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Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*

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Abstract. The western Pacific leatherback turtle (*Dermochelys coriacea*), one of three genetically distinct stocks in the Indo-Pacific region, has declined markedly during past decades. This metapopulation nests year-round at beaches of several western Pacific island nations and has been documented through genetic analysis and telemetry studies to occur in multiple regions of the Pacific Ocean. To provide a large-scale perspective of their movements, high-use areas, and habitat associations, we report and synthesize results of 126 satellite telemetry deployments conducted on leatherbacks at western Pacific nesting beaches and at one eastern Pacific foraging ground during 2000–2007. A Bayesian switching state-space model was applied to raw Argos-acquired surface locations to estimate daily positions and behavioral mode (either transiting or area-restricted search) for each turtle. Monthly areas of high use were identified for post-nesting periods using kernel density estimation. There was a clear separation of migratory destinations for boreal summer vs. boreal winter nesters. Leatherbacks that nested during boreal summer moved into Large Marine Ecosystems (LMEs) of the temperate North Pacific Ocean or into tropical waters of the South China Sea. Turtles that nested during boreal winter moved into temperate and tropical LMEs of the southern hemisphere. Area-restricted search occurred in temperate and tropical waters at diverse pelagic and coastal regions exhibiting a wide range of oceanographic features, including mesoscale eddies, coastal retention areas, current boundaries, or stationary fronts, all of which are known mechanisms for aggregating leatherback prey. Use of the most distant and temperate foraging ground, the California Current LME, required a 10–12 month trans-Pacific migration and commonly involved multiple years of migrating between high-latitude summer foraging grounds and low-latitude eastern tropical Pacific wintering areas without returning to western Pacific nesting beaches. In contrast, tropical foraging destinations were reached within 5–7 months and appeared to support year-round foraging, potentially allowing a more rapid return to nesting beaches. Based on these observations, we hypothesize that demographic differences are likely among nesting females using different LMEs of the Indo-Pacific. The differences in movements and foraging strategies underscore the importance of and the need for ecosystem-based management and coordinated Pacific-wide conservation efforts.

Key words: California, USA; *Dermochelys coriacea*; foraging habitat; Indo-Pacific; movements; Papua Barat Indonesia; Papua New Guinea; satellite telemetry; seasonality; Solomon Islands; state-space model; western Pacific leatherback.

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Introduction

The conservation of wide-ranging marine species has recently received increasing attention as awareness has grown that anthropogenic activities are affecting species far away from coastal areas (Hyrenbach et al. 2000, Ferraroli et al. 2004, Lewison et al. 2004, Halpern et al. 2008). Telemetry studies have provided insight into the movements of diverse marine predators including sharks, tunas, pinnipeds, whales, seabirds, and turtles (Shaffer et al. 2006, Bailey et al. 2009, Walli et al. 2009, Jorgensen et al. 2010, Simmons et al. 2010, Witt et al. 2011). In some cases, the results of such studies have contributed to the development of conservation strategies (e.g., Howell et al. 2008).

Leatherback turtles (*Dermochelys coriacea*) are found worldwide in pelagic and neritic waters of temperate and tropical regions. Their large range and extensive movements spanning entire ocean basins and national waters of many countries has complicated conservation and management efforts that are largely local or national in nature (Dutton and Squires 2008). Primary threats have included intentional harvest and habitat degradation at nesting beaches and incidental catch in coastal and pelagic fisheries (Suarez and Starbird 1996, Spotila et al. 2000, Dutton et al. 2007, Hitipeuw et al. 2007). Effective conservation efforts require a combination of protection of leatherback turtles at nesting beaches and knowledge of at-sea movement patterns and areas of high use (Benson et al. 2007*b*, Shillinger et al. 2008). This is particularly important for Pacific leatherback turtles, which are Critically Endangered (Sarti Martinez 2000) and have experienced severe declines at several nesting beaches during the past two decades (Crowder 2000, Spotila et al. 2000). Genetic studies (Dutton et al. 1999, 2007) have identified three distinct stocks of leatherback turtles in the Pacific: (1) an eastern Pacific stock that nests primarily in Mexico and Costa Rica, (2) a western Pacific stock that is known to nest in Papua Barat, Indonesia (PBI), Papua New Guinea (PNG), Solomon Islands (SI), and Vanuatu, and (3) a Malaysian stock. The most dramatic declines have been well-documented in the eastern Pacific (Spotila et al. 1996, 2000) and in Malaysia, where the population is now considered functionally extinct (Chan and Liew 1996). Less severe declines at western Pacific beaches have been inferred from recent nesting counts and anecdotal reports by nearby villagers (Hitipeuw et al. 2007).

Eastern Pacific leatherback turtles nest during the boreal winter (December–March), and post-nesting movements have been documented from beaches in Mexico and Costa Rica to pelagic waters of the eastern South Pacific (Eckert and Sarti 1997, Shillinger et al. 2008). In contrast, western Pacific leatherback turtles form a diverse metapopulation that nests year-round at beaches scattered across several western Pacific island nations and has been documented through genetic analysis and telemetry studies to occur in multiple regions of the Pacific, including waters of the eastern and central North Pacific, the western South Pacific, the South China Sea, and the Sea of Japan (Dutton et al. 2000, 2007, Benson et al. 2007*a*, *c*). Linkages have not yet been established between other areas of the Indo-Pacific region where leatherback turtles are known to occur (e.g., Kei Island, Indonesia; Suarez and Starbird 1996) or waters off both coasts of Australia (Robins et al. 2002, Limpus 2009). The objective of this study is to synthesize results of telemetry deployments conducted during 2000–2007 on leatherback turtles at multiple western Pacific nesting beaches and one northeastern Pacific foraging ground, to provide a large-scale perspective of movements,

high-use areas, and habitat associations of the western Pacific metapopulation. Nesting beach deployments were conducted during both the boreal winter (December–February, henceforth 'Winter') and the boreal summer (July–August; 'Summer') to provide information on year-round movement patterns of this leatherback turtle metapopulation. The comprehensive nature of this study is intended to provide a broad ecological context in support of conservation and management of this species.

Materials and Methods

Field methods

We selected tagging locations and dates based on knowledge of reliable occurrence of nesting or foraging leatherback turtles. Telemetry deployments at nesting beaches included two beaches along the northern Bird's Head coast in PBI (Jamursba-Medi, 0°21′ S, 132°33′ E; Wermon; 0°26′ S, 132°50′ E), two beaches in the Huon Gulf of PNG (Kamiali Wildlife Management Area, 7°16′ S, 147°8′ E; and Maus Buang, 6°54′ S, 146°57′ E), and three beaches in SI (Sasakolo, Santa Isabel Island, 7°48′ S, 158°41′ E; Litoghahira, Santa Isabel Island, 7°54′ S, 158°48′ E; Baniata, Rendova Island, 8°38′ S, 157°15′ E). Deployments were concentrated after the peak of each nesting season to maximize the amount of post-nesting movement data. We also conducted at-sea captures and telemetry deployments in neritic waters of Monterey Bay and San Mateo County, California, USA (approximately 37° N, 122° W). Between 2000 and 2007, we deployed a total of 89 tags at nesting beaches and 37 at the foraging grounds (Table 1).

We deployed a variety of satellite-linked transmitters on leatherback turtles during the study period, including the following platform transmitter terminals (PTT) models: Wildlife Computers (Washington, USA) SDR-SSC3 (n = 21), MK10 (n = 11), SDR-T16 (n = 9), SPLASH (n = 7), SPOT2 (n = 1), SPOT3 (n = 3), and SPOT5 (n = 3); Telonics (Arizona, USA) ST14 (n = 2), ST18 (n = 3) and ST20 (n = 14); Sirtrack (New Zealand) Kiwisat 101 (n = 23); and Sea Mammal Research Unit (SMRU, U.K.) Satellite Relay Data Logger (SRDL) (n = 29). All PTTs featured a salt-water switch that suppressed transmission while submerged and were duty-cycled to optimize battery life, reporting positions via the Argos system every 1–3 d.

We attached PTTs to leatherback turtles with the aid of a flexible harness (Eckert and Eckert 1986) that consisted of soft nylon webbing with flexible polyvinyl tubing over the shoulder straps and a corrodible pin designed to release the harness within 18–24 months. Before attaching transmitters we visually assessed each turtle for signs of injury or compromised health and only selected turtles that appeared to be in normal condition. To minimize impacts on nesting females, we waited until turtles began laying eggs, well into the nesting process when females enter a trance-like state, before sampling and attaching the transmitters. At the California foraging grounds, we located male and female leatherback turtles with the aid of a spotter aircraft and captured them from a boat using a specially designed break-away hoop. Our primary capture boat was a 9-m aluminum Munson, which featured a custom made bowsprit that provided a platform for deploying the hoopnet as well as a retractable bow that when lowered to the waterline provided access to the captured turtles and a slide for pulling them on board. Once the turtle was on board, we measured curved carapace length (CCL) and width (CCW), applied PIT and flipper tags (Dutton and McDonald 1994, Bolten 1999), and attached the harness.

Analytical methods

State-space model.—We applied a Bayesian switching state-space model (SSSM) to all of the raw Argos-acquired surface locations for each of the leatherback turtle tracks to obtain daily position estimates. The SSSM is a time-series model that accounts for Argos errors and estimates at regular time intervals the most likely true location and the animal's behavior (Jonsen et al. 2005, Bailey et al. 2008, Patterson et al. 2008). This method couples two models, the measurement and transition equations. The measurement equation accounts for the errors in the observed satellite locations, indicated by the Argos location quality classes and based on published estimates (Vincent et al. 2002). The transition equation is based on a correlated random walk model and includes a process model for each of two behavioral modes (Jonsen et al. 2005). The

Table 1. Summary of telemetry deployments by location and deployment group, 2000–2007.

Metric	2000	2001	2002	2003	2004	2005	2006	2007	Total
Foraging (n = 37)									
CCA									
No. deployments	2	2	8	6	7	5	...	7	37
Durations (days)									
Mean	252	72	288	245	318	98	...	327	255
SD	286	55	219	124	212	75	...	46	172
Min	49	33	65	96	46	47	...	268	33
Max	454	111	769	463	648	225	...	416	769
Summer nesting (n = 44)									
PBI-J									
No. deployments	...	...	...	9	2	11	3	14	39
Durations (days)									
Mean	...	...	...	241	84	293	304	266	261
SD	...	...	...	167	103	222	36	165	175
Min	...	...	...	79	11	9	272	10	9
Max	...	...	...	639	157	531	343	520	639
PBI-W									
No. deployments	...	...	...	...	...	...	5	...	5
Durations (days)									
Mean	...	...	...	...	...	...	327	...	327
SD	...	...	...	...	...	...	207	...	207
Min	...	...	...	...	...	...	69	...	69
Max	...	...	...	...	...	...	645	...	645
Winter nesting (n = 45)									
PBI-W									
No. deployments	...	...	...	...	...	13	...	5	18
Durations (days)									
Mean	...	...	...	...	...	210	...	323	241
SD	...	...	...	...	...	103	...	28	102
Min	...	...	...	...	...	62	...	294	62
Max	...	...	...	...	...	346	...	360	360
PNG									
No. deployments	...	7	...	9	...	1	...	...	17
Durations (days)									
Mean	...	62	...	71	...	10	...	...	64
SD	...	43	...	72	...	n/a	...	...	59
Min	...	9	...	5	...	n/a	...	...	5
Max	...	110	...	241	...	n/a	...	...	241
SI									
No. deployments	...	...	...	...	...	...	10	...	10
Durations (days)									
Mean	...	...	...	...	...	...	271	...	271
SD	...	...	...	...	...	...	155	...	155
Min	...	...	...	...	...	...	28	...	28
Max	...	...	...	...	...	...	503	...	503

