

Stable isotope analysis reveals migratory origin of loggerhead turtles in the Southern California Bight

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ABSTRACT: Loggerhead turtles *Caretta caretta* in the North Pacific are listed as Endangered under the US Endangered Species Act and the IUCN Red List. Due partly to their imperiled status, the US National Marine Fisheries Service established a time-area closure in 2003 for the California drift gillnet (CDGN) fishery operating within the Southern California Bight (SCB) to avoid incidental captures. This closure is triggered when sea surface temperatures are above normal, generally caused by El Niño-derived warm-water conditions, which is the time when loggerheads are thought to enter the SCB. Knowledge of the previous foraging grounds of loggerheads incidentally captured by the CDGN fishery in the SCB will help elucidate the oceanographic mechanisms that may influence turtle movement into this region and can assist in optimizing the environmental triggers for implementation of the SCB fishing closure. Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis was used to determine the previous foraging grounds of loggerheads encountered in the SCB. Skin samples from loggerheads captured in the CDGN fishery were compared with skin from loggerheads in the central North Pacific, incidentally caught in the Hawaii-based longline fishery, as well as skin from turtles sampled during in-water research along the Baja California Peninsula, Mexico. The stable isotope values of CDGN-caught turtles were more similar to those from the central North Pacific than to those from Baja, indicating movements from the central North Pacific to the SCB. We elaborate on potential oceanographic mechanisms by which turtles access the SCB and provide insights that can inform future management decisions for the time-area closure.

KEY WORDS: *Caretta caretta* · Carbon · Nitrogen · California drift gillnet fishery · Hawaii-based longline fishery · Baja California Peninsula · Time-area closure · California Current Large Marine Ecosystem

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INTRODUCTION

Mitigating incidental catch of endangered species in commercial fisheries is a major challenge for developing successful management and protection plans. As a consequence, efforts are underway to reduce these impacts on a variety of taxa, including marine mammals, seabirds, and sea turtles (Lewison et al. 2004, Moore et al. 2009). Several measures have

been implemented globally to reduce turtle bycatch, including controlling fishing effort, time-area closures, gear modifications, and a map-tool providing thermal ranges for turtles (Epperly et al. 1995, Gilman et al. 2006, Dietrich et al. 2007, Read 2007, Gardner et al. 2008b, Howell et al. 2008, McClellan et al. 2009, Wallace et al. 2010). However, the effective implementation of such management strategies will benefit from additional knowledge of the loca-

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tion and timing of movements of marine species, as well as information about the environmental drivers that influence their biology (Lewison et al. 2004, Carreras et al. 2006, Etnoyer et al. 2006, McClellan & Read 2007, 2009, Gardner et al. 2008a, Wallace & Saba 2009).

In the North Pacific, the loggerhead turtle *Caretta caretta* is among the primary species of concern for fisheries management and bycatch reduction efforts (Dietrich et al. 2007, Peckham et al. 2007). Following a status review initiated in 2008, loggerheads in the North Pacific were up-listed to endangered status (identified as the North Pacific 'distinct population segment' in 2011 under the US Endangered Species Act; Conant et al. 2009), whereas the species as a whole is listed as Endangered on the International Union for Conservation of Nature (IUCN) Red List (www.iucnredlist.org). Loggerheads in the North Pacific constitute a distinct genetic stock (Bowen et al. 1995, Dutton 2007, LeRoux et al. 2008, Watanabe et al. 2011), with nesting occurring almost exclusively in Japan. At sea, individuals use broadly separated localities and various habitats during their lifetime. Juvenile loggerheads inhabit 2 distinct regions: the oceanic waters of the central North Pacific (Polovina et al. 2000, 2004) and neritic and oceanic habitats along the Pacific coast of the Baja California Peninsula (BCP), Mexico (Seminoff et al. 2004, Peckham et al. 2008, 2011). Once they are close to sexual maturity, loggerheads migrate back to foraging areas near their breeding grounds in the western Pacific (Resendiz et al. 1998, Nichols et al. 2000, Ishihara et al. 2011).

Interactions between loggerheads and fisheries occur throughout the eastern Pacific, with hotspots identified in waters of Chile, Peru, and Mexico (Peckham et al. 2007, Donoso & Dutton 2010, Alfaro-Shigueto et al. 2011). Whereas loggerheads foraging off Chile and Peru belong to the South Pacific distinct population segment (Conant et al. 2009) of turtles that nest in eastern Australia and New Caledonia (Kelez et al. 2003, Alfaro-Shigueto et al. 2004, Boyle et al. 2009), those found off the coasts of Mexico and the US originate from the North Pacific breeding stock, of which most individuals nest in Japan (Bowen et al. 1995, Dutton 2007, LeRoux et al. 2008, Watanabe et al. 2011).

Along the US west coast, observers of the California drift gillnet (CDGN) fishery operating within the Southern California Bight (SCB) have documented few loggerhead interactions ($n = 16$ in 4165 observed sets in the SCB from 1990 to 2010, average of 3.8 loggerhead turtles caught per 1000 observed sets within

the SCB; Carretta & Barlow 2011, Carretta & Enriquez 2012), with the recorded bycatch largely occurring during El Niño Southern Oscillation (ENSO) conditions (NMFS 2000, Carretta et al. 2003, Carretta & Enriquez 2007). To reduce gillnet fishery interactions with loggerhead turtles, the US National Marine Fisheries Service (NMFS) established a time-area closure for the CDGN fishery operating within the SCB in 2003 (NOAA 2007), which is implemented during above average warm-water periods brought on by ENSO events (June, July, and/or August during forecasted or realized ENSO years; NOAA 2007). Non-ENSO years are excluded from the closure, as it is likely that the SCB is too cold in relation to temperature ranges associated with satellite tracked or fishery-caught loggerheads in the central North Pacific (Polovina et al. 2000, 2004, Howell et al. 2008). To date, this closure has yet to be implemented, because the sea surface temperature (SST) threshold for triggering the month-by-month closure has not been reached since the publication of this regulation. Fishing effort has decreased over time, and therefore, more recent bycatch rates are lower. Nonetheless, bycatch of loggerheads in the SCB has occurred as recently as 2006 when ENSO conditions were identified during the period of the interaction, yet SSTs were normal. Therefore, a better understanding of migratory pathways and habitat use by loggerhead turtles in the SCB would help refine this adaptive management tool.

One technique to examine migratory origin is the analysis of stable isotope ratios in animal tissue (Hobson & Wassenaar 1999). The isotopic compositions of consumer tissues integrate information from foraging environments, which allows these animals to be recorders of the prevailing isotope regime (often referred to as an 'isoscape') within which they live (DeNiro & Epstein 1981, Hobson & Wassenaar 2008, Ruiz-Cooley & Gerrodette 2012). When an animal moves among spatially discrete food webs that are isotopically distinct, the stable isotope analysis (SIA) of tissues with slow turnover rates (e.g. skin; Newsome et al. 2010, Reich et al. 2008) can provide unambiguous information about the animal's previous location(s) (Hobson & Wassenaar 2008, Newsome et al. 2010). Indeed, the large-scale movements of sea turtles have been tracked previously using the SIA technique (McClellan et al. 2010, Reich et al. 2010, Zbinden et al. 2011, Seminoff et al. 2012).

