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Scott R. Benson

NOAA National Marine Fisheries Service Southwest Regional Office

Karin A. Forney

San Jose State University, karin.forney@sjsu.edu

Jeffrey E. Moore

NOAA National Marine Fisheries Service Southwest Regional Office

Erin L. LaCasella

NOAA National Marine Fisheries Service Southwest Regional Office

James T. Harvey

Moss Landing Marine Laboratories, james.harvey@sjsu.edu

See next page for additional authors

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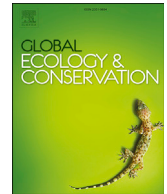
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Original Research Article

A long-term decline in the abundance of endangered leatherback turtles, *Dermochelys coriacea*, at a foraging ground in the California Current Ecosystem

Scott R. Benson^{a, b, *}, Karin A. Forney^{a, b}, Jeffrey E. Moore^c, Erin L. LaCasella^c, James T. Harvey^b, James V. Carretta^c

^a Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Moss Landing, CA, 95039, USA

^b Moss Landing Marine Laboratories, San Jose State University, Moss Landing, CA, 95039, USA

^c Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla, CA, 92037, USA



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ABSTRACT

Pacific leatherback turtles (*Dermochelys coriacea*) are critically endangered, and declines have been documented at multiple nesting sites throughout the Pacific. The western Pacific leatherback forages in temperate and tropical waters of the Indo-Pacific region, and about 38–57% of summer-nesting females from the largest remaining nesting population in Papua Barat (Indonesia) migrate to distant foraging grounds off the U.S. West Coast, including neritic waters off central California. In this study, we examined the trend in leatherback abundance off central California from 28 years of aerial survey data from coast-wide and adaptive fine-scale surveys. We used a Bayesian hierarchical analysis framework, including a process model of leatherback population density and an observation model relating leatherback observations to distance sampling methods. We also used time-depth data from biologists deployed on 21 foraging leatherback turtles in the study area to account for detection biases associated with diving animals. Our results indicate that leatherback abundance has declined at an annual rate of –5.6% (95% credible interval –9.8% to –1.5%), without any marked changes in ocean conditions or prey availability. These results are similar to the nesting population trends of –5.9% and –6.1% per year estimated at Indonesian index beaches, which comprise 75% of western Pacific nesting activity. Combined, the declining trends underscore the need for coordinated international conservation efforts and long-term population monitoring to avoid extirpation of western Pacific leatherback turtles.

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* Corresponding author. NOAA/SWFSC, 7544 Sandholdt Rd., Moss Landing, CA, 95039, USA.

E-mail addresses: Scott.Benson@noaa.gov (S.R. Benson), Karin.Forney@noaa.gov (K.A. Forney), Jeff.E.Moore@noaa.gov (J.E. Moore), Erin.LaCasella@noaa.gov (E.L. LaCasella), harvey@mlml.calstate.edu (J.T. Harvey), Jim.Carretta@noaa.gov (J.V. Carretta).

1. Introduction

Multi-decadal declines of endangered Pacific leatherback turtle populations (*Dermochelys coriacea*) have been documented at nesting sites in the eastern and western Pacific (Spotila et al., 2000; Sarti Martinez et al., 2007; Tapilatu et al., 2013; Santidrián-Tomillo et al., 2017; Martin et al., 2020), and a formerly large nesting population in Malaysia is now functionally extinct (Chan and Liew 1996). The eastern Pacific population is predicted to virtually disappear by 2040 based on the current rate of decline (Wallace et al., 2013a; The Laúd OPO Network 2020), whereas the larger western Pacific population is projected to decline 96% by 2040 (Tiwari et al., 2013). These population declines have primarily been attributed to fisheries bycatch, direct harvest of leatherback eggs and meat, and degradation of nesting habitat from various causes (Wallace et al., 2011).

In the western Pacific, there is a single genetic metapopulation that originates from multiple nesting sites located in Papua New Guinea, Solomon Islands, Vanuatu, and Indonesia (Dutton et al., 2007), with 75% of nesting activity occurring at two beaches (Jamursba Medi and Wermon) on the north coast of Bird's Head Peninsula, West Papua, Indonesia (Tapilatu et al., 2013). Nesting occurs year-round, with a July peak at Jamursba Medi, and peaks during July and January at Wermon (Hitipeuw et al., 2007). Between 1984 and 2011, the number of nesting females at Jamursba Medi declined by 78.3%; a similar 62.8% decline was documented at Wermon between 2002 and 2011, with a combined annual trend of -5.9% (Tapilatu et al., 2013). More recently, Martin et al. (2020) estimated an annual trend of -6.1% per year for this same population based on 2001–2017 nesting data, with a median estimated number of 790 nesting females (95% credible interval 666–942) during 2015–2017.

Satellite tracking of post-nesting western Pacific leatherback turtles revealed that this population has a complex migratory behavior. Foraging destinations vary by nesting season and include multiple large marine ecosystems in temperate and tropical waters of the Pacific Ocean and Indo-Pacific region (Benson et al., 2011). Boreal summer (henceforth 'summer') nesters forage in various regions of the northern hemisphere including the eastern North Pacific, the Kuroshio Extension and North Pacific Transition Zone, and the South China, Sulu, and Sulawesi Seas. In contrast, boreal winter ('winter') nesters forage in equatorial waters of Indonesia and temperate regions of the southern hemisphere, including the Tasman Sea and East Australia Current Extension. The most distant foraging grounds are located in the eastern North Pacific adjacent to the West Coast of North America (primarily California, Oregon, and Washington, USA), and are utilized by 38–57% of summer nesters in Papua Barat (Benson et al., 2011; Seminoff et al., 2012; Lontoh 2014). Adult and sub-adult leatherbacks of both sexes forage in these temperate habitats seasonally during summer and fall (Stinson 1984; Starbird et al., 1993; Benson et al., 2007a, 2011), with documented site fidelity and an approximate female:male ratio of 3:1 (Benson et al., 2011; Seminoff et al., 2012; Hetherington et al., 2019). The only foraging ground that has been monitored regularly is located in neritic waters off central California (Peterson et al., 2006; Benson et al., 2007a). Female leatherback turtles from this foraging ground return to beaches at Bird's Head Peninsula, and to a lesser extent Solomon Islands, during the summer nesting season (Benson et al., 2011) every 2–6 years (Lontoh 2014), following one or more years at the foraging grounds. Male leatherback turtles also appear to have similar movement patterns, either returning to the foraging grounds or migrating to the western Pacific during breeding season (Benson et al., 2011).

