MARINE MAMMAL SCIENCE, 21(3):429–445 (July 2005)

ESTIMATES OF SPERM WHALE ABUNDANCE IN THE NORTHEASTERN TEMPERATE PACIFIC FROM A COMBINED ACOUSTIC AND VISUAL SURVEY

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ABSTRACT

We estimate the abundance of sperm whales in a 7.8 million km^2 study area in the eastern temperate North Pacific using data from a ship-based acoustic and visual line-transect survey in spring 1997. Sperm whales were detected acoustically using a hydrophone array towed at 15 km/h and 100 m depth. The hydrophone array was towed for 14,500 km, and locations were estimated acoustically for 45 distinct sperm whale groups. Whales producing slow clicks (>2-s period) were detected at greater distance (up to 37 km), and the estimation of effective strip widths was stratified based on initial click period. Visual survey effort (using 25× binoculars and naked eyes) covered 8,100 km in Beaufort sea states 0–5 and resulted in only eight sightings. The effective strip width for visual detections was estimated from previous surveys conducted using the same methods and similar vessels in the eastern Pacific. Estimated sperm whale abundance in the study area was not significantly different between acoustic (32,100, CV = 0.36) and visual (26,300, CV = 0.81) detection methods. Acoustic techniques substantially increased the number of sperm whales detected on this line-transect survey by increasing the range of detection and allowing nighttime surveys; however, visual observations were necessary for estimating group size.

Key words: acoustic survey, visual survey, hydrophone array, line-transect, abundance, density, sperm whale, North Pacific, *Physeter macrocephalus*.

Most previous ship surveys of cetacean abundance have relied on line-transect methods (Buckland *et al.* 2001) using visual searching (Holt 1987, Buckland *et al.* 1992, Wade and Gerrodette 1993, Barlow 1995, Schweder *et al.* 1996). Many have suggested that passive acoustic surveys offer potential advantages over visual methods in detecting submerged animals, extending search distances, and allowing nighttime surveys (Gordon and Steiner 1992, Leaper *et al.* 1992). Despite recent advances in acoustic survey methods, few acoustic surveys have actually produced estimates of whale abundance.

Of all cetaceans, sperm whales (*Physeter macrocephalus*) are most amenable to acoustic detection and survey methods. Sperm whale sounds have been classified as "usual" clicks (0.4–1.0-s period), slow clicks (5–8-s period), codas (patterned clicks), and creaks (a series of very rapid clicks) (Weilgart and Whitehead 1988). The usual clicks are relatively loud (180–223 dB re: 1 μP @ 1 m) (Watkins 1980, Møhl *et al.* 2000), and previous studies have shown these sounds to be detectable at 10–16 km under optimal conditions (Watkins 1980, Madsen *et al.* 2002). The slow clicks are thought to be produced only by males (Weilgart and Whitehead 1988) and are predicted to propagate up to 60 km (Madsen *et al.* 2002). Codas and creaks, which are of lesser amplitude, are not detectable far from their source. The frequency distribution of clicks (<100 Hz to 30 kHz, Watkins 1980) extends above the dominant range of ship and flow noise, making these sounds easier to detect with a towed array system than the lower frequency sounds of baleen whales. Sperm whale clicks have a rapid rise time (<1 ms) which improves the precision of localization methods based on time-of-arrival difference between two hydrophones. A significant fraction of sperm whales are unavailable to visual observers (Kasamatsu and Joyce 1995, Barlow and Sexton 1996) because they can dive for an hour or more (Leatherwood *et al.* 1982); therefore, acoustic surveys are potentially more valuable for sperm whales than for many other species.

Our survey was designed primarily to estimate the breeding-season abundance of sperm whales in the eastern temperate North Pacific (between 20°N and 45°N) and to collect biopsy samples for genetic analysis of sperm whale population structure within this area. This study area was chosen because the majority of North Pacific sperm whales were predicted to be south of 40°N (Berzin 1971, Rice 1974) and in this area during their breeding season. Preliminary genetic analyses show some evidence of population structure within the North Pacific (Mesnick *et al.* 1999). Abundance estimates presented in this report apply to a specific geographic area and season and should not be interpreted to represent a discrete biological population.

Methods

Line-transect methods were followed with independent visual and acoustic teams on the 53-m National Oceanographic and Atmospheric Administration (NOAA) research vessel *McArthur* from 9 March to 8 June 1997. Transect lines were established prior to the survey to uniformly cover the defined study area, both spatially and seasonally. When sperm whales were detected by one team, the survey design called for turning the vessel only after the other team had been given an opportunity to detect them (*i.e.*, after they had passed abeam).

Visual Survey Methods

The standard Southwest Fisheries Science Center (SWFSC) protocol was used for visual surveys (Holt 1987, Wade and Gerrodette 1993, Barlow 1995). Two visual observers searched during daylight hours using port and starboard pedestal-mounted 25× binoculars on the flying bridge deck (10 m above sea level at eye level). A third visual observer recorded data and searched with unaided eyes and (occasionally) a hand-held 7× binocular. Observers maintained 40-min consecutive watches in each of these three observer positions and then rested for 2 h before their next watch. Variables related to survey effort (observer positions, Beaufort sea state, weather conditions, course, and speed) were recorded at the start of every watch and