Notes: CCA = Central California, USA; PBI-J = Papua Barat, Indonesia (Jamursba-Medi); PBI-W = Papua Barat, Indonesia (Wermon); PNG = Papua New Guinea; SI = Solomon Islands. See text and Fig. 1 for location details. Mean durations are the number of days with positions derived from the state-space model. "..." indicates no data.

transition equation was specified as (Jonsen et al. 2007):

$$\mathbf{d}_t \sim N_2[\gamma_{b_t}\mathbf{T}(\theta_{b_t})\mathbf{d}_{t-1}, \mathbf{\Sigma}] \quad (1)$$

where $\mathbf{d}_{t\text{-}1}$ is the distance between the locations $\mathbf{x}_{t\text{-}1}$ and $\mathbf{x}_{t\text{-}2}$ and $\mathbf{d}_t$ is the difference between $\mathbf{x}_t$ and $\mathbf{x}_{t-1}$. N_2 is a bivariate Gaussian distribution with covariance matrix $\mathbf{\Sigma}$ that represents the randomness in the animal's behavior (Breed et al. 2009). The parameter γ is the autocorrelation in speed and direction, ranging from 0 to 1. $\mathbf{T}(\theta)$ is a transition matrix that provides the rotation required to move from $\mathbf{d}_{t-1}$ **to** $\mathbf{d}_t$, where θ is the mean turning angle. The index b_t denotes the behavioral mode, where mode 1 is considered to represent transiting or migration, and mode 2 is indicative of inter-nesting, foraging or area-restricted search behavior (Bailey et al. 2008, 2009). Area-restricted search (ARS) is based on the hypothesis that once an animal encounters prey, it will remain within the area by increasing its turning angle and/or decreasing its speed (Kareiva and Odell 1987). We specified prior distributions on the parameters in the model

assuming that during migration turn angles should be closer to 0 and autocorrelation in speed and direction should be higher than when foraging (Jonsen et al. 2007).

We ran the model using the R software package (R Development Core Team 2008) and WinBUGS software (Lunn et al. 2000). We ran two chains in parallel, each for a total of 20,000 Markov Chain Monte Carlo samples, with the first 15,000 discarded as a burn-in and the remaining samples thinned, retaining every tenth sample to reduce autocorrelation. Thus, posterior distributions for each parameter were based on 500 samples from each chain, giving a total of 1000 independent samples. When there were 20 or more days of missing satellite positions, we removed the corresponding SSSM positions and divided the track into sections, as the error in the SSSM mean positions increases rapidly when there are such large data gaps (Bailey et al. 2008). 'Effective transmission durations' for each track were defined as the total number of daily positions estimated from the SSSM. From the model output we obtained the mean position estimates, their 95% credible limits (a measure of uncertainty), and posterior distributions of behavioral mode at daily intervals.

In a previous study of leatherback turtle behavior derived from satellite telemetry data, Jonsen et al. (2007) classified mean behavioral modes below 1.25 as transiting and values greater than 1.75 as foraging or inter-nesting behavior. Values between 1.25 and 1.75 were classified as uncertain. In this study, rather than discarding locations with intermediate values, we used the posterior distribution of behavioral mode for each daily location to compute a daily probability of transit (P_{tran}). This is similar to the approach of Jonsen et al. (2005) and Bailey et al. (2008), but provides a probability of transit to infer transiting or foraging/inter-nesting behavior. Locations with a probability of transit less than or equal to 0.5 ($P_{tran} \leq 0.5$) were considered to represent ARS behavior, whereas locations with $P_{tran} > 0.5$ were considered to indicate transiting behavior.

Kernel density estimation.—We used kernel density estimation (KDE) to identify areas of high use and examined temporal patterns based on further stratification of the data. We initially scrutinized the locations determined by the state-space models to separate inter-nesting and non-nesting periods for those transmitters deployed at nesting beaches. We determined high-use areas near nesting beaches by computing a kernel density for periods representing inter-nesting data, whereas for ARS and transit behavior we excluded inter-nesting periods. For all KDE analyses, resolutions and bandwidths were selected by trial and error, starting from the values given by the Normal Reference Rule (Scott 1992). Because of the sparse data points in some areas, it was not possible to estimate these parameters for each location. We used the same value for all areas, which allowed us to compare the spatial spread of the estimated density among locations without the influence of different parameter values. The selected combinations provided smooth contours at the spatial scales of interest without locally manipulating the parameters. For the inter-nesting periods, we separated locations into summer and winter nesting according to the deployment records (Table 1), and we used a resolution of 0.05 degrees in latitude and longitude and a bandwidth of 0.3 degrees. For periods of transit or ARS behavior, which spanned a much broader geographic area, we used a resolution of 0.5 degrees in latitude and longitude and a bandwidth of 1.5 degrees in latitude and longitude. To determine temporal changes in the distributions of leatherback turtles throughout the Pacific, we divided locations outside of inter-nesting periods into 12 temporal strata of 30 or 31 d, roughly corresponding to calendar months. Within each temporal stratum, we categorized data and KDE results as ARS or transit behavior according to the probability of transit described previously.

Characterization of habitat use.—We obtained a suite of habitat variables that have previously been linked to the distribution of marine turtles (e.g., Polovina et al. 2000, 2001, 2004, Shillinger et al. 2008), including bathymetric depth, sea surface temperature (SST), Chlorophyll-a concentration (CHL), sea surface height (SSH) variation (as measured by SSH root-mean-square, SSHrms), eddy kinetic energy (EKE), and Ekman pumping (EKP). We averaged Pathfinder version 5 SST (Kilpatrick et al. 2001) and CHL from the Moderate Resolution Imaging Spectrometer (MODIS) (O'Reilly et al. 2000) within the 95% credible limits for each daily

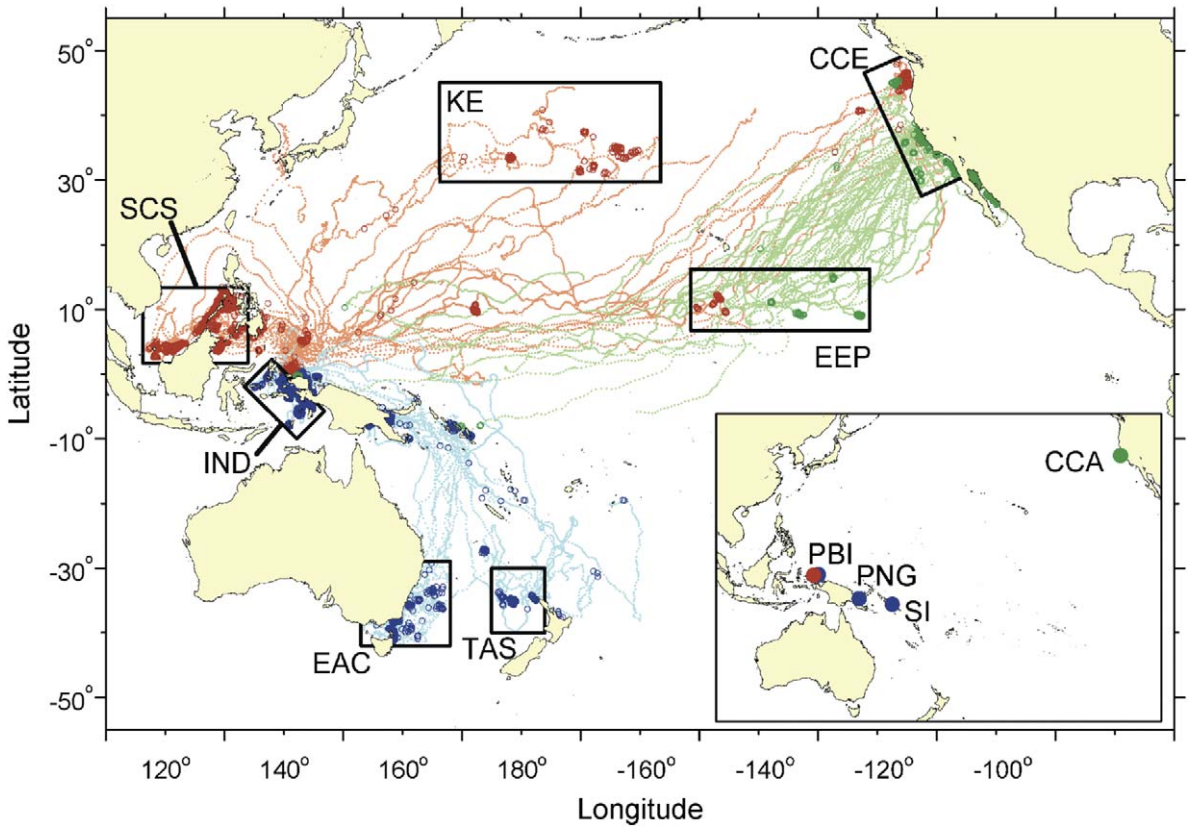

Fig. 1. All 126 deployments presented as probability of transit. Large, darker circles indicate Area Restricted Search (ARS) behavior; small, lighter dots indicate transiting behavior. Color of track indicates deployment season: red = summer nesters, blue = winter nesters, green = deployments at central California foraging grounds. Inset shows deployment locations; PBI = Papua Barat, Indonesia, PNG = Papua New Guinea, SI = Solomon Islands, CCA = central California. Black boxes represent ecoregions for which habitat associations were quantitatively examined (see text): SCS = South China, Sulu and Sulawesi Seas, IND = Indonesian Seas, EAC = East Australia Current Extension, TAS = Tasman Front, KE = Kuroshio Extension, EEP = equatorial eastern Pacific, and CCE = California Current Ecosystem.

position from the SSSM using an 8-d temporal composite centered on the position's date. Derived variables included SSHrms, calculated from the Archiving, Validation and Interpretation of Satellite Oceanographic Data (AVISO) SSH data located within a 2 × 2 degree box around the estimated daily position, and EKE, calculated as $1/2(U^2+V^2)$, where U and V are meridional and zonal geostrophic current components, respectively (Ducet et al. 2000). We also estimated EKP, a measure of wind-driven upwelling, from wind stress following the method of Xie and Hsieh (1995).

To identify habitat variables that are associated with ARS behavior within each region of interest (see Results and Fig. 1), we examined whether mean values of each variable differed for locations with transit behavior vs. ARS behavior using a two-sample permutation test (Efron and Tibshirani 1993). This type of test is free of many of assumptions associated with parametric tests, and provides a simple method for evaluating the significance of patterns within the data. We created permutation samples of all locations within each region (n = 10,000) by randomly shuffling the values of P_{tran} among all available locations. We then computed the mean value for each habitat variable for the permuted ARS locations to provide a distribution of the expected means if ARS behavior occurred randomly

among all available locations. The achieved significance level (ASL), defined as the probability of obtaining an outcome at least as extreme as the actual value, was estimated from the percentiles of the distribution of permuted means. An ASL of $P = 0.05$ provides reasonably strong evidence of a significantly non-random association of ARS behavior with respect to each habitat variable, while an ASL of $P = 0.01$ provides very strong evidence and $P = 0.10$ provides weak evidence (Efron and Tibshirani 1993). We plotted the permuted distributions, mean values for ARS locations in the actual tracks, and ASL values together by region and variable to show whether ARS behavior was associated with high or low values of each variable of interest.

Table 2. Mean (and standard error) posterior quantiles for the switching state-space model parameters, based on $n = 126$ leatherback telemetry tracks.