Benson et al., 2007a estimated the abundance of foraging leatherbacks off California during 1990–2003 based on aerial line-transect surveys within neritic waters. Annual abundance was variable (12–366 turtles) and linked to the strength of upwelling in each year, indicating that the number of turtles, and the proportion of the overall western Pacific population, vary based on ocean conditions and individual nesting cycles. Over time, however, the central California foraging ground can serve as an index area to examine population trends, because this represents an important foraging destination for western Pacific leatherbacks. Benson et al., 2007a did not identify a long-term population trend for the period 1990–2003, but aerial surveys have continued off central California through 2017, providing a 28-year time series to re-examine the long-term population trend. In this study, we assess the trend in abundance of foraging leatherbacks off central California for the years 1990–2017 using a Bayesian hierarchical modeling framework (de Valpine and Hastings 2002; Royle and Dorazio 2008; Moore and Barlow, 2011, 2013, 2014). This provides a unique opportunity to examine the population trend for both male and female turtles at one of their foraging grounds, relative to trends documented for females at nesting beaches.

2. Methods

2.1. Field methods

Two sets of aerial line-transect data for neritic central California waters are included in this study. The first set was established as part of a long-term monitoring program for harbor porpoise, *Phocoena phocoena*, and follows a zig-zag pattern between the coast and the 92-m (50-fathom) isobath (Forney et al. 1991, 2014), roughly within 30 km of the coast (Fig. 1A). During these harbor porpoise aerial surveys (HPAS), leatherback turtles were recorded systematically along with harbor porpoises and other cetaceans. As part of the porpoise monitoring program, the transects were replicated 4–7 times per year between mid-August and mid-November during 9 years (1990, 1991, 1993, 1995, 1997, 1999, 2002, 2007, 2011; Forney et al., 2014). During 13 additional years between 2000 and 2017, the same transects were flown once or twice annually as part of a program to study leatherback turtles in waters off central California, roughly between Point Sur (36° 18.4'N) and Point Arena (38° 57.3'N).

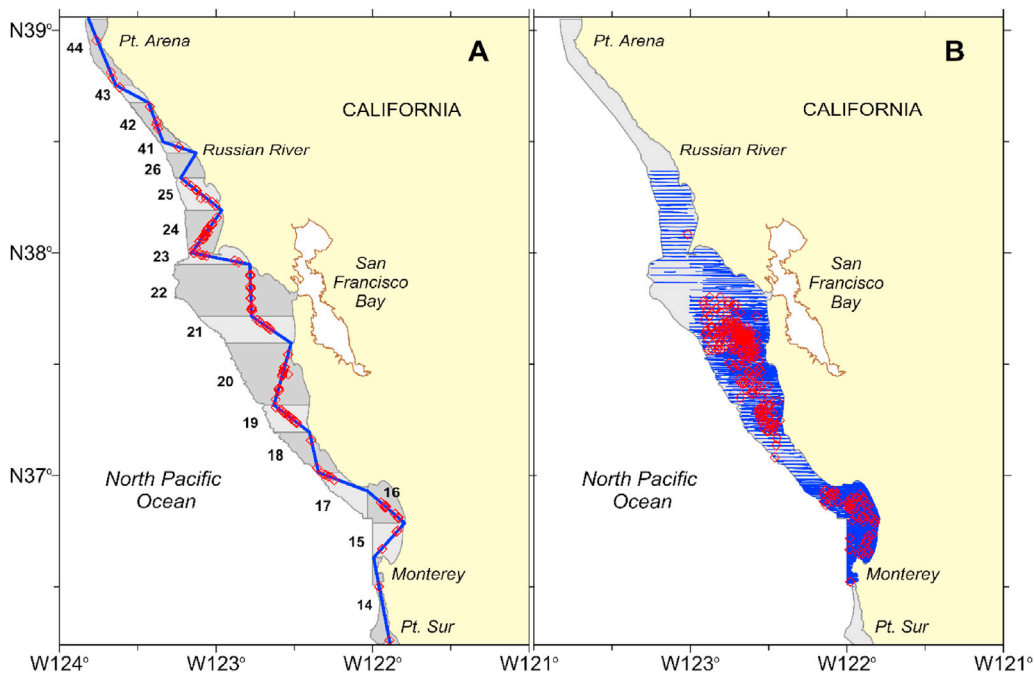


Fig. 1. Aerial survey coverage (A) along harbor porpoise transects, 1990–2017 and (B) along adaptive fine-scale surveys that primarily covered waters from Monterey Bay to San Francisco, 2000–2017. Blue lines show transects; red diamonds show leatherback sightings. Analysis strata are shown in alternating light and medium gray shading in panel (A), with stratum/transect numbers shown alongside. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The second survey set was flown adaptively during summer and fall of 2000–2017 and was designed to provide sampling in support of separate vessel-based leatherback tagging and capture operations (described in Benson et al., 2011). These fine-scale (FINE) transects were oriented east-west and spaced every 1 min of latitude from Monterey (36° 35.0'N) to the Russian River (38° 27.0'N), extending from the coast to approximately the 100-m isobath except in Monterey Bay, where nearshore portions of the deeper Monterey Canyon were included for simplicity (Fig. 1B). A subset of these transects, focusing on the areas where leatherback turtles or their primary prey, brown sea nettles (*Chrysaora fuscescens*) were found, was flown one or multiple times during the years 2000–2014, and 2016–2017. Survey protocols, aircraft, and many observers were identical to those used during the first survey set.

