Abstract—Leatherback turtles (*Dermochelys coriacea*) are regularly seen off the U.S. West Coast, where they forage on jellyfish (Scyphomedusae) during summer and fall. Aerial line-transect surveys were conducted in neritic waters (<92 m depth) off central and northern California during 1990–2003, providing the first foraging population estimates for Pacific leatherback turtles. Males and females of about 1.1 to 2.1 m length were observed. Estimated abundance was linked to the Northern Oscillation Index and ranged from 12 (coefficient of variation [CV]=0.75) in 1995 to 379 (CV=0.23) in 1990, averaging 178 (CV=0.15). Greatest densities were found off central California, where oceanographic retention areas or upwelling shadows created favorable habitat for leatherback turtle prey. Results from independent telemetry studies have linked leatherback turtles off the U.S. West Coast to one of the two largest remaining Pacific breeding populations, at Jamursba Medi, Indonesia. Nearshore waters off California thus represent an important foraging region for the critically endangered Pacific leatherback turtle.

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Abundance, distribution, and habitat of leatherback turtles (*Dermochelys coriacea*) off California, 1990–2003

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The leatherback turtle (*Dermochelys coriacea*) is listed as a critically endangered species on the World Conservation Union Red List 2006 (IUCN[1]). The Pacific population is at risk of extirpation because of over-harvest of eggs, commercial and residential development on nesting beaches, and incidental bycatch in fisheries (Spotila et al., 2000). Declines have been documented at nesting beaches in the eastern Pacific and throughout the Indo-Pacific region, where there has been a complete loss of the Malaysian nesting population (Chan and Liew, 1996), severe declines at nesting beaches in Costa Rica (Spotila et al., 2000) and Mexico (Sarti et al., 1996), and lesser declines at western Pacific nesting beaches (Hitipeuw et al., 2007).

Research on leatherback turtles in the Pacific has typically been limited to nesting beaches and few studies have been conducted in foraging areas. In the eastern North Pacific, the leatherback turtle is the most common sea turtle sighted north of Mexico (Stinson, 1984), although no nesting occurs at these latitudes. Sightings and incidental capture data indicate that this species is found as far north as Alaska but has been most frequently encountered off the coast of central California (Stinson, 1984; Starbird et al., 1993). Genetic analyses of tissues from leatherback turtles stranded on California beaches or caught incidentally in the California-Oregon drift gillnet fishery indicate that these turtles originate from nesting beaches in the western Pacific (Dutton et al., 2000, 2007). Thus, leatherback turtles travel thousands of kilometers from western Pacific beaches to forage on season-

[1] IUCN (World Conservation Union). 2006. Species Survival Commission. Red List database 2006. Website: http://www.iucnredlist.org/ (accessed 19 November 2006).

ally abundant jellyfish (Scyphomedusae) along the West Coast of North America (Eisenberg and Frazier, 1983; Shenker, 1984), where coastal upwelling creates a dynamic and highly productive ecosystem.

The California Current ecosystem is dominated by seasonal upwelling that is most intense between Pt. Conception and Cape Mendocino and gradually abates between July and October (Bakun et al., 1974). Previous studies of sighting patterns have linked leatherback turtle distribution and occurrence off the West Coast of North America to sea surface temperatures of 15–16°C during late summer and early fall (Stinson, 1984; Starbird et al., 1993). In particular, Monterey Bay, California, was identified as an area where leatherback turtles can be found during August, according to incidental sighting information collected by recreational boaters, researchers, and whale-watching operators. The spatially biased nature of these observations, however, precluded the estimation of overall leatherback turtle density and abundance.

In this study, we report the results of systematic aerial surveys conducted over coastal California waters between 1990 and 2003 and provide the first estimates of abundance for foraging leatherback turtles along the California coast. We also describe the density, distribution, and interannual variability of leatherback turtles off California during the peak period of occurrence in late summer and fall, examine oceanographic factors related to their occurrence in this region, and evaluate the potential significance of this foraging area to the western Pacific stock. Knowledge of leatherback foraging habitats is essential for the recovery of this critically endangered species, and the results of this study provide a basis for identifying and examining other potential foraging regions in the northeastern Pacific.

Materials and methods

Field methods

Aerial line-transect surveys for marine mammals and sea turtles were conducted between 15 August and 15 November in 10 of 14 years between 1990 and 2003. The primary objective of these surveys was to estimate abundance and trends of harbor porpoise (*Phocoena phocoena*), a small, cryptic nearshore cetacean; however, turtle sightings were also recorded systematically. Surveys were restricted to good weather days, defined as days with clear to partly cloudy skies and winds of less than about 12 kt (Beaufort sea states of 0–3). The transects followed a zigzag pattern designed to survey systematically between the coast and the 92-m (50-fathom) isobath, located less than 30 km offshore, and covering the primary habitat for harbor porpoise (Fig. 1). During each survey year, 26 transects between Pt. Conception and the Russian River (38°27′N) were replicated 4–8 times, depending on weather conditions. An additional 17 transects were surveyed 1–3 times a year off northern California between the Russian River and the California-Oregon border. Total transect length was 916 km, and under good weather conditions all transects were surveyed in two days. The full set of 43 transects was surveyed during the years 1990, 1991, 1993, 1995, 1997, 1999, and 2002. A subset of the transect lines (between Pt. Sur and Pt. Arena) was surveyed during 2000, 2001, and 2003 to provide further information on leatherback turtle occurrence off central California during these years.

Details of the survey methods have been reported elsewhere (Forney et al., 1991), and only a summary of key methods is provided here. The survey platform was a high-wing, twin-engine Partenavia P-68 aircraft, with two bubble windows for lateral viewing and a belly port for downward viewing. The survey team consisted of three observers (one on the left, right, and belly) and one data recorder. Distances to sighted animals were calculated from the declination angle to the sighting when abeam of the aircraft (obtained with a hand-held clinometer) and the aircraft's altitude. Surveys were flown at 167–185 km/h (90–100 kt) airspeed and 213 m (700 ft) altitude. Sighting information and environmental conditions, including Beaufort sea state, percentage cloud cover, and horizontal sun position (to measure glare direction) were recorded and updated throughout the survey by using a laptop computer connected to the aircraft's LORAN or GPS navigation system.