The central North Pacific and Pacific waters of the BCP are the 2 potential foraging regions for loggerheads incidentally caught in the SCB, with the Pacific water off Baja being the likely source for logger-

heads in the SCB due to the close proximity of the BCP to California and the fact that both are sub-regions within the California Current Large Marine Ecosystem (CCLME; NMFS 2000). Waters of the CCLME are characterized by high phytoplankton $\delta^{15}\text{N}$ values in surface waters (Liu & Kaplan 1989, Castro et al. 2001, Voss et al. 2001, Somes et al. 2010) caused by denitrification in the eastern tropical North Pacific Ocean (Voss et al. 2001) and advection of this water mass northward (Liu & Kaplan 1989), whereas the central North Pacific exhibits lower baseline $\delta^{15}\text{N}$ values in oceanic food webs (Liu & Kaplan 1989). The baseline stable nitrogen isotope values of these 2 regions differ by approximately 3‰ (Liu & Kaplan 1989). These disparate baseline $\delta^{15}\text{N}$ values suggest that SIA is an excellent tool to determine the origin of loggerheads in the SCB.

In this study, we used SIA of loggerhead skin samples combined with knowledge of prevailing regional isoscapes to determine the migratory origin of loggerhead turtles found in the SCB. Similar to previous studies of sea turtles (Blumenthal et al. 2009, Godley et al. 2010), identification of the recent foraging ground locations and movement patterns of juvenile loggerheads may elucidate the oceanographic conditions at the time of loggerhead presence and can help clarify the most appropriate environmental triggers for implementation of the CDGN fishing closure to minimize loggerhead bycatch while reducing undue hardships to fishers. Ultimately, these findings will be useful for the management of the endangered North Pacific loggerhead stock. The isotopic patterns identified in our results underscore the value of SIA for addressing endangered species management concerns and policy decisions.

MATERIALS AND METHODS

Turtle sampling and body size

Skin tissue samples were obtained from loggerhead turtles that were incidentally caught by US commercial fisheries or purposely caught during research operations in 3 different regions (central North Pacific [$n = 20$ turtles], SCB [$n = 8$], and BCP [$n = 9$]; Fig. 1). Samples from the central North Pacific were obtained in January and December 1998, January, February, and December 1999, and Janu-

ary, February, and August 2000 from turtles caught by the Hawaii-based longline (HLL) fishery. HLL fishing occurs primarily outside of the exclusive economic zones (EEZ) between the Hawaiian Archipelago and outside the west coast EEZ of the USA. Samples from the SCB were obtained from loggerheads incidentally caught by the CDGN fishery during August and October 1997, August 1998, August 2001, and October 2006. Samples off the west coast of the BCP were collected from loggerhead turtles captured during research operations in July and August 2004 and 2005. Of the 26 loggerhead turtles stranded in the SCB from 1990 to 2010, 24 were measured for body size. The size (curved carapace length, CCL) of all turtles was obtained whenever possible. Straight carapace length (SCL) measurements obtained for the stranded turtles ($n = 17$) were converted to CCL using the conversion equation derived by Peckham et al. (2008).

Sample collection and preparation

Skin was obtained from each turtle using a razor or biopsy punch. All but 4 samples (3 BCP and 1 CDGN) were preserved in 20% dimethyl sulfoxide (DMSO) solution in saturated salt (NaCl); the other 4 were preserved in a saturated salt solution. All samples

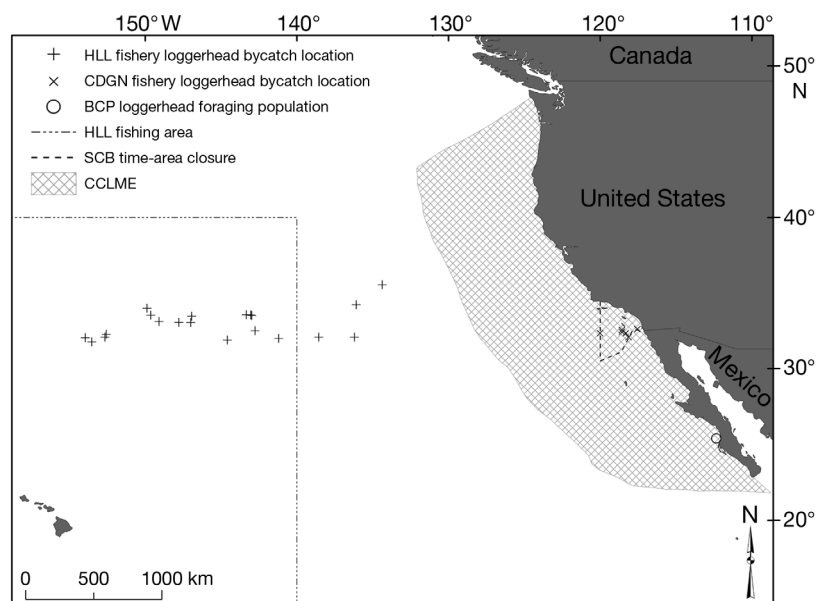


Fig. 1. *Caretta caretta*. Foraging area of loggerhead turtles off the Baja California Peninsula (BCP) and locations of turtle captures by the Hawaii-based longline (HLL) fishery and the California drift gillnet (CDGN) fishery. Also included for reference are the north-east corner of the HLL fishing area in the central North Pacific region, the southern California bight (SCB) time-area closure, and the California Current Large Marine Ecosystem (CCLME)

were frozen (-80°C) after collection. Although DMSO has been shown to affect stable isotope values (Barrow et al. 2008), based on studies by Todd et al. (1997) and Ruiz-Cooley et al. (2011), we assumed our samples were free of DMSO after lipid extraction. Further, the difference in stable isotope values between control (dried at 60°C for 24 h) samples and those preserved in DMSO decreased after samples were stored for >60 d (Barrow et al. 2008). Because our samples were preserved over 60 d in DMSO and virtually all samples had the same preservation technique, DMSO did not likely change our results.

Skin samples were thawed, rinsed with distilled water, and freeze-dried at -50°C for a minimum of 8 h in a lyophilizer (BenchTop K, VirTis, SP Industries). An accelerated solvent extractor (Model 200, Dionex) removed lipids from the skin samples using petroleum ether (one 30 min cycle). Following lipid extraction, samples were freeze-dried at -50°C for ~ 3 h to remove any residual solvent. Sub-samples of prepared tissue were then cut with a razor blade into small grains, weighed with a microbalance (0.6 to 1.0 mg), and packed in tin capsules for mass spectrometric analysis.