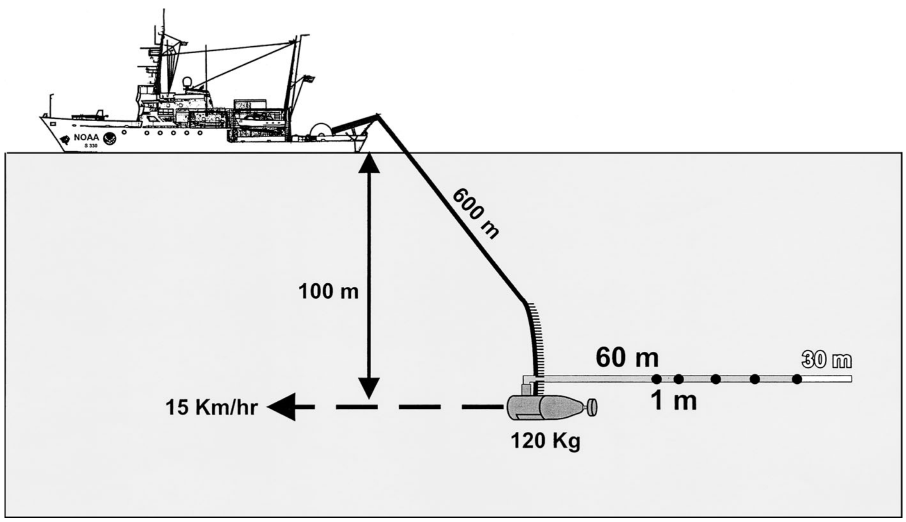

Figure 1. Diagram showing the tow cable, depressor weight, and horizontal hydrophone array used for the acoustic survey (not to scale). The lower 30 m of the tow cable was fared to reduce drag and cable strum. A nylon rope was used to stabilize the last 30 m at the tail of the array.

were updated whenever conditions changed. When marine mammals were seen, observers recorded their bearing relative to the bow (using a calibrated collar on the base of the 25× binoculars) and their distance from the ship (using reticles in the oculars of the 25× and 7× binoculars) (Kinzey and Gerrodette 2001).

Group size was estimated visually by up to six observers. Although a few groups were observed rafting at the surface and could be easily counted, most groups were comprised of asynchronously diving clusters (subgroups of 2–10 whales in close proximity to one another). Clusters were often spread over several square kilometers. Estimation of total group size was difficult because these diving groups were never simultaneously at the surface together. Groups were typically observed for 90 min prior to making group size estimates. During this time, at least five observers maintained a 360° watch around the ship. When a cluster surfaced, an observer would give location and number of individuals within clusters to a central recorder who plotted the data in real time on a computer. All observers had access to this information, which formed the basis for their independent "best," "high," and "low" estimates of the number of whales present, and independent "best" estimates by each observer were averaged.

Acoustic Survey Methods

For acoustic surveys, technicians listened to sounds received from a towed hydrophone array while they visually monitored the spectrogram and waveform of these sounds on a computer display. The hydrophone array consisted of a 60-m, 5-element, solid array (made by Innovative Transducers, Inc.[1]) that was attached to a 120-kg depressor weight (Fig. 1). Hydrophone elements were located 30 m, 31

[1] Use of trade names is not an endorsement by the U.S. National Marine Fisheries Service.

m, 33 m, 37 m, and 45 m from the depressor weight. A 30-m nylon rope (1.9 cm diameter) was attached to the tail of the array to stabilize it. Inside the depressor weight, an electronics package (from GeoAcoustics, Inc.[1]) digitized two of the five signals (16 bit resolution at 32,000 samples/s each) and transmitted them to the ship *via* a thin (1.1 cm) coax tow cable. The digitized signals were transmitted from the cable on the winch drum to a deck cable *via* slip rings. The thin cable system allowed greater tow depth and speed by reducing drag. Experiments using a time/depth recorder (TDR) demonstrated that by deploying 600 m of tow cable at a tow speed of 15 km/h, the array could be maintained at our standard tow depth of 100 m. The array was towed approximately 22 h per day and was typically retrieved only when the vessel stopped for its daily oceanographic station (~0400–0600), when the vessel was stopped for dive time, biopsy, and other studies of sperm whales, or when swell height was greater than 4 m. During retrieval, the hydrophone array was detached from the depressor weight and was reeled onto a separate drum.

The acoustic technician could choose two of the five hydrophone elements to monitor. We used hydrophone spacings of 3–7 m, which were sufficient to obtain good angular resolution, but not so great as to create ambiguity between clicks from different whales (Leaper *et al.* 1992). The digital signals were converted back into analog signals on the ship. These stereo analog signals were amplified, passed through a 1 kHz high-pass filter, and routed to the input of a Data Translation[1] DT-3809 digital signal processing (DSP) board in a Pentium[1]-based computer. Spectral analysis of one channel was performed on the DSP board and the results were passed, along with the wave-form data, to the Pentium processor running custom software which displayed a scrolling spectrum (0–10 kHz, oversampled at 40,000 samples/s). When the signal amplitude in a user-specified window exceeded a critical level (set by the operator), software on the Pentium processor would be triggered to display the stereo waveforms, to calculate the time delay between the two peaks in each waveform, and to calculate and display a temporal cross-correlation between the waveforms. Bearing angles to sperm whale clicks were estimated using two time-of-arrival methods (peak matching and cross-correlation).

Each of four technicians monitored signals for three consecutive hours, with 9-h rests between watches. The acoustic monitoring station was located in the plot room behind the pilot house and was isolated from the bridge officers and the visual observers. The acoustic technician listened to the 1 kHz high-pass filtered sounds from one hydrophone with one ear (to emphasize sperm whale clicks) and the unfiltered sounds from the other hydrophone with the other ear (to emphasize humpback whale songs and other lower-frequency sounds). When a sperm whale click was heard with appropriate spectral and waveform characteristics, the operator signaled the computer to plot bearing angles estimated by one of two methods (typically cross-correlation produced more stable estimates than peak-matching). Bearing angles and vessel tracks were plotted on a separate computer display. As the vessel continued along its course, multiple bearing lines converged at the whale's estimated location (Fig. 2). During daylight hours, small turns (5°–10°) were initiated to resolve the left-right ambiguity in whale location, and the ship was directed to that location to obtain visual estimates of group size.