Visibility of submerged leatherback turtles is dependent upon water clarity and color contrast of the animals. When viewed from the air, this species generally exhibits considerable contrast to the surrounding waters within the California study area. To approximate the visibility of turtles at varying depths below the surface, a calibration experiment was conducted by using a set of multiple light-colored Secchi disks submerged at 1 m, 2 m, 3 m, and 4 m depth. During overflights, observers recorded the maximum visible Secchi disk depth. The proportion of time leatherback turtles spent within the visible depth range was estimated from dive data obtained during 2005 on free-swimming turtles, using a suction cup apparatus containing a VHF transmitter and a Lotek LTD 1110 time-depth-recorder (TDR) (Lotek, St. John's, Newfoundland, Canada). The suction cup apparatus (280 g weight in air) was attached to the dorsal surface of three leatherback turtles by using a pole from a small vessel, without capturing or handling the animal. The TDRs recorded depth every 5 sec at a resolution of 0.5 m and with an accuracy of ±1%. Tagged turtles were tracked for several hours until the tag disengaged from the animal or was actively removed with the pole, creating little or no disturbance to the animal. Potential posttagging effects were examined by visually inspecting the full dive profile, and by analysis of variance to test for differences in the time spent within the estimated visual depth range between the first 30 minutes and subsequent 30-minute periods. All deployments occurred during daylight hours between 12:00 and 16:30 local time.

Analytical methods

For analysis of regional patterns of leatherback turtle density and distribution, the study area was divided into five geographic strata, near prominent features of the coastline, to capture variation in bathymetric and oceanographic characteristics (Fig. 1): north coast (3765 km^2), Pt. Arena (772 km^2), Gulf of the Farallones (4189 km^2), Monterey Bay (908 km^2), and south central California (1849 km^2).

Leatherback turtle sighting rates were evaluated for potential effects of sea state, glare, and cloud cover, by using a two-way extension of the Kruskal-Wallis nonparametric analysis of variance (Scheirer et al., 1976), because these factors can influence one's ability to detect marine animals. Glare conditions were categorized as either optimal, when the sun position was behind the aircraft or directly ahead and did not affect the primary field of view, or marginal, when the sun position was just ahead of or perpendicular to the aircraft's travel direction. Cloud cover was divided into four categories: clear (<25% cloud cover), partly cloudy (26–50%), mostly cloudy (51–75%), and overcast (76–100%). Data collected in sea states greater than Beaufort 3 were excluded from the analysis; cloud cover and glare did not appear to exhibit any effect (see "Results" section) and were not considered further.

The detection function of leatherback turtles was estimated from the pooled perpendicular distances by using DISTANCE software (Thomas et al.[2]). Truncation of the 5–10% most distant sightings was investigated but it did not improve precision or model fit, and the final models included all data without truncation. Hazard, half-normal, and uniform models with and without cosine adjustment terms were fit to the ungrouped perpendicular distance data. The best model was selected according to Akaike's information criterion, AIC (Akaike, 1973), and visual inspection of goodness-of-fit.

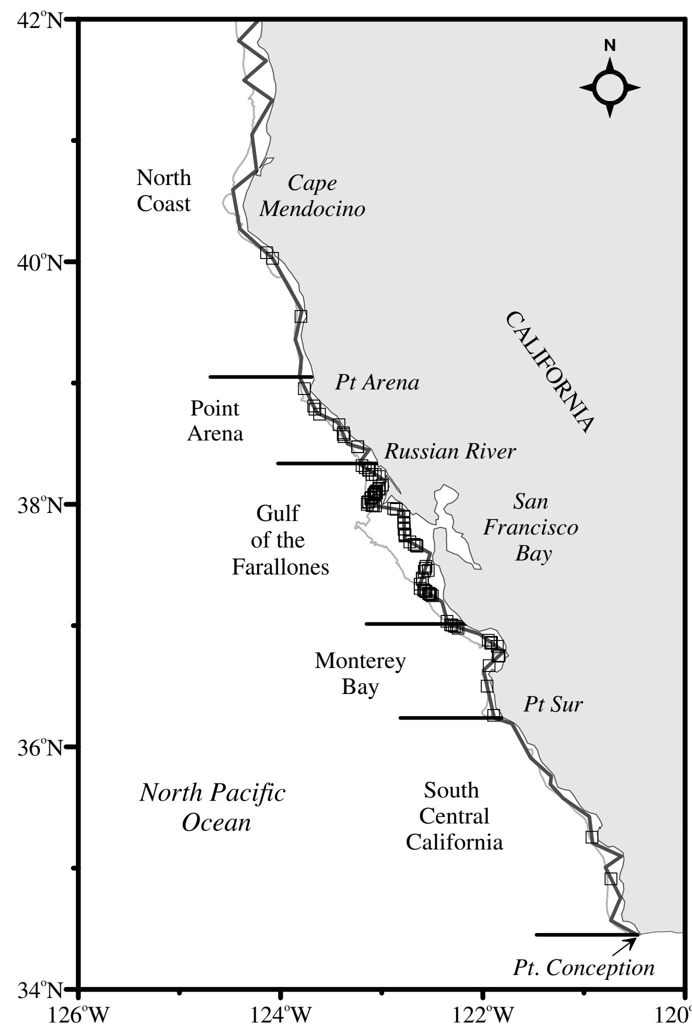

Figure 1

California study area with survey transects and geographic strata. Open squares represent locations of leatherback turtle (*Dermochelys coriacea*) sightings during systematic surveys. Thin gray line denotes the 90-m isobath.

The density (D) and abundance (N) of leatherback turtles within each geographic stratum, j, were estimated by using standard line-transect formulae (Buckland et al., 2001):

$$D_j = \frac{n_j f(0)}{2L_j g(0)}, \qquad (1)$$

$$N_j = D_j A_j, \qquad (2)$$

where n_j = the total number of turtles seen during systematic surveys;
$f(0)$ = the probability density function evaluated at zero perpendicular distance;
L_j = the linear distance surveyed in km;
$g(0)$ = the probability of detection at zero perpendicular distance, estimated from leatherback turtle dive data (see below); and
A_j = the area size in km^2.

Although we attempted to complete each transect the same number of times, weather conditions often resulted in uneven coverage. To avoid this potential within-stratum source of bias, encounter rates (n_j/L_j) for each geographic stratum were calculated from the individual transect encounter rates, weighted according to the proportional contribution of each transect:

[2] Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, and J. R. B. Bishop. 2004. Distance 4.1. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. Website: http://www.ruwpa.st-and.ac.uk/distance/ (accessed 19 November 2006).

Table 1

Number of leatherback turtle (*Dermochelys coriacea*) sightings and kilometers of trackline surveyed by geographic stratum, 1990–2003 (SC=South Central California, MB=Monterey Bay, GF=Gulf of the Farallones, PA=Pt. Arena, NC=North Coast).