Sample analysis

The samples were sent to the Stable Isotope Laboratory at the University of Florida, Gainesville, USA, to be analyzed by a continuous-flow isotope-ratio mass spectrometer. A Costech ECS 4010 elemental combustion system interfaced via a ConFlo III device (Finnigan MAT) to a Deltaplus gas isotope-ratio mass spectrometer (Finnigan MAT) was used to determine stable isotope values. A conventional delta (δ) notation in parts per thousand (‰) was used to express the stable isotope ratios of the samples relative to the isotope standards: $\delta = ([R_{\text{sample}}/R_{\text{standard}}] - 1)(1000)$, where the corresponding ratios of heavy to light isotopes ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) in the sample and standard are represented by R_{sample} and R_{standard} , respectively. R_{standard} for ^{13}C was Baker acetanilide ($\text{C}_8\text{H}_9\text{NO}$; $\delta^{13}\text{C} = -10.4\text{‰}$) calibrated monthly against the Peedee Belemnite limestone formation international standard; R_{standard} for ^{15}N was IAEA N1 ammonium sulfate ($(\text{NH}_4)_2\text{SO}_4$; $\delta^{15}\text{N} = +0.4\text{‰}$) calibrated against atmospheric N_2 and USGS nitrogen standards. After every 6 to 7 samples, standard materials were included for each run in order to calibrate the system and compensate for any drift over time. Measurement errors of the standard materials in replicate assays were 0.05‰ for carbon and 0.095‰ for nitrogen.

SST

SSTs at the locations of loggerhead bycatch events were examined to determine the thermal environment of SCB waters when loggerheads were present. The SST data were obtained from NOAA's coastwatch browser (<http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp>) using the data set 'SST, Pathfinder Ver 5.0, Day and Night, 4.4 km, Global, Science Quality*'. SST data were compiled for each date (averaged over 7 to 8 d for $\pm 1^{\circ}$ latitude/longitude, centered at the location of bycatch) on which a loggerhead was incidentally caught in the SCB.

Statistical analysis

To compare body size between all groups of loggerhead turtles, as well as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among the 3 sampled groups (HLL, CDGN, and BCP), a Bayesian equivalent of a 1-way analysis of variance was used. The mean values were modeled as a linear function among the different groups (Kéry 2010). OpenBUGS (Lunn et al. 2009) was used to sample the joint posterior distribution of parameters. Marginal posterior distributions were computed by using kernel density estimates of the posterior samples. Large overlap between 2 posterior distributions of the means indicated a similarity between the 2 means. To quantify the difference between 2 means, we report the difference interval (D95) by listing the 2.5th and 97.5th percentiles. If the difference interval includes zero, the 2 means are considered to be similar. Results are presented as mean \pm standard error (SE) of the mean where applicable.

RESULTS

Turtle body size

Of the turtles for which size data were collected (see Table 1), all (except 2 stranded loggerheads) were classified as juveniles based on their CCL (relative to the mean size of nesting adults in Japan, ≥ 84.8 cm SCL; Ishihara et al. 2011). Mean body size varied among turtle sampling locations (Table 1). The loggerheads caught by the CDGN fishery were significantly smaller than those in the other groups, viz. the HLL-caught turtles ($D_{95} = [5.62, 21.91]$), those foraging off the BCP ($D_{95} = [3.29, 32.86]$), and stranded turtles ($D_{95} = [10.82, 26.46]$). There was no difference in

body size between the HLL- and BCP-captured turtles ($D_{95} = [-10.13, 18.78]$), or stranded turtles versus HLL ($D_{95} = [-2.30, 12.03]$) or BCP ($D_{95} = [-13.67, 14.77]$).

Stable isotope analysis

The isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of loggerhead skin tissues from the 3 study regions are provided in Table 1. The $\delta^{13}\text{C}$ ratios were statistically different for all 3 pairwise comparisons among the 3 groups (HLL vs. CDGN: $D_{95} = [-1.21, -0.20]$; HLL vs. BCP: $D_{95} = [1.31, 2.27]$; CDGN vs. BCP: $D_{95} = [0.50, 1.68]$, Fig. 2A). For $\delta^{15}\text{N}$, there was a significant difference for the pairwise comparisons of 2 groups: CDGN vs. BCP ($D_{95} = [3.44, 5.67]$, Fig. 2B) and HLL vs. BCP ($D_{95} = [4.06, 5.90]$, Fig. 2B). There was no difference between $\delta^{15}\text{N}$ values for HLL vs. CDGN ($D_{95} = [-1.38, 0.53]$, Fig. 2B).

Southern California Bight SST

The average SST within the SCB for each bycatch date (± 7 to 8 d) was $19.7 \pm 0.5^\circ\text{C}$ (18.6 to 21.2°C , $n = 5$; note that 2 bycatch dates are included in the same 7 to 8 d period). The SST around each bycatch location ($\pm 1^\circ$

latitude/longitude) on the date of bycatch was $20.3 \pm 0.6^\circ\text{C}$ (18.5 to 22.4°C , $n = 6$; note that 3 loggerheads were caught at the same location in August 1998).

DISCUSSION

Loggerhead turtles that migrate to the SCB most likely move in from the central North Pacific, based on the isotopic comparisons among the 3 study groups. Specifically, the $\delta^{15}\text{N}$ values for loggerheads caught in the SCB were nearly identical to turtles caught in the HLL fishery. The mean $\delta^{15}\text{N}$ values of these 2 groups were significantly lower than that of

Table 1. *Caretta caretta*. Loggerhead turtle size (curved carapace length, CCL) and stable isotope (SI) values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of skin samples obtained from turtles caught by the California drift gillnet (CDGN) or Hawaii-based longline (HLL) fisheries, from a foraging location off the Baja California Peninsula (BCP), Mexico, or from turtles that stranded in the Southern California Bight. Values are mean \pm SE, with ranges in parentheses. Size measurements were not obtained for all turtles sampled and not all turtles measured for size were sampled for SI analysis. (–) data not available

	n_{CCL}	CCL (cm)	n_{SI}	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
HLL	19	59.4 ± 2.0 (48.0 to 82.5)	20	-18.0 ± 0.1 (-18.6 to -17.3)	11.0 ± 0.3 (7.7 to 12.8)
CDGN	14	45.6 ± 2.2 (35.5 to 59.0)	8	-17.3 ± 0.4 (-18.7 to -16.1)	11.4 ± 0.2 (10.7 to 12.3)
BCP	3	63.8 ± 7.6 (50.0 to 76.0)	9	-16.2 ± 0.2 (-17.2 to -15.7)	15.9 ± 0.3 (14.2 to 16.7)
Stranded	24	64.3 ± 3.0 (25.5 to 97.7)		–	–

