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Trophic ecology of green sea turtles in a highly urbanized bay: Insights from stable isotopes and mixing models

Garrett Lemons [a], Rebecca Lewison [b], Lisa Komoroske [b], Alexander Gaos [b], Chun-Ta Lai [b], Peter Dutton [a], Tomoharu Eguchi [a], Robin LeRoux [a], Jeffrey A. Seminoff [a,*]

[a] NOAA-National Marine Fisheries Service, Southwest Fisheries Science Center, 3333 N. Torrey Pines Ct., La Jolla, CA 92037, United States
[b] Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182, United States

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ABSTRACT

The green turtle, *Chelonia mydas*, is a circumglobal species that is susceptible to overexploitation as a food resource, incidental mortality in fisheries, and coastal foraging habitat degradation, all of which have contributed to its listing as Endangered on the IUCN Red List. Efforts to recover regional green turtle populations have been hampered by a lack of information on their biology. In particular, temporal patterns of diet intake and habitat use in neritic foraging areas are not well understood. Historical paradigms suggest that adult green turtles are obligate herbivores with diets consisting of seagrasses and/or marine algae. However, these insights are largely based on conventional diet analysis techniques that only yield snapshots of recently consumed foods. Stable isotope analysis has been used to determine contributions of various potential food resources to a consumer's diet, and this approach is commonly applied to identify diet composition and long-term trophic relationships of a species. In this study, we measured the stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of 86 green turtles and seven putative prey species (e.g., algae, seagrass, invertebrates) collected from 2003 to 2008 in San Diego Bay, California, USA, an urbanized coastal bay in the temperate eastern Pacific Ocean. The $\delta^{13}C$ and $\delta^{15}N$ values in skin of green turtles in this study ranged from −18.9‰ to −13.7‰ and 11.0‰ to 19.3‰, respectively, whereas the values for potential foods ranged from −22.6‰ to −11.5‰ for $\delta^{13}C$ and 10.4‰ to 15.9‰ for $\delta^{15}N$. We applied a leading multisource stable isotope mixing model (Stable Isotope Analysis in R), to determine the main contributors to, and annual variation in, green turtle diet based on comparisons of isotope values of turtles and putative prey species. Mixing model outputs indicated that green turtles consumed an omnivorous diet during all years of this study. Mobile invertebrates had the greatest median dietary distribution (38%), whereas seagrasses (26%) and sessile invertebrates (12%) were also found to be major dietary contributors. Red algae and green algae were also identified as feasible prey species, although at reduced levels. When coupled with information on prey species' spatial distributions, these data also provide insights about the types of habitats visited by foraging green turtles. Local seagrass pastures appear to be of high value, serving as a major food resource and providing habitat for other green turtle prey. Protection of the remaining seagrass habitat in and around San Diego Bay is thus considered essential for local green turtle management, and restoration of degraded seagrass habitats in this highly urbanized bay should be considered a top conservation priority.

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1. Introduction

The green turtle (*Chelonia mydas*) is one of the most widely distributed of all marine turtles, occurring in coastal habitats throughout temperate to tropical regions worldwide. Among the many disparate green turtle populations in neritic habitats, there is a broad array of major foods consumed (Bjorndal, 1997), with dietary composition often dependent on the local availability of prey resources (Bjorndal, 1997; Hatase et al., 2006; Seminoff et al., 2002). Although green turtles have historically been considered 'the only herbivorous turtle' (Parsons, 1962; Bjorndal, 1982; and references therein), recent field studies have indicated that at least some green turtle populations found in neritic habitats of the eastern Pacific Ocean are at times omnivorous, with diets consisting of combinations of invertebrates, marine algae, and seagrass (Amorcho and Reina, 2007; Carrion-Cortez et al., 2010; Lopez-Mendilaharsu et al., 2005). Indeed, controlled studies have documented the ability of green turtles to digest sponges and other invertebrate foods (Amorcho and Reina, 2008; Bjorndal, 1990). However, even with this observed diet diversity, seagrasses and/or marine algae have constituted the bulk of adult green turtle diet in neritic habitats in all studies to date (e.g., Bjorndal, 1980; Forbes, 1993; Mortimer, 1981; Seminoff et al., 2002).

Seagrass pastures have been demonstrated as fundamentally important in the foraging ecology of green turtles. Broadly dispersed

* Corresponding author. Tel.: +1 858 546 7152; fax: +1 858 546 7003.
E-mail address: jeffrey.seminoff@noaa.gov (J.A. Seminoff).

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turtlegrass (*Thalassia testudinum*) pastures are the prototypical foraging habitat for green turtles throughout the western North Atlantic and Caribbean Sea (Bjorndal, 1997; Mortimer, 1981; Williams, 1988), whereas eelgrass (*Zostera marina*) is the predominant seagrass found in green turtle foraging habitats of the eastern North Pacific (Lopez-Mendilaharsu et al., 2005). Additionally, declines in green turtle populations have been linked to a drop in the condition of seagrass pastures around the world (Jackson et al., 2001) highlighting the critical relationship between these two ecosystem components. Seagrass habitats by definition occur in shallow, near shore areas and act as important shelter for larval fish, habitat for invertebrates and control for sediment deposition and coastal erosion (Spalding et al., 2003) Seagrass habitats found adjacent to urban centers are vulnerable to a myriad of anthropogenic threats, including anchor damage, eutrophication, pollution, coastal construction, overfishing, and rising sea level (Duarte, 2002; Spalding et al., 2003) Correspondingly, there is a growing threat of seagrass habitat degradation in these and other regions due these direct and indirect human impacts (Spalding et al., 2003). Loss of seagrass is accelerating along many coasts worldwide and is likely to impact green turtles due to the decrease in food availability and from the degradation of benthic structure that provides habitat for other diet resources (Hughes et al., 2009).