	1990	1991	1993	1995	1997	1999	2000	2001	2002	2003
No. of leatherback turtles										
SC	0	0	0	1	0	0	0	0	1	0
MB	4	0	0	1	0	1	2	0	8	0
GF	21	1	5	0	11	12	1	3	11	4
PA	3	0	0	0	2	5	0	0	0	0
NC	0	2	1	0	0	0	0	0	0	0
Total	28	3	6	2	13	18	3	3	20	4
Km surveyed										
SC	1605	922	1643	1197	1492	1317	0	0	1652	0
MB	655	509	860	730	860	585	74	368	812	334
GF	1316	293	1273	1030	1343	1026	197	482	1664	668
PA	343	107	287	192	328	327	12	179	475	27
NC	806	517	762	477	814	777	0	0	549	0
Total	4724	2347	4826	3626	4837	4032	283	1030	5151	1030

$$\frac{n_j}{L_j} = \sum_{i=1}^{k} \frac{t_{ij}}{T_{ij}} \frac{n_{ij}}{L_{ij}}, \quad (3)$$

where k = the total number of transects within geographic stratum j;
t_{ij} = the length (in km) of the ith transect in stratum j;
T_{ij} = the total length of all transects in stratum j;
n_{ij} = the number of turtles seen on transect i in stratum j; and
L_{ij} = the actual distance flown on transect i within stratum j.

The probability of detecting a leatherback turtle at zero perpendicular distance, $g(0)$, is primarily influenced by the proportion of time a turtle is unavailable to be seen by the aerial survey team because it is diving (availability bias; Marsh and Sinclair, 1989). In other cases, animals may be present at or near the surface, but missed by observers for other reasons, such as fatigue or poor viewing conditions (perception bias). In this study, no correction was available for perception bias. Availability bias was estimated from leatherback turtle dive data and the estimated visible depth range from the visibility calibration experiment. Variances for D and N were calculated on basis of the variances of n, $f(0)$, and $g(0)$, according to the method of Buckland et al. (2001). The variance in number of sightings, n, was expected to differ by year and stratum because of differences in mean turtle density; however, it was not possible to calculate stratum-specific and year-specific variances empirically because not all transects were replicated in all years. The variance of leatherback turtle detections, therefore, was assumed to follow a Poisson distribution, with $\hat{var}(n) = n$. The variance of $f(0)$ was estimated analytically with DISTANCE software, and the variance of $g(0)$ was estimated from the individual $g(0)$ estimates for the three tagged turtles.

Overall abundance estimates for the entire study area were calculated as the sum of the stratum-specific abundance estimates for the seven full survey years: 1990, 1991, 1993, 1995, 1997, 1999, and 2002. During the three years when surveys were flown only off central California (2000, 2001, and 2003), coastwide abundance of leatherback turtles was estimated as the sum of the abundances for the Monterey Bay and Gulf of the Farallones strata, divided by the mean proportion of the total abundance found in these two strata during full survey years. The variance in this proportion was estimated across years (n=7) and incorporated into the variance of N and D by using standard formulae. Abundance estimates were examined for trends and potential large-scale environmental influences by linear least squares regression that included year and the 12-month average Northern Oscillation Index (NOI; Schwing et al., 2002) as predictor variables. Regressions were performed for all years, and for the subset of seven full survey years, because there was greater uncertainty in the abundance estimates for 2000, 2001, and 2003.

Results

Survey summary

A total of 31,885 km were surveyed in Beaufort sea states of 0–3 during 1990–2003 (Table 1), and annual totals ranged from 2347 to 5151 km during the full survey years when all strata were surveyed, and from 283 to 1030 km during the partial survey years, when only waters between Pt. Sur and Pt. Arena were surveyed. Weather conditions varied by year and were the primary determinant of the level of survey coverage achieved. Leatherback turtle encounter rates were identical for Beaufort sea states 0–1, 2, and 3 (0.003 turtles/km). Cloud cover and glare categories did not have a significant effect on encounter rates (P=0.08 and P=0.23, respectively).

The number of leatherback turtles seen per year ranged from 2 to 28, and totaled 100 individuals for all years (Table 1). The majority of turtles were subjectively estimated to be 5–7 ft (1.5–2.1 m) in total length, but only three smaller individuals (3.5–4.5 ft; 1.1–1.4 m) and one very large individual, estimated to be about 7.5 ft (2.3 m), were also recorded. Whenever possible, the presence of a long tail (indicating an adult male) was noted; however, this feature was often difficult to determine from the aircraft. In particular, males with tails of intermediate length may have had a greater likelihood of being recorded as "tail length undetermined." The proportion of identified males, 6 of 44 (14%), therefore, is a minimum proportion of males in the study area. Greatest concentrations of leatherback turtles were observed in the Gulf of the Farallones stratum, but turtles were observed in all geographic strata (Fig. 1).

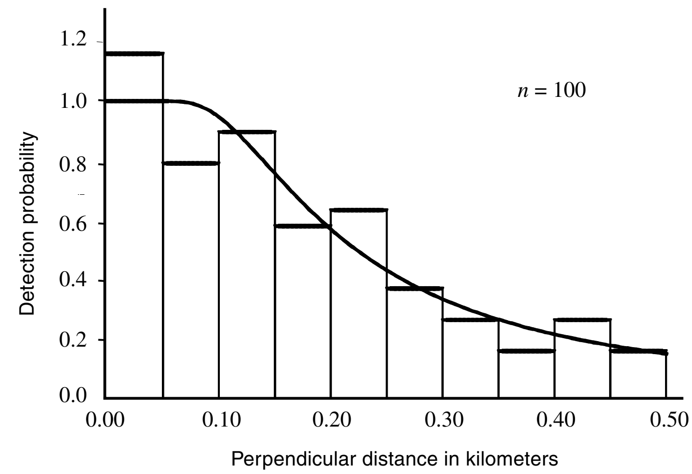

Figure 2

Detection probability function (Hazard rate model) and distribution of perpendicular distances for 100 leatherback turtle (*Dermochelys coriacea*) sightings.

Estimation of line-transect parameters

All three detection function models yielded similar estimates of $f(0)$, and AIC values were within one point. The Hazard rate model (Buckland et al., 2001) was selected because it provided the best fit, especially near the transect line (Fig. 2), yielding an estimated $f(0)$=4.465 (coefficient of variation, CV=0.136).