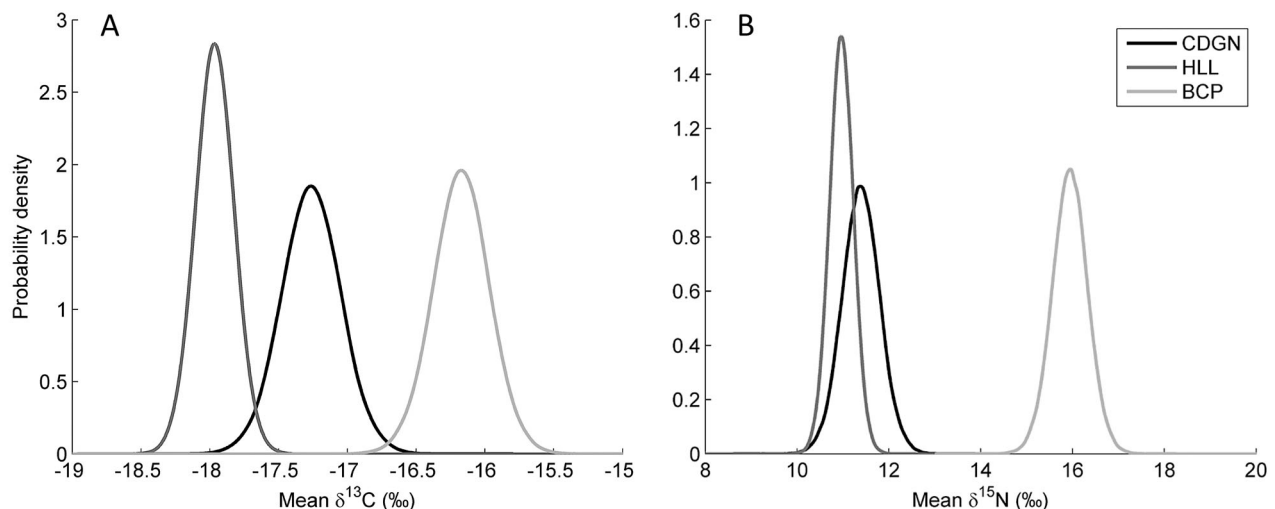


Fig. 2. *Caretta caretta*. Posterior distributions of the mean of (A) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$ ratios in skin samples of loggerhead turtles incidentally caught by Hawaii-based longline (HLL, $n = 20$) and California drift gillnet (CDGN, $n = 8$) fisheries as well as from a foraging population off the Baja California Peninsula (BCP, $n = 9$), Mexico

turtles sampled in the waters off the BCP (Fig. 2B). This finding is useful for answering management-related queries regarding the origin of loggerhead turtles caught by the CDGN fishery in the SCB and illustrates how isotopes can be used to decipher animal movements (Hobson & Wassenaar 2008).

Stable isotope values of any tissue are affected by how quickly they change as animals move to a different isoscape (turnover rates). Although empirical isotope turnover rates are unavailable for the size classes of turtles examined in this study, insights about turnover rates of large juvenile loggerheads can be gained by examining the isotope turnover rates that are available for post-hatchlings coupled with our understanding of the influence of growth rates on turnover rates. For example, Reich et al. (2008) found that stable nitrogen turnover in skin is on the order of 45 d for post-hatchling turtles (mean SCL = 10.6 ± 1.4 cm). Considering that such small turtles grow rapidly relative to larger immature turtles (Chaloupka 1998), protein turnover, and thus isotopic residence time, would likely be longer for larger turtles. The average size of CDGN-caught loggerheads (45.6 ± 2.2 cm CCL) relative to the hatchlings in the study by Reich et al. (2008) suggests that turnover rate for these larger animals is on the order of 5 to 6 mo (K. Reich pers. comm.). This implies that any loggerhead turtle moving northward from the Pacific coast of Baja would retain a relatively high $\delta^{15}\text{N}$ 'Baja' signal for several months after entrance into the SCB. High $\delta^{15}\text{N}$ would also be expected for animals that have been in the SCB for extended periods (longer than the isotopic turnover rate), because the SCB is characterized by high baseline $\delta^{15}\text{N}$ (Voss et al. 2001). The fact that CDGN-caught loggerheads possess low $\delta^{15}\text{N}$ values is indicative of a turtle coming from an isotope regime that differs from that of the CCLME. Moreover, when taken in the context of knowledge regarding isotope turnover, the turtles encountered in the SCB are likely recent arrivals to the area (within 5 to 6 mo).

The nitrogen isotope dichotomy in loggerhead turtles is likely due to differences in nitrogen biogeochemistry in the central North Pacific versus the CCLME (Liu & Kaplan 1989, Somes et al. 2010). Loggerheads in the central North Pacific are in an area with relaxed N_2 fixation and low denitrification, where source nitrogen has a lower isotopic composition (Deutsch et al. 2001, Montoya 2007). Turtles residing in the CCLME that are centered off Baja California Sur, Mexico, to take advantage of this area's productive and warm waters (Voss et al. 2001, Peckham et al. 2011) are in a region characterized by high

baseline $\delta^{15}\text{N}$ (Rau et al. 2003). More recent studies have used SIA of loggerhead skin samples to reveal oceanic differences in baseline isotope values (Pajuelo et al. 2010, 2012). Similarly, loggerheads sampled in denitrified southeast Pacific Peruvian waters had bulk tissue $\delta^{15}\text{N}$ values ($17.1 \pm 0.9\%$ $\delta^{15}\text{N}$, Pajuelo et al. 2010) more in line with values from the BCP ($15.9 \pm 0.3\%$ $\delta^{15}\text{N}$) than the other 2 groups sampled in our study. These studies underscore the role of nitrogen cycling regimes in driving observed patterns of marine turtle nitrogen isotopic compositions.

We found a significant difference in $\delta^{13}\text{C}$ skin values among the 3 groups of turtles. Lower $\delta^{13}\text{C}$ values in oceanic versus neritic systems (Hobson et al. 1994), correlate with our finding that HLL-caught loggerheads have the lowest $\delta^{13}\text{C}$ skin values among all 3 groups; however, the reasons for significant differences in $\delta^{13}\text{C}$ between BCP and SCB turtles are unclear. Perhaps the greater $\delta^{13}\text{C}$ of BCP turtles versus SCB turtles relates to the lesser influence of oceanic isotope signals along the Pacific coast of the BCP. Whereas water depths along the BCP where loggerheads typically forage is <75 m (Peckham 2009), depths at the loggerhead bycatch locations in the SCB range to >500 m (Hanan et al. 1993). However, the fact that CDGN- and HLL-sampled turtles differ in $\delta^{13}\text{C}$ but are consistent in $\delta^{15}\text{N}$ suggests that other factors may be at play. The differences between $\delta^{13}\text{C}$ of CDGN- and HLL-caught turtles may relate to the fact that these study groups included turtles from different years. While this would not be an issue for $\delta^{15}\text{N}$ due to consistency in nitrogen values of turtle skin tissue through time, $\delta^{13}\text{C}$ is highly variable among years (Lemons et al. 2011). Therefore, the difference in carbon between HLL- and CDGN-caught turtles is not due to spatial differences, but perhaps instead to temporal differences when turtles were sampled. To clarify the observed difference in $\delta^{13}\text{C}$, we recommend additional stable isotope-specific studies on tissue turnover rates for loggerhead turtles that are within the size range of turtles in this study as well as investigations on the changes in baseline $\delta^{13}\text{C}$ through time.