Digital audio (DAT) recordings were kept for most acoustic detections of sperm whales. These stereo recordings allowed additional bearing angles to be determined after the cruise to augment those estimated in "real time" during the cruise. Plots of

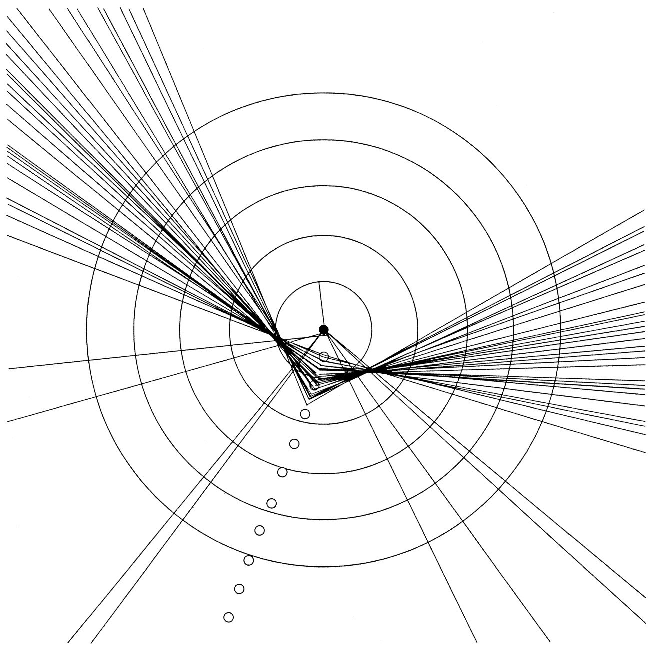

Figure 2. Ships track (small open circles) and bearing lines to an acoustically located sperm whale. Small filled circle represents the final ship's location. Concentric circles are 1.85 km (1 nmi) apart and are used to indicate scale. The likely locations of the sperm whale are at the convergence of the majority of bearing lines. In this example, insufficient bearing lines were measured after the ship changed course to eliminate the left/right ambiguity in the whale's location.

bearing lines and ship's tracks (Fig. 2) were made after the cruise for all sperm whale detections. Tapes were replayed and additional bearing lines were added to the plots for 23 detections. Estimated locations of sperm whale groups were plotted by hand at the approximate center of the group of intersecting lines, and perpendicular distances from the trackline to these estimated positions were measured on these plots.

Our bearings represent conical bearing angles, and perpendicular distance estimated by these methods is the distance in three dimensions from the path traced by the towed array. Line-transect methods are based on two-dimensional distances from the trackline, measured at the surface. From the perspective of estimating line-transect density, acoustic perpendicular distances are biased and would be greater than the perpendicular distance at the surface unless the sperm whales were vocalizing at the exact depth of the array. Because sperm whales dive to great depths, this bias may not be trivial. Unfortunately, the bias cannot be corrected without knowing the depth of the vocalizing animals. We explored the likely magnitude of this bias by assuming that vocalizing sperm whales were at 600 m depth (slightly greater than the mean dive depth of 500 m reported by Whitehead (2003) and 500 m below the depth of the array) and by using the Pythagorean formula to estimate perpendicular distance at the surface from the acoustically estimated perpendicular distance.

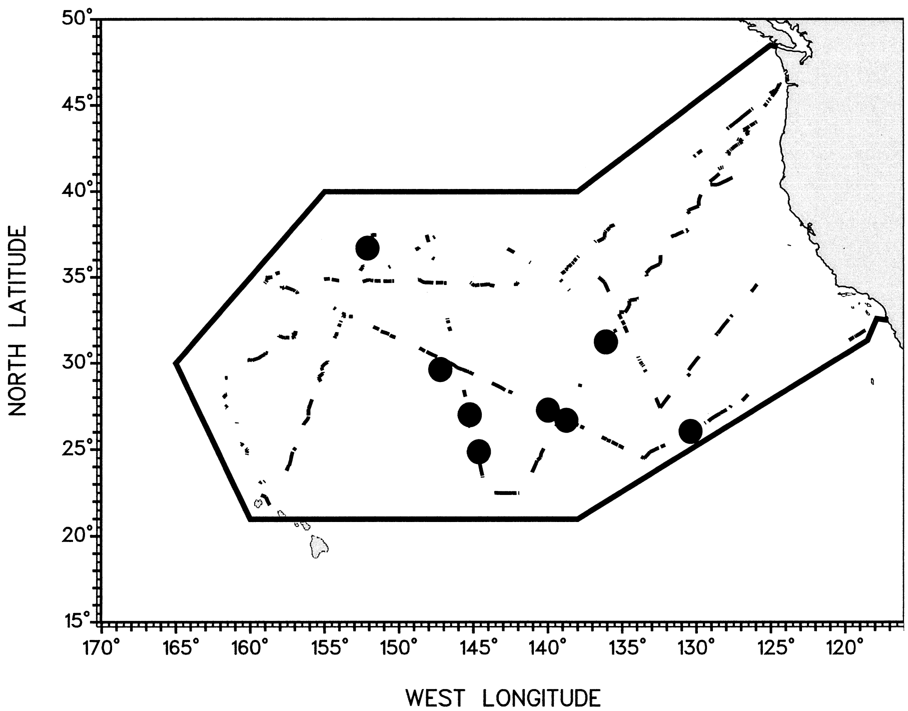

Figure 3. Visual survey effort (fine dark lines) and locations of visually detected sperm whales (closed circles) during acceptable sea state conditions (Beaufort 0–5). Bold line indicates the margin of the defined study area.

Analytical Methods

Line-transect methods (Buckland *et al.* 2001) were applied separately to the visual and acoustic survey data. Abundance (N) within the study area (A) was estimated as

$$N = \frac{A \cdot n \cdot E(S) \cdot f(0)}{2 \cdot L \cdot g(0)} \tag{1}$$

where n = number of visual or acoustic detections, $E(S)$ = expected group size, $f(0)$ = sighting probability density at zero perpendicular distance, $g(0)$ = probability of detecting a sperm whale on the transect line, and L = length of transect surveyed. The defined study area (Fig. 3) covers 7,786,000 km^2. The mean size for each group that was seen was estimated as the average of the observers' independent "best" estimates of the number present. The expected group size was estimated as a simple arithmetic mean of the groups that were visually detected before turning towards them (for visual line-transect estimates) or as the mean of the groups that were acoustically detected in daylight hours (for acoustic line-transect estimates). Sightings (n) and effort (L) were based only on "acceptable" conditions (sea states less than or equal to Beaufort 5 for visual surveys; sea states less than or equal to Beaufort 6 and swell heights less than or equal to 4 m for acoustic surveys). $f(0)$ was estimated by fitting a function to the observed distribution of perpendicular detection distances using the Hazard rate and half-normal key functions in the program DISTANCE (Laake *et al.* 1994), and the best model was selected using AIC. For visual surveys, there were insufficient sightings to estimate $f(0)$ directly from this survey, so it was estimated based on 281 sightings of sperm whales from previous surveys in the eastern North Pacific using the same survey methods on the same ship or a very similar ship (the NOAA research vessel *David Starr Jordan*) (Wade and Gerrodette 1993, Barlow 1995). These data were truncated at a perpendicular sighting distance of 7 km to improve the fit of a detection function (Buckland *et al.* 2001). The low number of visual detections did not allow a direct approach to estimating $g(0)$. We assume that $g(0) = 1.0$ for acoustic surveys (but see Discussion), and we use the Barlow and Sexton (1996) estimate of $g(0) = 0.87$ (CV $= 0.09$) for visual surveys. The latter estimate is based on synchronously diving whales with a 30-min dive cycle (25-min dives followed by 5 min at the surface).