During the visibility calibration experiment, only the Secchi disk at 1 m depth was visible to the aerial observers; therefore, the depth at which leatherback turtles were detected was estimated to be about 1 m. Time-depth recorders (TDRs) were attached to three turtles (1 male, 2 females) on 29 September (for 153 minutes), 30 September (167 minutes), and 13 October, 2005 (229 minutes). There was no visible reaction by the turtles to the application of the tag, and the proportion of time spent within 1 m of the surface did not differ between the first 30 minutes and subsequent 30-minute periods of tag deployment (P=0.08). The parameter $g(0)$ was, therefore, estimated from the complete TDR dive record as the average proportion of time leatherbacks spent at or above 1 m depth. The three individuals exhibited a remarkably similar proportion of time spent within the upper meter of the sea surface (Table 2), and $g(0)$ was estimated as 0.471 (CV=0.029). Corrected estimates of abundance thus are about twice the uncorrected values (Fig. 3).

Abundance and density

Estimated leatherback turtle abundance was variable among years (Fig. 3; Table 3), ranging from 12 (CV=0.74) during 1995 to 379 (CV=0.23) during 1990. The greatest proportion of turtles was encountered within the two central California strata (Monterey Bay and Gulf of the Farallones), accounting for an average of 72% (range 31–97%, CV=0.37) of the total abundance. In partial survey years, when only these two strata were surveyed, total abundance within the study area was estimated as the central California abundance divided by the mean percentage (72%). For all years combined, estimated leatherback turtle abundance averaged 140 (CV=0.17) within the central California strata and 178 (CV=0.15) for the entire study area (Table 3). Although the Gulf of the Farallones stratum contributed the most to overall abundance because of its larger size, turtle densities were only slightly less for the Monterey Bay and Pt. Arena strata (Table 3). The South Central California and North Coast strata had the lowest densities. Monthly encounter rates of leatherback turtles by stratum (Fig. 4) were consistent with past reports of frequent sightings in Monterey Bay during August (Starbird et al., 1993); however, in our study, encounter rates were also high during September in the Monterey Bay and Gulf of the Farallones strata, and during October within the Gulf of the Farallones. Encounter rates decreased markedly throughout the study area during November. Interannual variability was least during September, and regionally within the Gulf of the Farallones stratum.

The estimates of abundance of leatherback turtles off California (Fig. 3) did not exhibit a trend between 1990 and 2003 (P=0.19 when data for all ten survey years were used, P=0.41 including only the seven coastwide survey years) but appeared to be related to the average annual NOI (Schwing et al., 2002), i.e, there were positive index values associated with greater leatherback turtle abundance and vice versa (Fig. 5; P=0.03 when

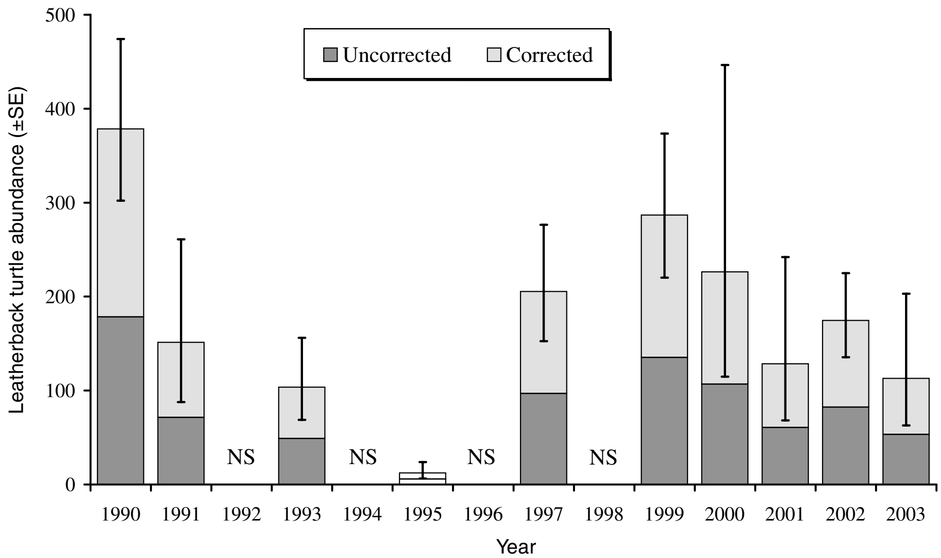

Figure 3

Estimated leatherback turtle (*Dermochelys coriacea*) abundance within the California study area, with and without $g(0)$ correction for diving behavior. Error bars indicate one standard error (SE); NS indicates no surveys were conducted during that year.

Table 2

Proportion of time spent in upper 5 meters of the water column by three foraging leatherback turtles (*Dermochelys coriacea*) tagged with time-depth recorders off central California during 2005. Dates and deployment times are provided for each turtle. "No. of intervals" represents the number of samples recorded by the depth logger (every 5 sec) within each depth category. The proportion of intervals within the upper 1 m was used for $g(0)$ estimation. CV = coefficient of variation.

	29 Sep 2005 (12:20–14:53)		30 Sep 2005 (13:28–16:16)		13 Oct 2005 (12:06–15:54)		Average	
Depth (m)	No. of intervals	Proportion of intervals	No. of intervals	Proportion of intervals	No. of intervals	Proportion of intervals	Porportion of intervals	CV
At surface	804	0.437	876	0.436	1099	0.400	0.425	0.029
≤1	35	0.456	124	0.498	164	0.460	0.471	0.029
≤2	104	0.513	260	0.628	219	0.540	0.560	0.062
≤3	63	0.547	123	0.689	150	0.595	0.610	0.069
≤4	220	0.666	229	0.803	287	0.699	0.723	0.057
≤5	76	0.708	92	0.849	91	0.732	0.763	0.057
>5	538	1.000	303	1.000	735	1.000	1.000	—

including all ten survey years; $P=0.04$ for only the seven coastwide survey years).

Discussion

The results of this study demonstrate the importance of neritic waters off California to foraging leatherback turtles and provide the first estimates of abundance for a Pacific foraging population of this critically endangered species. The aerial line-transect surveys, although not originally designed to census this species, provided quantitative data during the summer and fall peak season of occurrence (Starbird et al., 1993). Absolute abundances of foraging Pacific leatherback turtles were estimated for the first time by applying a new telemetry-based correction factor to account for submerged animals. Corrected densities in this study were 2.1 times greater than uncorrected densities. This contrasts markedly with the correction factor of 7.6 derived from dive data for a single leatherback turtle off St. Croix, U.S. Virgin Islands

Table 3

Estimated density and abundance of leatherback turtles (*Dermochelys coriacea*) by year and geographic stratum (SC=South Central California, MB = Monterey Bay, GF=Gulf of the Farallones, PA=Pt. Arena, NC=North Coast. Central CA includes MB and GF). CV = Coefficient of variation.