The influence of nitrogen cycling on the $\delta^{15}\text{N}$ values in marine turtle tissues has been suggested previously (Wallace et al. 2006, Pajuelo et al. 2010); however, these studies could not eliminate the possibility that differences in $\delta^{15}\text{N}$ values were the result of trophic variation among foraging groups – a major constraint of most SIA studies. In our study, the observed $\geq 4.5\%$ difference in skin $\delta^{15}\text{N}$ values between BCP and SCB/HLL loggerheads is suggestive of at least a full trophic-step difference between these

groups based on the loggerhead skin tissue discrimination factors presented by Reich et al. (2008). However, while loggerheads are known to be opportunistic foragers, it is unlikely that potential differences in diet would be sufficient to create the observed $\delta^{15}\text{N}$ disparity between turtles foraging within the BCP or SCB/central North Pacific. Whereas a variety of prey species have been identified in the diet of loggerheads throughout the Pacific (Nichols 2003, Parker et al. 2005, Peckham et al. 2011), all of these taxa, with the exception of fish (loggerheads eat fish discarded by fishers; Peckham et al. 2011), are of similar trophic status (Peterson & Fry 1987, Jennings et al. 1997, McClellan et al. 2010) and are therefore unlikely to be influential in the difference in nitrogen content between the groups of turtles (BCP and SCB/HLL). As explained in the previous 2 paragraphs, the more likely explanation is the difference in isoscapes between the central North Pacific and BCP.

Previous satellite tracking studies in the eastern North Pacific corroborate our findings that turtles sampled in the SCB most likely came from the central North Pacific and are not from the BCP. For example, despite the proximity of the BCP to the SCB, none of the 40 loggerheads tracked while foraging along the Pacific coast of Baja from 1996 to 2007 moved north into US waters (Peckham et al. 2011). This is particularly relevant considering that this time period encompassed at least one major ENSO event (1997–1998). The results of Peckham et al. (2011) underscore the strong tendency for loggerheads to maintain their presence in the waters off Mexico after arrival from the nesting beaches in Japan. The apparent absence of northward movements of tracked turtles may be due to the equatorial flow of the California Current (Lynn & Simpson 1987), which would require northbound turtles off the BCP to swim directly into the southerly currents. In addition to potential impediments to northward movement in the form of the prevailing southerly current, loggerheads may stay in the BCP 'hotspot' due to consistently high productivity and prey availability (Peckham et al. 2011, Wingfield et al. 2011) and also because juvenile loggerheads show site fidelity to foraging areas (Avens et al. 2003).

There is a possible bias in our data due to small sample sizes. The number of samples obtained for the loggerheads caught in the SCB by the CDGN fishery is limited by the number of observed turtles caught ($n = 16$), and therefore SIA could only be performed on

the samples obtained ($n = 8$) from the loggerheads. However, increasing our sample size would likely bolster our findings that turtles from the central North Pacific move to the SCB.

The occurrence of ENSO could be the driving force in the presence of loggerhead turtles in the SCB. Indeed, 7 out of 8 loggerhead captures by the CDGN fishery coincided with ENSO events (Fig. 3). Changes in fishing effort by the CDGN fishery during ENSO years likely did not influence the number of interactions with loggerhead turtles in the SCB, as the percentage of observed drift gillnet sets within the SCB has increased over the years (>50% since 2000), while only 2 out of the 16 interactions with loggerheads occurred since 2000 (Carretta & Barlow 2011, Carretta & Enriquez 2012). Specifically, the percentage of observed sets within the SCB during the ENSO events was 29% in 1992/1993 (7 loggerhead interactions) and 46% in 1997/1998 (7 loggerhead interactions), while during the 2006 El Niño, 77% of observed sets occurred within the SCB (1 loggerhead interaction). Although the ENSO-driven movement hypothesis is plausible, loggerhead turtles also enter the SCB and are taken by fisheries or found stranded during non-El Niño years (NOAA 2007, LeRoux et al. 2012; Fig. 3). Furthermore, although stranding events are rare, over half (14 out of 26 or 1.3 yr^{-1} from 1990 to 2010) of the strandings of loggerhead turtles along the coast of the SCB occurred during non-El Niño events (all years except 1992–1993, 1997–1998 and 2006). Therefore, El Niño events and changes in fishing effort within the SCB may not be the contributing factors which influence

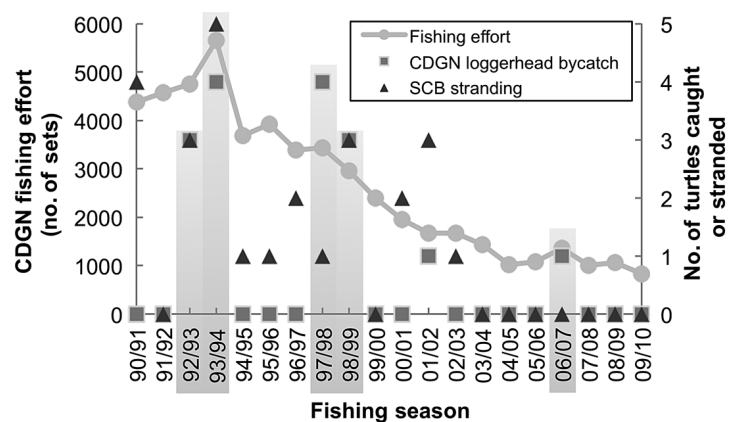


Fig. 3. *Caretta caretta*. Estimated fishing effort (number of drift gillnet sets) and the number of loggerhead turtles incidentally caught by the California drift gillnet (CDGN, $n = 16$) fishery per fishing season as well as the number of stranded turtles ($n = 26$) along the southern California coast in the Southern California Bight (SCB). Fishing seasons coinciding with El Niño Southern Oscillation events are designated by gray bars

interactions between loggerheads and the CDGN fishery.

Due to loggerhead turtles being caught or stranded in the SCB during and outside of ENSO events, and because changes in loggerhead distribution due to varying SST have been described previously (Epperly et al. 1995, Polovina et al. 2004, Howell et al. 2008), SST within the SCB was examined as a potential mechanism for their movement into the region. SST has been suggested as a good predictor for fishery interactions with loggerhead turtles (Braun-McNeill et al. 2008, Murray 2009). For all of the samples collected ($n = 8$), the SSTs in the SCB when loggerheads were incidentally caught by the CDGN fishery (mean: 19.7°C, range: 18.6 to 21.2°C) were similar to central North Pacific SSTs that were associated with loggerhead turtle interactions with the HLL fishery (mean: 17.9°C, range: 15.1 to 20.1°C, Howell et al. 2008), implying that SCB waters are within the turtles' normal temperature range even outside of ENSO events. Specifically, for the samples obtained from the 2001 and 2006 bycatch events, the SSTs in the SCB were at or below the average of 18.7°C (<http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp>; data set: SST Anomaly, Blended, Optimum Interpolation, Ver. 2, NCDC AVHRR, 0.25 degree, Global*), but they still were within the temperature range (15.0 to 22.0°C) in which loggerhead turtles were caught by the HLL fishery in the central North Pacific (15.1 to 20.1°C). Therefore, the temperature range of SCB waters may be suitable for this turtle species. If so, the existing management framework using temperature-threshold implementation of fishery closure for the SCB needs to be reconsidered.

