines represent standard error and "n" represents number of transects completed in each section (A: total=73) and random depth locations plotted within each section (B); total=584).

Discussion

Population and density estimates of harbor porpoise were based on several assumptions of line transect theory. Relevant assumptions included the following: 1) study area was sampled randomly (transect lines placed randomly with respect to the distribution of objects) or animals were randomly distributed; 2) all animals on the trackline were detected; 3) group size was estimated without error; 4) locations were measured accurately for each individual or group; and 5) animals did not move in response to the survey vessel or were detected before they moved (Burnham et al., 1980).

The first assumption of line transect theory was met by employing a stratified random sampling design within the study area. This design was chosen so that the 8-km transects would adequately cover the entire study area. By using fixed length straight transects, however, certain areas of sections B and
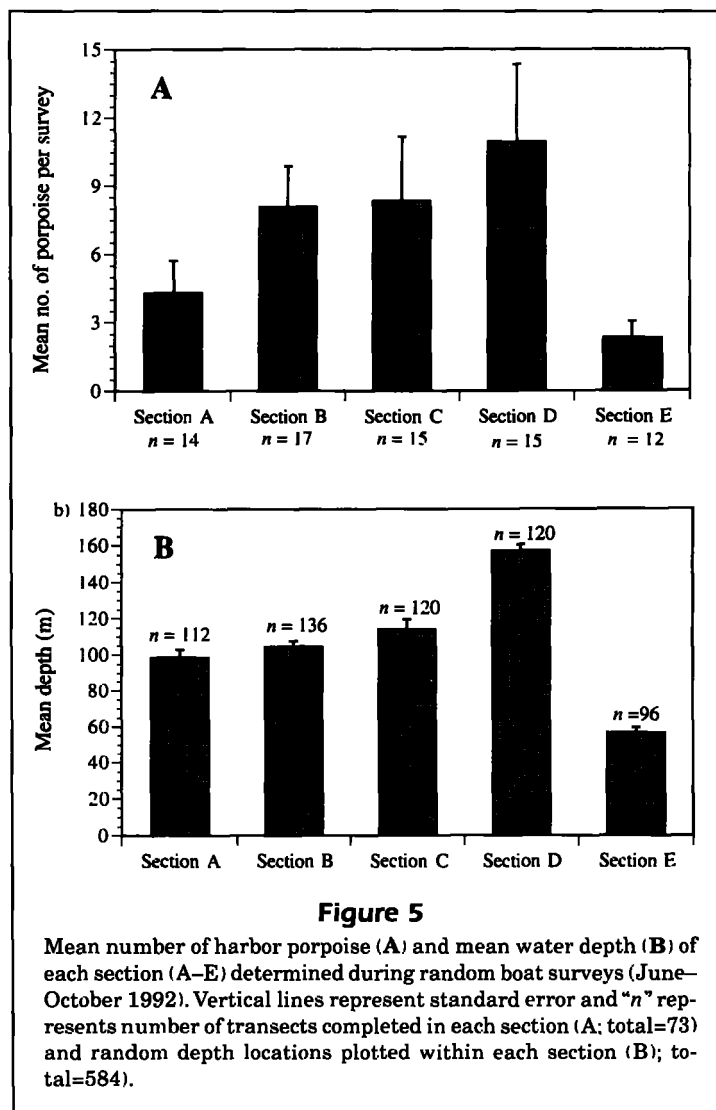
C were not adequately sampled. The habitat features of these areas were similar to the rest of the study area, and portions of section C not sampled during random surveys were sampled during fixed transect surveys 5 and 6. A study design that incorporated shorter transects (4 km) would allow more complete coverage of all areas within strata. If this study were replicated, we recommend incorporating 4-km transects to cover the areas that we missed. We do not believe, however, that our study design affected the results of the habitat correlates. By randomly surveying within a defined region off the northern San Juan Islands, we adequately sampled oceanographic features of interest (depth, seafloor slope, surface temperature, tides).