Parameter	Posterior quantiles		
	0.025	0.500	0.975
θ_1	−0.198 (0.026)	0.014 (0.014)	0.223 (0.026)
θ_2	2.222 (0.069)	3.241 (0.056)	4.268 (0.055)
γ_1	0.711 (0.007)	0.784 (0.005)	0.850 (0.003)
γ_2	0.291 (0.006)	0.477 (0.006)	0.669 (0.006)
α_1	0.770 (0.027)	0.909 (0.014)	0.987 (0.002)
α_2	0.055 (0.006)	0.338 (0.023)	0.671 (0.033)

Notes: θ is the mean turning angle in radians, and γ is the autocorrelation in speed and direction. The subscripts denote behavioral mode 1 and mode 2. The parameter α estimates the probability of switching between behavioral modes; α_1 is the probability of being in mode 1 at time t given it was also in this mode at time $t - 1$, and α_2 is the probability of being in mode 1 at time t given it was in mode 2 at $t - 1$.

Results

Telemetry results

We tagged similar numbers of leatherbacks during boreal winter nesting ($n = 45$), boreal summer nesting ($n = 44$), and boreal summer foraging periods ($n = 37$). Our summer deployments of PBI post-nesters occurred during July 2003, 2005–2007, and August 2004 at Jamursba-Medi ($n = 39$) and during July 2006 at Wermon ($n = 5$). Our winter post-nesting deployments were conducted during December 2001, February 2003, and January 2005 in PNG ($n = 17$), during February 2005 and January 2007 at Wermon, PBI ($n = 18$), and during December 2006 at SI ($n = 10$). PTT deployments from foraging grounds off central California occurred during August–September 2000–2005 and 2007 and included 27 females and 10 males. The 126 PTT deployments yielded transmission durations of 4 to 946 d, although data gaps and intermittent reporting resulted in shorter effective transmission durations. In some cases, including the longest deployment, there were transmission gaps lasting from several days to over one year, presumably because of biofouling on the PTT's saltwater switch. The switching state-space model parameters (Table 2) were similar to those previously reported for eastern Pacific and Atlantic leatherbacks (Bailey et al. 2008), and effective transmission durations ranged from 9 to 645 d with a mean duration of 269 d for boreal summer post-nesters, 5 to 503 d with a mean duration of 181 d for boreal winter post-nesters, and 33 to 769 d with a mean duration of 255 d for deployments at the California foraging grounds (Table 1). Combined, the tracks spanned large areas throughout the Pacific Ocean basin (Fig. 1).

Leatherback movements

Inter-nesting movements.—Although this study focused on post-nesting movements and high-use areas, we were also able to obtain some data on inter-nesting movements. Movements of female turtles immediately following PTT deployment at the nesting beaches were concentrated in waters adjacent to the beaches as individuals returned to lay additional clutches during the inter-nesting period (Fig. 2). Summer nesters at PBI primarily remained within 170–315 km of the nesting beaches, in waters between northwest Bird's Head Peninsula and the Raja Ampat Islands, while PBI winter nesters spent inter-nesting intervals between the northeastern coast of Bird's Head Peninsula and Cenderawasih Bay, within about 120–300 km of the nesting beach. Inter-nesting activity in PNG was mostly limited to the Huon Gulf, and turtles remained within 140–300 km of the nesting beach. Movements of SI leatherbacks were concentrated around Santa Isabel and Malaita Islands, and turtles traveled slightly farther from the nesting beaches (about 200–400 km). Upon completion of nesting activity, movements away from the beaches were diverse and differed notably by nesting season.

Post-nesting movements.—Among the PBI summer nesters with tracks of sufficient duration to

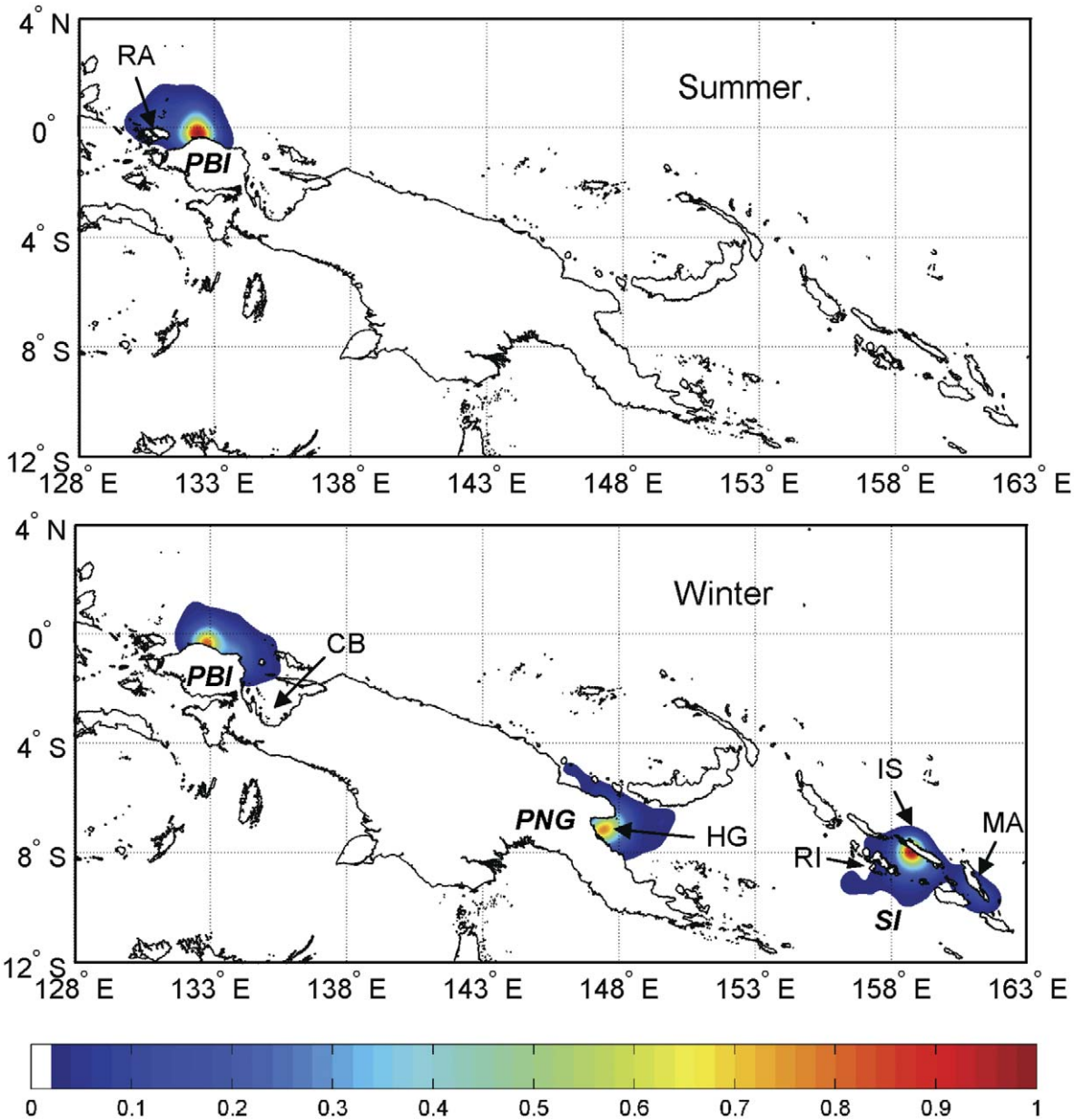

Fig. 2. High-use areas of western Pacific leatherbacks during inter-nesting periods, derived using kernel density estimation (KDE) for 89 satellite telemetry tracks from nesting deployments. Warmer colors represent greater KDE values. Locations are abbreviated as follows: PBI = Papua Barat, Indonesia (Bird's Head Peninsula), PNG = Papua New Guinea, SI = Solomon Islands, RA = Raja Ampat Islands, CB = Cenderawasih Bay, HG = Huon Gulf, IS = Santa Isabel Island, RI = Rendova Island, and MA = Malaita Island.

determine movement patterns ($n = 37$, Fig. 1), 23 (62%) initially moved east or northeastward towards the North Pacific. Sixteen of these turtles reached temperate North Pacific waters, approaching either the Kuroshio Extension region ($n = 6$) or the California Current Ecosystem ($n = 10$), with 5 leatherbacks completing trans-Pacific movements between the western Pacific and the west coast of North America. Seven turtles had tracks that were too short to identify specific

destinations within the North Pacific region. The second most frequent pattern (13 turtles, or 35%) involved westward movement to shelf regions of the South China Sea, adjacent to Malaysian Borneo and Palawan Island, Philippines. Access to the South China Sea was primarily through the Sulawesi and Sulu Seas (11 turtles), although two individuals entered the South China Sea from the north after passing through the Luzon Strait between Taiwan and the Philippines. One leatherback (3%) traveled northward into the Sea of Japan.

Among winter nesters, post-nesting movements (Fig. 1) of turtles tagged in PNG ($n = 17$) and SI ($n = 10$) were southward through the Coral Sea, into or approaching high-latitude waters of the western South Pacific Ocean or Tasman Sea. The only exception was one turtle from SI that moved westward through the Coral Sea and remained in tropical waters of the Gulf of Papua until transmission ceased after 266 d. Winter nesters from PBI with sufficiently long track durations ($n = 17$) exhibited two distinct movement patterns. Eleven (65%) moved westward around Bird's Head Peninsula and then south into the Halmahera, Ceram or Banda Seas, where they remained for weeks to months. The remaining six animals (35%) moved along the north side of New Guinea and then southeast into or approaching high latitude waters of the western South Pacific Ocean or Tasman Sea, similar to SI and PNG turtles.

Movements from California foraging grounds.— Movements of turtles captured and tagged at central California foraging areas were less diverse ($n = 37$; Fig. 1). Following release, 33 turtles (89%) moved immediately southwest towards the equatorial eastern Pacific (EEP), although three individuals (8%) initially moved northward and spent time in other areas off California or Oregon before moving towards the EEP. In addition, one male leatherback initially moved southwestward to about 26° N but then returned to southern California before moving south along Baja California, Mexico and into the Gulf of California. Once turtles reached the EEP, there were two dominant patterns of continued movement. Seven of the 25 turtles with tracks of sufficient duration (28%) continued moving westward, presumably towards western Pacific nesting beaches. Transmissions ceased prior to arrival at nesting beaches for all except two turtles, which nested at Santa Isabel Island (SI) the following May, and Jamursba-Medi (PBI) the following July, respectively. The majority (17 turtles, 72%), however, remained in the EEP for approximately 2–3 months and then moved back towards the California coast, typically arriving in the southern California Bight during spring and traveling nearshore as they approached the central California foraging areas from the south.

High-use post-nesting areas

The high-use post-nesting areas identified by the KDE (Fig. 3) represent areas with greater occurrence of ARS behavior by multiple tagged individuals or by some individuals for prolonged periods. The areas used represent diverse ecoregions with varying oceanic processes, and leatherbacks associated with different suites of habitat features across all regions. To examine the habitats and how leatherbacks use them, we defined seven ecoregions of interest in which ARS was observed frequently (Fig. 1). Each will be considered separately below to summarize associations between leatherbacks and regional habitat features, based on the permutation test results (Fig. 4).