Survey protocols followed those previously described by Benson et al., 2007a, and we provide a brief summary here. The aerial survey team consisted of four people. Two observers searched on either side of the aircraft through bubble windows, and one observer searched through a window in the belly of the aircraft to provide additional coverage directly on the transect line. A data recorder logged survey effort, viewing condition information, and sighting details directly into a laptop computer connected to a Global Positioning System (GPS). Declination angles to each sighting were measured using handheld Suunto clinometers to allow calculation of perpendicular distances to each sighting. Surveys were conducted when viewing conditions for detecting leatherback turtles were good, with light winds (Beaufort sea states 0–3) and mostly when skies were clear or partly cloudy (Benson et al., 2007a).

2.2. Estimation of availability bias, $g(0)$

For diving marine species, the accurate estimation of animal abundance and density from aerial surveys requires an estimation of availability bias, or the proportion of time an animal is visible near the surface ($g(0)$; Buckland et al., 2001). Dive data from tagged animals have been used to estimate $g(0)$, based on the proportion of time spent at or near the surface (e.g., Pollock et al., 2006; Benson et al., 2007a; Seminoff et al., 2014; Fuentes et al., 2015). Benson et al., 2007a presented a preliminary estimate of $g(0)$ based on three time-depth recorder (TDR) deployments on leatherback turtles off California. In our study, we conducted 18 additional TDR deployments using the same methods as Benson et al., 2007a, to improve the estimate of this important line-transect parameter. The TDR tags were attached with a suction cup to the carapace of free-swimming turtles with the aid of a pole (no capture or handling) as described in Benson et al., 2007a. The Starr-Oddi brand *DST milli-TD* TDRs were programmed to record depth every 2–30 s, depending on deployment, at a resolution of 0.07 m and an accuracy of $\pm 0.6\%$. Tagged turtles were tracked for hours to days until the tag disengaged from the animal or was actively removed with the pole. For estimation of $g(0)$, only deployments of at least 30 min were included, and any apparent dive response following tag attachment was removed from the dive record before processing. Data were filtered to include only daylight hours

between 08:30 and 17:30, when aerial surveys took place. To examine potential differences in time spent at or near the surface by time of day, we divided the data into three 3-hr blocks (08:30–11:30, 11:30–14:30 and 14:30–17:30) and conducted a Kolmogorov–Smirnov test of the cumulative number of minutes spent by all turtles a) at the surface, b) within 1 m of the surface, when they would still be visible to aerial observers, or c) at 2+ m depth, when they would be too deep to be seen. Zero-offset corrections (ZOC) were applied to each dive record to adjust for small baseline discrepancies that are common in time-depth recorders (Hazel et al., 2009). Estimates of $g(0)$ were derived from each dive record as the proportion of time each turtle spent within 1 m of the surface (Benson et al., 2007a).

2.3. Analytical methods

We conducted a trend analysis of leatherback abundance using Bayesian hierarchical models in R (v. 3.5.1, R Core Team 2018) and OpenBUGS (v. 3.22). Our methods followed those initially described by Moore and Barlow (2014) and subsequently adapted by Forney et al. (2020) to assess harbor porpoise trends with the same aerial survey data used in this study. Markov Chain Monte Carlo (MCMC) simulations were run with a process model for population growth and an observation model based on the line-transect (Distance) sampling (Buckland et al., 2001). Two MCMC chains were run for 100,000 time steps with a thinning rate of 10 to minimize autocorrelation and a 50,000 step burn-in. Model convergence was initially ascertained visually, to ensure chains were stable and well-mixed for parameters of interest and resulting posterior distributions were smooth. Convergence was also confirmed quantitatively using the R package *coda* by (a) testing for equality of the means of the first and last parts of the Markov chain (Geweke 1992) and (b) calculating Gelman scores, which indicate good convergence within the range of 1.00–1.05 (Gelman and Rubin 1992).

2.3.1. Process model

The process model describing population change was specified as a Markov process:

$$N_t = N_{t-1} \times \exp(r + \varepsilon_t)$$

$$\varepsilon_t \sim \text{Normal}(0, \sigma_{\text{process}}^2)$$

where N_t is leatherback abundance at time t , r is the parameter for mean annual population growth rate, and ε_t is the process error. The process error represents changes in abundance due to demographic and movement processes, and is assumed to be normally distributed on a log scale with a mean of zero and a process variation $\sigma_{\text{process}}^2$. The long-term annual growth rate, λ , was estimated as the geometric mean of the individual realized annual growth estimates, λ_t :

$$\lambda_t = N_t / N_{t-1}$$

Leatherback density is $D_t = N_t/A$, where A is the size of the study area (6842 km²); however, density varies spatially and our survey coverage was biased towards higher density regions because we also sought to locate leatherbacks for telemetry studies. To avoid bias in the resulting abundance estimates, we modeled stratum-specific density effects when linking the process and observation models. Each HPAS transect line represented a separate along-shore stratum, with boundaries located at the ends of each zig-zag line as shown in Fig. 1A. The fine-scale lines (Fig. 1B) were assigned to these strata based on their respective locations.

Leatherback density in stratum i at time t is described by $D_{i,t} = D_t \times c_i$, where c_i is a stratum-specific, time-independent multiplier that accounts for persistent leatherback density differences (i.e., some strata consistently have better foraging habitat than others, based on the interaction of coastal bays and headlands with local ocean processes; Graham et al., 2001). Overdispersion was included in the observation model using a Poisson-gamma distribution (see Section 2.3.2 below) to allow for annual departures from this expectation. There were two important constraints when specifying Bayesian priors for the c_i . First, stratum-area weights were calculated as $w_i = a_i/A$, where a_i are the stratum area sizes in km² (Supplemental Table S1), and the sum of the $c_i \times w_i$ was constrained to be equal to 1. This ensures that the overall study area density equals the area-weighted average of the individual stratum densities: $D_t = \sum \frac{D_{i,t} a_i}{A} = \sum D_{i,t} c_i w_i$. Second, the c_i for each stratum were constrained to be less than or equal to its respective $1/w_i$, because if any $c_i > 1/w_i$, that would imply that all leatherbacks were within this single stratum.