To investigate potential biases, two stratification methods were investigated. Because visual detection distances are affected by Beaufort sea state and because sea states during this survey were rougher on average than during previous surveys that were used for estimating $f(0)$, analyses were also completed separately using four sea state strata (Beaufort 0–2, 3, 4, and 5). Overall population size from visual detections was estimated as an average of the Beaufort-stratified estimates, weighted by the inverse of their variances. Because acoustic detection distances appeared to be strongly affected by the initial click rate (click rate when first heard), acoustic abundance was estimated separately for groups with initial click periods of greater than or less than 2 s. These two strata can be considered to be exclusive; overall population size from acoustic detections was estimated as the sum of the two strata and variances were assumed to be additive.

Results

Visual Survey

Visual survey effort in acceptable survey conditions (Beaufort 0–5) covered 8,080 km (Fig. 3) and resulted in only eight on-effort sightings of sperm whales. Distributions of perpendicular sighting distances are available for 316 sperm whale sightings from previous surveys in the eastern Pacific. The truncation distance of 7 km eliminated the most distant 12% of sightings. Effective strip width was estimated for the remaining 281 sightings pooled and stratified by sea state. In each case, the program DISTANCE (Laake *et al.* 1994) chose the half-normal model as giving the best fit to the pooled and stratified data. Effective strip widths ($1/f(0)$) ranged from 4.6 km at Beaufort 0–2 to 3.6 km at Beaufort 5 (Table 1); the unstratified estimate was 4.3 km. The prior surveys on which these estimates were based showed an almost uniform distribution of search efforts in each of these four sea state categories, whereas current search effort was predominately in Beaufort 4 and 5 (Table 1). The geographic distribution of search effort within sea state categories was relatively uniform (Fig. 4). From a practical perspective, there is little difference between the unstratified estimate of abundance and the weighted average of the stratified estimates, but the unstratified estimate may be biased because it is based on surveys with a different distribution of sea state during search effort. For the current survey, the 7-km truncation distance eliminated two of the eight sightings. The average group size of the remaining six sightings was 30.9 sperm whales (Table 1). We will refer to the stratified estimates of density

Table 1. Estimates of sperm whale abundance in the 7.8 million km^2 study area (Fig. 3) for visual and acoustic survey methods. Detections outside the truncation distances (7 km for visual detections, 18.5 km for acoustic detections of usual clicks, and 37 km for acoustic detection of slow clicks) were excluded. Averages of stratified abundance and density estimates for visual surveys are weighted by the distances surveyed in each sea state.

	Number sightings n	Expected group size E(S)	Distance surveyed L (km)	Effective strip width $1/f(0)$ (km)	Trackline detection probability $g(0)$	Density (#/1,000 km^2)	Abundance	CV abundance
Visual surveys								
Beaufort 0–2	0	0	668	4.63	0.87	0.00	0	1.00
Beaufort 3	2	34.8	1,309	4.04	0.87	7.56	58,891	0.71
Beaufort 4	1	53.8	2,866	4.14	0.87	2.61	20,308	1.00
Beaufort 5	3	20.6	3,265	3.56	0.87	3.06	23,859	0.81
Stratified weighted average						3.38	26,292	0.81
Unstratified	6	30.9	8,107	4.32	0.87	3.04	23,668	0.49
Acoustic surveys								
Click period <2 s	17	23.4	14,500	4.52	1.00	2.86	22,236	0.43
Click period >2 s	18	39.8	14,500	19.56	1.00	1.26	9,832	0.67
Stratified sum							32,068	0.36
Unstratified	35	28.1	14,500	7.99	1.00	4.25	33,060	0.40

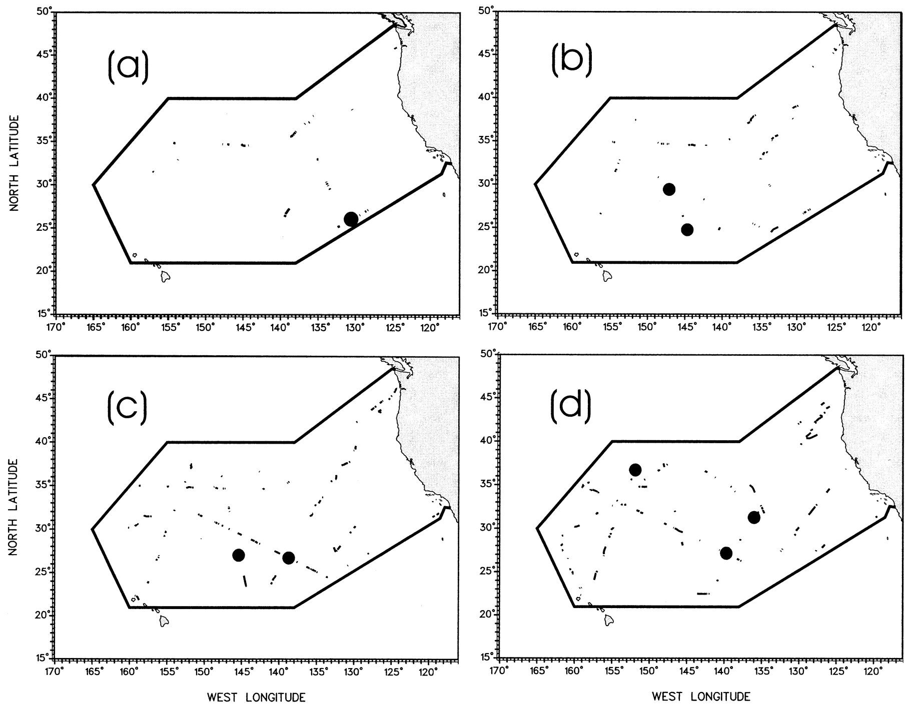

Figure 4. Geographic distribution of visual survey effort (fine dark lines) and locations of visually detected sperm whales (closed circles) during sea state conditions: (a) Beaufort 0–2, (b) Beaufort 3, (c) Beaufort 4, and (d) Beaufort 5. Bold line indicates the margin of the defined study area.