Two tropical ecoregions, the South China, Sulu, and Sulawesi Seas (SCS) and Indonesian seas (IND), were associated with year-round ARS behavior that was highly concentrated in shallow waters adjacent to islands ($P < 0.001$, Figs. 4–5). Within the SCS, ARS behavior occurred for 59% of the daily locations, associated with warm water ($P < 0.001$), in lower EKP (downwelling, $P < 0.001$) and greater SSH variation ($P = 0.029$). There was no significant association with respect to CHL or EKE. There were two primary ARS areas within the SCS, one along the northern and western coasts of Palawan Island and one on the shelf off northwestern Borneo (Fig. 5). Leatherbacks engaged in ARS behavior off Palawan exhibited a seasonal shift (Fig. 3), arriving at the northern tip of Palawan Island (about 11° N and 119° E) in October–January, and then shifting southward along the western coast from June through September. In contrast, leatherbacks using the shelf off Borneo remained in the same area year-round. Some additional short-term ARS behavior was identified during September–January in the western Sulawesi Sea off Borneo

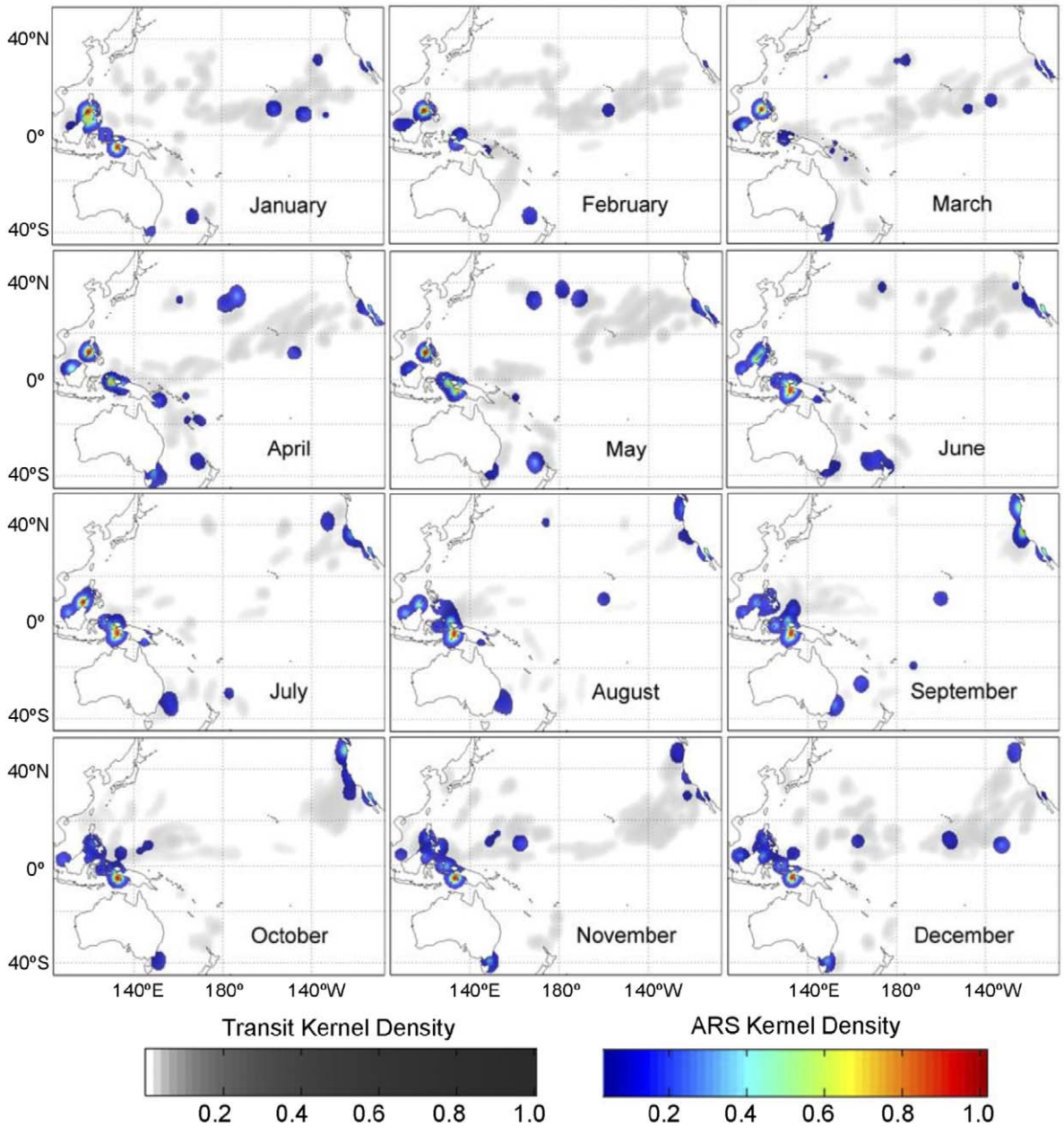

Fig. 3. High-use areas of western Pacific leatherbacks during post-nesting periods, derived using kernel density estimation for 126 satellite telemetry tracks. Blue-yellow-red indicates increasing density of ARS behavior (presumed foraging). Gray indicates transiting behavior.

and throughout the Sulu Archipelago. ARS behavior in the IND occurred for 78% of daily locations and was significantly associated with the coolest water ($P < 0.001$), high CHL ($P < 0.001$) and low EKE ($P < 0.001$), while EKP and SSH variation showed no relationship with ARS behavior. ARS behavior occurred year-round throughout the eastern Banda, Ceram, Halmahera, and Molucca Seas (Figs. 3, 5), with turtles moving among islands but exhibiting the most ARS behavior off the islands of Kei, Aru, Tanimbar, and Ceram.

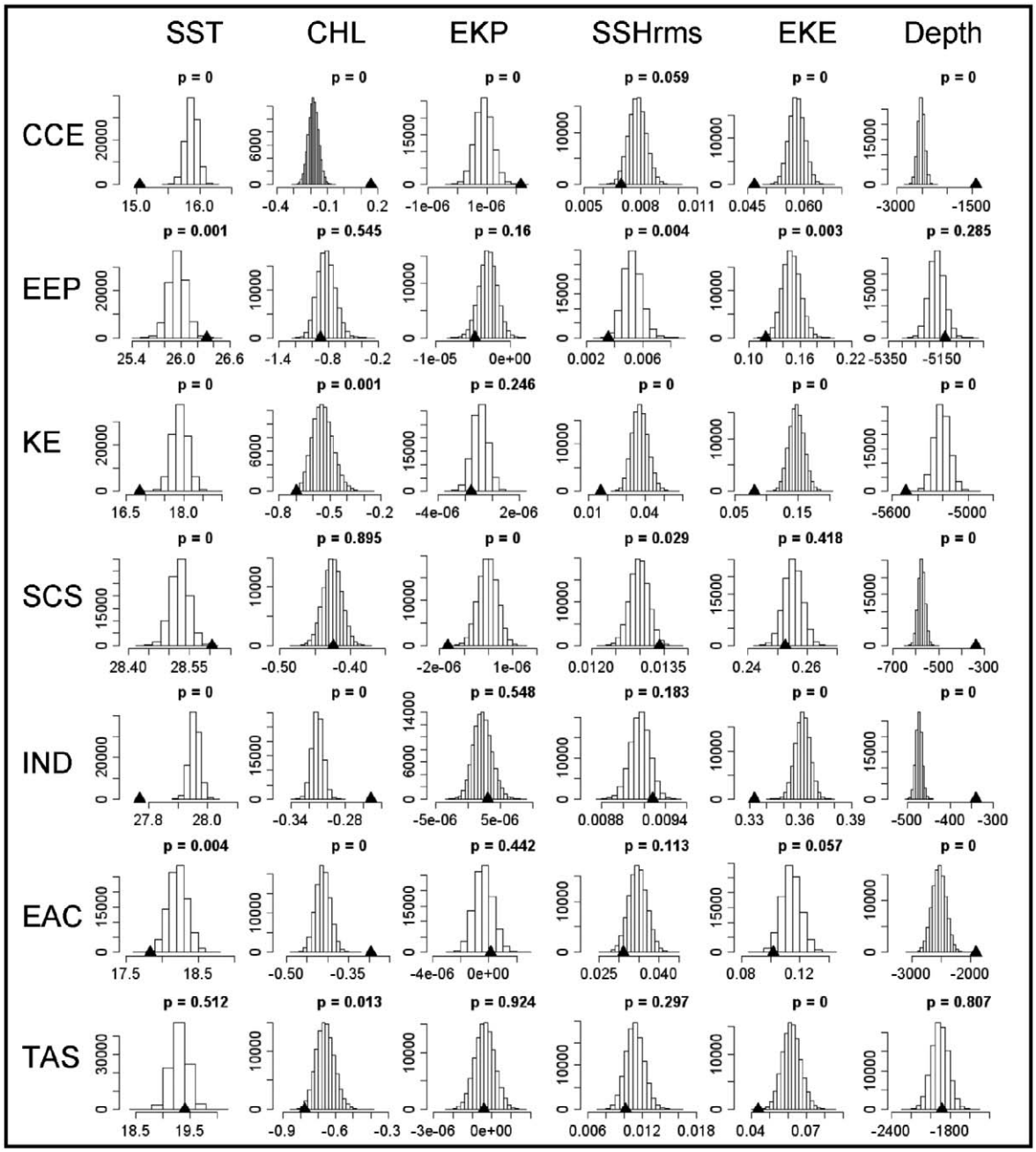

Fig. 4. Results of randomization tests for turtle locations within each ecoregion. Histograms represent means for random ARS behavior; triangles indicate means for actual ARS locations. See text for abbreviations for ecoregions and oceanographic variables.

Four ecoregions were occupied seasonally by leatherbacks exhibiting ARS behavior, including one tropical region (EEP) and three temperate regions: the California Current Ecosystem (CCE), the East Australian Current Extension (EAC), and the Tasman Front (TAS). Within the CCE, ARS behavior occurred in habitats that were cool, shallow, and characterized by high CHL, high EKP, and low EKE ($P < 0.001$ for all habitat variables, Fig. 4). SSH variation was only weakly