The assumption that all animals are detected on the trackline is often violated during marine mammal surveys. Animals with long durations of submer-

gence have a high probability of remaining undetected during the passage of an aircraft or vessel, resulting in availability bias (Marsh and Sinclair, 1989). Several studies (e.g. Marsh and Sinclair, 1989) of harbor porpoise have indicated, on the basis of perception bias, that the probability of detecting a harbor porpoise on the trackline, $g(0)$, is less than one (Barlow, 1988; Palka, 1993; Calambokidis[3]). Using an independent team of three observers,

Barlow (1988) reported an estimated 22% of harbor porpoise that surfaced on the trackline were missed by a team of five observers (perception bias) traveling on a vessel at 18.5 km/h. Using three observers per survey, Calambokidis[3] and Palka (1993) estimated the probability of observing a group of harbor porpoise on the trackline, $g(0)$, was less than 0.5. We assumed $g(0)$ was one during our study because we were unable to determine availability or perception bias. It is probable that some porpoise did avoid the vessel and might have been submerged for up to five minutes (Raum-Suryan, 1995). It is, therefore, likely that $g(0)$ is less than one and harbor porpoise abundance is underestimated.

The ability to estimate group size can vary by the number of animals within the group and by the species of interest. Data from land-based calibration studies off the Washington coast indicated that observers on ves-
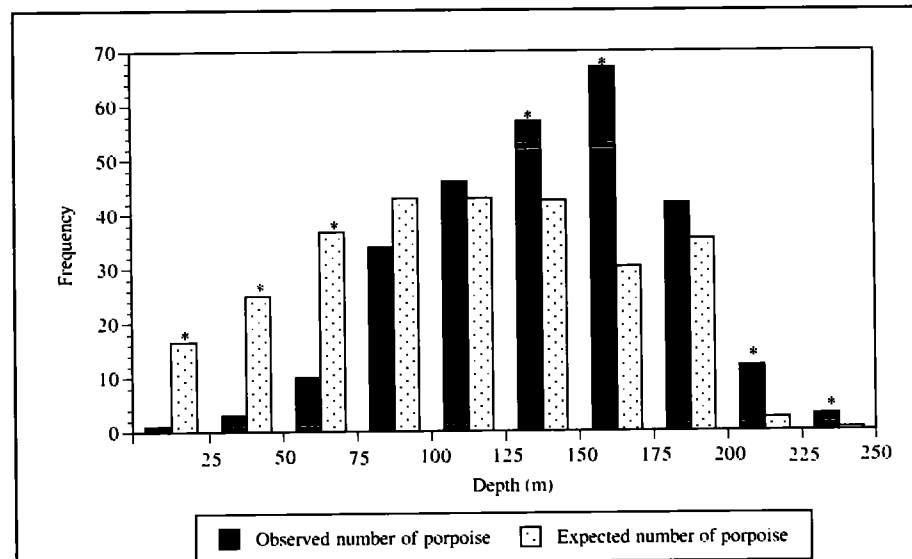

Figure 6

Depth distribution of 275 harbor porpoise sightings determined from random boat surveys (June to October 1992) in relation to expected distribution of harbor porpoise if they were distributed randomly with depth (as determined from depths at 584 random locations). An asterisk (*) designates a significant ($P<0.05$) difference determined with chi-square goodness-of-fit analyses.

[3] Calambokidis, J. 1991. Vessel surveys for harbor porpoise off the Washington coast. *In* H. Kajimura (ed.). Harbor porpoise interactions with Makah Salmon set net fishery in coastal Washington waters, 1988–89. National Marine Mammal Laboratory Processed Report, National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

Table 2

Mean, standard error (SE), number of sightings, and number of harbor porpoise determined during fixed boat surveys in 1991 and 1992. In 1992, the number of harbor porpoise observed (Obs.) are presented, as are values from four randomly chosen surveys used in analysis (Anal.), comparing mean number of harbor porpoise sighted along each transect in 1991 and 1992). n refers to the number of transect "sides" (bow out to 90° on port or starboard) surveyed.