One area where loss of seagrass habitat has been a concern is San Diego Bay, a highly urbanized inlet located along the U.S. west coast that hosts a year-round population of green turtles (Eguchi et al., 2010; Fig. 1). Much of this Bay is impacted by industrial development, including numerous shipyards, two military bases, and a major cruise ship terminal. Resident turtle populations are also subject to the impact from the South Bay Power Plant (SBPP), a once-through-cooling power generating facility located in the extreme southern portion of this bay. Through flushing warm effluent directly into its waters, this power plant has artificially warmed the southern portion of San Diego Bay for more than five decades, starting in 1960. Environmental data from prior to its construction are scarce, but it is believed that the long-term thermal impacts throughout the Bay have resulted in a re-distribution of seagrass habitat and other benthic communities. As ectotherms, green turtles are thought to benefit from the abnormally high water temperatures in San Diego Bay, as the warmer temperatures confer an advantage for digestion and assimilation of ingested nutrition. As a result, green turtles have thrived in San Diego Bay, frequenting the SBPP's effluent channel during winter months since at least the late 1960s (Dutton et al., 1993; Eguchi et al., 2010; Stinson, 1984). In the case of green turtles, knowledge of diet and the value of eelgrass habitats is compulsory for effective management and protection, although few such data are available for San Diego Bay.

Stable isotopic analyses (SIA) have been increasingly used to explore the foraging ecology of many marine vertebrates, including cetaceans (Ruiz-Cooley et al., 2004), pinnipeds (Kurle, 2002), seabirds (Hobson, 1993), sharks (Estrada et al., 2003), teleosts (Thomas and Cahoon, 1993), and sea turtles (Godley et al., 1998). The value of this technique for answering ecological questions stems from the fact that isotopic composition of consumer body tissues is derived from its prey and the environment within which it lives (DeNiro and Epstein, 1978, 1981; Hobson and Clark, 1992; Michener and Schell, 1994). Whereas conventional stomach content analyses provide a limited temporal window or 'snapshot' into diet trends, stable isotopes incorporate signatures of nutrients ingested and assimilated over broader temporal periods (e.g., from weeks to months; Peterson and Fry, 1987; Hobson et al., 1996; Reich et al., 2008). Stable isotope signatures of predators and their prey are not identical, and there is usually some degree of isotopic enrichment that occurs with each trophic step due to a differential retention of heavier isotopes during a predator's digestive processes (DeNiro and Epstein, 1978, 1981). Whereas carbon (^{13}C) enrichment has been noted as minimal (−1‰ to 1‰ per trophic step), nitrogen (^{15}N) enrichment has been estimated at 3‰ to 5‰ per trophic level for higher-order consumers (DeNiro and Epstein, 1977, 1978, 1981; Hobson, 1993).

Analyses of consumer trophic status and diet complexity are among the most salient applications of SIA. With diet composition often an amalgam of multiple prey species that fluctuates through space and time, an expanding SIA approach is to apply isotope mixing models that determine the importance of different prey groups based

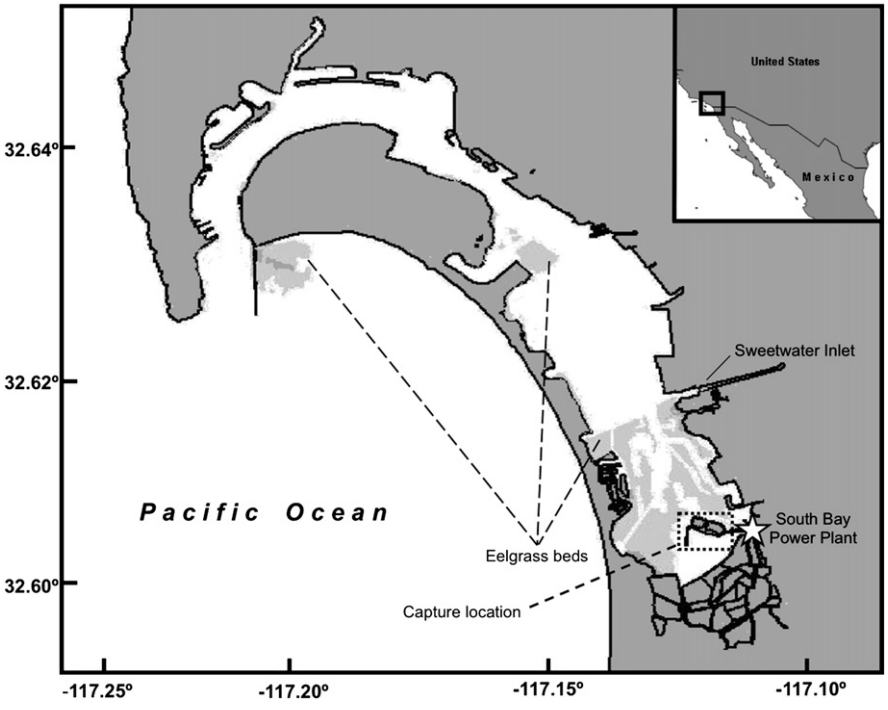

Fig. 1. Map of the San Diego Bay study area. The San Diego Bay Nature Preserve starts south Sweetwater Inlet. The green turtles' capture location is shown in near proximity to the South Bay Power Plant.

on their isotopic signatures versus those of the consumer in focus (Phillips and Gregg, 2003; Inger et al., 2010b). Through Bayesian and parametric statistical approaches, mixing models integrate consumer and prey isotope data to yield a distribution of 'feasible solutions' for each putative prey species' dietary contribution. The model outputs from these packages provide insights about trophic niche width and dietary complexity of consumer diet that is unachievable via conventional data analysis. To date, stable isotope mixing models have been applied in studies of sea turtles (McClellan et al., 2010; Wallace et al., 2009), marine fishes (Benstead et al., 2006), and waterfowl and seabirds (Inger et al., 2010a; Moreno et al., 2010).