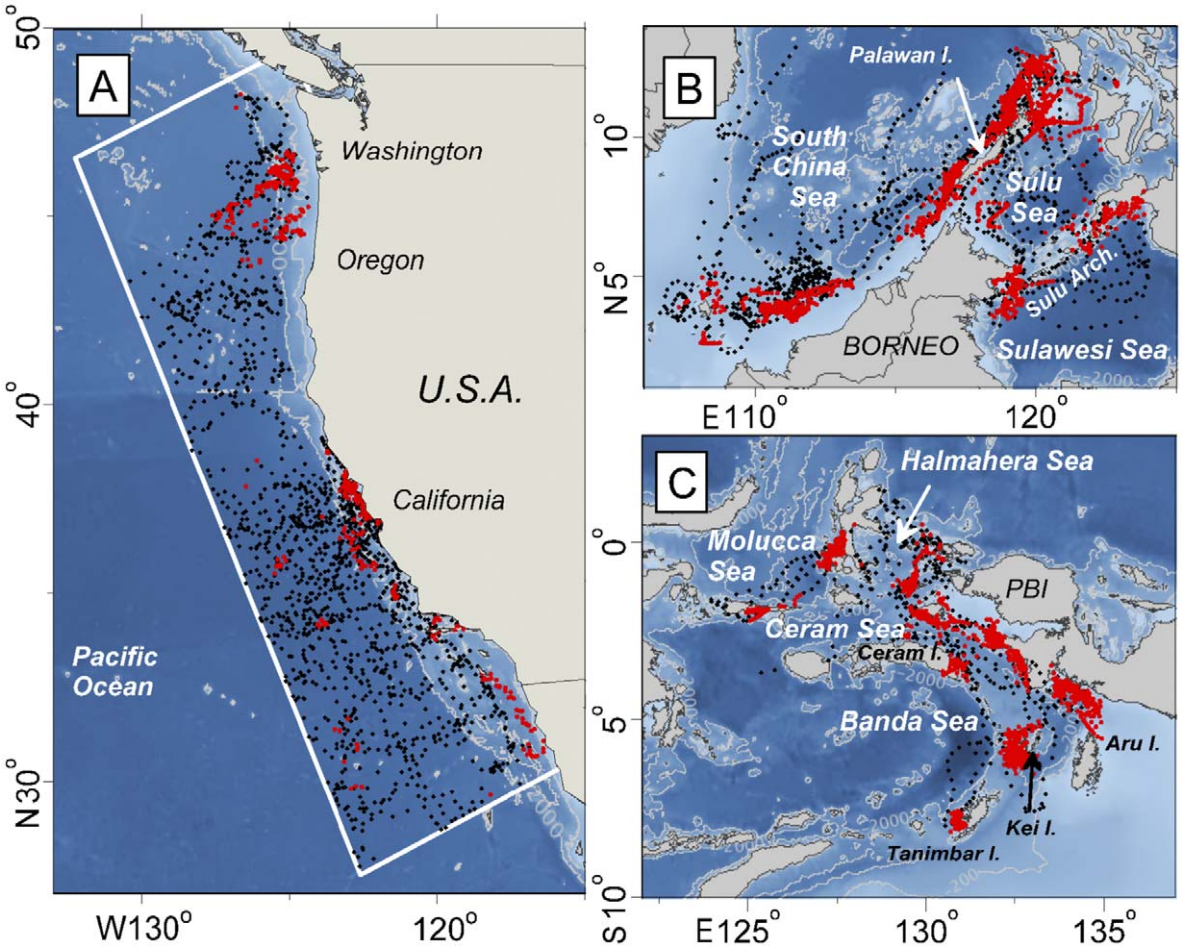

Fig. 5. Leatherback telemetry locations with ARS behavior (red dots) and transit behavior (black dots) relative to bathymetry in high-use areas (A) CCE ($n = 40$ turtles), (B) SCS ($n = 13$), and (C) IND ($n = 18$), with 200-m and 2000-m isobaths. Only locations within each defined ecoregion (Fig. 1) are included. PBI = Papua Barat, Indonesia (Bird's Head Peninsula).

associated with ARS behavior ($P = 0.059$) (Fig. 4). Seasonality was pronounced, with leatherbacks arriving in April–July and engaging in ARS behavior 21% of the time off California, Oregon, and Washington (USA) through late November. After departing these ARS areas, leatherbacks moved directly southwestwards into waters of the EEP, which they occupied seasonally from about December through April, until they either returned northeastward to the CCE or continued westwards towards nesting beaches. Within the EEP, less ARS behavior was identified (only 6% of daily locations), and it was associated with habitats characterized by low EKE ($P = 0.003$), low SSH variation ($P = 0.004$), and higher SST ($P = 0.001$). Some ARS behavior was also identified in the EEP during August–September for two post-nesting leatherback turtles as they crossed the Pacific.

We obtained fewer telemetry tracks for animals that moved to temperate southern hemisphere waters, but some seasonal patterns were nonetheless evident. Within the EAC, ARS behavior was identified for 23% of daily positions, primarily over cool ($P = 0.004$), shelf/slope waters ($P < 0.001$) with greater CHL ($P < 0.001$). EKE was weakly associated with ARS behavior ($P = 0.057$), while SSH variation and EKP were not significant ($P = 0.113$ and $P = 0.442$, respectively). ARS behavior was most frequent in high-latitude

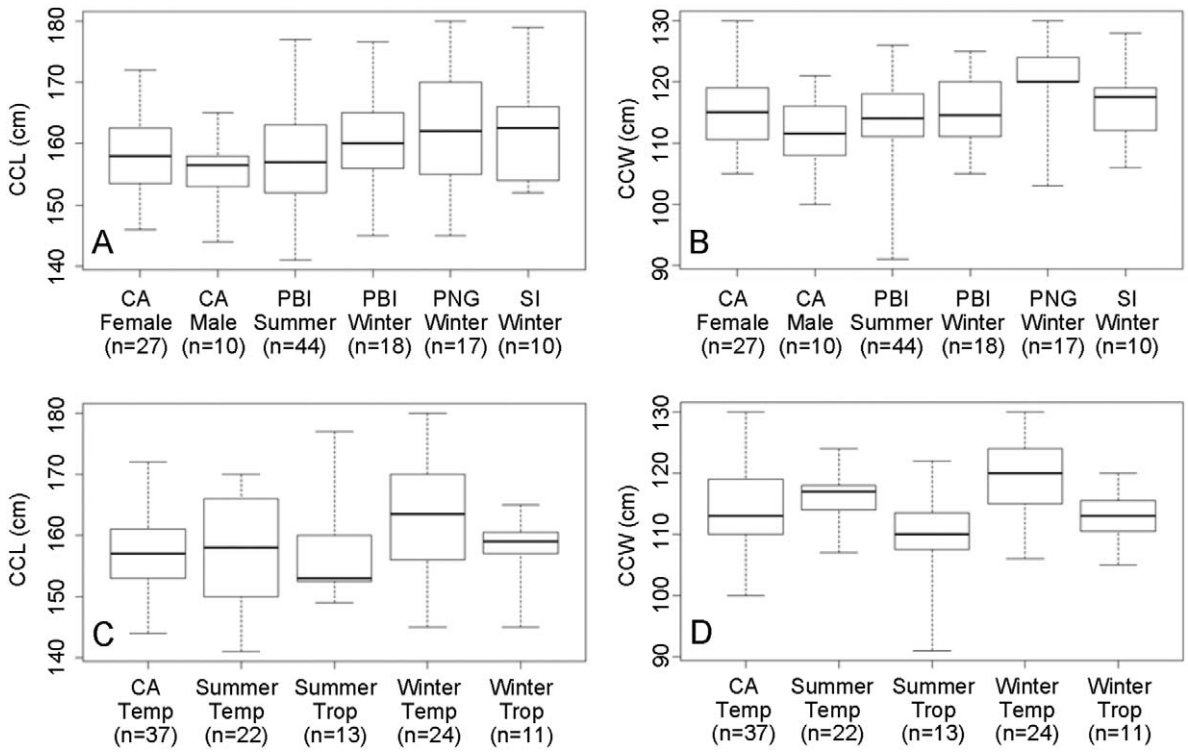

Fig. 6. Means, quartiles, and ranges of curved carapace length (CCL, left panels A and C) and curved carapace width (CCW, right panels B and D) for leatherbacks tagged and measured in this study, by deployment (location, season, gender; top panels A and B) and destination type (Trop = tropical; Temp = temperate; bottom panels C and D). CA Temp includes male and female turtles tagged at California foraging grounds. Winter nesters had significantly greater CCL (panel A, $P = 0.021$) and CCW (panel B, $P = 0.037$) than summer nesters. Temperate foragers for both seasons had significantly greater CCW than tropical foragers (panel D, $P = 0.001$).

shelf waters during March–June and September–January. Between these austral fall and spring periods, ARS occurred further north over deeper waters. Transmission durations were not sufficient for inference during February. Only three leatherbacks reached the TAS region, so inference for this region is limited. ARS behavior was identified between January and June for 21% of locations within this region, and it was significantly associated with low EKE regions ($P < 0.001$) and low CHL ($P = 0.013$).

The final ecoregion in which leatherbacks exhibited substantial ARS behavior was the Kuroshio Extension (KE), but only four turtles engaged in ARS behavior in this region and transmission durations were insufficient to provide a complete year-round picture of ARS behavior. Leatherbacks departing nesting beaches in August arrived within the KE between November and April, and ARS behavior was identified only during March–August. ARS occurred for 17% of all locations and was significantly associated with lower values for SST, EKE, SSH variation, and depth (all $P < 0.001$) as well as CHL ($P = 0.001$). The longest track exhibited northward movement between July and September before transmissions ceased, but the turtle was no longer engaged in ARS behavior during September.

Leatherback size patterns

Variation in CCL and CCW among deployment locations and destination type was evident in the morphometric data (Fig. 6). Mean CCL and CCW were similar among the three winter nesting locations (overall mean CCL = 161.6 cm, SE = 1.3, CCW = 116.9 cm, SE = 1.0), and we combined them for subsequent analyses. We

Table 3. Results of the analysis of variance (ANOVA) tests comparing curved carapace length (CCL) and curved carapace width (CCW) of leatherbacks by season, destination type, and sex: (a) two-way ANOVA: nesting season and destination type (temperate, tropical, unknown); (b) one-way ANOVA: sex (at California foraging grounds).

Response	Predictor	Df	Sum Sq.	Mean Sq.	F	*P*
a) Two-way ANOVA						
CCL	Season	1	363.3	363.34	5.5099	0.021
	Destination type	2	175.6	87.79	1.3314	0.270
	Residuals	78	5143.5	65.94		
CCW	Season	1	156.9	156.91	4.5259	0.037
	Destination type	2	576.1	288.07	8.3090	0.001
	Residuals	76	2634.9	34.67		
b) One-way ANOVA						
CCL	Sex	1	52.2	52.18	1.2698	0.268
	Residuals	35	1438.3	41.09		
CCW	Sex	1	85.7	85.65	2.1717	0.150
	Residuals	35	1380.4	39.44		

Notes: Df = degrees of freedom, Sum Sq. = sum of squares, Mean Sq. = mean square error, *P* = level of significance.

compared leatherback sizes by nesting season (winter or summer), destination type (temperate, tropical, or unknown), and sex (at California foraging grounds only). Combined mean CCL for winter nesters was significantly greater than for summer nesters (mean CCL = 157.4 cm, SE = 1.3, CCW = 114.1 cm, SE = 1.0), but there was no significant difference in CCL among nesting females that moved to temperate vs. tropical destinations post-nesting (Table 3a). Mean CCW was significantly greater for winter nesters and for nesting turtles that moved to temperate destinations post-nesting. There was no significant difference in size between male and female turtles sampled off the central California coast (Table 3b; female mean CCL = 158.0 cm, SE = 1.3, CCW = 114.7 cm, SE = 1.2; male mean CCL = 155.2 cm, SE = 1.7, CCW = 111.3 cm, SE = 2.0).

Discussion

High-use inter-nesting areas

Between successive nesting events, leatherbacks in this study remained within relatively narrowly defined areas adjacent to nesting beaches (Fig. 3). The Huon Gulf west of 149° E was heavily used by PNG turtles during the December–February inter-nesting period. Leatherbacks nesting during these months at SI also remained largely in the vicinity of nesting beaches at Santa Isabel, Malaita, and Rendova Islands, although the region west of Santa Isabel Island was most heavily used. Along the north coast of PBI, where leatherbacks nest year-round (Hitipeuw et al. 2007), inter-nesting females generally remained south of 1° N but ranged about 1° longitude farther westward during summer than winter (130–134° E vs. 131–135° E, respectively). We hypothesize that this shift is related to the seasonal reversal of the New Guinea Coastal Current (Wyrtki 1961). In all areas, the timing and extent of inter-nesting movements are sufficiently well-defined to allow for effective local conservation efforts, as needed. For example, in areas where bycatch of leatherbacks is of concern, conservation measures might include adaptive management strategies to reduce spatial and temporal overlap with turtles. In the case of PBI, most fishing occurs during the eastern monsoon, which coincides with peak nesting at Jamursba-Medi beach (Hitipeuw et al. 2007). Compared to the challenges posed with protecting large migratory and foraging areas, relatively small time-area closures of the marine areas associated with nesting would provide effective protection during peak inter-nesting periods in the Huon Gulf, PNG, off the north coast of PBI, and within the Solomon Islands archipelago. The results of this study can inform the development of conservation measures designed to protect breeding leatherbacks during the nesting season.