(3.38 per 1,000 km^2) and abundance (26,300) in the remainder of this paper (Table 1). Ideally, the fraction of animals missed on the transect line, $g(0)$, (Barlow and Sexton 1996) should also be stratified by sea state, but available data are insufficient to make stratified estimates of this parameter.

Acoustic Survey

Acoustic surveys in acceptable conditions covered 14,500 km. Approximately half of the first leg (San Francisco to Hawaii) was lost due to storms and equipment malfunctions. Several other shorter segments of search effort were lost due to very poor weather or abnormally high noise levels. The resulting effort did, however, cover the majority of the study area, and sperm whale groups were detected at 60 distinct locations (Fig. 5). Locations relative to the trackline could be determined (from converging bearing lines) for 45 of these detections.

Initial click periods showed a bimodal pattern, with usual clicks showing a sharp peak at 0.5–1.0 s and slow clicks showing a broad mode from 2.5–9.0 s (Fig. 6). During the survey, it was noted that slow clicks were often detected at much greater range than the usual sperm whale clicks. Typically only one individual in a group would be making slow clicks, and, when approaching a slow clicking individual,

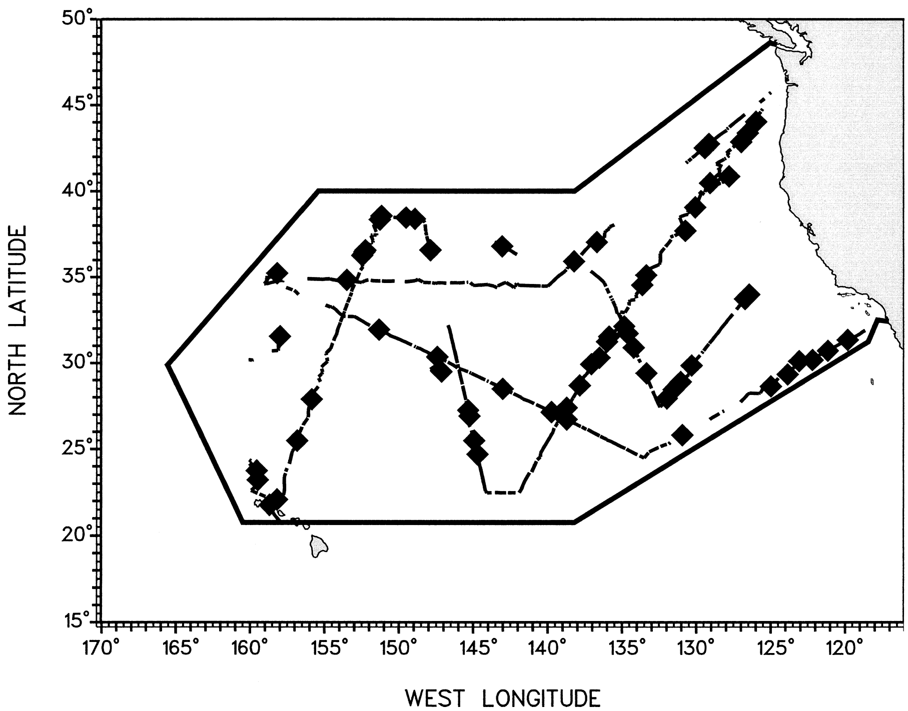

Figure 5. Acoustic survey effort (fine dark lines) and locations of acoustically detected sperm whales (filled diamonds) during acceptable survey conditions (Beaufort sea state 0–6, swell height <4 m). Bold line indicates the margin of the defined study area.

the other individuals in that group were not heard until the ship was within approximately 4 km. As expected, distributions of perpendicular sighting distances varied with initial click period (Fig. 7).

Detection functions were fit to the distributions of perpendicular sighting distance, both stratified by initial click period (<2 s *vs.* >2 s) and pooled. AIC values were consistently lower for the stratified analyses, so these estimates are favored. Different truncation distances were chosen for slow clicks (37 km) and for usual clicks and pooled data (18.5 km), and effective strip widths were much greater for slow clicks (19.6 km) than for usual clicks (4.5 km). A half-normal detection key function was found to be the best fitting model in all three cases, with cosine adjustment terms in two cases. The mean visual estimate of group size was 28.1 (CV = 0.31) based on 21 sperm whale groups. The resulting estimate of sperm whale abundance in the study area is approximately 32,100 (CV = 0.36) (Table 1).

Effective strip widths were also estimated with revised perpendicular distances based on an assumed whale depth of 500 m below the hydrophone array. For comparability, models were constrained to the half-normal key function. These effective strip widths differed from those given in Table 1 by less than one percent. For typical sperm whale acoustic detection distances, the effect of whale depth appears to have a trivial effect on density and abundance estimation.