	1990	1991	1993	1995	1997	1999	2000[1]	2001[1]	2002	2003[1]	Mean	CV
Density (no./100 km^2)												
SC	0.0	0.0	0.0	0.4	0.0	0.0	—	—	0.3	—	0.1	0.72
MB	2.8	0.0	0.0	0.5	0.0	1.0	7.2	0.0	4.9	0.0	1.3	0.29
GF	7.7	1.1	1.9	0.0	4.3	5.4	2.3	2.2	3.0	1.9	3.6	0.18
PA	4.1	0.0	0.0	0.0	3.5	6.6	0.0	0.0	0.0	0.0	2.3	0.35
NC	0.0	2.8	0.6	0.0	0.0	0.0	—	—	0.0	—	0.3	0.59
Total area	3.3	1.3	0.9	0.1	1.8	2.5	2.0	1.1	1.5	1.0	1.6	0.15
Abundance												
SC	0	0	0	8	0	0	—	—	6	—	2	0.72
MB	25	0	0	4	0	9	66	0	45	0	15	0.29
GF	321	47	80	0	179	227	97	92	124	81	125	0.18
PA	32	0	0	0	27	51	0	0	0	0	14	0.35
NC	0	105	23	0	0	0	—	—	0	—	18	0.59
Total area	379	151	104	12	205	287	226	129	175	113	178	0.15
CV	0.23	0.59	0.43	0.74	0.30	0.27	0.77	0.70	0.26	0.64		
Central CA	347	47	80	4	179	236	162	92	169	81	140	0.17
CV	0.24	1.01	0.47	1.01	0.33	0.31	0.67	0.59	0.26	0.52		
% of total	92%	31%	78%	36%	87%	82%	—	—	97%	—	72%	0.37

[1] In these years, only central California was surveyed. Abundance estimates for the total area were extrapolated from central CA estimates based on the mean proportion of leatherbacks in central California during full survey years.

(Keinath and Musick, 1993) and applied to aerial survey density estimates for Atlantic leatherback turtles (Keinath et al., 1996). The correction used in the Keinath and Musick study, however, was based on the proportion of time the transmitter was above the water surface (and wave action), not the estimated proportion of time a turtle would have been visible to an aerial survey team (to about 1 m depth), as in this study. Furthermore, St. Croix represents a nesting area, and leatherback diving behavior may differ between nesting and foraging areas.

Average uncorrected densities of leatherback turtles off California during our study (0.75 turtles/100 km^2) are within the range of 0.21 to 2.2 leatherback turtles/100 km^2 reported during 1978–82 along the U.S. Atlantic coast (Shoop and Kenney, 1992), although the Atlantic study reported monthly estimates, not a seasonal average, and encompassed a larger study area. Average uncorrected densities in a smaller foraging area off North Carolina during August–November 1986–91 (0.80 leatherback turtles/100 km^2; Keinath et al., 1996), were similar to those observed in this study.

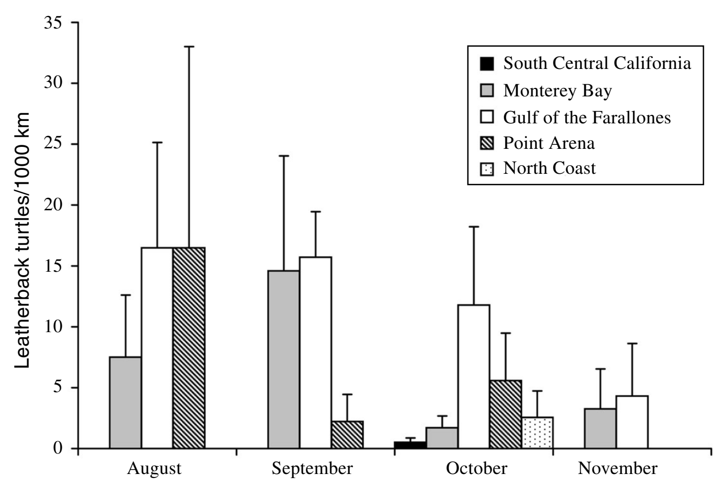

Figure 4

Average monthly leatherback turtle (*Dermochelys coriacea*) encounter rates (turtles / 1000 km surveyed) by geographic stratum, 1990–2003. Error bars indicate one standard error.

Leatherback turtles along the U.S. West Coast are part of the western Pacific genetic stock (Dutton et al., 2000, 2007), which is known to nest in Papua (Indonesia), Papua New Guinea, Solomon Islands, and on other western Pacific islands (Dutton et al., 2007). The western Pacific metapopulation was estimated to contain roughly 1800 nesting females in 1995 (Spotila et al., 1996); however, a more comprehensive evaluation indicates that the total western Pacific metapopulation may contain 2700–4500 breeding females (Dutton et al., 2007). Satellite telemetry studies have linked leatherback turtles foraging along the U.S. West Coast with one of the two largest remaining nesting beaches, Jamursba Medi (Papua, Indonesia) (Benson et al., 2007a), which experiences peak nesting activity during the austral winter. No links to the U.S. West Coast have been identified for animals nesting during the austral summer at nearby Wermon, Papua, Indonesia (S. Benson and P. Dutton, unpubl. data) or in Papua New Guinea (Benson et al., 2007b).

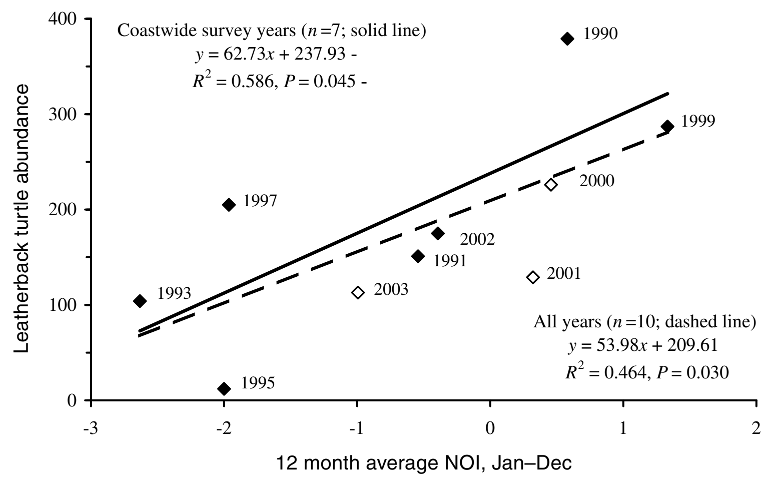

Figure 5

Regression of estimated leatherback turtle (*Dermochelys coriacea*) abundance versus 12 month average Northern Oscillation Index (NOI; Schwing et al., 2002) for the period January–December of each survey year (indicated next to the points). Filled symbols represent years in which surveys were conducted coastwide; open symbols represent years in which estimates of coastwide abundance were based on central California abundance (see "Materials and methods" section).