High-use foraging destinations

Western Pacific leatherbacks exhibited extraordinarily diverse movement patterns spanning coastal and pelagic habitats throughout the Indo-Pacific region. Areas of high use and inferred foraging, where turtles exhibited ARS movements ($P_{tran} < 0.5$), included several large marine ecosystems (Longhurst 2007), each discussed separately below. Summer nesters used tropical and temperate northern hemisphere foraging regions, while destinations of winter nesters included tropical waters and temperate regions of the southern hemisphere. A recent analysis of seasonal currents in the western Pacific suggests that differential transport of hatchlings may explain this striking difference (P. Gaspar et al., *unpublished manuscript*). The larger size of southern hemisphere winter nesters may be attributable to energetic differences associated with each region, i.e., summer nesters used more distant temperate and tropical habitats (Fig. 1).

CA Current Ecosystem (CCE).—The CCE, a highly productive eastern boundary current dominated by seasonal wind-driven upwelling (Chelton et al. 1982, Lynn and Simpson 1987), was the most distant post-nesting destination for nesters from western Pacific nesting beaches. Upwelling favorable winds tend to be most persistent during boreal spring and early summer months, transitioning to intermittent or 'relaxed' conditions during the late summer and fall, when water temperatures are warmest. Leatherbacks forage in this area from early summer to late fall, when water temperatures reach their warmest annual levels and large jelly aggregations develop (Graham et al. 2001). Turtles begin to depart the CCE when water temperatures drop in October–November and productivity decreases (Thomas and Strub 2001).

Three main areas of high use were identified within the CCE. Leatherbacks off California used relatively cool water (14–16°C) over the coastal shelf (<200 m) characterized by elevated levels of CHL and low EKE, particularly off central California (Fig. 5). This is consistent with results of previous aerial surveys (Benson et al. 2007*b*). Off Oregon and Washington, we identified ARS behavior in continental shelf and slope habitat (200–2000 m), particularly in waters adjacent to the Columbia River Plume. Both of these CCE foraging areas support seasonal dense aggregations of gelatinous prey, e.g., *Chrysaora fuscescens* and *Aurelia* spp., in retention areas created by points, headlands, and frontal regions (Shenker 1984, Graham et al. 2001). We identified some additional ARS behavior in offshore waters of central and northern California, where SST fronts are pronounced during the boreal spring and summer in deeper offshore regions (Costelao et al. 2006). This area was used by several leatherbacks during early summer prior to arriving in neritic waters and by two leatherbacks tagged in PBI that arrived off California during 2006 when delayed upwelling reduced seasonal productivity (Goericke et al. 2007) and jelly prey were scarce (S. R. Benson, *unpublished data*).

Leatherback turtles within the CCE indicated strong site fidelity to the central California foraging area: all returning turtles with deployments of sufficient duration ($n = 11$) came back to waters off central California in one or more subsequent years. Nine returned the following summer (minimum 2-yr foraging period), and two turtles tagged during 2004 returned to the California coast during both 2005 and 2006 (minimum 3-yr foraging period). Further, four of the 37 turtles tagged off central California were recaptured at or near their original capture location (two with harnesses one year later and two without harnesses 4 yr later), and two stranded dead along California beaches (without harness) 2–5 yr following tagging. The use of this very distant and limited seasonal foraging area by western Pacific leatherbacks is unique and appears to be paired with the use of EEP waters between successive CCE foraging seasons. Although leatherbacks retain metabolic heat (Paladino et al. 1990) and are capable of withstanding cooler water temperatures (Mrosovsky 1980), we hypothesize that the cold waters and limited prey availability of the CCE during winter require animals to 'overwinter' in warmer tropical waters between successive foraging seasons. A similar pattern has been documented through telemetry studies of Atlantic leatherback turtles (James et al. 2005) as well as eastern Pacific sharks (Weng et al. 2008, Jorgensen et al. 2010).

Equatorial Eastern Pacific (EEP).—The EEP was not a primary foraging destination for turtles departing nesting beaches, but rather its use was seasonal (December–February) and limited to northeastern Pacific foragers. This region is the

closest area to the CCE that has warmer water and mesoscale features that might aggregate zooplankton prey. Productivity is markedly lower than in other open-ocean foraging regions used by western Pacific leatherbacks, such as KE, TAS, and EAC (Polovina et al. 2001, Fiedler and Talley 2006, Longhurst 2007, Baird et al. 2008), but eastern Pacific leatherbacks have also been documented in waters of low productivity within the South Pacific gyre (Shillinger et al. 2008). Very little ARS behavior was identified (only 6% of daily locations), centered around 9–12° N latitude in areas with significantly lower SSH variation, lower EKE, and higher SST (Fig. 4). This suggests either that foraging is only taking place opportunistically and for short periods of time in areas of convergence or low current velocities, or that the features in which leatherback turtles forage within the EEP are themselves mobile and the state space model does not identify these portions of the track as ARS behavior. Further analysis of the tracks, dive data, and oceanography will be required to resolve this question.

Kuroshio Extension (KE).—The KE and North Pacific Transition Zone are part of a highly dynamic marine region with eastward propagating eddies and meanders (Polovina et al. 2001, 2006). This region is known to be an important pelagic longline fishing area and a foraging area for many species, including loggerhead turtles (*Caretta caretta*), albatross (*Phoebastria* spp.), tunas (*Thunnus* spp.), swordfish (*Xiphias gladius*), and elephant seals (*Mirounga angustirostris*) (Polovina et al. 2000, 2004, Hyrenbach et al. 2002, Seki et al. 2002, Simmons et al. 2010). Four of the six leatherback turtles from PBI that moved towards the KE engaged in ARS behavior, and only one of the four tracks was more than 12 months duration, so inference for this region is limited. ARS behavior was only documented during spring (April–May) at about 35–38° N latitude. The strongest patterns identified were that ARS behavior occurred primarily in areas of low SSH variation and low EKE, as in the EEP, and in areas of lower SST and deeper waters. (Fig. 4). Although the KE is known to be a region of higher productivity (Polovina et al. 2001, 2006), ARS behavior was highly associated with areas of lower rather than higher CHL (Fig. 7). This may be due to the mechanisms of productivity and retention for zooplankton prey along the front, which is characterized by a zone of north-to-south surface convergence with cool, vertically mixed, high-CHL surface water sinking beneath warm stratified low-CHL water. The habitat associations of the ARS locations suggest that leatherback turtles are likely foraging in areas of convergence on the south side of the chlorophyll front, moving northward throughout the summer as the front moves north (see most northerly track in Fig. 1). This is consistent with patterns identified previously for loggerhead turtles (Polovina et al. 2000, 2004, 2006).

East Australian Current Extension (EAC).—The East Australian Current is a western boundary current system characterized by vigorous, southward moving eddies and a surface flow that varies seasonally in strength (Ridgway and Godfrey 1997) and is strongest south of about 25° S during the austral summer. Eddy mass transports can be several times the mean transport, leading to strong recirculation patterns (Mata et al. 2006). At about 30° S, the current splits into the eastward flowing Tasman Front (Andrews et al. 1980) and the southward flowing EAC. ARS behavior by leatherbacks was identified in two seasonally distinct areas within the EAC: a southern area near Bass Strait that was used during austral spring, summer and fall months (Figs. 4, 8), and a northern area that was occupied seasonally during the austral winter (July–September). Similar to patterns described for the CCE, leatherbacks within the EAC performed seasonal movements between a productive, high latitude region and an offshore lower latitude overwintering area, although the two areas are geographically much closer together within the EAC than the CCE and EEP. In this case, the high-latitude foraging is concentrated in waters along the eastern shelf of Bass Strait (38–41° S), where a wintertime cascade (Tomczak 1985, Luick et al. 1994) produces downwelling and enhanced surface CHL (see Fig. 8, August) and where productivity is enhanced during spring through autumn (Fig. 8, October and April). Leatherbacks departed this area in June, possibly associated with a sharp drop in SST and the initiation of the Bass Strait Cascade, and spent June–August between about 30° S and 37° S associated with the cool-water, high-CHL margins of warm offshore eddies (Fig. 8).

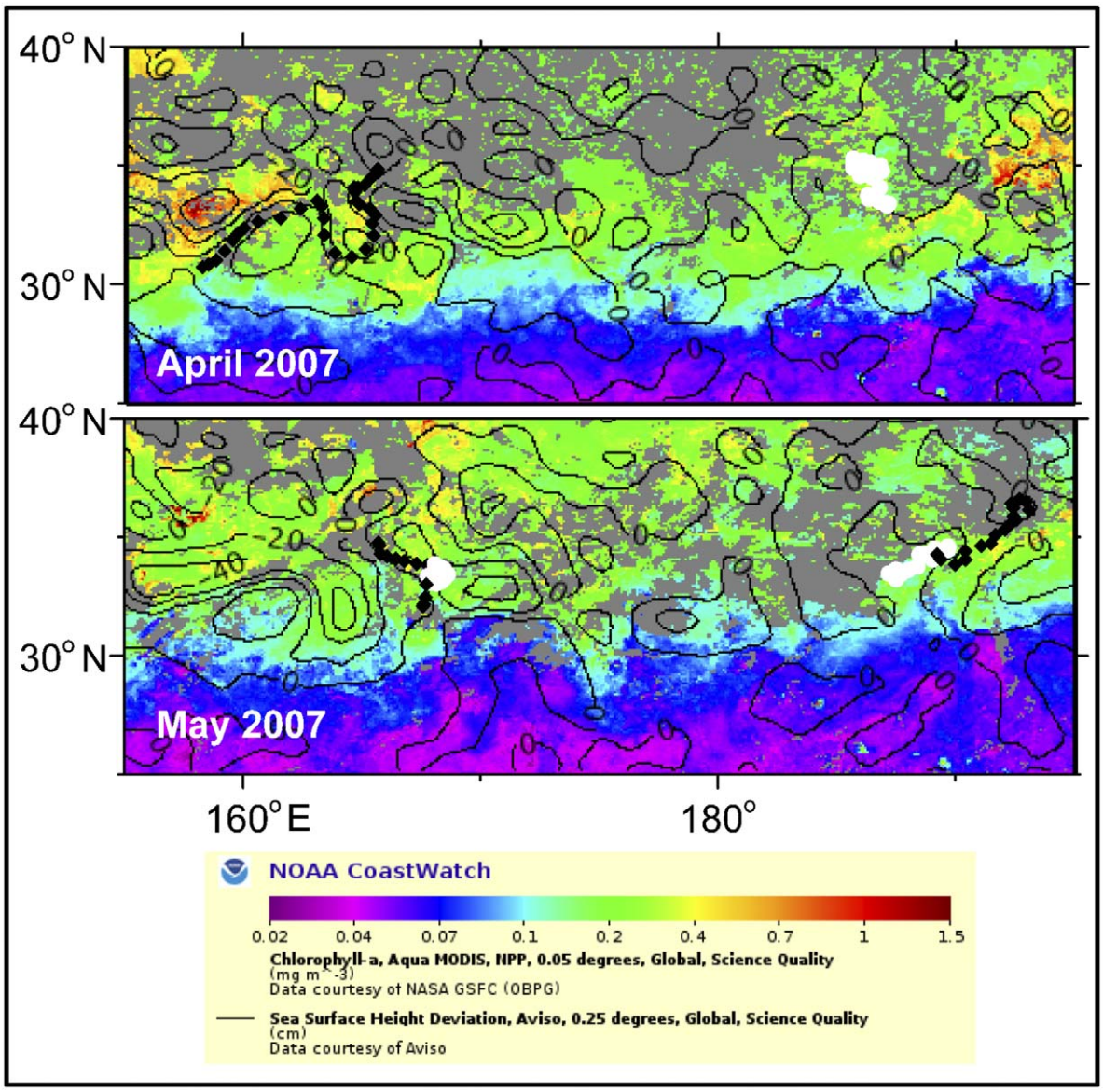

Fig. 7. Telemetry locations with ARS behavior (white dots) and transit behavior (smaller black dots) for two leatherback turtles relative to chlorophyll concentrations and sea surface height variation during April and May 2007 in the Kuroshio Extension (KE) high-use area.