| Transect no. | 1991 | | | | | 1992 | | | | | | | | | | | |
| | Mean | SE | n | No. of sightings | No. of porpoise | Mean | | SE | | n | | No. of sightings | | No. of porpoise | | Probability |
						Obs.	Anal.	Obs.	Anal.	Obs.	Anal.	Obs.	Anal.	Obs.	Anal.	
1	2.20	0.80	5	11	18	2.50	2.00	0.42	0.41	8	4	20	8	31	13	$P = 0.843$
2	1.83	0.48	6	11	16	1.25	1.25	0.45	0.63	8	4	10	5	22	17	$P = 0.474$
3	1.00	0.38	7	7	13	0.13	0.25	0.13	0.25	8	4	1	1	1	1	$P = 0.200$
5	2.83	0.54	6	17	29	2.25	3.00	0.49	0.58	8	4	18	12	25	18	$P = 0.844$
6	0.60	0.40	5	3	6	0.88	0.50	0.40	0.29	8	4	7	2	12	3	$P = 0.853$
7	1.75	0.63	4	7	10	1.50	1.00	0.82	0.41	8	4	12	9	26	19	$P = 0.356$

sels underestimated true group size of harbor porpoise, missing up to 60% or more of animals (Calambokidis et al.[4]). However, these results were based on a very small sample size and the survey vessel traveled at twice the speed of our vessel. In our study, mean group size (1.91 porpoise) was only 5% different from that detected from concurrent shore-based surveys (2.01 porpoise; Raum-Suryan, 1995). We are, therefore, confident that any biases in group size estimates are small.

Accurately measuring the locations of marine mammals from vessels can be affected by the height of observers above water (Polacheck and Smith, 1989) and the use of reticle and compass binoculars (Smith, 1982; Barlow and Lee, 1994). From a low height above the water, angles are greatly affected by small deviations in reticle estimates. As radial distances to harbor porpoise decrease, however, errors in reticle estimates (sighting angles) have progressively less effect on distance calculations. The majority (78%) of our radial and perpendicular sighting distances were less than 350 m. At 350 m an error of ±0.1 reticle was equal to 50 m (the range of our data groupings which best fitted the model). Therefore, although the platform height of our survey vessel was low (2.68 m), we were able to obtain accurate sighting data by conducting surveys only during optimal sighting conditions (Beaufort ≤1), and because there was both a lack of ocean swell and the majority of sightings were less than 350 m distant.

Harbor porpoise are small, inconspicuous animals that avoid boats (Amudin and Amudin, 1974; Gaskin, 1977; Prescott and Fiorelli, 1980; Barlow, 1988). Detection of harbor porpoise before they become aware of the survey vessel is often difficult without prior knowledge of their locations. Polacheck and Thorpe (1990) observed harbor porpoise swimming away from their survey vessel a significant
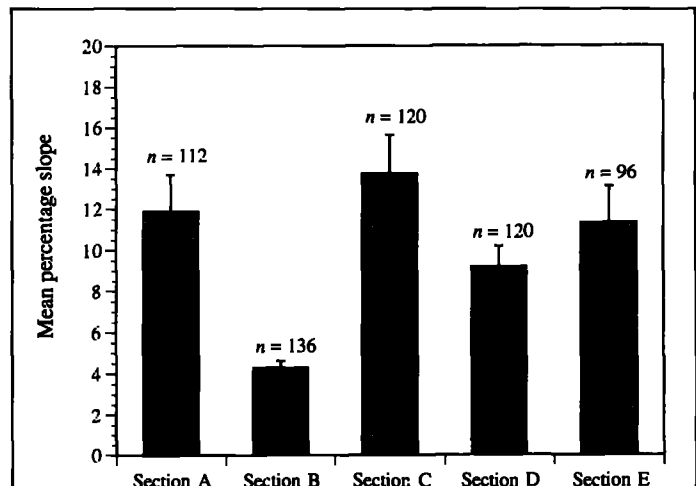