2.3.2. Observation model

The observation model linking the above process to the observed data followed distance sampling methods, with the expected number of leatherbacks, $E[n_{i,t}] = \mu_{i,t}$, described as:

$$E[n_{i,t}] = \mu_{i,t} = 2 \times L_{i,t} \times ESW \times g(0) \times D_{i,t}$$

where $L_{i,t}$ are the lengths of the transect lines (km) surveyed within the strata, $g(0)$ is the probability of detecting a leatherback on the transect line, and ESW is the effective strip half-width (km). The effective strip half width (ESW) was estimated from the combined leatherback sighting data using R version 3.5.1 (R Core Team 2018) and the package *Distance* 0.9.7, evaluating both conventional and multi-covariate approaches to include potential weather covariates (e.g., sea state, glare). We

evaluated detection functions based on Akaike's Information Criterion (AIC; Akaike 1973), choosing the simplest model when multiple approaches yielded similar AIC values ($\Delta \text{AIC} < 1$). The resulting effective strip half-width, along with its standard error, was included in the trend analysis as an informed prior with a normal distribution. The probability of detecting animals on the transect line, $g(0)$, was estimated from the TDR dive behavior data as the proportion of time a leatherback was within 1 m of the surface, following the methods of Benson et al., 2007a, and specified as a beta distribution in our model. The observed number of leatherbacks $n_{i,t}$, was assumed to follow a negative binomial distribution using a Poisson-gamma specification with $n_{i,t} \sim \text{Poisson}(\mu_{i,t} \times \rho_{i,t})$, and $\rho_{i,t} \sim \text{gamma}(\alpha, \alpha)$.

2.3.3. Priors and estimation

We specified uniform priors for the process model as follows: initial leatherback population size, $N_0 \sim \text{Uniform}(0, 2000)$, annual growth rate $r \sim \text{Uniform}(-1, 1)$, and process variation $\sigma_p \sim \text{Uniform}(0, 2)$. To conform to the constraints described above, prior specifications for the c_i were more complex:

$$c_1 \sim \text{uniform}(0, 1/w_1)$$

$$c_i \sim \text{uniform}\left(0, \frac{1 - \sum_{j=1}^{i-1} c_j w_j}{w_i}\right), \text{ for } i=2, 3, \dots, k-1, \text{ where } k \text{ is the number of strata}$$

$$c_k = \frac{1 - \sum_{j=1}^{k-1} c_j w_j}{w_k}$$

For the observation model, ESW was specified based on the estimated detection function (see Results below): $\text{ESW} \sim \text{Normal}(0.2615, 0.097)$. The negative binomial overdispersion parameter, α , was specified as $\alpha \sim \text{Uniform}(1, 10)$.

2.4. Environmental data

To evaluate the estimated leatherback population trend in the context of coastal ocean processes that influence leatherback prey and habitat (e.g., the strength of upwelling), we obtained two habitat indices from NOAA's California Current Integrated Ecosystem Assessment website¹: (1) the Northern Oscillation Index (NOI), which correlates with upwelling intensity and zooplankton production, and which was previously linked to leatherback abundance (Benson et al., 2007a); and (2) a 1990–2017 time-series of catch per unit effort (CPUE) for brown sea nettles off central California, derived from spring trawl stations during NOAA's Rockfish Recruitment and Ecosystem Assessment Surveys (Ralston et al., 2013).

3. Results

Survey coverage varied during the study period (Table 1), with HPAS transects dominating the early years (1990–2000), and FINE transects contributing a much greater level of effort after 2000. Leatherback turtles were observed in 20 of the 22 years that had survey coverage, although sighting rates varied inter-annually. A total of 358 sightings were recorded, ranging from zero to 43 animals per year. Some intra-annual sightings may represent re-sightings of the same individuals.

We conducted 18 TDR deployments during 2007–2013 to update the estimate of $g(0)$ for abundance estimation. Combined with the three 2005 deployments reported by Benson et al., 2007a, this resulted in a new estimate of $g(0) = 0.607$ (SE = 0.040) (Table 2). The proportion of time tagged turtles spent at the surface, within 1 m, and at depths of at least 2 m was not significantly different by time of day ($p \geq 0.10$). The simplest detection function that minimized AIC was the half-normal without covariates, resulting in an estimate of $\text{ESW} = 261.5$ m (SE = 9.7) across all years. Truncation distances of 400–700 m were explored, and the best model fit was achieved without any data truncation, similar to previous marine turtle surveys (Benson et al., 2007a; Eguchi et al., 2018).

The MCMC chains achieved convergence, as indicated by Gelman statistics within the recommended range of 1–1.05, non-significant Geweke scores, and smooth posterior distributions, as shown in Fig. 2 for three key parameters: the realized growth rate, λ , the process error, $\sigma_{process}^2$, and the overdispersion parameter, α . Posterior distributions for the stratum-specific density multipliers, c_i , were consistent with observed geographic patterns of leatherback density and variation therein (Supplemental Figure S1); in particular, the greatest densities were in strata 20 and 21 (see Fig. 1A). The overall trend analysis indicated a long-term decline in the abundance of leatherback turtles off central California (Fig. 3), with a median annual growth rate ($\lambda - 1$) of -5.6% (95% credible interval -9.8% to -1.5%) between 1990 and 2017. The decline was not monotonic as abundance varied across years, with peaks during years with positive or increasing Northern Oscillation Index values (Fig. 4A). This is consistent with the findings of Benson et al., 2007a; however, the magnitude of these abundance peaks has decreased over time (Fig. 4B and C). The most recent peak abundance of 106 leatherbacks during 2016 (95% credible interval: 51–221) was markedly less than the 1990 peak, when there were an estimated 298 leatherbacks (95% credible interval: 154–600). The relative abundance of the leatherback's primary prey in this region also was variable throughout our study

¹ <https://www.integratedecosystemassessment.noaa.gov/regions/california-current-region/indicators/climate-and-ocean-drivers.html>.

Table 1

Summary of 1990–2017 aerial survey effort and leatherback sightings for both transect sets (harbor porpoise transects, Fig. 1A, and adaptive fine-scale transects, Fig. 1B). Surveys were conducted from mid-August to mid-November in each year sampled.