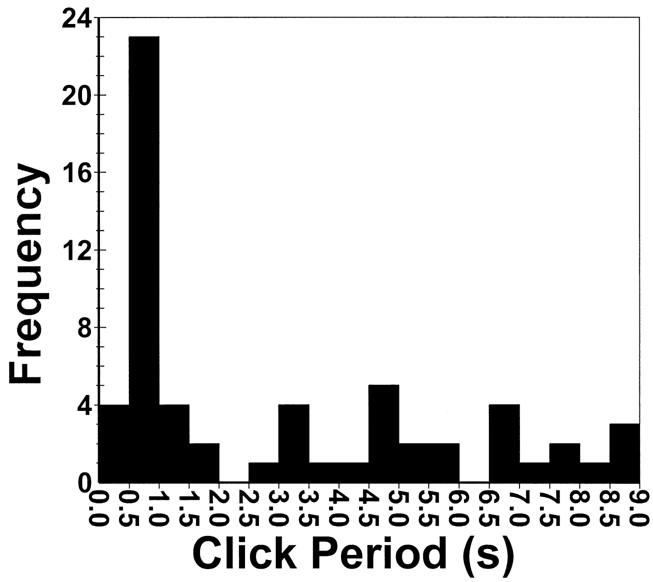

Figure 6. Frequency distribution of numbers of sperm whale groups detected acoustically based on initial click periods.

Combined Visual and Acoustic Results

Attempts to maintain independent visual and acoustic searches were largely unsuccessful. There were only two occasions when visual observers detected sperm whales prior to the acoustic team. On both occasions, which occurred during the last two weeks of the cruise, they turned the ship immediately instead of waiting for the whales to pass abeam (apparently, they just got too excited at finally seeing something). On both occasions, the acoustic team heard the whales soon after the vessel was turned, so it is likely that the whales would have been detected both acoustically and visually. Similarly, on several occasions, the acoustic team turned the vessel before the whales passed abeam. In some cases this was because the ship's course was limited by large swells and the return to a group of whales would have been difficult after they had passed abeam. In other cases, people seemed to have just "forgotten" the protocol. Prior to the next survey of this type, more emphasis needs to be placed on establishing and enforcing protocols for maintaining independence of visual and acoustic teams.

DISCUSSION

Group Size Estimates

Group size estimates are problematic for sperm whales because of their complex social behavior and long dive times. Most of the sperm whales encountered on this survey were in asynchronously diving clusters. Each cluster was composed of synchronously diving individuals. Occasionally, entire sperm whale groups are seen to dive synchronously, but this was not observed on this survey except for very

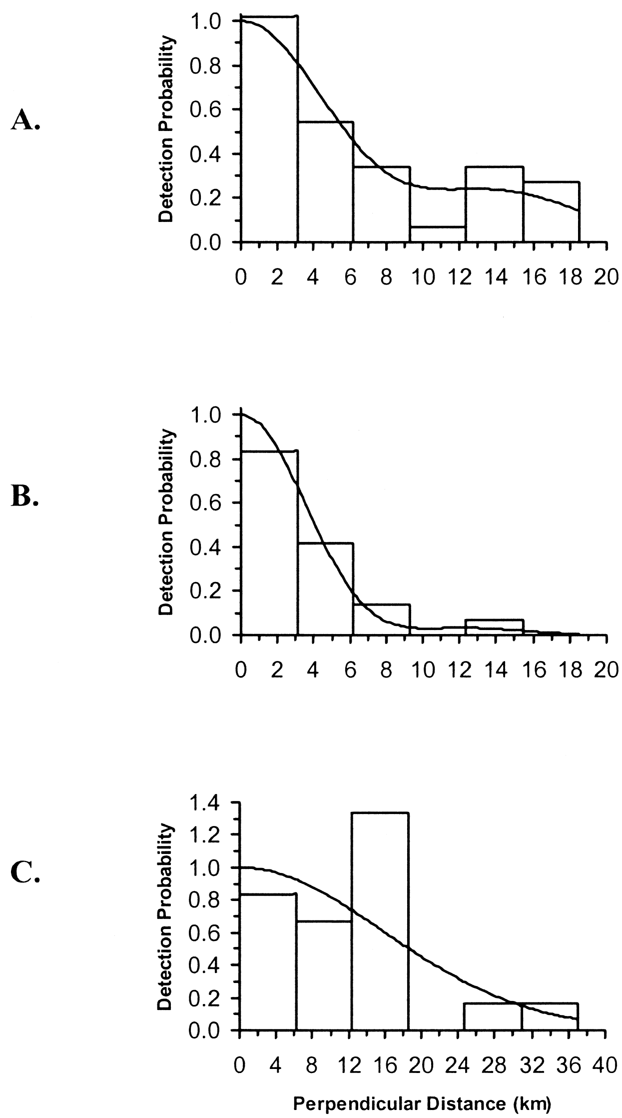

Figure 7. Distributions of perpendicular acoustic detection distances for (A) all detections pooled, (B) usual and unmeasured clicks, and (C) slow clicks. The smoothed line represents the best model fit to these data. Truncation distances were 18.5 km (A and B) and 37 km (C).

small groups. The modal dive times for sperm whales is approximately 40–45 min and the modal surface time between dives is approximately 8–10 min (Whitehead *et al.* 1992, Gordon and Steiner 1992, Jaquet *et al.* 1998, Whitehead 2003). This combination of long and asynchronous diving makes group size estimation difficult and uncertain. Biases may exist in our group size estimates, and we are almost certainly overestimating the precision with which we estimate group sizes. The CV for abundance does not include this uncertainty.

Mean group sizes for this dedicated sperm whale survey (~30 individuals) are much higher than for previous SWFSC surveys (~10 individuals). Previous estimates were likely to be low. By taking group size estimates after 90 min of observation, we can be reasonably sure that all individuals surfaced at least once. Although previous group size estimates were probably low because insufficient time was spent observing groups (usually <30 min on previous surveys), all observers on this survey had been observers on past SWFSC cruises, and they expressed their belief that group sizes for this survey were actually larger. The difference in group size could be a seasonal effect as past cruises were conducted in fall while this survey was conducted in the spring breeding season, or the difference could be geographical. Even though the negative bias may not have been as large as indicated by just comparing mean group sizes for the different cruises, there is no doubt that group size was underestimated in the past.