In a recent analysis of nest counts at Jamursba Medi, an average of about 750 females were estimated to nest annually between 1993 and 2004 (Hitipeuw et al., 2007). Efforts are underway to determine the relationship between the number of females nesting annually and the total number of females in the Jamursba-Medi nesting population; however, it is thought that this population currently has at least 1000–2000 nesting females (Spotila et al., 1996; Dutton et al., 2007). Capture studies off central California during 2000–2005 documented that about 67.5% (27 of 40) of foraging leatherback turtles were female (S. Benson and P. Dutton, unpubl. data). Our average annual estimate of 178 leatherback turtles along the California coast, therefore, should correspond to approximately 120 females. It is difficult, however, to evaluate this number in relation to the total Jamursba-Medi nesting population, because insufficient data are available on migration intervals between nesting beaches and foraging grounds. If each nesting year corresponds to one year at the California foraging grounds, then an average of about 16% of Jamursba-Medi females (120 divided by 750) potentially use the California foraging area; however there is evidence that leatherback turtles do not alternate nesting and foraging at such regular intervals. Remigration intervals to nesting beaches can range up to seven years (Price et al., 2004; Dutton et al., 2005), and some turtles have returned to forage off the U.S. West Coast during consecutive years without nesting (S. Benson and P. Dutton, unpubl. data). Further studies of remigration patterns and foraging site fidelity of western Pacific leatherback turtles will be required to resolve the proportion of these turtles that forage off California.

Estimates of foraging abundance in this study vary markedly among years (Fig. 3) and have a number of known sources of downward bias. First, the California study area includes only the nearshore environment to a water depth of about 92 m (50 fm), but leatherback turtles also have been captured incidentally in drift gill nets set in deeper waters (Julian and Beeson, 1998; Carretta et al., 2005). Second, the estimate calculated in this article represents an average snapshot abundance, and will be an underestimate of the true number of individuals using the area to the extent that residence times in the study area are less than our three-month study season. For example, if leatherback turtles forage within the study area for two months, then turtles observed in August would likely be different individuals from those observed during October or November, but average line-transect densities would only reflect the presence of a single turtle. Similarly, if leatherback turtle density is not constant throughout the three-month study period, the pooled estimate presented in this study will be lower than the peak seasonal abundance. Lastly, no estimate of perception bias was available for leatherback turtles in this study; however, small groups of small dolphins and porpoises are missed about 33% of the time (Forney et al., 1995). Therefore, it is likely that the detection of available turtles along the transect line is less than 100%.

The estimate of $g(0)$ developed in this study is the first to be based on dive records of leatherback turtles within a foraging region. Although the three turtles exhibited remarkably similar proportions of time within near-surface waters (Table 2), there is some uncertainty in the estimate because it is based on limited afternoon deployments (n=3) within a single year (2005). Furthermore, the depth to which turtles are visible to aerial observers may vary in space and time, as turbidity changes. The estimated $g(0)$ =0.471 should, therefore,

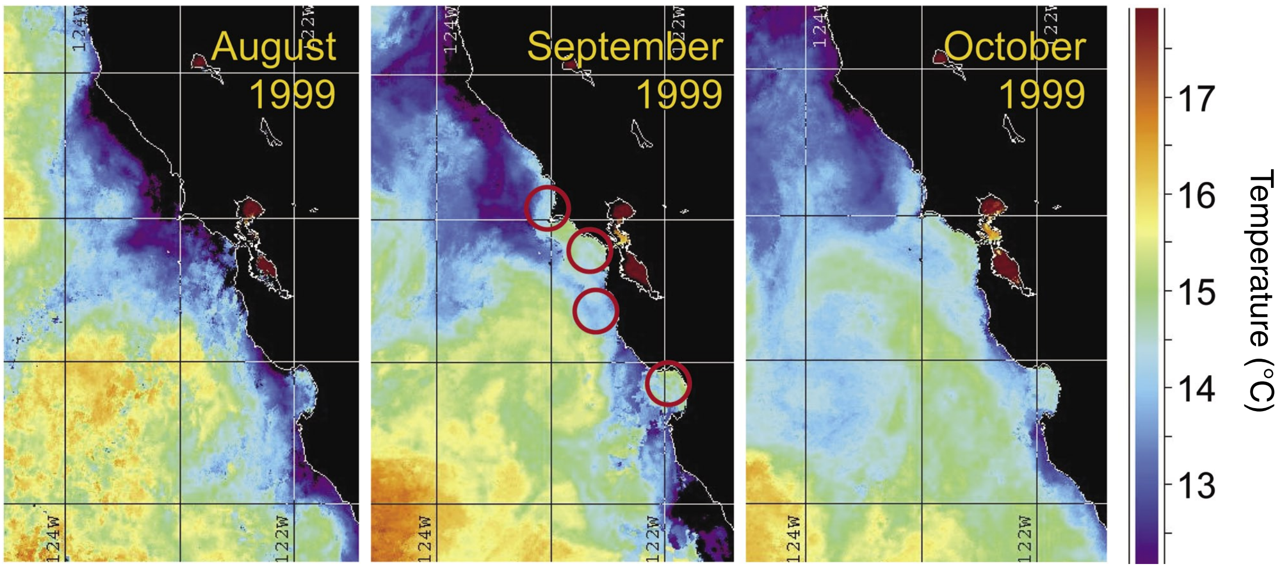

Figure 6

Pattern of upwelling and retention along the central California coast, illustrated with monthly satellite-derived sea surface temperature images for August, September, and October 1999. Leatherback turtles (*Dermochelys coriacea*) and Scyphomedusae were primarily found in areas of retention (circled in middle panel). High resolution monthly composite satellite images courtesy of NOAA CoastWatch, West Coast Node.

be considered provisional, pending further TDR deployments and calibration experiments.