Figure 7

Mean percentage slope of seafloor for each section (A– E) determined from random boat surveys. Vertical lines represent standard error and "*n*" represents the number of random slope locations plotted within each section (total=584).
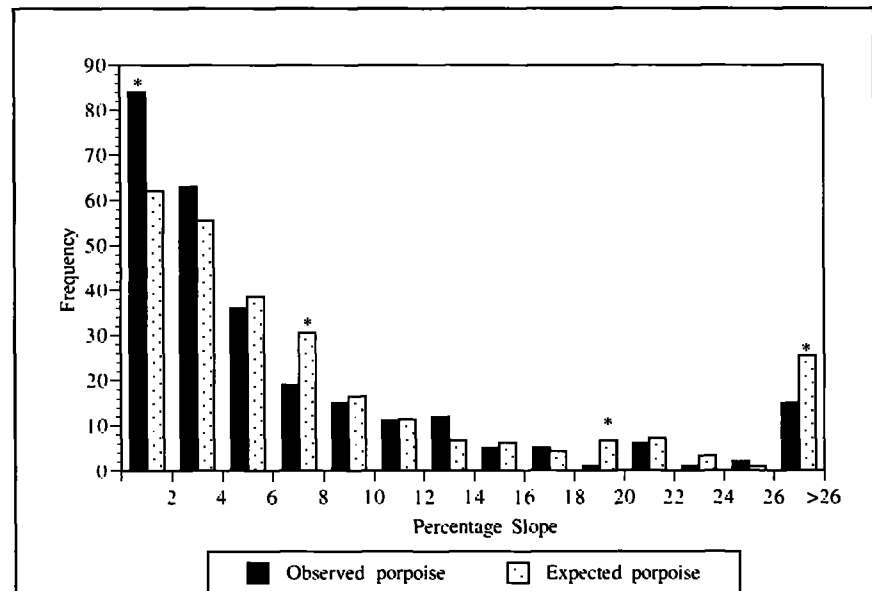

Figure 8

Harbor porpoise sightings (*n*=275) from random boat surveys (June–October 1992) in relation to expected distribution if porpoise were distributed randomly with slope (as determined from slopes at 584 random locations). An asterisk (*) designates a significant (*P*<0.05) difference, determined with chi-square goodness-of-fit analyses.

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[4] Calambokidis, J., S. R. Melin, and D. J. Rugh. 1991. Land-based calibrations of harbor porpoise sightings from a vessel along the northern Washington coast. *In* H. Kajimura (ed.), Harbor porpoise interactions with Makah Salmon set net fishery in coastal Washington waters, 1988–89. National Marine Mammal Laboratory Processed Report. National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

proportion of time. Barlow (1988) reported that harbor porpoise quickly avoid a closely approaching survey vessel. Vessel avoidance by harbor porpoise may result in animals remaining undetected by observ-
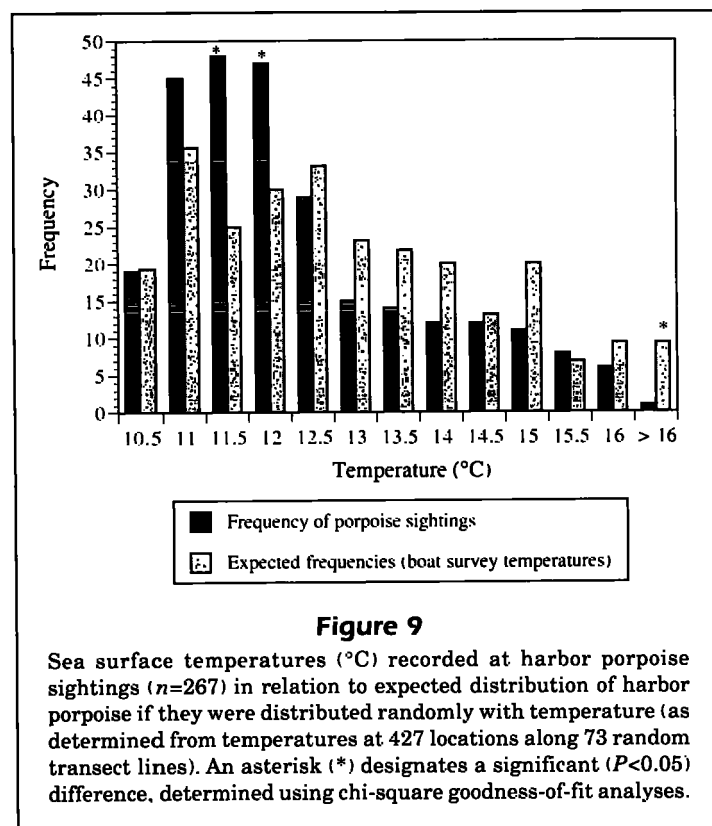
Figure 9