Leatherbacks that departed nesting beaches in Solomon Islands during January–February arrived in waters of the EAC in March–April, sufficiently early to reach Bass Strait for 1–2 months of foraging before winter. In contrast, PBI nesters did not reach the EAC until May–June, and spent June–August within the offshore eddies prior to continuing south to Bass Strait during spring. Notably, turtles from Solomon Islands and PNG were the largest recorded in our study (Fig. 6), perhaps related to their ability to return quickly to nearby high-latitude foraging grounds following nesting. Further, water temperatures within the high latitude foraging areas of the EAC are warmer than temperate waters frequented by leatherbacks in the northern hemisphere, thus potentially providing an energetic advantage.

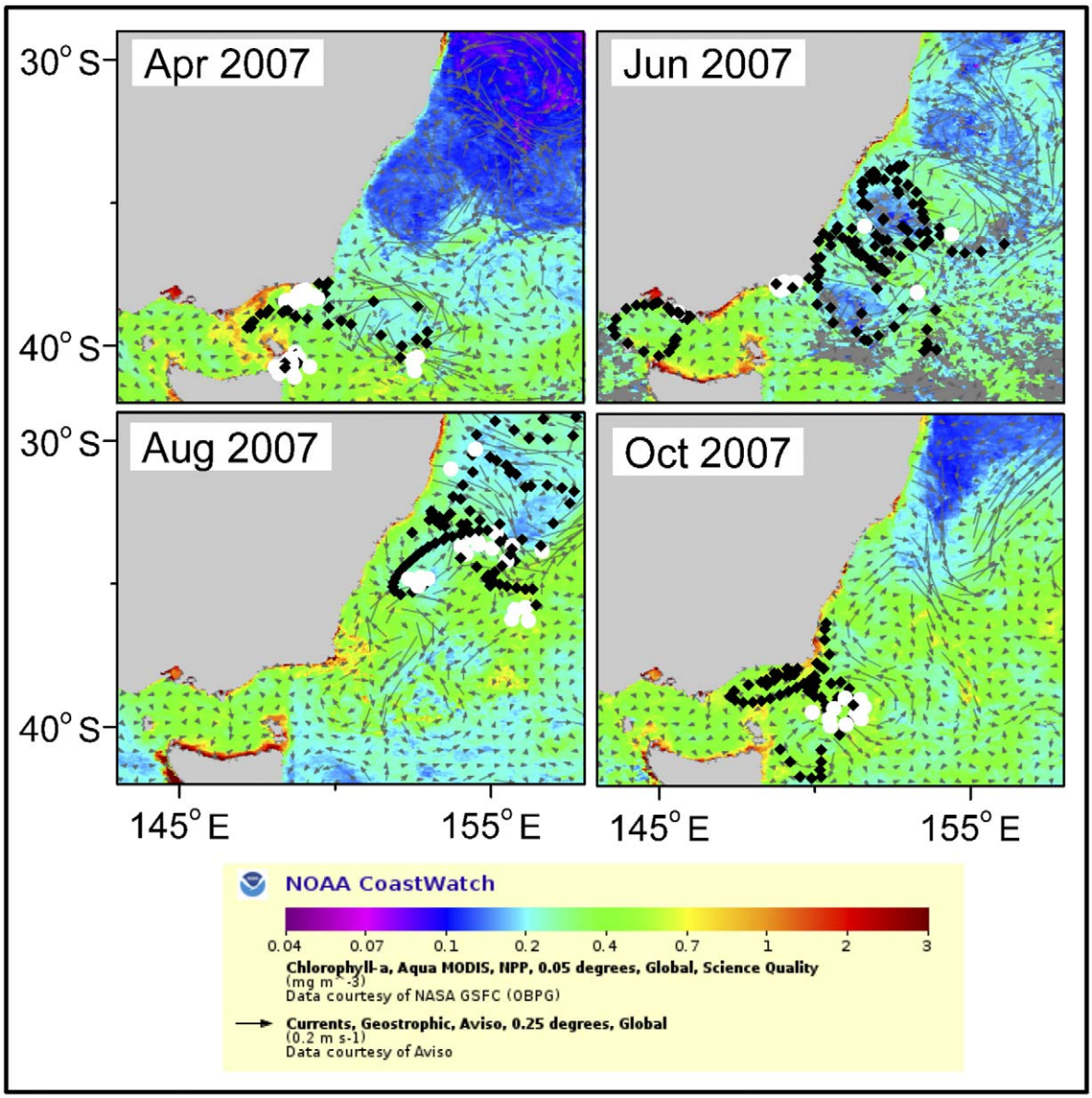

Fig. 8. Leatherback turtle telemetry locations with ARS behavior (white dots) and transit behavior (black dots) relative to chlorophyll concentrations and geostrophic currents (from which eddy kinetic energy is calculated) during April–October 2007 in the East Australia Current Extension (EAC) high-use area.

Tasman Front (TAS).—The TAS is a semi-permanent frontal feature created by the East Australia Current as it moves eastward and offshore, and is characterized by marked meanders and eddies and a zone of enhanced CHL (Andrews et al. 1980, Tilburg et al. 2001, Belkin and Cornillon 2007, Baird et al. 2008). Two leatherbacks from SI nesting beaches arrived in the TAS region during April–June and engaged in ARS behavior in an area of low current-velocity and potential zooplankton retention just south of the TAS prior to passing New Zealand's North Cape (Fig. 9). As in the KE, leatherback ARS behavior occurred within areas of lower CHL directly adjacent to a region of enhanced CHL. This pattern of association with low CHL is

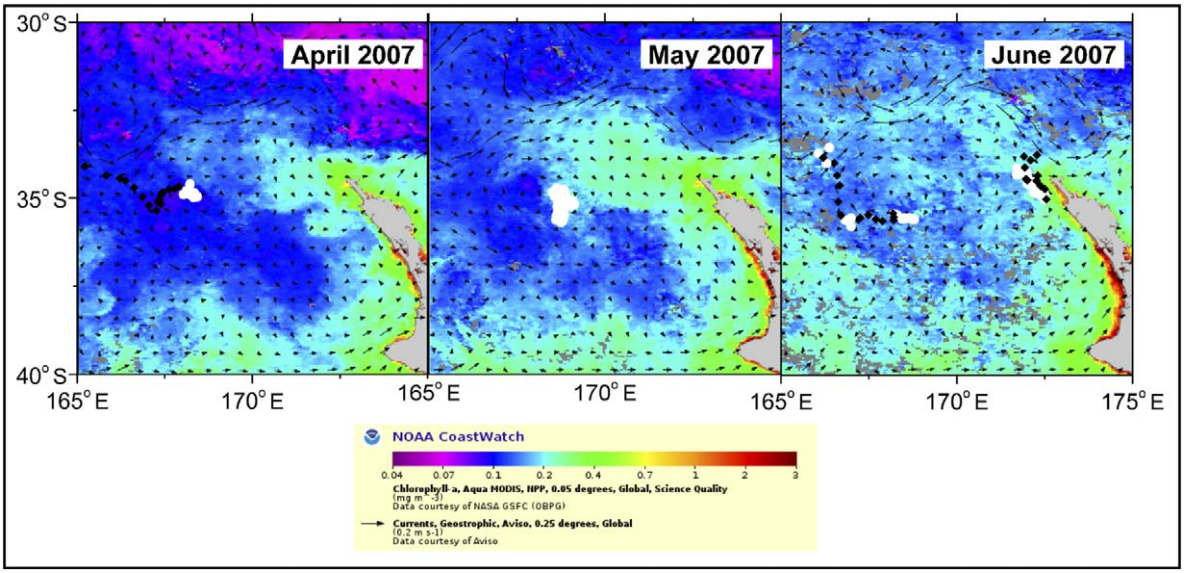

Fig. 9. Telemetry locations with ARS behavior (white dots) and transit behavior (black dots) for two leatherback turtles relative to chlorophyll concentrations and geostrophic currents (from which eddy kinetic energy is calculated) during April–June 2007 in the Tasman Front (TAS) high-use area.

opposite to that identified for the CCE, EAC, and Indonesian Seas. Although sample sizes are small (only three turtles moved into the TAS region) track durations of two turtles were sufficiently long to reveal subsequent northward movement during the austral winter (July–September) and a return to the TAS region the following October–June (Figs. 1, 4). This suggests that leatherbacks foraging in the TAS might undertake seasonal north/south movements and return to higher latitudes during at least two consecutive years, as in the other temperate regions identified in this study (CCE and EAC).

Indo-Pacific Archipelago (SCS and IND).—Tropical seas of the Indo-Pacific Archipelago (Longhurst 2007) include the closest foraging destinations to Indonesian nesting beaches and were occupied by post-nesting leatherbacks throughout the year. Leatherback ARS behavior occurred in over half of all recorded positions within these regions and was highly concentrated over shallow waters (<400 m, Figs. 4–5). There was, however, a marked geographic separation between boreal summer nesters, which moved to SCS, and boreal winter nesters, which moved to IND, west and south of PBI. These tropical, semi-enclosed seas contain numerous islands and are connected to each other and to the Pacific and Indian Oceans via multiple straits. They are characterized by complex bathymetry and dynamic currents dominated by seasonal monsoon winds (Wyrtki 1961, Longhurst 2007). The difference in foraging destinations for summer vs. winter nesters may be attributable to the seasonal monsoon-related current reversals and their effects on the dispersal of hatchlings (P. Gaspar et al., *unpublished manuscript*). Particularly given the proximity of the SCS and IND foraging regions, the lack of crossover among seasonal nesting populations strongly suggests that leatherbacks develop fidelity for specific foraging regions based on juvenile dispersal patterns, as has been suggested for Atlantic leatherback populations and loggerhead turtles (Fossette et al. 2010, Hays et al. 2010).

The SCS region was used by the largest number of post-nesting turtles tagged in PBI during summer (13 of 37), however the proximity of this region to nesting beaches likely allowed a greater number of turtles to reach this destination prior to transmitter failure vs. the more distant temperate foraging regions. Within the SCS, ARS behavior was most frequent over narrow shelf waters adjacent to Palawan Island, over the broad shelf west of Borneo, and to a

lesser extent, the Sulu archipelago (Fig. 4). These are all regions where shelf-slope fronts have been identified (Belkin and Cornillon 2003, 2007). Leatherbacks occupied the northernmost areas off Palawan Island during fall through spring when the regional thermocline is deepest (Longhurst 2007). The southward seasonal movement of leatherback ARS behavior along the western shelf of Palawan Island coincided with monsoon-driven changes in surface winds and a shallowing of the thermocline within the South China Sea during the boreal summer (Wyrtki 1961, Longhurst 2007). Seasonal changes in thermocline depth within the Sulu Archipelago are less pronounced (Longhurst 2007), and leatherback movements did not present a clear seasonal pattern other than use of these areas while en route to the South China Sea. The broad shelf region off western Borneo was occupied year-round. The association of ARS behavior with slightly warmer waters in areas of downwelling and greater SSH variation suggests leatherbacks are foraging in areas of convergence and retention within this dynamic SCS region, but a detailed study of the tracks, dive records, and local oceanography will be required to resolve the local processes involved.