In this study, we used stable isotope analysis and applied a Bayesian mixing model (Inger et al. 2010b; Parnell et al. 2010) to determine the trophic status of green turtles in San Diego Bay. Our goals were to characterize the dietary diversity of green turtles and elucidate the value of eelgrass habitats as foraging sites for local green turtles. By exploring the trophic variability and the importance of putative foraging habitats, this study will help refine green turtle conservation and management efforts in San Diego Bay and shed light on green turtle biology in similar habitats along the Pacific coast of North America.

2. Materials and methods

2.1. Study site

San Diego Bay lies along the extreme southern coast of California, 6 km north of the U.S.–Mexico border (32°N, 117°W; Fig. 1). The Bay extends ca. 25 km north to south, and has 4262 ha of open water and 1788 ha of inter-tidal area (Merkel and Associates, 2009). The Bay's southern section is significantly shallower than its northern section, where deep shipping channels (23+ m) are located. It is largely an ecological reserve south of the Sweetwater Inlet (Fig. 1), where water depth averages <5 m below the mean lower low water (MLLW; U.S. Navy and Port of San Diego, 2007). Multiple habitat types exist among the Bay's wide range of depths and varied coastline, types including salt marshes, tidal and subtidal habitats, eelgrass beds, mud and sand bottom invertebrate communities, as well as man-made habitat including rock rip rap and marine floats (U.S. Navy and Port of San Diego, 2007).

2.2. Turtle capture

From 2003 to 2008 we captured green turtles along the shallow perimeter of southern San Diego Bay approximately every two weeks from November to April. Capture efforts occurred near the effluent of the South Bay Power Plant (Fig. 1) using entanglement nets (100 m × 6 m, mesh size = 50 cm stretched). Net-soak time ranged from 1 to 5 h during diurnal periods, and nets were monitored at 0.5-h to 0.75-h intervals. Upon capture, turtles were disentangled and transported to shore (<1 km) where they were processed (e.g., individual identification, body measurements, general health assessment, tagging, tissue sampling). Curved carapace length (CCL; ±0.1 cm) was measured from the nuchal notch to the posterior-most edge of the marginal scutes using a flexible measuring tape, and body weight (±0.5 kg) was measured using an electronic balance.

2.3. Sample collection and preparation

We collected skin tissue (stratum corneum) from the dorsal surface of the neck of each captured turtle using a razor or biopsy punch. Skin samples were promptly preserved in saturated salt (NaCl) solution and placed on ice for transport to the laboratory where they were stored at −20 °C until preparation and analysis. Prior to stable isotope analysis, skin samples were thawed, rinsed with distilled water, dried at 60 °C for 48 h, and then ground with a razor blade into small grains. Tissue from putative prey species (hereafter referred to as habitat samples) was collected during SCUBA line-transects at areas of interest throughout the Bay (L. Komoroske, unpubl. data), as well as opportunistically during field efforts. We collected entire organisms (i.e. whole body) for all but eelgrass, for which only the blades were gathered. These habitat samples were cleaned with distilled water and frozen at −10 °C. Prior to analysis, habitat samples were thawed, weighed (wet weight), and dried at 60 °C until sample weight remained constant (i.e. dry weight), then were homogenized into a fine powder using a mortar and pestle. Lipids were removed from skin samples and a portion of each habitat sample using a Soxhlet apparatus with a 1:1 solvent mixture of petroleum ether and ethyl ether for at least two 10-h cycles. Samples then were dried at 60 °C for 24 h to remove any residual solvent.

2.4. Sample analysis

Approximately 1.0 mg of green turtle skin or habitat samples were loaded into sterilized tin capsules and analyzed by a continuous-flow isotope-ratio mass spectrometer in the Stable Isotope Laboratory at the University of Florida, Gainesville USA. We used a Costech ECS 4010 elemental combustion system interfaced via a ConFlo III device (Finnigan MAT, Bremen, Germany) to a Deltaplus gas isotope-ratio mass spectrometer (Finnigan MAT, Bremen, Germany). Sample stable isotope ratios relative to the isotope standard are expressed in the following conventional delta (δ) notation in parts per thousand (‰)

$$\delta = \left(\left[R_{sample} / R_{standard}\right] - 1\right) \quad (1000)$$

where R_{sample} and $R_{standard}$ are the corresponding ratios of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and standard, respectively. $R_{standard}$ for ^{13}C was Baker Acetanilide (C_8H_9NO; $\delta^{13}C = -10.4‰$) calibrated monthly against the Peedee Belemnite (PDB) limestone formation international standard; $R_{standard}$ for ^{15}N was IAEA N1 Ammonium Sulfate ($(NH_4)_2SO_4$; $\delta^{15}N = +0.4‰$) calibrated against atmospheric N_2 and USGS Nitrogen standards. All analytical runs included samples of standard materials inserted every 6 to 7 samples to calibrate the system and compensate for any drift over time. Replicate assays of standard materials indicated measurement errors of 0.05‰ and 0.095‰ for carbon and nitrogen, respectively. In addition to stable isotope ratios, we measured %C and %N for each diet and tissue sample. Samples were combusted in pure oxygen in the elemental analyzer. Resultant CO_2 and N_2 gasses were passed through a series of thermal conductivity detectors and element traps to determine percent compositions. Acetanilide standards (10.36% N, 71.09% C) were used for calibration.