Visual Abundance Estimates

Visual survey methods for cetaceans are well established. The most controversial aspect of our treatment of these data is our use of an effective strip width and a trackline detection probability derived from previous surveys. Effective strip half-width ($1/f(0)$) for sperm whales is among the greatest estimated for any species on SWFSC surveys in the eastern tropical Pacific (Wade and Gerrodette 1993). Similar detection distances have been found for sperm whales on all of our subsequent surveys. The precision gained in using the much larger sample of detection distances from previous cruises, rather than trying to make an estimate from six sightings, certainly outweighs the potential loss in accuracy. Sea state is one variable that clearly affects detection distances, and the potential bias in using detection distances from another survey is minimized by using sea state stratification. Similarly, $g(0)$ might be lower in rougher sea states which, if we could correct for this, would also tend to increase our estimates of abundance from the visual surveys. The estimated coefficient of variation (CV) is lower for the visual survey than for the acoustic survey, but this is largely an artifact of using the estimates of $f(0)$ and $g(0)$ based on other studies with much larger sample sizes. The true CV is likely to be underestimated by doing so.

Acoustic Abundance Estimates

Acoustic methods have been used only twice before to estimate the density of sperm whales. Gillespie and Leaper (1997) used the Hiby cartwheels algorithm to empirically estimate detection distances for their survey of sperm whales around the Azores archipelago. Leaper *et al.* (2000) used the same method as we did (convergence of bearing angles) to estimate an effective strip width for sperm whales south of 50°S near South Georgia Island. The astonishing similarity between their estimate (ESW = 8.0 km) and our pooled estimate (ESW = 7.99 km) is likely to be coincidental.

Results from this survey show that the empirical distribution of perpendicular detection distances (Fig. 7) initially decreases rapidly with distance from the trackline but has a long tail with detections at greater than 18.5 km. Others have also found long tails in their distributions of perpendicular detection distances (Leaper *et al.* 2000). This pattern is not predicted by simple sound propagation models. Such unanticipated results show the importance of localizing sperm whale groups and directly measuring the observed distribution of perpendicular detection distances. Our unusual distribution of perpendicular distances could have resulted from varying intensity of source levels produced by the whales (Watkins 1980), directionality of sperm whale clicks (Møhl *et al.* 2000), or could have been the result of varying propagation of signals due to oceanographic features such as near-surface sound channels. We found that slow clicks (2–8 s) were detected at ranges up to 37 km, whereas the usual sperm whale clicks (0.4–1.0 s period) were typically heard at less than 9 km. This result corroborates the predictions of Madsen *et al.* (2003) that slow clicks should propagate approximately four times farther than regular clicks.

Additional analyses may improve acoustic abundance estimation methods. The location of sperm whale groups relative to the transect line was estimated by eye, based on the convergence of bearing lines. Of course, all bearing lines did not converge at a single point because sperm whale groups have some physical dimension (in our experience up to 4 km radius, but see Whitehead (2003) for additional information) and because sperm whale groups are usually moving (typically 3.5–6.0 km/h, Whitehead (2003)). Given that our methods should approximate the geometric centrum of a group with a physical dimension and that whale group speed is typically slow compared to survey speed (15 km/h), any biases due to these effects are likely to be small. Nonetheless, a maximum likelihood approach could be used to estimate location more objectively by explicitly incorporating these uncertainties. Information on group speed and direction from visual observations might also improve estimates of the location at the time of initial acoustic detection. Line-transect analysis of sperm whale density from acoustics may benefit from stratification by other variables, such as sea state, which can affect ambient noise and propagation distances (Gordon *et al.* 1998).

Previous Density and Abundance Estimates

Sperm whale density and abundance has been previously estimated for various other areas of the North Pacific using visual line-transect surveys. Wade and Gerrodette (1993) estimated 22,700 sperm whales (1.2 per 1,000 km^2) based on summer/fall ship surveys in the eastern tropical Pacific, an area more than twice as large as our study area and completely south of it. Within portions of our study area, Barlow (1995) estimated 756 sperm whales (0.9 per 1,000 km^2) based on summer/fall ship surveys within 300 nmi of the coast of California. Whitehead (2002) reviewed sperm whale density estimates worldwide and found an overall average of 1.4 whales per 1,000 km^2. All of these estimates show lower densities than we found in our study area (3.0–4.2 whales per 1,000 km^2). Recall that our survey was designed to capture the breeding season when sperm whale density should be highest (and when whales should be in breeding aggregations suitable for genetic analysis of stock separation). Given that some of the density difference between this and past surveys could have resulted from biased estimates of group size on past surveys, it is likely that sperm whales are not strikingly concentrated during the breeding season. Sperm whales were found fairly uniformly distributed throughout the study area. Future research should extend the study area, and the best survey season should be reconsidered for better sighting conditions.

Combined Visual and Acoustic Estimates

Ideally, visual and acoustic detections would be integrated seamlessly into a single approach to estimating abundance. We intended to collect data to be used in such analyses, but the visual survey effort fell short in the required number of sightings, and necessary protocols were not always followed. Based on a small sample size, we can say that most visual sightings will also be detected acoustically, so $g(0)$ for the acoustic surveys will be close to 1.0. However, when we followed one group of sperm whales over a 36-h period, we observed a 3-h period of silence in early morning hours. At dawn, the animals were observed surfacing quiescently less than a mile from the vessel; blows were barely visible. Based on this and other published reports of quiescent periods (Whitehead 2003), we anticipate that some trackline groups will evade acoustic detection. Perhaps the best approach to estimating the fraction missed acoustically would be to use the visual observers as a "tracking platform" (Buckland and Turnock 1992) which would monitor the locations of a group of sperm whales from far in front of the vessel until they passed abeam and were either detected or missed by the acoustic listener. This approach allows estimation of correction factors for both missed detections and for directed movement in response to the vessel (Buckland and Turnock 1992). Because the entire acoustic record can be easily recorded on a stereo tape, subsequent playback could help determine whether missed acoustic detections were caused by silent whales (availability bias) or by listener error (perception bias). We hope to gather additional information for this purpose on future surveys using joint acoustic and visual methods.