Sea surface temperatures (°C) recorded at harbor porpoise sightings (n=267) in relation to expected distribution of harbor porpoise if they were distributed randomly with temperature (as determined from temperatures at 427 locations along 73 random transect lines). An asterisk (*) designates a significant (P<0.05) difference, determined using chi-square goodness-of-fit analyses.
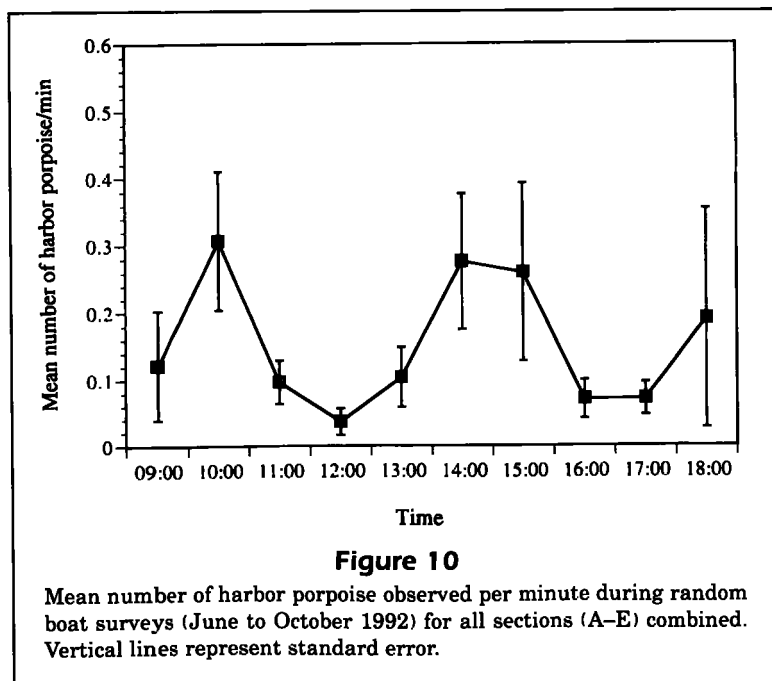
Figure 10

Mean number of harbor porpoise observed per minute during random boat surveys (June to October 1992) for all sections (A–E) combined. Vertical lines represent standard error.

ers or may affect estimates of perpendicular distance of harbor porpoise from the vessel. If the frequency of harbor porpoise sightings were greatest near the trackline and decreased with increasing perpendicular distance during this study, it appeared that most harbor porpoise were detected before potentially significant vessel avoidance occurred. If porpoise did avoid the vessel, our abundance estimates would be underestimated. Ship avoidance was likely constant throughout the survey period, however, and would not have affected results of habitat correlates.

Density estimates of harbor porpoise (1.26 porpoise/km^2) within the study area (237 km^2) were greater than densities reported by Calambokidis et al.[2] (0.42 porpoise/km^2) for waters off the San Juan Islands and part of the Strait of Georgia (2291 km^2) but were similar to density estimates of Flaherty and Stark[1] (0.85 to 1.63 porpoise/km^2) for the north and west San Juan Islands (1005 km^2). Density estimates reported by Calambokidis et al.[2] were based on an initial $g(0)$ equal to 0.324 (CV= 0.171) multiplied by a correction factor of 3.1 and yielding a $g(0)$ of one. Green et al.[5] surveyed an extensive area within the 100-m isobath off the coast of Oregon and Washington and also reported a much lower density of harbor porpoise (0.17 porpoise/km^2) than reported here. These differences probably result from Green et al.[5] and Calambokidis et al.[2] including regions of high and low harbor porpoise abundance in contrast to our focus on high density areas off the northern San Juan Islands.

Prey or habitat requirements often limit distribution of cetaceans to regions that may vary daily, seasonally, or yearly, depending on an individual's foraging, mating, or behavioral requirements. During this study, surveys were conducted only within the summer months (June to October) and thus may account for the relatively high density estimates of harbor porpoise within our study area. Flaherty and Stark[1] sighted harbor porpoise during all months of the year off the San Juan

[5] Green, G. A., J. J. Brueggeman, C. E. Bowlby, R. A. Grotefendt, M. L. Bonnell, and K. T. Balcomb III. 1992. Cetacean distribution and abundance off Oregon and Washington, 1989–1990. In J. J. Brueggeman (ed.), Final report prepared by Ebasco Environmental and Ecological Consulting, Inc. for Minerals Management Service, Pacific OCS Region. Offshore Continental Shelf (OCS) Study MMS 91-0093, 100 p.