2.5. Statistics and mixing model analysis

The $\delta^{13}C$ and $\delta^{15}N$ values for green turtle skin tissue were compared among all years using ANOVA to gauge the consistency in isotopic values through time. If a significant difference was detected among years, we used a Tukey post-hoc comparison among means to determine which years were significantly different. To establish the probable dietary groups consumed and assimilated by green turtles, we used the isotope mixing model Stable Isotope Analysis in R (SIAR) and ran the model option incorporating elemental concentrations (e.g., %C and %N; Inger et al., 2010b). Prior to analysis with SIAR, we grouped our putative prey items into categories based on similarities in life history. Tunicates and poriferans were grouped as 'sessile invertebrates' because of the similarities in their filter feeding strategy (Bergquist, 1978; Fiala-Medioni, 1978). We also grouped the California aglaja (*Navanax inermis*) and the California bubble snail (*Bulla gouldiana*) as 'mobile invertebrates' due to life history similarities. As the only marine angiosperm analyzed, eelgrass was kept as a separate source in the analysis. Likewise, the study area's two dominant algae species (*Ulva*

lactuca and *Gracilaria* sp.), a green alga and red alga, respectively, were also modeled as separate prey groups due to their respective C_3 and C_4 photosynthetic pathways (Beer and Israel, 1986; Cole and Sheath, 1990) that could affect $\delta^{13}C$ signatures (Table 3). With SIAR we generated a series of prey contribution distributions, which proportionally integrated the variance of green turtle and habitat $\delta^{13}C$, and $\delta^{15}N$ values based on the %C and %N for each prey group. Elemental concentrations for prey items from the primary foraging habitats in the south bay region were used. Since different tissues are shown to incorporate isotopes at different rates (Reich et al. 2008), prior to model generation we applied green turtle skin-specific correction factors (−0.17‰ for $\delta^{13}C$, +2.80‰ for $\delta^{15}N$; Seminoff et al. 2006) to our data to account for consumer–prey isotopic discrimination.

3. Results

3.1. Turtle capture

A total of 86 green turtles were captured, with 4 to 20 turtles captured each season (mean = 14.5 ± 5.9, Table 1). Curved carapace length of captured turtles ranged from 49 to 115 cm in CCL (n = 74; mean = 89.9 ± 21.2), and body weight ranged from 14 to 133 kg (n = 65; mean = 107.4 ± 63.9). Mean annual CCL and body weight were consistent among all years of this study (CCL: $F_{5,73} = 1.43$, $p = 0.22$; weight: $F_{5,64} = 1.12$, $p = 0.31$).

3.2. Elemental concentrations and stable isotope ratios

The elemental concentrations (%C and %N) and isotope values ($\delta^{13}C$ and $\delta^{15}N$) of green turtle skin tissues collected and used in analyses from 2003 to 2008 are shown in Table 1. Whereas %C in skin samples ranged from 31.6% to 59.3%, %N was from 8.4% to 16.5%. All elemental concentration values were within ranges reported previously in a controlled green turtle feeding study (Seminoff et al., 2006). With respect to stable isotope results, skin $\delta^{13}C$ ranged from −18.9‰ to −13.7‰ (overall mean = −15.1 ± 1.1‰). There was significant variability in mean $\delta^{13}C$ among years ($F_{5,82} = 9.25$, $p = 0.0001$; Fig. 2), with 2003 having the highest $\delta^{13}C$ (−14.6 ± 1.1‰) and 2007 the lowest $\delta^{13}C$ (−17.2 ± 0.9‰). A Tukey post-hoc comparison among means revealed the years 2003 and 2006 were significantly different (Table 3). Skin $\delta^{15}N$ ranged from 8.7‰ to 19.3‰ (overall mean = 16.9 ± 1.3‰) and annual mean $\delta^{15}N$ was consistent among all years ($F_{5,82} = 1.2$, $p = 0.3$; Fig. 2).

Stable carbon and nitrogen values as well as elemental concentrations were determined for seven prey species. $\delta^{13}C$ values for the seven species ranged from −22.6‰ to −11.1‰ and $\delta^{15}N$ ranged from 10.4‰ to 15.9‰. Elemental concentrations ranged from 20.4% to 51.1% for carbon and 3.5% to 10.4% for nitrogen. All species were common in the study area and considered to be putative prey species of local green turtles due to their presence in the diet of green turtles at other foraging areas (Table 2). For carbon, eelgrass had the most enriched $\delta^{13}C$ value (−11.1 ± 1.0‰), whereas sessile invertebrates had the most depleted $\delta^{13}C$ value (−22.1 ± 0.8‰; Table 2). For nitrogen, mobile invertebrates had the most enriched $\delta^{15}N$ values (15.8 ± 1.0‰), whereas eelgrass had the most depleted $\delta^{15}N$ value (10.4 ± 1.1‰; Table 2).

Table 2
Mean stable isotope values for prey groups used in the mixing model analyses. All means are presented with standard deviation.