Leatherback turtle populations at many Pacific nesting beaches have decreased dramatically during the last decade (Spotila et al., 2000), but decreases at Jamursba-Medi have been less pronounced (Hitipeuw et al., 2007), and the abundance of turtles foraging off California does not exhibit a trend between 1990 and 2003 (Fig. 3). The California study area is a dynamic upwelling environment that exhibits great interannual variability in oceanographic conditions (Chelton et al., 1982; McGowan et al., 1998) and distribution of marine vertebrates (e.g., Ainley et al., 1993; Benson et al., 2002). Links have been proposed elsewhere between large-scale environmental indices, such as the Southern Oscillation Index and the North Atlantic Oscillation, and sea turtles (Limpus and Nicholls, 1988; Rivalan, 2004) or their prey (Lynam et al., 2004). In this study, leatherback turtle abundance off California exhibited a positive relationship with the average annual NOI (Fig. 5). Positive NOI values correspond with conditions favorable to upwelling along the California coast, leading to increased zooplankton production (Schwing et al., 2002) and the development of large aggregations of gelatinous zooplankton (Graham, 1994), which are known to be the primary prey of leatherback turtles (Eisenberg and Frazier, 1983).

Although we did not measure underlying physical and biological processes, central California has been the focus of numerous oceanographic studies that shed light on potential trophic links between physical processes and leatherback turtles. Strong northwest winds during late spring and early summer lead to wind-driven upwelling (Bakun et al., 1974), particularly near points and headlands. These prominences can interact with local hydrographic features to create localized retention areas (upwelling shadows; Graham, 1994), where nutrient-rich, upwelling-modified water is entrained nearshore, particularly during wind relaxation. This process creates favorable conditions for phytoplankton growth and increases retention of zooplankton, larval fish, crabs, and gelatinous organisms (Wing et al., 1995; Graham et al., 2001). Dense aggregations of jellyfish (Scyphomedusae), primarily *Chrysaora fuscescens*, *C. colorata*, and *Aurelia* spp., have been observed regularly in these nearshore regions (Graham, 1994; this study). Similar processes have been reported off Oregon, where Scyphomedusae become denser and larger in size during summer, when the movement of surface and near-surface waters concentrates plankton in nearshore retention areas (Shenker, 1984). During our surveys, Scyphomedusae were common in retention areas between Pt. Reyes and Monterey Bay (Fig. 6), where leatherback turtles were most frequently encountered and observed feeding on *C. fuscescens*, *C. colorata*, and *Aurelia* spp. (Starbird et al., 1993; this study). We hypothesize that variability in the expression of these physical and trophic processes leads to interannual and seasonal variability in observed leatherback turtle abundance off central California, with densities greatest during periods of significant upwelling and subsequent relaxation events.

Previous researchers have linked leatherback turtle occurrence at high latitudes to the 15–16°C isotherm (Stinson, 1984; McMahon and Hays, 2006). Off central California, this reported pattern may reflect the presence of >15°C waters during summer and fall relaxation events and in upwelling shadows where jellyfish aggregations are found (Graham, 1994; Graham and Largier, 1997), rather than a physiological limitation of leatherback turtles. The broad shallow area of retention in the Gulf of the Farallones consistently exhibited greater abundances of leatherback turtles during our study. In contrast, few turtles were observed south of Pt. Sur, where the shelf is extremely narrow and cooler waters dominate along a nearly straight coastline where there are limited retention zones.

Many questions remain unanswered regarding the role of physical and biological factors and their influence on leatherback turtle abundance and distribution along the U.S. West Coast. Upwelling shadows and relaxation events probably affect leatherback turtle occurrence, but directed studies are needed to establish trophic links. Furthermore, the potential influence and role of the San Francisco Bay outflow on this nearshore foraging area is unknown. Results of this study provide a means for designing finer-scale surveys in key index areas of reliable leatherback turtle occurrence, such as the Gulf of the Farallones and Monterey Bay. Aerial surveys of these index areas should be coupled with telemetry studies and investigations of environmental variables that affect leatherback turtle foraging behavior to provide insights into the relevant trophic processes.

Ultimately, successful conservation efforts for leatherback turtles must include both protection of nesting beaches and mitigation of at-sea threats in foraging areas and along migratory routes. This study has demonstrated that waters off central California are a critical foraging area for one of the largest remaining Pacific nesting populations. Fortunately, threats such as coastal gillnet and longline fisheries that may incidentally catch leatherback turtles have largely been eliminated within our nearshore study area although pelagic driftnet and longline fisheries remain along the migratory pathways to and from the coast (e.g., Spotila et al., 1996; Carretta et al., 2005). Continued efforts to identify and characterize Pacific foraging areas are critical for mitigating at-sea threats, monitoring population trends, and, ultimately, for the successful recovery of Pacific leatherback turtle populations.

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Literature cited

Ainley, D. G., W. J. Sydeman, R. H. Parrish, and W. H. Lenarz.
1993. Oceanic factors influencing distribution of young rockfish (*Sebastes*) in central California: a predator's perspective. CalCOFI Rep. 34:133–139.

Akaike, H.
1973. Information theory and an extension of the maximum likelihood principle. *In* Second international symposium on information theory (B. N. Petran and F. Csàaki, eds.), p. 267–281. Akadèemiai Kiadi, Budapest, Hungary.

Bakun, A., D. R. McLain, and F. V. Mayo.
1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. Fish. Bull. 72:843–844.

Benson, S. R., D. A. Croll, B. Marinovic, F. P. Chavez, and J. T. Harvey.
2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997–98 and La Niña 1999. Prog. Oceanogr. 54:279–291.

Benson, S. R., P. H. Dutton, C. Hitipeuw, B. Samber, J. Bakarbessy, and D. Parker.
2007a. Post-nesting migrations of leatherback turtles (*Dermochelys coriacea*) from Jamursba-Medi, Bird's Head Peninsula, Indonesia. Chelonian Conserv. Biol. 6(1):150–154.

Benson, S. R., K. M. Kisokau, L. Ambio, V. Rei, P. H. Dutton, and D. Parker.
2007b. Beach use, internesting movement, and migration of leatherback turtles, *Dermochelys coriacea*, nesting on the north coast of Papua New Guinea. Chelonian Conserv. Biol. 6(1):7–14.

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, 432 p. Oxford Univ. Press, Inc., New York, NY.