Loggerheads caught by the CDGN fishery within the SCB were significantly smaller in size relative to those in the other areas (Table 1), and it is possible that ocean current patterns may facilitate movement of smaller turtles into the region. The sub-sample of HLL-caught loggerheads used in this study (larger individuals) may not be representative of the population because smaller animals are caught in the HLL and high-seas driftnet fisheries in the central North Pacific (Polovina et al. 2000, Parker et al. 2005). Perhaps the smaller turtles are more likely to become entrained in prevailing currents, although even small turtles can swim counter-current for some period (Polovina et al. 2000). The mean size (64.3 ± 3.0 cm) of stranded loggerhead turtles in the SCB was larger than that of the 3 turtle groups used for SIA (Table 1). Therefore, although small juvenile turtles do migrate to the SCB, the smaller size of the CDGN-caught tur-

tles may be an artifact of gillnet fishery-dependent sampling bias.

An alternate, although not mutually exclusive, mechanism by which loggerheads may enter SCB waters from the central North Pacific is via the turtles' close affinity with frontal zones, which are known to be areas of prey aggregation (Polovina et al. 2000). However, while associations with ocean fronts have been shown for loggerheads in the central North Pacific (Polovina et al. 2000, 2001, 2004), frontal zone location and movements within the SCB are not well understood during our study period. Finally, it is possible that loggerhead turtles exist in the SCB continuously at low density. Given the strong affinity to their foraging grounds during the juvenile stage at other locations, some juvenile loggerhead turtles may remain in the area until they mature. For future studies, we encourage additional efforts to determine the ocean current and frontal zone patterns within the SCB throughout the year with respect to locations of loggerhead turtles.

Management implications

Loggerhead turtle bycatch in the North Pacific is of growing concern due to the endangered status of this species. While loggerheads are relatively rare in the SCB compared to identified foraging 'hotspots' in the north Pacific (Peckham et al. 2011, Wingfield et al. 2011), from a fisheries-management perspective it is important to understand when they occur in the SCB and what brings them there. The findings of this study assist in understanding the movement patterns of loggerhead turtles and in addressing marine turtle management concerns and policy. SIA can assist in determining the foraging location of turtles prior to their entry into the SCB. Future research into fishery-bycatch issues should examine existing data on incidentally captured species and include investigation of multiple environmental influences (i.e. chlorophyll *a*, SST, or frontal zone location) that may affect bycatch of certain species.

At present, an SCB fishery closure would only take place during summer months when there are warmer than normal SSTs (which usually occur during ENSO events) in the 1 or 2 months prior to June, July, and/or August (NOAA 2007). These criteria have not been met in the time since these regulations were established. Therefore, other environmental variables in addition to SST should be investigated from the central Pacific to the US and BCP west coasts throughout the year to determine factors that affect

movements of loggerhead turtles in this area. Such studies would provide essential information for developing a better management tool for the species and improved fishing operations.

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LITERATURE CITED

- Alfaro-Shigueto J, Dutton PH, Mangel J, Vega D (2004) First confirmed occurrence of loggerhead turtles in Peru. *Mar Turtle News* 103:7–11
- Alfaro-Shigueto J, Mangel JC, Bernedo F, Dutton PH, Seminoff JA, Godley BJ (2011) Small-scale fisheries of Peru: a major sink for marine turtles in the Pacific. *J Appl Ecol* 48:1432–1440
- Avens L, Braun-McNeill J, Epperly SP, Lohmann KJ (2003) Site fidelity and homing behavior in juvenile loggerhead sea turtles (*Caretta caretta*). *Mar Biol* 143:211–220
- Barrow LM, Bjorndal KA, Reich KJ (2008) Effects of preservation method on stable carbon and nitrogen isotope values. *Physiol Biochem Zool* 81:688–693
- Blumenthal JM, Abreu-Grobois FA, Austin TJ, Broderick AC and others (2009) Turtle groups or turtle soup: dispersal patterns of hawksbill turtles in the Caribbean. *Mol Ecol* 18:4841–4853
- Bowen BW, Abreu-Grobois FA, Balazs GH, Kamezaki N, Limpus CJ, Ferl RJ (1995) Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. *Proc Natl Acad Sci USA* 92:3731–3734
- Boyle MC, FitzSimmons NN, Limpus CJ, Kelez S, Velez-Zuazo X, Waycott M (2009) Evidence for transoceanic migrations by loggerhead sea turtles in the southern Pacific Ocean. *Proc Biol Sci* 276:1993–1999
- Braun-McNeill J, Sasso CR, Epperly SP, Rivero C (2008) Feasibility of using sea surface temperature imagery to mitigate cheloniid sea turtle–fishery interactions off the coast of northeastern USA. *Endang Species Res* 5:257–266
- Carreras C, Pont S, Maffucci F, Pascual M and others (2006) Genetic structuring of immature loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea reflects water circulation patterns. *Mar Biol* 149:1269–1279
- Carretta JV, Barlow J (2011) Long-term effectiveness, failure rates, and 'dinner bell' properties of acoustic pingers in a gillnet fishery. *Mar Technol Soc J* 45:7–19
- Carretta JV, Enriquez L (2007) Marine mammal and sea turtle bycatch in the California/Oregon thresher shark and swordfish drift gillnet fishery in 2006. Administrative Report LJ-07-06. Southwest Fisheries Science Center, NOAA NMFS, La Jolla, CA
- Carretta JV, Enriquez L (2012) Marine mammal and seabird bycatch in California gillnet fisheries in 2010. Administrative Report LJ-12-01. Southwest Fisheries Science Center, NOAA NMFS, La Jolla, CA
- Carretta JV, Forney KA (1993) Report of the two aerial surveys for marine mammals in California coastal waters utilizing a NOAA DeHavill and Twin Otter aircraft. NOAA Tech Memo NOAA-TM-NMFS-SWFSC-185
- Carretta JV, Price T, Petersen D, Read R (2003) Estimates of marine mammal, sea turtle, and seabird mortality in the California drift gillnet fishery for swordfish and thresher shark, 1996 – 2002. *Mar Fish Rev* 66:21–30
- Castro CG, Chavez FP, Collins CA (2001) Role of the California undercurrent in the export of denitrified waters from the eastern tropical North Pacific. *Global Biogeochem Cycles* 15:819–830
- Chaloupka M (1998) Polyphasic growth in pelagic loggerhead sea turtles. *Copeia* 1998:516–518
- Conant TA, Dutton PH, Eguchi T, Epperly SP and others (2009) Loggerhead sea turtle (*Caretta caretta*) 2009 status review under the US Endangered Species Act. Report of the Loggerhead Biological Review Team to the National Marine Fisheries Service, August 2009
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- Deutsch C, Gruber N, Key RM, Sarmiento JL (2001) Denitrification and N₂ fixation in the Pacific Ocean. *Global Biogeochem Cycles* 15:483–506
- Dietrich K, Cornish VR, Rivera KS, Conant TA (2007) Best practices for the collection of longline data to facilitate research and analysis to reduce bycatch of protected species. In: Report of a workshop held at the International Fisheries Observer Conference, Sydney, Australia. NOAA Technical Memorandum NMFS-OPR-35
- Donoso M, Dutton PH (2010) Sea turtle bycatch in the Chilean pelagic longline fishery in the southeastern Pacific: opportunities for conservation. *Biol Conserv* 143:2672–2684
- Dutton PH (2007) Genetic stock composition of loggerheads (*Caretta caretta*) encountered in the Hawaii-based longline fishery using mtDNA analysis. In: North Pacific Loggerhead Sea Turtle Expert Workshop, December 19–20, 2007, Honolulu, Hawaii. Western Pacific Regional Fishery Management Council and NOAA, Honolulu, HI, p 17–19
- Epperly SP, Braun J, Chester AJ, Cross FA, Merriner JV, Tester PA (1995) Winter distributions of sea turtles in the vicinity of Cape Hatteras and their interactions with the summer flounder trawl fishery. *Bull Mar Sci* 56:547–568
- Etnoyer P, Canny D, Mate B, Morgan L, Ortega-Ortiz J, Nichols WJ (2006) Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep-Sea Res II* 53:340–358