Prey item	N	%C	%N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Seagrass					
Zostera marina	46	39.4 ± 10.1	3.5 ± 0.6	−11.1 ± 1.0	10.4 ± 1.1
Macroalgae					
Ulva lactuca	22	51.1 ± 10.2	6.2 ± 1.2	−15.7 ± 2.6	12.5 ± 1.2
Gracilaria sp.	32	39.5 ± 7.6	5.3 ± 1.0	−20.1 ± 4.5	11.7 ± 1.0
Sessile invertebrates					
Tunicates	24	20.4 ± 31.6[a]	10.4 ± 22.8[a]	−22.1 ± 0.8[a]	2.9 ± 0.8[a]
Porifera	50				
Mobile invertebrates					
Bulla gouldiana	4	33.5 ± 6.2[a]	8.7 ± 2.2[a]	−16.6 ± 1.2[a]	15.8 ± 1.0[a]
Navanax inermis	2				

[a] denotes aggregated values used in SIAR analyses.

3.3. Mixing model outputs

All green turtle values were initially plotted with putative prey groups in SIAR to show a preliminary relationship (Fig. 3). Our model indicated that three prey groups contributed most substantially to green turtle diet. Mobile invertebrates appeared the most important diet group, with SIAR-modeled proportional distributions of feasible contributions ranging from 24% to 56% of the 1–99th percentile of feasible proportions and a median proportional contribution of 38% (Fig. 4). Eelgrass was also a significant diet group, with diet contribution ranging from 14% to 38% of the 1–99th percentile of feasible proportions and a median proportional contribution of 26%. Sessile invertebrate distribution ranged from 2% to 32% of the 1–99th percentile of feasible proportions, with a median proportional contribution occurring at 12%. SIAR outputs revealed lesser contributions from *Gracilaria* sp. and *Ulva lactuca*, with most probable median proportion densities at 14% for each. Densities for both algal groups are significantly lower than the other prey items and no solutions were generated for complete minimum distribution ranges for both of these algal groups (Fig. 4).

When examined on an annual basis, mobile invertebrates were shown by SIAR to be the primary diet group in 2003, 2005, 2006, and 2008, whereas eelgrass and sessile invertebrates were the primary diet components in 2004 and 2008, respectively (Fig. 5). During years of lesser apparent consumption of mobile invertebrates, eelgrass and sessile invertebrates were the two diet groups that consistently showed an increase in their possible contributions (Fig. 5). *Gracilaria* sp. and *Ulva lactuca* contribution was minimal throughout all years

Table 1
Mean stable isotope ($\delta^{13}C$, $\delta^{15}N$) values for green turtle skin samples collected from 2003 to 2008 in San Diego Bay. The present table does not include the presumed recent arrivals into San Diego Bay (n = 3; see Discussion).

Year	n	%C		%N		$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
		Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
2003	12	41.2 ± 4.82	27.5 to 47.5	12.8 ± 1.71	7.7 to 14.0	−14.6 ± 1.05	−15.9 to −11.6	17.7 ± 0.64	16.7 to 18.6
2004	19	46.1 ± 2.10	41.5 to 48.9	14.1 ± 0.94	12.7 to 15.8	−16.0 ± 0.76	−16.9 to −14.7	16.7 ± 1.26	14.7 to 19.0
2005	20	42.9 ± 7.45	22.1 to 59.3	13.0 ± 2.11	6.5 to 15.2	−16.0 ± 0.69	−17.3 to −14.7	17.1 ± 1.30	14.9 to 19.2
2006	11	43.6 ± 2.91	38.0 to 49.7	12.3 ± 1.56	8.7 to 14.2	−15.6 ± 1.28	−17.7 to −13.7	17.5 ± 0.59	16.2 to 18.1
2007	4	46.3 ± 2.99	44.3 to 50.7	12.9 ± 1.53	10.8 to 14.3	−17.2 ± 0.87	−18.4 to −16.4	16.5 ± 2.15	13.2 to 17.7
2008	17	43.1 ± 7.24	31.6 to 50.8	13.7 ± 3.28	8.4 to 16.5	−16.5 ± 0.80	−18.9 to −15.4	17.0 ± 2.30	11.0 to 19.3
Total	83	44.0 ± 4.93	22.1 to 59.3	13.5 ± 1.77	6.5 to 16.5	−15.9 ± 1.06	−18.9 to −13.7	17.1 ± 1.33	11.0 to 19.3

Table 3
Results from the Tukey post-hoc comparison test for mean annual skin tissue $\delta^{13}C$. Positive values show pairs of means that are significantly different.

Abs(Dif)-LSD	2003	2004	2005	2006	2007	2008
2003	−1.01	0.35	0.42	−0.59	0.87	1.10
2004	0.35	−0.80	−0.73	−0.16	−0.28	−0.10
2005	0.42	−0.73	−0.28	−0.10	−0.33	−0.15
2006	−0.59	−0.16	−0.10	−1.11	0.59	0.35
2007	1.10	−0.10	−0.33	0.35	−0.66	−1.76
2008	0.87	−0.28	−0.15	0.59	−0.85	−0.66

and only elevated in 2007 when all other forage items (in relation to each other) showed an overall consistency in potential dietary contribution.

4. Discussion

4.1. Green turtle trophic status

Establishing trophic position and important forage resources of green turtles in San Diego Bay bolsters knowledge about the biology of this endangered species and builds a better understanding of the importance of different geographic regions they utilize. Effective conservation decisions rely on the understanding of how different life stage habitats interrelate with green turtle behavior. When examined on an annual basis, these data can depict variation in foraging trends and temporal stability of specific diet resources, which is a central need for green turtle conservation. Coupling these data with information on prey distribution provides fundamental information to local management authorities (e.g., Unified Port of San Diego, U.S. National Marine Fisheries Service) to better manage and mitigate current and future human impacts within San Diego Bay.