Carretta, J. V., T. Price, D. Petersen, and R. Read.
2005. Estimates of marine mammal, sea turtle, and seabird mortality in the California drift gillnet fishery for swordfish and thresher shark, 1996–2002. Mar. Fish. Rev. 66(2):21–30.

Chan, E. H., and H. C. Liew.
1996. Decline of the leatherback population in Tereng-

ganu, Malaysia, 1956–1995. Chelonian Conserv. Biol. 2(2):196–203.

Chelton, D. B., P. A. Bernal, and J. A. McGowan.
1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40:1095–1125.

Dutton, D. L., P. H. Dutton, M. Chaloupka, and R. H. Boulon.
2005. Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. Biol. Conserv. 126(2):186–194.

Dutton, P. H., A. Frey, R. LeRoux, and G. Balazs.
2000. Molecular ecology of leatherbacks in the Pacific. *In* Sea turtles of the Indo-Pacific. Research, management and conservation (N. Pilcher, and G. Ismael, eds.), p. 248–253. Asean Academic Press Ltd, London, UK.

Dutton, P. H., C. Hitipeuw, M. Zein, S. R. Benson, G. Petro, J. Pita, V. Rei, L. Ambio, and J. Bakarbessy.
2007. Status and genetic structure of nesting populations of leatherback turtles (*Dermochelys coriacea*) in the western Pacific. Chelonian Conserv. Biol. 6(1):47–53.

Eisenberg, J. F., and J. Frazier.
1983. A leatherback turtle (*Dermochelys coriacea*) feeding in the wild. J. Herpetol. 17:81–82.

Forney, K. A., J. Barlow, and J. V. Carretta.
1995. The abundance of cetaceans in California coastal waters. Part II: Aerial surveys in winter and spring of 1991 and 1992. Fish. Bull. 93:15–26.

Forney, K. A., D. A. Hanan, and J. Barlow.
1991. Detecting trends in harbor porpoise abundance from aerial surveys using analysis of covariance. Fish. Bull. 89:367–377.

Graham, W. M.
1994. The physical oceanography and ecology of upwelling shadows. Ph.D. diss., 205 p. Univ. California, Santa Cruz, CA.

Graham, W. M., and J. L. Largier.
1997. Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. Cont. Shelf Res. 17(5):509–532.

Graham, W. M, F. Pagès, and W. M. Hamner.
2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451:199–212.

Hitipeuw, C., P. H. Dutton, S. R. Benson, J. Thebu, and J. Bakarbessy.
2007. Population status and internesting movement of leatherback turtles (*Dermochelys coriacea*) nesting on the northwest coast of Papua, Indonesia. Chelonian Conserv. Biol. 6(1):28–36.

Julian, F., and M. Beeson.
1998. Estimates of marine mammal, turtle and bird mortality for two California gillnet fisheries: 1990–1995. Fish. Bull. 96:271–284.

Keinath, J. A, and J. A. Musick.
1993. Movements and diving behavior of a leatherback turtle, *Dermochelys coriacea*. Copeia 1993: 1010–1017.

Keinath, J. A, J. A. Musick, and D. E. Barnard.
1996. Abundance and distribution of sea turtles off North Carolina. OCS Study/MMS 95-0024, 156 p. U. S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, 1201 Elmwood Park Boulevard, New Orleans, LA 70123-2394.

Limpus, C. J., and N. Nicholls.
1988. The Southern Oscillation regulates the annual numbers of green turtles (*Chelonia mydas*) breeding around northern Australia. Austral. J. Wildl. Res. 15(2):157–161.

Lynam, C. P., S. J. Hay, and A. S. Brierley.
2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnol. Oceanogr. 49:637–643.

Marsh, H., and D. F. Sinclair.
1989. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. J. Wildl. Manage. 53:1017–1024.

McGowan, J. A., D. R. Cayan, and L. M. Dorman.
1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science 281:210–217.

McMahon, C. R., and G. C. Hays.
2006. Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. Global Change Biol. 12:1–9.

Price, E. R., B. P. Wallace, R. D. Reina, J. R. Spotila, F. V. Paladino, R. Piedra, and E. Vélez.
2004. Size, growth, and reproductive output of adult female leatherback turtles *Dermochelys coriacea*. Endang. Species Res. 5:1–8.

Rivalan, P.
2004. Population dynamics of leatherback turtles in French Guiana: Research on relevant factors and application to the establishment of conservation strategies. [In French.] Ph.D. diss., 249 p. Univ. Paris XI Orsay, Paris.

Sarti, L., S. A. Eckert, N. García, and A. R. Barragan.
1996. Decline of the world's largest nesting assemblage of leatherback turtles. Mar. Turtle Newsl. 74:2–5.

Scheirer, C. J., W. S. Ray, and N. Hare.
1976. The analysis of ranked data derived from completely randomized factorial designs. Biometrics 32:429–434.

Schwing, F. B., T. Murphree, and P. M. Green.
2002. The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. Prog. Oceanogr. 53(2):115–139.

Shenker, J. M.
1984. Scyphomedusae in surface waters near the Oregon coast, May–August, 1981. Estuar. Coastal Shelf Sci. 19:619–632.

Shoop, C. R., and R. D. Kenney.
1992. Seasonal distributions and abundances of loggerhead and leatherback sea turtles in waters of the northeastern United States. Herpetol. Monogr. 6:43–67.

Spotila, J. R, A. E. Dunham, A. J. Leslie, A. C. Steyermark, P. T. Plotkin, and F. V. Paladino.
1996. Worldwide population decline of *Dermochelys coriacea*: Are leatherback turtles going extinct? Chelonian Conserv. Biol. 2(2):209–222.

Spotila, J. R., R. D. Reina, A. C. Steyermark, P. T. Plotkin, and F. V. Paladino.
2000. Pacific leatherback turtles face extinction. Nature 405:529–530.

Starbird, C. H., A. Baldridge, and J. T. Harvey.
1993. Seasonal occurrence of leatherback sea turtles (*Dermochelys coriacea*) in the Monterey Bay region, with notes on other sea turtles, 1986–1991. Calif. Fish Game 79(2):54–62.

Stinson, M. L.
1984. Biology of sea turtles in San Diego Bay, California, and the north eastern Pacific Ocean. M.S. thesis, 578 p. San Diego State Univ., San Diego, CA.

Wing, S. R., J. L. Largier, L. W. Botsford, and J. F. Quinn.
1995. Settlement and transport of benthic invertebrates in an intermittent upwelling system. Limnol. Oceanogr. 40:316–329.