Acknowledgments

Funding for this survey was provided by NOAA National Marine Fisheries Service's Office of Protected Resources and by the Office of Naval Research. The survey coordinator was Alex VonSaunder. John Hildebrand was co-principal investigator for acoustic survey efforts. Cruise leaders included Jim Carretta and Lisa Ballance (also B.T.). Visual observers included Jim Cotton, Doug Kinzey, Greg O'Corry-Crowe, Paula Olson, Jon Peterson, Bob Pitman, Todd Pusser, and Scott Sinclair. The acoustic team consisted Mark McDonald, Duncan McGehee, Laura Morse, Aviva Rosenberg, Sarah Mesnick, and Olaf Jaeke (also J.B.) and was lead by Tom Norris. Trent Apple aided in post-cruise analysis of acoustic survey data. This manuscript was improved by helpful comments from Trent Apple, Megan Ferguson, Dick Neal, Tom Norris, Hal Whitehead, the editor, and one anonymous reviewer.

Literature Cited

Barlow, J. 1995. The abundance of cetaceans in California waters. Part I: Ship surveys in summer and fall of 1991. Fishery Bulletin, U.S. 93:1–14.

Barlow, J., and S. Sexton. 1996. The effect of diving and searching behavior on the probability of detecting track-line groups, g_o, of long-diving whales during line-transect surveys. NOAA National Marine Fisheries Service, Southwest Fisheries Center Administrative Report LJ-96-14. 21 pp.

Berzin, A. A. 1971. The sperm whale. Pishchevaya Promyshlennost, Moscow. (A. W. Yablokov, ed.). [Translation by Israel Programme for Scientific Translations. 394 pp.]

BUCKLAND, S. T., AND B. J. TURNOCK. 1992. A robust line transect method. Biometrics 48:901–909.

BUCKLAND, S. T., K. L. CATTANACH AND T. GUNNLAUGSSON. 1992. Fin whale abundance in the North Atlantic, estimated from Icelandic and Faroese NASS-87 and NASS-89 data. Report of the International Whaling Commission 42:645–651.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS AND L. THOMAS. 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford, U.K.

GILLESPIE, D., AND R. LEAPER. 1997. An acoustic survey for sperm whales in the Southern Ocean Sanctuary conducted from the RSV *Aurora Australis*. Report of the International Whaling Commission 47:897–907.

GORDON, J., AND L. STEINER. 1992. Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. Report of the International Whaling Commission 42: 561–565.

GORDON, J., A. MOSCROP, C. CARLSON, S. INGRAM, R. LEAPER, J. MATTHEWS AND K. YOUNG. 1998. Distribution, movements and residency of sperm whales off the Commonwealth of Dominica, Eastern Caribbean: Implications for the development and regulation of the local whalewatching industry. Report of the International Whaling Commission 48:551–557.

HOLT, R. S. 1987. Estimating density of dolphin schools in the eastern tropical Pacific Ocean using line transect methods. Fishery Bulletin, U.S. 85:419–434.

JAQUET, N., S. DAWSON AND L. SLOOTEN. 1998. Seasonal distribution and diving behavior of male sperm whales off Kaikura: Foraging implications. Canadian Journal of Zoology 78:407–419.

KASAMATSU, F., AND G. G. JOYCE. 1995. Current status of odontocetes in the Antarctic. Antarctic Science 7:365–379.

KINZEY, D. P., AND T. GERRODETTE. 2001. Conversion factors for binocular reticles. Marine Mammal Science 17:353–361.

LAAKE, J. L., S. T. BUCKLAND, D. R. ANDERSON AND K. P. BURNHAM. 1994. DISTANCE User's Guide Version 2.1. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO.

LEAPER, R., O. CHAPPELL AND J. GORDON. 1992. The development of practical techniques for surveying sperm whale populations acoustically. Report of the International Whaling Commission 42:549–560.

LEAPER, R., D. GILLESPIE AND V. PAPASTAVOU. 2000. Results of passive acoustic surveys for odontocetes in the Southern Ocean. Journal of Cetacean Research and Management 2:187–196.

LEATHERWOOD, S., K. GOODRICH, A. L. KINTER AND R. M. TRUPPO. 1982. Respiration patterns and 'sightability' of whales. Report of the International Whaling Commission 32:601–613.

MADSEN, P., M. WAHLBERG AND B. MØHL. 2002. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: Implications for echolocation and communication. Behavioral Ecology and Sociobiology 53(1):31–41.

MESNICK, S. L., B. L. TAYLOR, B. NACHENBERG, A. ROSENBERG, S. PETERSON, J. HYDE AND A. E. DIZON. 1999. Genetic relatedness within groups and the definition of sperm whale stock boundaries from the coastal waters off California, Oregon and Washington. Southwest Fisheries Science Center Administrative Report LJ-99-12 available from SWFSC, 8604 La Jolla Shores Dr., La Jolla, CA 92037.

MØHL, B., M. WAHLBERG AND P. T. MADSEN. 2000. Sperm whale clicks: directionality and source level revisited. Journal of the Acoustic Society of America 107:638–648.

RICE, D. W. 1974. Whales and whale research in the eastern North Pacific. Pages 170–195 *in* W. E. Schevill, ed. The whale problem: A status report. Harvard Press, Cambridge, MA.

SCHWEDER, T., G. HAGEN, J. HELGELAND AND I. KOPPERVIK. 1996. Abundance estimation of northeastern Atlantic minke whales. Report of the International Whaling Commission 46:391–405.

WADE, P. R., AND T. GERRODETTE. 1993. Estimates of cetacean abundance and distribution in the eastern tropical Pacific. Report of the International Whaling Commission 43: 477–493.

WATKINS, W. A. 1980. Acoustics and the behavior of sperm whales. Pages 283–290 *in* R.-G. Busnel and J. F. Fish, eds. Animal sonar systems. Plenum Publishing Corp., New York, NY.

WEILGART, L. S., AND H. WHITEHEAD. 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). Canadian Journal of Zoology 66:931–937.

WHITEHEAD, H. 2002. Estimates of the current global population size and historical trajectory for sperm whales. Marine Ecology Progress Series 242:295–304.

WHITEHEAD, H. 2003. Sperm whales: Social evolution in the ocean. University of Chicago Press, Chicago, IL.

WHITEHEAD, H., S. BRENNAN AND D. GROVER. 1992. Distribution and behavior of male sperm whales on the Scotian Shelf, Canada. Canadian Journal of Zoology 70:912–918.

Received: 10 February 2004
Accepted: 5 January 2005