With a mean skin $\delta^{15}N$ value of 16.9‰, green turtles in San Diego Bay have the most enriched nitrogen values yet reported for this species. Arthur et al. (2008) found skin $\delta^{15}N$ from 6.0‰ to 12.0‰ for green turtles in Australia. Cardona et al. (2009) and Hatase et al. (2006) showed mean $\delta^{15}N$ of 8.6‰ and 11.4‰, respectively, although caution should be made considering they used different tissues. Occasionally, elevated $\delta^{15}N$ signatures can been attributed to poor nutrition, caused by metabolism of a consumer's own protein tissue due to starvation (Hobson,1993). However, no sign of starvation was seen or has been recorded in this population of green turtles (Eguchi et al., 2010; P. Dutton, pers. comm.). Farther south (200–400 km) in the California Current Large Marine Ecosystem, along the Pacific coast of the Baja California Peninsula, Mexico, green turtles have substantially more depleted $\delta^{15}N$ than those for San Diego Bay, despite the fact that the primary forage species in this region are similar to those at our study site (Lopez-Mendilaharsu et al., 2005; Lewis, 2009; J. Seminoff, unpubl. data). In light of the highly urbanized nature of San Diego Bay, the elevated $\delta^{15}N$ of green turtle skin and habitat values suggest that this system may be impacted by anthropogenic nitrogen loading. Indeed, commercial shipyards, naval shipyards and storm drain runoffs have been documented to contain high levels of pollutants for this system (Fairey et al., 1998), some of which have also been found in green turtle body tissues during a recent health and contaminant study (Komoroske et al., in press). In fact, recently a sewage spill of 8 million gallons was discovered to have entered the San Diego watershed after heavy rains (Lee, 2011). Presuming that these point sources of pollution contain sewage runoff, this could lead to an enrichment of ^{15}N in affected habitats (Valiela et al., 1999). Specific SIA studies of selected areas within San Diego Bay along with comparable contaminant data would facilitate a better understanding of the extent of nitrogen loading in this system.

Although the broad range in isotopic values is suggestive of varied foraging tactics within San Diego Bay, we acknowledge that isotopic influences from outside the study area may have affected our results. Considering that the minimum $\delta^{15}N$ of foods analyzed in the study area is 10.4‰, and that green turtles should exhibit tissue isotope values that are ^{15}N-enriched relative to their diet (Seminoff et al.,

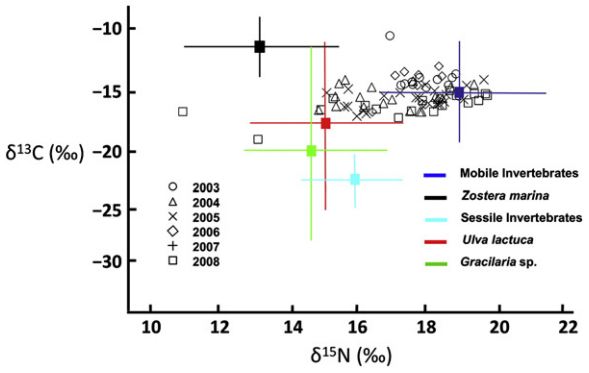

Fig. 3. Plot of all green turtles' values accounting for discrimination factors by year with prey items.

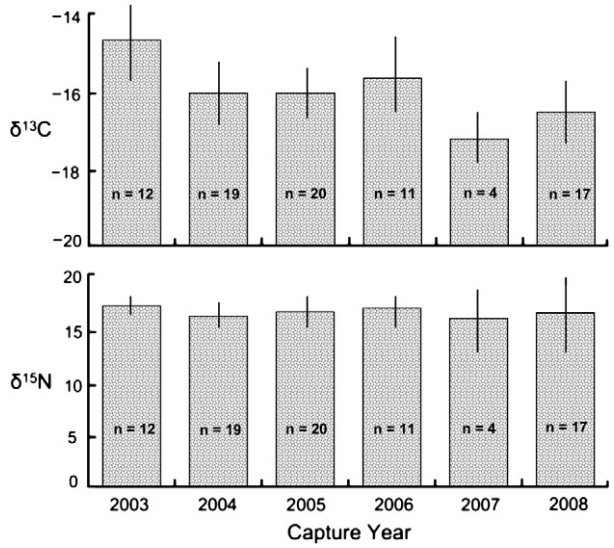

Fig. 2. Annual mean stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values for skin tissue of green turtles captured in San Diego Bay from 2003 to 2008.

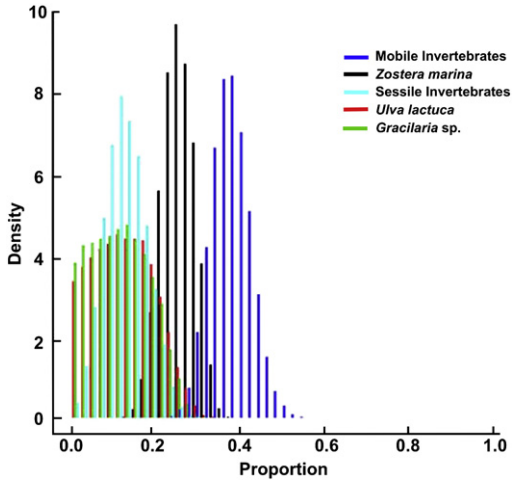

Fig. 4. SIAR output incorporating elemental concentration of five source dietary contribution distributions for years 2003 to 2008.