- Gardner B, Sullivan PJ, Epperly S, Morreale SJ (2008a) Hierarchical modeling of bycatch rates of sea turtles in the western North Atlantic. *Endang Species Res* 5: 279–289
- Gardner B, Sullivan PJ, Morreale SJ, Epperly SP (2008b) Spatial and temporal statistical analysis of bycatch data: patterns of sea turtle bycatch in the North Atlantic. *Can J Fish Aquat Sci* 65:2461–2470
- Gilman EL, Zollett E, Beverly S, Nakano H and others (2006) Reducing sea turtle by-catch in pelagic longline fisheries. *Fish Fish* 7:2–23
- Godley BJ, Barbosa C, Bruford MW, Broderick AC and others (2010) Unravelling migratory connectivity in marine turtles using multiple methods. *J Appl Ecol* 47:769–778
- Hanan DA, Holts DB, Coan AL (1993) The California drift gill net fishery for sharks and swordfish, 1981–82 through 1990–91. *Fish Bull* 175:1–95
- Helvey M, Fahy CC (2012) Fisheries management off the U.S. West Coast: a progressive model for sea turtle conservation. In: Seminoff JA, Wallace BP (eds) *Sea turtles of the eastern Pacific: advances in research and conservation*. University of Arizona Press, Tucson, AZ, p 113–135
- Hobson KA, Wassenaar LI (1999) Stable isotope ecology: an introduction. *Oecologia* 120:312–313
- Hobson KA, Wassenaar L (2008) *Tracking animal migration with stable isotopes*. Academic Press, London
- Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786–798
- Howell EA, Kobayashi DR, Parker DM, Balazs GH, Polovina JJ (2008) TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endang Species Res* 5: 267–278
- Ishihara T, Kamezaki N, Matsuzawa Y, Iwamoto F and others (2011) Reentry of juvenile and subadult loggerhead turtles into natal waters of Japan. *Curr Herpetol* 30: 63–68
- Jennings S, Reñones O, Morales-Nin B, Polunin NVC, Moranta J, Coll J (1997) Spatial variation in the ¹⁵N and ¹³C stable isotope composition of plants, invertebrates and fishes on Mediterranean reefs: implications for the study of trophic pathways. *Mar Ecol Prog Ser* 146: 109–116
- Kelez S, Velez-Zuazo X, Manrique C (2003) New evidence on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758) in Peru. *Ecol Appl* 2:141–142
- Kéry M (2010) *Introduction to WinBUGS for ecologists*. Academic Press, San Diego, CA
- Lemons G, Lewison RL, Komoroske L, Gaos AR and others (2011) Trophic ecology of green sea turtles in a highly urbanized bay: insights from stable isotopes and mixing models. *J Exp Mar Biol Ecol* 405:25–32
- LeRoux RA, Pease VL, LaCasella EL, Frey A, Dutton PH (2008) Longer mtDNA sequences uncover additional genetic variation among North Pacific loggerheads. In: Rees AF, Frick M, Panagopoulou A, Williams K (eds) *Proc 27th Ann Symp Sea Turtle Biol Conserv*. NOAA Tech Memo NMFS-SEFSC-569, p 129–130
- LeRoux RA, Fahy C, Cordaro J, Norberg B and others (2012) Marine turtle strandings on the U.S. West Coast. In: Jones TT, Wallace BP (eds) *Proc 31 Ann Symp Sea Turtle Biol Conserv*. NOAA Tech Memo NOAA NMFS-SEFSC-631, p 256
- Lewison RL, Crowder LB, Read AJ, Freeman SA (2004) Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol Evol* 19:598–604
- Liu KK, Kaplan IR (1989) The eastern tropical Pacific as a source of ¹⁵N-enriched nitrate in seawater off southern California. *Limnol Oceanogr* 34:820–830
- Lunn D, Spiegelhalter D, Thomas A, Best N (2009) The BUGS project: evolution, critique and future directions. *Stat Med* 28:3049–3067
- Lynn RJ, Simpson JJ (1987) The California Current System: the seasonal variability of its physical characteristics. *J Geophys Res* 92:12947–12966
- McClellan CM, Read AJ (2007) Complexity and variation in loggerhead sea turtle life history. *Biol Lett* 3:592–594
- McClellan CM, Read AJ (2009) Confronting the gauntlet: understanding incidental capture of green turtles through fine-scale movement studies. *Endang Species Res* 10:165–179
- McClellan CM, Read AJ, Price BA, Cluse WM, Godfrey MH (2009) Using telemetry to mitigate the bycatch of long-lived marine vertebrates. *Ecol Appl* 19:1660–1671
- McClellan CM, Braun-McNeill J, Avalos CD, Wallace BP, Read AJ (2010) Stable isotopes confirm a foraging dichotomy in juvenile loggerhead sea turtles. *J Exp Mar Biol Ecol* 387:44–51
- Montoya JP (2007) Natural abundance of ¹⁵N in marine planktonic ecosystems. In: Michener R, Lajtha K (eds) *Stable isotopes in ecology and environmental science*, 2nd edn. Blackwell Publishing, Oxford, p 176–201
- Moore JE, Wallace BP, Lewison RL, Zydelis R, Cox TM, Crowder LB (2009) A review of marine mammal, sea turtle and seabird bycatch in USA fisheries and the role of policy in shaping management. *Mar Policy* 33:435–451
- Murray KT (2009) Characteristics and magnitude of sea turtle bycatch in US mid-Atlantic gillnet gear. *Endang Species Res* 8:211–224
- Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. *Mar Mamm Sci* 26:509–572
- Nichols WJ (2003) *Biology and conservation of sea turtles in Baja California, Mexico*. PhD dissertation, The University of Arizona, Tucson, AZ
- Nichols WJ, Resendiz A, Seminoff JA, Resendiz B (2000) Transpacific migration of a loggerhead turtle monitored by satellite telemetry. *Bull Mar Sci* 67:937–947
- NMFS (National Marine Fisheries Service) (2000) *Biological Opinion. Endangered Species Act Section 7 consultation on authorization to take listed marine mammals incidental to commercial fishing operations under section 101(a)(5)(E) of the Marine Mammal Protection Act for the California/Oregon Drift Gillnet Fishery*. http://swr.nmfs.noaa.gov/bo/lb/Drift_gillnet_BO_2000.pdf
- NOAA (National Oceanic and Atmospheric Administration) (2007) *Fisheries off West Coast states; highly migratory species fisheries*. *Fed Regist* 72:31756–31757
- Pajuelo M, Bjørndal KA, Alfaro-Shigueto J, Seminoff JA, Mangel JC, Bolten AB (2010) Stable isotope variation in loggerhead turtles reveals Pacific–Atlantic oceanographic differences. *Mar Ecol Prog Ser* 417:277–285
- Pajuelo M, Bjørndal KA, Reich KJ, Arendt MD, Bolten AB (2012) Distribution of foraging habitats of male loggerhead turtles (*Caretta caretta*) as revealed by stable isotopes and satellite telemetry. *Mar Biol* 159:1255–1267
- Parker DM, Cooke WJ, Balazs GH (2005) Diet of oceanic loggerhead sea turtles (*Caretta caretta*) in the central North Pacific. *FAO Fish Bull* 103:142–152