Islands but observed more harbor porpoise in summer months (June to August) than other times of the year. Surveys of harbor porpoise throughout the year along the east and west coasts of the United States have indicated a seasonal pattern among various regions (Neave and Wright, 1968; Gaskin and Watson, 1985; Barlow, 1988; Green et al.[5]). Results of fixed transect surveys conducted in our study indicated no change in distributions of harbor porpoise between July and August 1991 and 1992. Clumped distribution of harbor porpoise along tracklines was likely associated with habitat features (harbor porpoise were sighted most often over deep water).

Among island regions, such as the Bay of Fundy, Glacier Bay, Alaska (Taylor and Dawson, 1984), and off the San Juan Islands, harbor porpoise are more often associated with deeper waters than along coastal regions of North America. Most harbor porpoise observed off the coast of California, Oregon, and Washington occurred at shallow water depths, and sightings decreased with increasing depth (Barlow, 1988; Dorfman, 1990; Calambokidis[3]; LaBarr and Ainley[6]). Incidental net entanglement of harbor porpoise within Washington waters occurred at the bottom of nets, at depths of 73 to 81 m (Scheffer and Slipp, 1948), and near the bottom or in the lower one-half of nets set from 11 to 18 m deep, indicating porpoise were foraging along the bottom or in deeper areas of the net (Gearin et al.[7]). The depth of water where harbor porpoise were sighted in this study may have been due to occurrence of prey within these areas.

The Pacific herring (*Clupea pallasi*) population in the Strait of Georgia is the largest known in Washington state, and herring are quite abundant in sections of the eastern Strait during summer, fall, and winter (Lemberg, 1978). During this study, harbor porpoise, harbor seals, and a minke whale were observed feeding on a school of Pacific herring. The dominant prey items in stomachs of harbor porpoise taken in a setnet fishery in summer off northern Washington were Pacific herring, market squid (*Loligo opalescens*), gadids, and osmerids (Gearin and Johnson[8]). Pacific herring and market squid migrate vertically within the water column, remaining close to the seafloor during

the day, and approach the surface at night (Hart, 1973; Blaxter, 1985; Flaherty and Stark[1]). Characteristics of these prey items and the greater occurrence of porpoise over deep waters may indicate that harbor porpoise feed in deep water during the day. Aggregations of surface schooling fish and associated harbor porpoise were rarely (1% of surveys) observed within our study area, further indicating that harbor porpoise were likely feeding on prey in deep water.

In our study, harbor porpoise were sighted most often in shallow sloping areas with little bathymetric relief. These results contrast with those of Flaherty and Stark,[1] in which 70% of harbor porpoise sighted were found in areas with seafloor relief greater than 40%, and with those of Calambokidis,[3] who observed significantly more harbor porpoise than expected within areas of uneven bottom topography off the outer Washington coast. It is likely that slope of the seafloor does not significantly affect the distribution of harbor porpoise or their prey in our study area. We believe that harbor porpoise and their prey are associated with deeper waters in this region which, in general, has shallow slopes.

Water temperature may influence the distribution of harbor porpoise. Calambokidis[3] reported harbor porpoise sightings in water temperatures ranging from 9° to 16°C off Washington. In the Bay of Fundy, Watts and Gaskin (1985) found a negative correlation between harbor porpoise abundance and mean August SST, and Watson (1981) reported that harbor porpoise occurred in water temperatures less than 15°C in the Bay of Fundy. It is unlikely, however, that SST alone would influence harbor porpoise distribution. Most harbor porpoise entered Fish Harbor, New Brunswick, Canada, when SST was between 9° and 10°C, a period when large numbers of juvenile herring were also entering the region (Gaskin and Watson, 1985). Within the Bay of Fundy, Watts and Gaskin (1985) found herring associated with vertically mixed waters and reduced surface temperatures. This association was possibly due to increased concentrations of zooplankton, which also occurred along convergent zones (Watts and Gaskin 1985). Sea surface temperatures off the northern San Juan Islands, therefore, were possibly related to tidal currents that may be associated with concentrations of harbor porpoise prey.