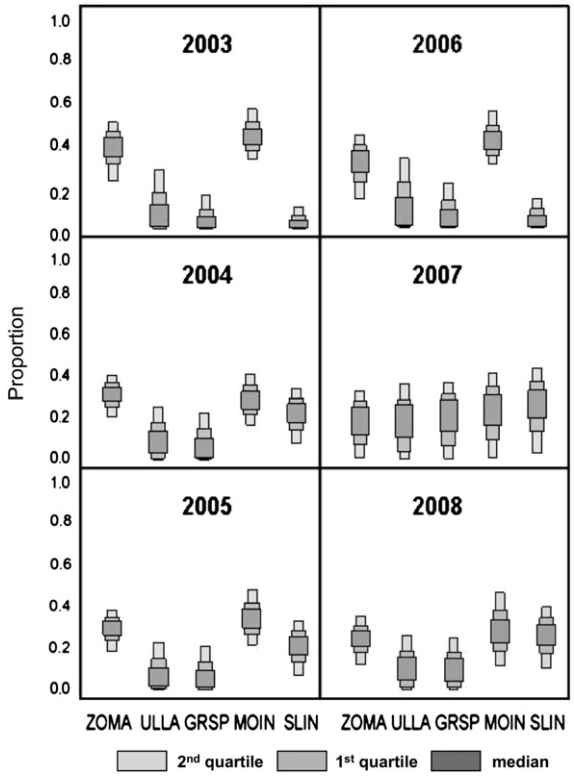

Fig. 5. Annual variation as illustrated by SIAR distributions with elemental concentrations. Box plots illustrating contribution ranges to green turtle diet by foraging items years 2003–2008. ZOMA (*Zostera marina*), ULLA (*Ulva lactuca*), GRSP (*Gracilaria* sp.), MOIN (mobile invertebrates), SLIN (sessile invertebrates).

2006), we believe that a $\delta^{15}N \leq 10.4‰$ is unlikely for a green turtle residing in San Diego Bay. This is a conservative minimum cutoff considering the presumed ^{15}N enrichment in green turtles versus their prey as reported by Seminoff et al. (2006; see above). We note that there were three turtles with values in this category, all of which are depicted as apparent outliers in Fig. 3. The %C and %N values — commonly used as a diagnostic to elucidate any 'problem samples' were within acceptable limits for all three individuals, suggesting these are accurate values and not the result of sample error. Thus, we suggest that these three turtles may have been recent arrivals to the study area, having acquired their stable isotopic makeup through foraging at a different habitat prior to arrival in San Diego Bay. This is conceivable when recognizing that all green turtles in San Diego Bay originate from nesting sites in Mexico, 1500 km to the south (P. Dutton, unpubl. data). Because these individuals may not have been resident to the Bay, we excluded them from the mixing model analyses. Although capture of turtles took place at one location throughout the study we feel it is unlikely capture location had any influence on our results as green turtles captured near the power plant effluent have been tracked at locations across the bay (B. Macdonald, unpubl. data).

Although mean annual $\delta^{15}N$ was consistently enriched among all years of this study, there was substantial individual variability for $\delta^{15}N$ (range = 11.0‰ to 19.8‰). Recall that the $\delta^{15}N$ range reflects individual values, as opposed to group means, thereby suggesting that our results may reflect individual dietary specialization among green turtles in San Diego Bay. With a $\delta^{15}N$ range among turtles >4‰ during four years of this six year study (all but 2003 and 2006), our data suggests that individual dietary specialization is common and persistent in San Diego Bay green turtles. Lewis (2009) found that green turtles in Bahia San Ignacio along the Baja Peninsula possessed variable foraging strategies, with some individuals demonstrating herbivory on seagrass while others were omnivorous, consuming seagrasses as well as benthic invertebrates. Similarly, Vander Zanden et al. (2010) used stable isotope analysis to highlight long-term individual diet and resource use specialization in a generalist population of loggerhead turtles (*Caretta caretta*).

Finally, because green turtles consuming eelgrass and/or marine algae would be one trophic step from baseline primary producers, green turtle skin tissues theoretically should reflect one trophic level of enrichment in $\delta^{15}N$ (2.8‰; Seminoff et al., 2006). Given that mean $\delta^{15}N$ of eelgrass, red algae and green algae in San Diego Bay are 10.4‰, 11.7‰, and 12.4‰, respectively, green turtle skin $\delta^{15}N$ should be roughly 13.2‰ to 15.2‰ if they are exclusively herbivorous. However, the range for green turtles excluding the three potential recent recruits (see above) is 11.0‰ to 19.8‰; thereby suggesting that at least some green turtles are consuming higher-trophic-level foods. In fact, of the 83 green turtles included in this study (not including the potential recent arrivals), 76 turtles had $\delta^{15}N > 15.2‰$, thereby indicating that the vast majority of green turtles in San Diego Bay are consuming an omnivorous diet, occupying both first and second order consumer trophic positions.

Although this study has provided valuable knowledge about green turtle trophic status in San Diego Bay, the digestive strategies of green turtles do underscore the need for future controlled foraging studies to validate field observations. Green turtles utilize microbial fermentation in their hindgut (Bjorndal et al., 1991) to break down cell walls of plants and algae ingested. Because nutrients from algal and plant foods are essentially made available to green turtles via this fermentative process, there is an additional step in digestive processing for green turtles that is not present in carnivorous marine turtles. However, the influence of microbial fermentation on consumer–prey isotope discrimination is unclear. We recommend additional studies that establish the relationship between diet, digestive strategy, and consumer–prey stable isotope discrimination.