Year	Harbor porpoise transects		Adaptive fine-scale transects		All surveys combined	
	Survey effort (km)	No. leatherbacks	Survey effort (km)	No. leatherbacks	Survey effort (km)	No. leatherbacks
1990	2316	28	0	0	2316	28
1991	909	1	0	0	909	1
1992	0	0	0	0	0	0
1993	2424	5	0	0	2424	5
1994	0	0	0	0	0	0
1995	1952	1	0	0	1952	1
1996	0	0	0	0	0	0
1997	2534	13	0	0	2534	13
1998	0	0	0	0	0	0
1999	1938	18	0	0	1938	18
2000	284	3	218	0	502	3
2001	1028	3	2813	6	3841	9
2002	2947	19	5220	20	8167	39
2003	1028	4	6222	39	7250	43
2004	301	0	9552	41	9853	41
2005	68	0	5966	25	6034	25
2006	584	2	3827	1	4411	3
2007	1526	7	3480	20	5006	27
2008	1065	5	1985	9	3050	14
2009	342	0	4487	8	4829	8
2010	290	0	1142	3	1432	3
2011	1244	0	2674	2	3918	2
2012	0	0	2011	0	2011	0
2013	238	1	3731	32	3969	33
2014	651	0	588	0	1239	0
2015	0	0	0	0	0	0
2016	1042	3	1322	31	2364	34
2017	385	0	1973	8	2358	8

Table 2

Summary of time-depth recorder (TDR) deployments and estimated mean proportion of time within 1 m of the surface, $g(0)$. * indicates deployments that were previously reported in [Benson et al., 2007a](#).

Deployment Date	Latitude (N)	Longitude (W)	Deployment ID	Minutes for $g(0)$ estimation	Sampling Interval (sec)	Percent of time within 1 m of surface
9/29/2005*	37.608	122.717	1	153	5	0.456
9/30/2005*	37.550	122.593	2	168	5	0.498
10/13/2005*	37.548	122.593	3	228	5	0.460
9/12/2007	37.568	122.670	4	213	10	0.877
9/13/2007	37.603	122.708	6	376	10	0.711
9/23/2007	37.235	122.501	7	226	30	0.386
9/24/2007	37.283	122.527	8	2574	30	0.507
9/26/2007	37.270	122.480	9	231	4	0.490
9/30/2007	37.549	122.700	11	44	2	0.656
9/4/2008	37.668	122.658	13	344	4	0.543
9/4/2008	37.618	122.620	14	205	4	0.837
10/13/2008	37.687	122.872	15	38	4	0.755
10/14/2008	37.684	122.771	16	49	4	0.426
10/14/2008	37.695	122.759	17	49	4	0.388
10/7/2010	36.792	121.924	18	41	2	0.287
10/14/2011	36.924	122.104	19	35	2	0.845
9/7/2013	36.855	121.863	20	54	2	0.905
9/7/2013	36.909	121.925	21	257	2	0.720
9/23/2013	37.575	122.833	24	107	2	0.752
9/27/2013	37.607	122.674	25	55	2	0.673
9/28/2013	37.603	122.563	27	818	20	0.576
					Mean	0.607
					S.E.	0.040
					CV	0.065

period and revealed unexpected asynchrony, with a weak negative correlation (Pearson's $r = -0.268$). The two largest peaks in brown sea nettle CPUE (1992 and 2010–2011) occurred during years with low leatherback abundance (Fig. 5). Conversely, the three years with peak leatherback abundance (1990, 1999, 2016) had relatively low CPUE of brown sea nettles.