The IND region was the most common destination for post-nesting turtles tagged in PBI during winter (11 of 17), although as for SCS, the proximity to nesting beaches likely allowed a greater number of turtles to reach this destination prior to transmitter failure compared to the more distant EAC and TAS. ARS behavior within this region was also highly concentrated along narrow shelf areas adjacent to islands, particularly at Kei, Tanimbar and Ceram Islands, but the dynamic habitat features associated with ARS (low SST, high CHL, and low EKE) differed markedly from those in the SCS. This might indicate that the mechanisms producing suitable foraging habitat differ, although the strong association with low EKE suggests that ARS within IND also takes place in areas of retention or convergence. As in SCS, frontal formation has been documented in association with sills and other topographic features within the Halmahera, Molucca and Banda Seas (Belkin and Cornillon 2007), and upwelling is enhanced during the southeast monsoon (May–August) within the eastern Banda Sea (Longhurst 2007). Leatherbacks did not reveal any systematic seasonal movements, and some individuals remained virtually 'stationary' for many consecutive months. In particular, a small area adjacent to the Kei Islands was occupied year-round and has supported a traditional hunt for free-swimming adult leatherbacks for centuries (Suarez and Starbird 1996).

High-use areas of passage

Western Pacific leatherbacks ranged widely, and no distinct 'migratory corridors' were identified (Fig. 1), but several regions stand out as areas of passage ($P_{tran} > 0.5$) used by many turtles traveling between nesting and foraging locations (darker gray shading in Fig. 3). Post-nesting females from PNG, SI, and winter PBI beaches rapidly moved towards temperate and tropical foraging areas, with key passage areas including the Halmahera, Bismarck, Solomon, and Coral Seas. In contrast, summer PBI nesters often spent weeks within the clockwise summertime circulation of the Halmahera Eddy north of Papua Barat (Arruda and Nof 2003) before moving in one of three predominant directions: westward through various passes in the Sulu and Sulawesi Seas, eastward along the equatorial currents, or northeastward into the KE. Use of the equatorial currents region included both the westward-flowing North Equatorial Current and the eastward-flowing North Equatorial Countercurrent, indicating that leatherbacks did not consistently travel with or against prevailing surface currents. Turtles accessing temperate northeastern Pacific waters of the CCE subsequently turned northeastward from the equatorial region between about 175° W and 155° W longitude. The seasonal roundtrip between CCE and EEP spanned a broad triangular region between the North American coast and Hawaii (Fig. 1), with animals moving southwestward from October–February and northeastward from about February–July (Fig. 3). Capture effects likely accelerated the initial departure from California foraging areas directly following tagging in September, and drag from the harness may have affected swim speeds for all turtles in this study (Fossette et al. 2008), but the observed seasonal patterns were consistent with independent observations where available (e.g., Starbird et al. 1993, Benson et al. 2007*a*, *b*).

Ecological implications

The sample size of telemetry deployments in our study ($n = 126$) is relatively large for a single study population, and the multi-year study period allowed us to identify overarching patterns of movement and habitat use across broad geographic areas. The diversity of observed movements limited inference for some destinations, and other, as yet unidentified areas are probably also used by this population. For example, three turtles exhibited distinctly different patterns (i.e., entering the Sea of Japan, the Gulf of Papua, and the Gulf of California), but these single observations are difficult to place into an ecological context. In other areas (e.g., the CCE), sample sizes are likely sufficient for further studies that evaluate interannual variability in leatherback movements and habitat use in relation to underlying ecological and oceanographic processes. The patterns that were revealed in this study, however, clearly demonstrate that western Pacific leatherbacks exploit resources in many areas where varying physical and biological mechanisms can produce aggregations of gelatinous zooplankton prey (Graham et al. 2001, Hamner and Dawson 2009). Mechanisms linked to areas of ARS behavior in this study included oceanic fronts, topographically-induced coastal retention zones, and mesoscale features, such as eddies. The common theme for all these areas are that they are regions of low physical energy, as demonstrated by the affinity of leatherbacks to exhibit ARS behavior in regions of low EKE, reduced SSH variation, or downwelling. Eastern Pacific leatherbacks have also been found to migrate to a low energy region, the South Pacific Gyre (Shillinger et al. 2008), and similar patterns have been documented for other wide-ranging marine species, such as loggerhead turtles, seabirds, and tunas (Polovina et al. 2001, Hyrenbach et al. 2002).

Although leatherbacks are widely distributed throughout the oceans, this study has demonstrated the critical importance of coastal areas throughout the Indo-Pacific basin to foraging leatherbacks. In these areas, coastal nutrient input, high productivity, and shallow waters are favorable for the life history of many species of Scypohomedusae that require a benthic life stage and are important prey for leatherbacks (Graham et al. 2001, James and Herman 2001, Hamner and Dawson 2009, Graham et al. 2010). Some of the coastal regions identified in this study as likely foraging areas for leatherbacks also support fisheries for jellyfish (Omori and Nakano 2001). Gelatinous zooplankton are generally considered relatively nutrient-poor (Doyle et al. 2007), and leatherbacks must consume large quantities of prey (20–30% of their body mass daily, Davenport and Balazs 1991). The reliable availability of abundant prey in relatively small geographic areas and associated with fixed or recurrent physical features is likely a key factor causing leatherbacks to travel great distances to reach coastal regions throughout the Indo-Pacific, at a comparable scale to other far-ranging marine predators, including sooty shearwaters (*Puffinus griseus*), which migrate from nesting areas in New Zealand to foraging areas off California (Shaffer et al. 2006), North Pacific albatross, which exploit areas with predictable mesoscale features (Hyrenbach et al. 2002), and white sharks (*Carcharodon carcharias*), which migrate between distant offshore and coastal areas (Jorgensen et al. 2010).

In contrast to coastal areas, prey patches in open ocean regions are likely more dynamic and ephemeral (Olson et al. 1994, Hyrenbach et al. 2000). Leatherbacks in this study covered markedly larger areas between bouts of ARS behavior in such open ocean regions. Leatherback ARS behavior in these areas was generally associated with low-CHL waters adjacent to high-CHL frontal regions, as previously identified for loggerhead turtles (Polovina et al. 2001, Kobayashi et al. 2008). Although this might appear to contradict the conclusions of H. Bailey et al. (*unpublished manuscript*), who found an association of Pacific leatherback ARS behavior with regions of higher CHL, it is, in fact, a reflection of ecological scale: leatherbacks are foraging in the low-CHL portions of productive (high CHL) ecoregions. It should also be noted that ARS behavior may have been underestimated in these regions (EEP, KE, EAC, TAS) if the mesoscale features associated with ARS were themselves dynamic. Future studies using state-space models may benefit from regional parameterization that can take this into account.

The diversity of foraging destinations and habitat characteristics also has implications for

the life history of western Pacific leatherbacks. Leatherbacks that exploit distant, seasonally abundant resources (CCE, EAC, TAS) would be expected to require multiple years of seasonal foraging before remigrating to nesting beaches. In contrast, leatherbacks exploiting geographically closer, year-round prey resources (SCS, IND) would have the potential to remigrate more quickly. Winter nesters in this study, which foraged relatively closer to the nesting beaches (IND, EAC, TAS), were documented to have greater CCL and CCW than summer nesters that moved to more distant tropical and temperate regions (CCE, KE, SCS). Regardless of nesting season, turtles that moved to temperate destinations had significantly greater CCW than turtles that moved to tropical destinations. Assuming there is foraging site fidelity (see *Discussion: California Current Ecosystem* and *Indo-Pacific Archipelago*), this would indicate that temperate foragers increase their body weight to a much greater extent before returning to nesting beaches. Although no studies have yet examined egg production or hatching success by foraging destination for western Pacific leatherback females, we hypothesize that within-year reproductive output should be greater for temperate foragers because they have stored greater energetic reserves. Thus, two life history strategies appear to exist in the western Pacific nesting population: (1) forage tropically and return more quickly with fewer stored energy reserves, or (2) forage in distant temperate locations and return less frequently but in markedly better body condition. Although an alternate explanation for the larger CCW of temperate foragers is that they must store greater reserves to handle the added energetic cost of distant migration, the largest turtles in our study were not the most distant temperate foragers (CCE), but rather the winter-nesting turtles (SI and PNG) foraging in the closest available temperate foraging grounds (EAC and TAS). Further study of foraging site fidelity, prey quality and quantity, prey consumption rates, and energetic cost of migration for each foraging area will be required to further elucidate the energetic mechanisms that create the above patterns.

Our tracking results show that the western Pacific genetic stock (Dutton et al. 2007) is likely comprised of demographically discrete foraging "units" that in the case of PBI nest on the same beaches at different times of year. The multiple dispersal strategies illustrated in our study for western Pacific leatherbacks are also found in Atlantic leatherback populations (Ferraroli et al. 2004, Hays et al. 2004, Eckert 2006, Witt et al. 2011), which are abundant and increasing (Dutton et al. 2005, Turtle Expert Working Group 2007). This contrasts dramatically with the severely depleted eastern Pacific genetic stock, which has a more limited distribution associated with foraging areas exclusively in the southeastern Pacific (Eckert and Sarti 1997, Shillinger et al. 2008), making this population more vulnerable to impacts from fishing (Alfaro-Shigueto et al. 2010). Further, these southeastern Pacific foraging areas are characterized by low productivity linked with frequent El Niño events (Saba et al. 2007). A diverse foraging strategy provides a greater buffer against adverse anthropogenic impacts and environmental perturbation in the marine environment, suggesting that the western Pacific stock is more likely to respond to conservation action on the nesting beaches directed at increasing hatchling production (Dutton et al. 2005) than has been evident for the eastern Pacific leatherback stock.

Conservation implications

This study provides insights into temporal and spatial patterns of high use for western Pacific leatherbacks and can guide efforts to minimize overlap between potentially harmful anthropogenic activities and leatherback turtles. For example, leatherbacks departed the CCE and traveled towards the EEP during fall and returned northeastward again in spring for summertime foraging off California, Oregon and Washington. Thus, risks in the transit area would be expected to be greatest during spring and fall, and lower when turtles are on the foraging grounds. A seasonal area closure that takes this movement pattern into account has successfully reduced the bycatch of leatherbacks in California drift gillnet fisheries since 2001 (Carretta et al. 2004). In the central North Pacific, a dynamic product is available on-line that displays near real time areas of likely overlap between longline fisheries targeting swordfish (*Xiphias gladius*) and loggerhead turtles (Howell et al. 2008) to allow fishermen to reduce bycatch.

A similar product may be feasible for leatherback turtles in the central Pacific and elsewhere, based on the results of this study that shows association of leatherbacks with low-energy regions.

In our study, transmission ceased prematurely for some deployments in all years (Table 1), but in most cases we cannot determine whether this is due to transmitter/harness failure or death of the turtle. However, seven of the 126 leatherbacks tagged in this study (5%) are known or suspected to have been subsequently killed either incidentally or intentionally by humans. We believe three PBI-nesters were likely killed in fisheries off Malaysia, Philippines, and Japan based on transmission signals or local reports (Benson et al. 2007*a*; Salinas et al. 2009; S. R. Benson, *unpublished data*). Two turtles were killed for subsistence hunting, one in PNG during 2001 (S. R. Benson, *unpublished data*) and one in the Kei Islands during 2008 (C. Hitipeuw, *unpublished data*). Two additional nesting turtles were killed by youths in PNG during 2006 (Papua New Guinea Post-Courier 2007). This is a high rate of documented anthropogenic mortality for a long-lived species, of particular concern given that these were breeding adults and therefore of high reproductive value to the population (see Wallace et al. 2008).

The extent of movements by western Pacific leatherbacks and the multiple threats they face throughout the Indo-Pacific illustrate that conservation efforts must consider both the nesting and at-sea portions of their life history in an ecosystem context (Dutton and Squires 2011). Protection of nesting beaches and enhancement of recruitment is critical to recovery of the species, but the conservation of diverse foraging units, as identified in this study, optimizes future potential for maintaining the western Pacific metapopulation.

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