- Peckham SH (2009) Demographic and conservation implications of alternative foraging strategies in juvenile loggerhead turtles (*Caretta caretta*) of the North Pacific Ocean. PhD thesis, The University of California, Santa Cruz, CA
- Peckham SH, Maldonado-Diaz D, Walli A, Ruiz G, Crowder LB, Nichols WJ (2007) Small-scale fisheries bycatch jeopardizes endangered Pacific loggerhead turtles. *PLoS ONE* 2:e1041
- Peckham SH, Maldonado-Diaz D, Koch V, Mancini A, Gaos A, Tinker MT, Nichols WJ (2008) High mortality of loggerhead turtles due to bycatch, human consumption and strandings at Baja California Sur, Mexico, 2003 to 2007. *Endang Species Res* 5:171–183
- Peckham SH, Maldonado-Diaz D, Tremblay Y, Ochoa R and others (2011) Demographic implications of alternative foraging strategies in juvenile loggerhead turtles *Caretta caretta* of the North Pacific Ocean. *Mar Ecol Prog Ser* 425:269–280
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Polovina JJ, Kobayashi DR, Parker DM, Seki MP, Balazs GH (2000) Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997–1998. *Fish Oceanogr* 9:71–82
- Polovina JJ, Howell EA, Kobayashi DR, Seki MP (2001) The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Prog Oceanogr* 49:469–483
- Polovina JJ, Balazs GH, Howell EA, Parker DM, Seki MP, Dutton PH (2004) Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fish Oceanogr* 13:36–51
- Rau GH, Ohman MD, Pierrot-Bults A (2003) Linking nitrogen dynamics to climate variability off central California: a 51 year record based on $^{15}\text{N}/^{14}\text{N}$ in CalCOFI zooplankton. *Deep-Sea Res II* 50:2431–2447
- Read AJ (2007) Do circle hooks reduce the mortality of sea turtles in pelagic longlines? A review of recent experiments. *Biol Conserv* 135:155–169
- Reich KJ, Bjorndal KA, Martínez del Rio C (2008) Effects of growth and tissue type on the kinetics of ^{13}C and ^{15}N incorporation in a rapidly growing ectotherm. *Oecologia* 155:651–663
- Reich KJ, Bjorndal KA, Frick MG, Witherington BE, Johnson C, Bolten AB (2010) Polymodal foraging in adult female loggerheads (*Caretta caretta*). *Mar Biol* 157:113–121
- Resendiz A, Resendiz B, Nichols WJ, Seminoff JA, Kamezaki N (1998) First confirmed east-west transpacific movement of a loggerhead sea turtle, *Caretta caretta*, released in Baja California, Mexico. *Pac Sci* 52:151–153
- Ruiz-Cooley RI, Gerrodette T (2012) Tracking large-scale latitudinal patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ along the E Pacific using epi-mesopelagic squid as indicators. *Ecosphere* 3:art63
- Ruiz-Cooley RI, Garcia KY, Hetherington ED (2011) Effects of lipid removal and preservatives on carbon and nitrogen stable isotope ratios of squid tissues: implications for ecological studies. *J Exp Mar Biol Ecol* 407:101–107
- Seminoff JA, Resendiz A, Resendiz B, Nichols WJ (2004) Occurrence of loggerhead sea turtles (*Caretta caretta*) in the Gulf of California, México: evidence of life-history variation in the Pacific Ocean. *Herpetol Rev* 35:24–27
- Seminoff JA, Benson SR, Arthur KE, Eguchi T, Dutton PH, Tapilatu RF, Popp BN (2012) Stable isotope tracking of endangered sea turtles: validation with satellite telemetry and $\delta^{15}\text{N}$ analysis of amino acids. *PLoS ONE* 7:e37403
- Somes CJ, Schmittner A, Galbraith ED, Lehmann MF and others (2010) Simulating the global distribution of nitrogen isotopes in the ocean. *Global Biogeochem Cycles* 24:GB4019, doi:10.1029/2009GB003767
- Todd S, Ostrom P, Lien J, Abrajano J (1997) Use of biopsy samples of humpback whale (*Megaptera novaeangliae*) skin for stable isotope ($\delta^{13}\text{C}$) determination. *J Northwest Atl Fish Sci* 22:71–76
- Voss M, Dippner JW, Montoya JP (2001) Nitrogen isotope patterns in the oxygen-deficient waters of the Eastern Tropical North Pacific Ocean. *Deep-Sea Res I* 48:1905–1921
- Wallace BP, Saba VS (2009) Environmental and anthropogenic impacts on intra-specific variation in leatherback turtles: opportunities for targeted research and conservation. *Endang Species Res* 7:11–21
- Wallace BP, Seminoff JA, Kilham SS, Spotila JR, Dutton PH (2006) Leatherback turtles as oceanographic indicators: stable isotope analyses reveal a trophic dichotomy between ocean basins. *Mar Biol* 149:953–960
- Wallace BP, Lewison RL, McDonald SL, McDonald RK and others (2010) Global patterns of marine turtle bycatch. *Conserv Lett* 3:131–142
- Watanabe KK, Hatase H, Kinoshita M, Omuta K and others (2011) Population structure of the loggerhead turtle *Caretta caretta*, a large marine carnivore that exhibits alternative foraging behaviors. *Mar Ecol Prog Ser* 424:273–283
- Wingfield DK, Peckham SH, Foley DG, Palacios DM and others (2011) The making of a productivity hotspot in the coastal ocean. *PLoS ONE* 6:e27874
- Zbinden JA, Bearhop S, Bradshaw P, Gill B, Margaritoulis D, Newton J, Godley BJ (2011) Migratory dichotomy and associated phenotypic variation in marine turtles revealed by satellite tracking and stable isotope analysis. *Mar Ecol Prog Ser* 421:291–302

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