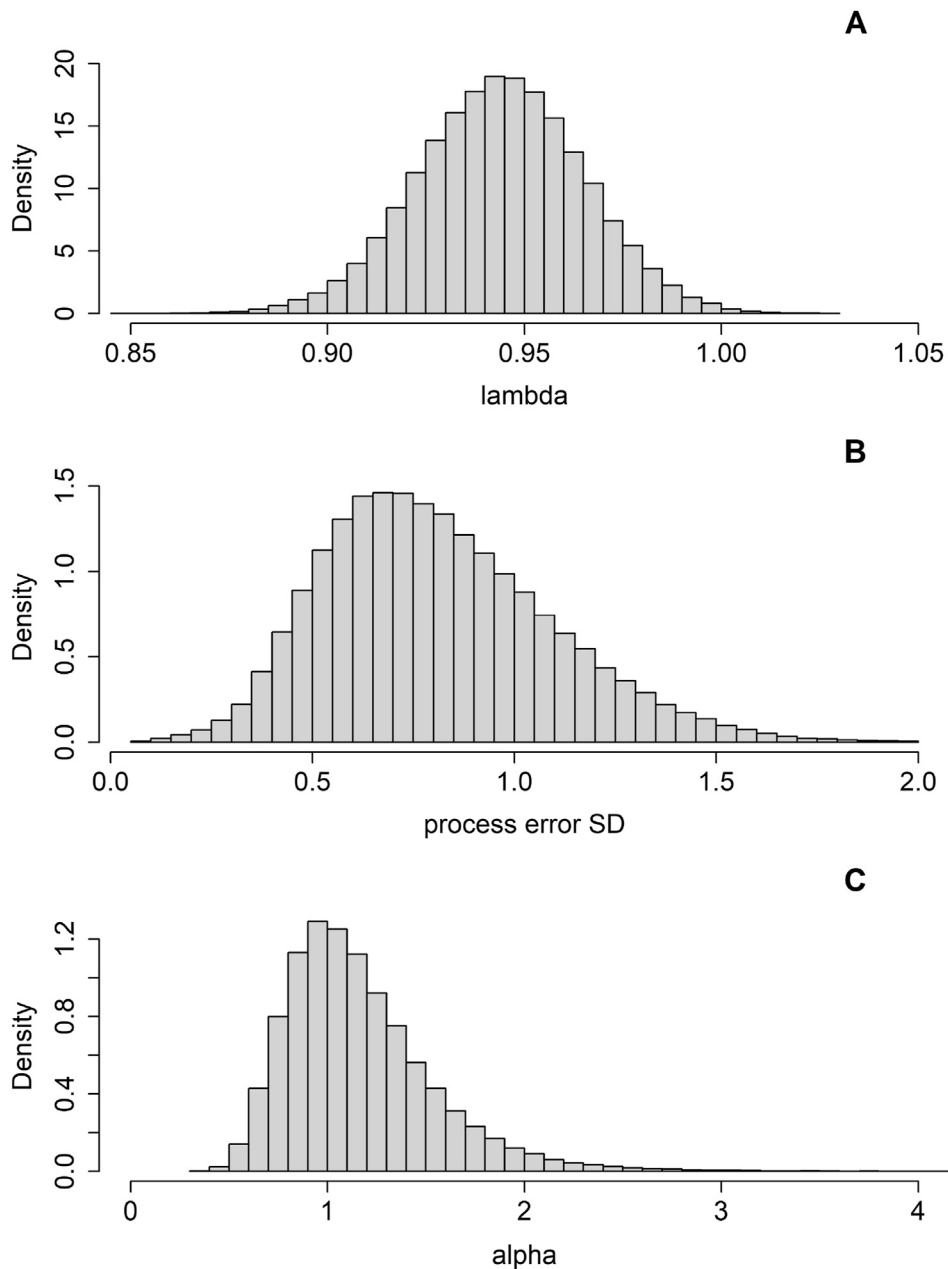


Fig. 2. Posterior distributions for (A) the realized growth rate, λ ; (B) the process error SD, $\sigma_{process}$; (C) the overdispersion parameter, α .

4. Discussion

4.1. Leatherback abundance patterns

The Bayesian hierarchical framework applied in this study combined data from relatively coarse, coast-wide surveys (HPAS transects) with data from adaptive fine-scale surveys within areas of greatest leatherback occurrence. The resulting abundance estimates are similar to previous estimates for 1990–2003 (Benson et al., 2007a), but the addition of adaptive transects and the improved estimate of $g(0)$ have allowed us to achieve robust annual abundance estimates for trend estimation within a highly variable ecosystem.

Leatherback abundance off California varies inter-annually, because individual turtles spend almost two years migrating to the nesting beaches and back, and subsequently return to the foraging grounds during one or more consecutive years. Variable habitat conditions and within-season foraging success likely determine the number of foraging seasons each

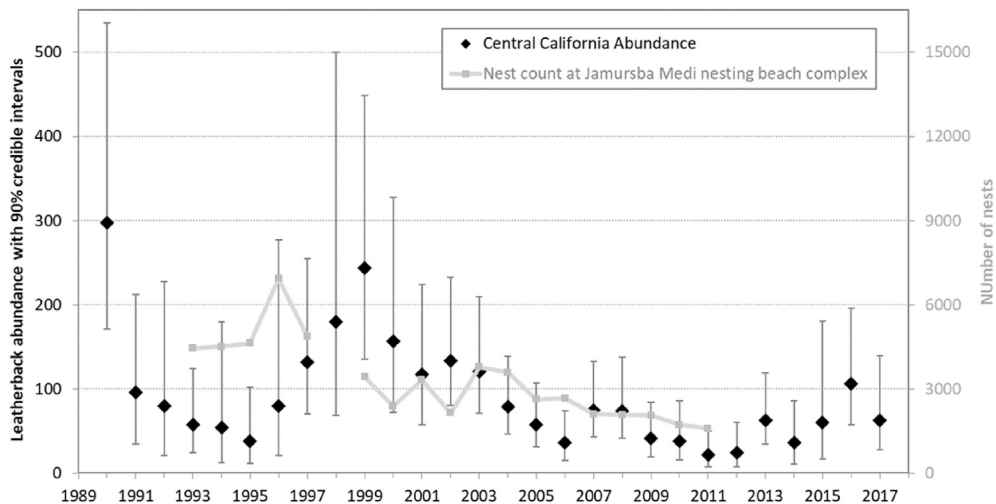


Fig. 3. Estimated leatherback abundance off central California, 1990–2017 (black diamonds, with 90% credible intervals; see Supplemental Table S2), and summer nest counts (gray line) at the largest remaining western Pacific nesting beach complex (Jamursba Medi, Birds Head Peninsula, Indonesia; from Tapilatu et al., 2013) for comparison.