[6] LaBarr, M. S., and D. G. Ainley. 1985. Depth distribution of harbor porpoise off central California: a report of cruises in April and May–June 1985. NMFS Contract No. 41 USC 252, 23 p.

[7] Gearin, P. J., M. A. Johnson, and S. Joner. 1991. Harbor porpoise interactions with the Makah Chinook Salmon Set-Net Fishery, 1988–89. *In* H. Kajimura (ed.), Harbor porpoise interactions with Makah salmon set net fishery in coastal Washington waters, 1988–89. National Marine Mammal Laboratory Processed Report. National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

[8] Gearin, P. J., and M. A. Johnson. 1991. Prey identified from stomachs of harbor porpoise and Chinook salmon from the 1988–89 Makah Salmon Set-Net Fishery. *In* H. Kajimura (ed.), Harbor porpoise interactions with Makah Salmon set net fishery in coastal Washington waters, 1988–89. National Marine Mammal Laboratory Processed Report. National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

In this study, SST was measured along tracklines and may not have represented water temperatures where harbor porpoise were sighted. Tide rips mixing water, or currents moving through the study area could have altered water temperatures by a few degrees between trackline and harbor porpoise locations. Sea surface temperature varied by 5°C from beginning to end of the 8-km tracklines. We assumed, however, less bias was introduced by collecting SST along the trackline than by continuously going off transect and potentially disturbing harbor porpoise ahead of the vessel. Because our methods were consistent over the study period, the comparison in use versus availability of SST is likely representative.

It is doubtful that time of day had a significant effect on the ability to sight harbor porpoise in our study; therefore, other environmental factors must have affected harbor porpoise distribution in relation to time of day. Occurrence of harbor porpoise appears closely associated with the strength of tidal currents. From shore-based surveys within our study area (Raum-Suryan, 1995), mean number of porpoise observed per minute was greatest two hours before each peak in the maximum flood tide, and significantly more ($P<0.05$) porpoise were observed per minute during flood than ebb tides. From June to October 1992, the majority of low tides in the northern San Juan Islands occurred in the early morning hours. The relation between the occurrence of harbor porpoise with tide and time of day indicates that porpoise movements may have been associated with concentrations of prey in flood currents and tide rips. It is possible that harbor porpoise range throughout Washington Sound but continue to return to northern San Juan Island waters as a primary foraging area.

We found a large proportion of the harbor porpoise population of Washington Sound located within our study area. Calambokidis et al.[2] estimated the population size of harbor porpoise for the San Juan Islands (2291 km²) at 960 animals (corrected as in density estimate). In approximately 10% (237 km²) of the area that Calambokidis et al.[2] surveyed, we estimated 30% (299 porpoise) of the harbor porpoise population. Given that our $g(0)$ was assumed to be one (thus underestimating the population size), the proportion of harbor porpoise within our study area is likely greater than 30% of the total population within the San Juan Island region. On the basis of pollutants detected in harbor porpoise tissues, porpoise along the west coast do not mix freely between California, Oregon, and Washington (Calambokidis and Barlow, 1991). In addition, Washington and California are considered repositories of genetic diver-

sity for harbor porpoise of the Northeast Pacific (Rosel et al., 1995) and also indicate that harbor porpoise ranges may be restricted. In addition to aerial surveys conducted over Washington waters (Calambokidis et al.[2]), our study area appears to be an important site for monitoring trends in distribution and abundance of harbor porpoise in inland water of Washington.

It is not clear why harbor porpoise are not as abundant in other areas of Washington Sound as they are in our study area. The relatively low abundance outside our study area may be due to factors other than food availability, such as pollution, fishing pressure, increased boat traffic, or other environmental changes. We believe that harbor porpoise are more abundant in our study area than in other parts of Washington Sound because certain environmental conditions (deep, cool water, and strong tidal mixing) influence the distribution of harbor porpoise prey. Future monitoring studies on oceanographic conditions and prey availability associated with harbor porpoise sightings would greatly assist in determining mechanisms affecting harbor porpoise abundance and distribution in this and other areas and help in managing this genetically important stock.

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