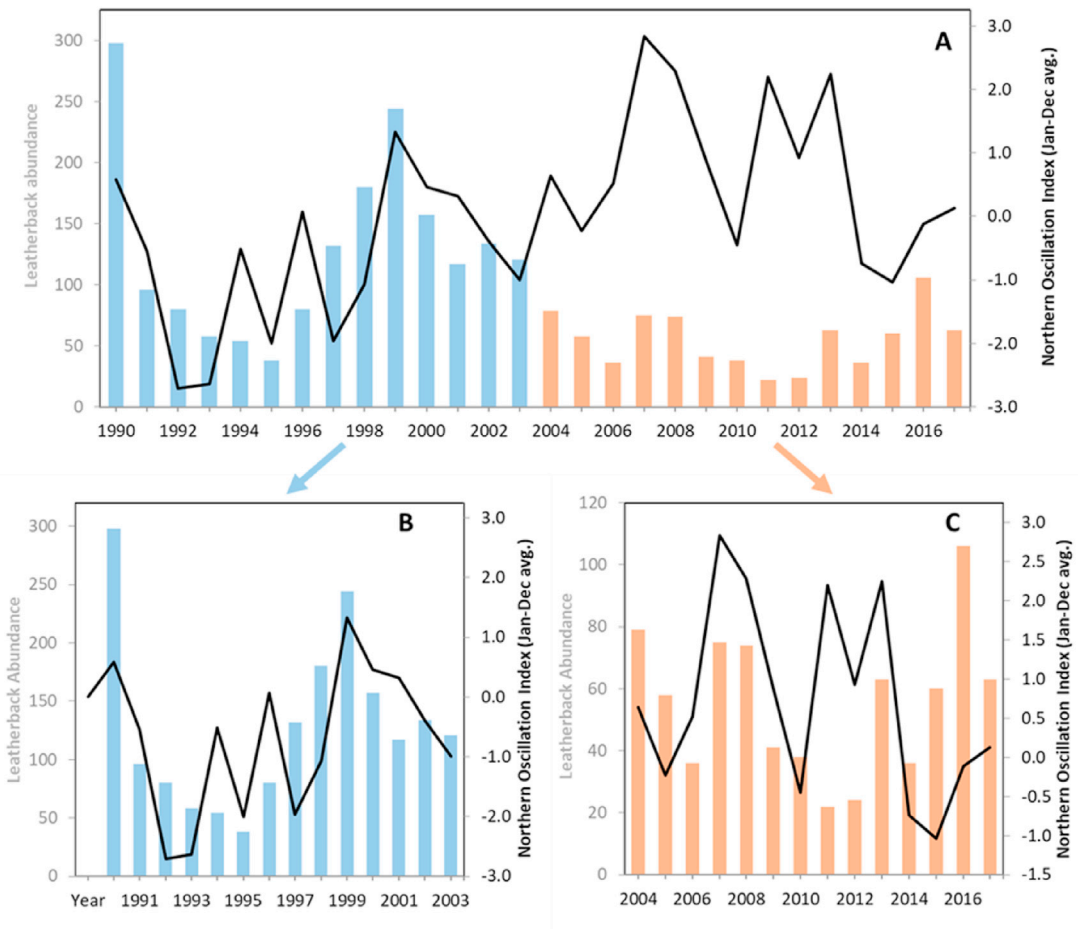


Fig. 4. Estimated leatherback abundance off central California, 1990–2017 (bars) relative to the average annual Northern Oscillation Index (black line), which was previously correlated with abundance during 1990–2003 (blue bars; Benson et al., 2007a). Panel (A) shows 1990–2017 on a single common y-axis scale, while panels (B) and (C) are scaled according to the range of abundances during 1990–2003 (blue) and 2004–2017 (orange), respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

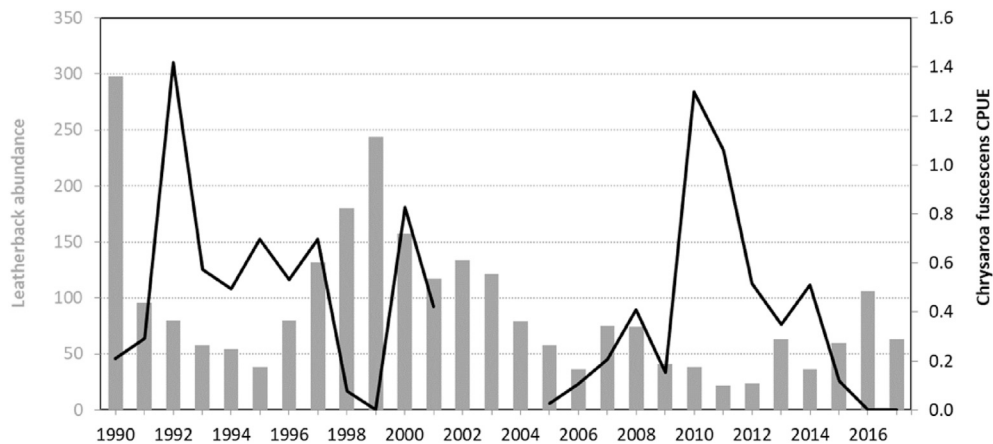


Fig. 5. Estimated leatherback abundance off central California, 1990–2017 (gray bars) relative to brown sea nettle (*Chrysaora fuscescens*) catch per unit effort (CPUE = $\ln(\text{catch}+1)$) within a standard 15-min trawl (black line) during NOAA's Rockfish Recruitment and Ecosystem Assessment Surveys (Ralston et al., 2013).

individual leatherback requires to meet energetic demands for reproduction, growth and migration (Lutcavage and Lutz, 1986; Rivalan et al., 2005; Saba et al., 2007; Benson et al. 2007b, 2011; Jones et al., 2012; Avens et al., 2020). Thus, the total number of leatherback turtles at California foraging grounds each year represents a subset of the entire California foraging cohort, with the remaining individuals engaged in migration to or from the distant nesting beaches. Currently, there are insufficient data to estimate what proportion of the total western Pacific leatherback population is foraging off central California on an annual basis, nor how many unique individuals are in the California foraging cohort.

The apparent cyclical patterns within our abundance time series (peaking roughly every eight years; Fig. 3) may reflect the above-described life-history patterns as well as variation in ocean productivity and forage conditions, although the magnitude of the peaks has declined. The results of our analysis indicate a long-term decline in the abundance of foraging central California leatherbacks, at an estimated rate of -5.6% per year or a total of -80% from 1990 to 2017.

4.2. Habitat conditions

Habitat conditions in the study area do not appear to be responsible for the declining trend, because we found no evidence of a deterioration of foraging habitat or prey abundance that might have caused a large-scale shift in leatherback use away from central California waters. The NOI and brown sea nettle CPUE from trawl surveys were variable during 1990–2017; however, neither indicated a systematic ecosystem change that might have influenced leatherbacks to become less abundant in the study area. Positive NOI values correspond with conditions favorable for upwelling along the California coast, leading to increased zooplankton production (Schwing et al., 2002). During 1990–2003, leatherback turtle abundance off California exhibited a positive relationship with the average annual NOI (Benson et al., 2007a). The NOI peaked in 2007, 2011, and 2013; however, leatherback abundance did not show a corresponding increase. Brown sea nettles are the primary prey item for leatherback turtles in neritic central California waters (Benson et al., 2007a; Hetherington et al., 2019). Data from trawl surveys of brown sea nettles did not correlate well with leatherback abundance at an inter-annual scale. For example, brown sea nettle CPUE was high in 2010–2011 when leatherback abundance was low. The poor correlation could be attributed to the patchy distribution of brown sea nettles in the California Current Ecosystem (Graham et al., 2001; Suchman and Brodeur 2005), and/or a spatio-temporal mismatch between the spring brown sea nettle trawls and summer/fall leatherback sampling. Despite the lack of within year correlation and high inter-annual variability, brown sea nettle trawl data did not show any systematic, long-term reduction in prey availability that could explain the long-term decline of leatherbacks.

4.3. Comparison to nesting beach trends

The long-term trend in the annual number of foraging leatherback turtles off central California (-5.6%) is similar to findings at the largest remaining nesting beach complex in the western Pacific, where most California leatherbacks originate (Dutton et al., 2000; Benson et al., 2011). Tapilatu et al. (2013) estimated a -5.9% annual rate of decline during 1984–2011, and Martin et al. (2020) estimated a -6.1% annual rate of decline during 2001–2017. At first glance, it might seem surprising that the trend at a single foraging ground would closely mirror overall nesting beach trends, given that individual leatherback turtles exhibit site fidelity to specific, diverse foraging grounds throughout the Indo-Pacific Basin (Seminoff et al., 2012; Lontoh 2014) and anthropogenic threat levels vary geographically (e.g., Roe et al., 2014). However, hatchling dispersal studies (Gaspar et al., 2012; Gaspar and Lalire, 2017) have shown that all foraging regions used by summer-nesting leatherback turtles in the western Pacific are indeed directly linked to each other (and to the summer nesting beaches), because each cohort of

hatchlings may disperse to any or all of the foraging grounds, effectively reshuffling the population each generation. Thus, concordance between foraging-ground and nesting-beach trends is not unexpected, underscoring the critical danger of extinction faced by this population throughout its Pacific range. Adverse impacts on leatherbacks in one region will – over time – be felt across all regions.

4.4. Causes and potential solutions

Causes of the western Pacific leatherback population decline are multi-faceted, including fishery bycatch, harvesting of eggs and adults, habitat degradation of nesting beaches leading to poor recruitment (Tiwari et al., 2013; Martin et al., 2020), and potentially poorly understood effects of climate variability (Saba et al., 2008). Direct anthropogenic threats span many nations and international waters throughout most of the Pacific and Indo-Pacific Basins, given the enormous range of this leatherback population (Harrison et al., 2018). Programs to protect leatherbacks and enhance reproductive output at nesting beaches have been successful in the Atlantic (Dutton et al., 2005) and are ongoing in the western Pacific (Pakiding et al., 2020), but fishery bycatch remains a significant conservation challenge (Wallace et al., 2013b; Swimmer et al., 2017). Peatman and Nicol (2020) provide annual rough estimates of 600–1900 leatherbacks caught incidentally during 2003–2018 within the Western and Central Pacific Fishery Commission Convention Area, but caution that limited and uneven fishery monitoring introduces substantial uncertainty.

Successful recovery of western Pacific leatherbacks will require Pacific-wide measures and multi-national coordination to reduce impacts. Curtis et al. (2015) demonstrated a local Limit Reference Point (LLRP) approach for assessing regional levels of sustainable impacts to leatherbacks; these LLRPs can provide regional mitigation targets for the implementation of coordinated, Pacific-wide population stabilization or recovery efforts. Along the U.S. West Coast, the LLRP (i.e., the maximum allowable mortality limit) that would allow recovery of this population (if human-caused mortality was similarly limited throughout the population range) is 4.7 turtles per 5 years (approximately one per year). Within this region, leatherback bycatch in the swordfish drift gillnet fishery was reduced dramatically by a seasonal fishery closure within the Pacific Leatherback Conservation Area (PLCA) established in 2001. Prior to that time, 104 leatherbacks were estimated to have been killed or injured in this fishery during 1990–2000, averaging 9.5 per year (Carretta et al., 2019). In contrast, the estimate for 2001–2017 was seven leatherbacks (averaging 0.4 per year), a 93% reduction. However, unmonitored set gillnet and fixed-gear (pot or trap) fisheries continue to pose a risk of entanglement and death to leatherbacks at their foraging grounds within waters of the U.S. West Coast Exclusive Economic Zone (EEZ) (National Marine Fisheries Service and U.S. Fish and Wildlife Service, 2020).

Bycatch reduction efforts within and beyond U.S. waters can benefit from new technologies that have been implemented or are being tested in some fisheries. For example, the requirement to use 16/0 circle hooks and dehooking devices to release hooked turtles, along with several other measures, has reduced leatherback bycatch in the Hawaii-based shallow-set fishery by 84% (Swimmer et al., 2017). If these practices were adopted Pacific-wide by longline fisheries from all nations, the collective reduction in bycatch could make a substantial positive impact on leatherback turtle population trends (Gilman et al., 2006). Other experimental techniques, such as deep-set buoy gear being tested off the U.S. West Coast, may also contribute to leatherback recovery if these techniques are successful and economically feasible in other regions (Sepulveda et al., 2015). Lastly, models and analyses that take into account ocean conditions, fishery distributions, and leatherback movement patterns (e.g., Roe et al., 2014; Howell et al., 2015; Hazen et al., 2018) can inform fishery management decision-making and increase our understanding of how the dynamic nature of the marine environment, particularly in a changing climate, may affect bycatch risks to leatherback turtles.

5. Conclusion

This study presents the first evidence of a long-term decline in leatherback turtle abundance at a major foraging ground along the U.S. West Coast. The estimated –5.6% annual rate of decline in the number of leatherbacks foraging off central California between 1990 and 2017 corresponds to an overall decline of 80% during the 28-year period. Our updated analysis provides an average estimate of 128 leatherbacks foraging off central California each year during the first half of our time series, 1990–2003, similar to the Benson et al., 2007a estimate of 140 but slightly lower because of the updated estimate of availability bias ($g(0)$). From 2004 to 2017, however, the average number of leatherbacks off central California dropped to 55 individuals, despite evidence from the NOI and sea nettle trawl samples that foraging conditions continued to be favorable. These results highlight the value of long-term monitoring to establish population trends, particularly for species like leatherbacks that have complex migration and life history characteristics. Our study's findings underscore the urgent need to increase leatherback conservation efforts throughout this population's range to avoid a continued population decline and the eventual extirpation of the western Pacific leatherback.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01371>.

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