4.2. Green turtle diet and habitat use

SIA coupled with a stable isotope mixing model provides insights about the primary food resources for green turtles in San Diego Bay. SIAR identified an omnivorous foraging strategy by green turtles, with mobile invertebrates showing a distribution of 24% to 56% (Fig. 4) of the diet of green turtles. Mobile invertebrate distribution solutions from SIAR surpassed those for all other putative prey groups for a majority of the study years (Fig. 5). When accounting for total invertebrate contribution ranges (mobile and sessile invertebrate prey groups), green turtles in San Diego Bay demonstrate the highest apparent level of invertebrate consumption reported to date for green turtles in the wild (e.g., Mortimer, 1981; Seminoff et al., 2002; Lopez-Mendilaharsu et al., 2005; Carrion-Cortez et al., 2010). Perhaps the greater availability of the mobile and sessile invertebrates, their relative ease of capture, and their high nutritional value, coupled with the low levels of algae within the Bay, led to their unprecedented dietary importance. We note, however, that mobile invertebrates have higher elemental nitrogen concentration relative to eelgrass (Table 2), such that green turtles would have to eat proportionally less biomass of mobile invertebrates to have this prey group's $\delta^{15}N$ content be reflected equally to seagrass in their own body tissue. We also acknowledge the possibility of incidental ingestion of eelgrass during the consumption of invertebrates.

Our results also shed light on the specific habitat types accessed by green turtles. Although few data are available on abundance and distribution of the putative prey groups included in this study, it is clear that eelgrass distribution is centered in the extreme southern portion of the Bay, with only a few smaller pastures located north of Sweet Water Inlet (Fig. 1; B. MacDonald, unpubl. data). Eelgrass beds in San Diego Bay are known to support a wide variety of benthic fauna including the California bubble snail, the California ajala, and other mobile invertebrates (Sirota and Hovel, 2006). While it is possible that these aforementioned species also occur away from eelgrass pastures,

we note that no specimens of either species were found during extensive transects in the Bay during a previous study (L. Komoroske, unpubl. data). Considering the mean proportion density of the eelgrass distributions (26%; Fig. 4) and the mean proportion density of mobile invertebrates (38%) living within these eelgrass pastures, the total contribution eelgrass-related forage items to the diet of green turtles is substantial. Although seagrass pastures have been cited as critical foraging areas for green turtles elsewhere (Mortimer, 1981; Williams, 1988), our results are the first to underscore their critical value in the eastern Pacific Ocean. Lopez-Mendilaharsu et al. (2005) found that eelgrass made up 9.2% of the diet of green turtles farther south along the Pacific coast and Lewis (2009) showed turtles consume eelgrass in foraging areas in Baja California, Mexico. Nevertheless, neither study depicted the value of eelgrass pastures as a host habitat for other food resources. Our results emphasize that eelgrass beds are a critical resource for green turtles in San Diego Bay, both as a forage item and as a structural feature that creates habitat for other green turtle prey species.

4.3. Annual variation in diet

The six years of stable isotope data for green turtles in San Diego Bay represent one of the longest isotopic time series for marine turtles, and as such, it allows us to explore trophic variability through time. During the majority of years in this study, mobile invertebrates were the most important food group consumed by green turtles, with the highest distribution range in 2003 (42% to 50%) and the lowest distribution range in 2007 (55% to 45%; Fig. 5). Sessile invertebrates and eelgrass were found to be consistent prey sources in all years except for sessile invertebrates in 2003 and 2006 (Fig. 5). These results correlate well with the overall distributions produce by SIAR (Fig. 4). Marine algae were also found to be inconsistently consumed over the duration of this study, with 2007 as the only year for which green algae was found to be a significant diet item.

Our study would have benefited from an understanding of annual variation in elemental concentrations and stable isotope values of putative foods within the study area. Clearly, annual information on %C, %N, $\delta^{13}C$ and $\delta^{15}N$ for each putative prey species would lead to a more robust examination of the annual variation in diet composition based on our mixing model approach. Unfortunately few data exists to confirm seasonal and annual isotopic fluctuation in the Bay. We note, however, that Kwak and Zedler (1997) profiled isotopic signatures of various habitat species in the San Diego watershed – including most of the putative prey species included in this study – and in all cases, the values reported therein were highly similar to our results, a notable similarity considering the long time duration between our study (2003–2008) and theirs (early to mid 1990s). This consistency supports a temporal stability in isotope signatures of the putative prey items and suggests that any such changes would be minimal for the species.

What causes the annual differences in diet composition? Yearly fluctuations may be due to opportunistic consumption of secondary, or less preferred prey species, when primary items are less available. Considering that mobile invertebrate populations can fluctuate due to different factors (Edgar, 1990), it is possible that years of greater seagrass, algae, and sessile invertebrate consumption were the result of diminished availability of mobile invertebrates. A greater understanding of local marine ecosystem dynamics and annual variability in prey availability would be instructive for better interpreting our current results and will be the focus of future green turtle diet studies in San Diego Bay.

5. Conclusions

Green turtles in San Diego Bay exhibit flexible foraging strategies, encompassing at least two trophic levels in this neritic foraging area. While Hatase et al. (2006) used SIA to show that green turtles in oceanic environments also consume an omnivorous diet, ours is the first study using SIA to show high levels of omnivory in a coastal neritic habitat. In this context, it would be interesting as a retrospective to employ SIA in historical studies that had identified obligate seagrass consumption by green turtles occupying seagrass habitats (e.g. Bjorndal, 1980, 1982; Forbes, 1993; Mortimer, 1981; Williams, 1988).

In addition to highlighting the importance of specific prey groups, our results underscore the need for eelgrass conservation in San Diego Bay and alert us to the potential nitrogen loading in this system. Specific spatial SIA studies of selected areas would facilitate a more specific determination of the extent of human influence in San Diego Bay. Since seagrass beds in coastal waters provide critical habitat and shelter for invertebrates and fish, including a variety of marine snails (Kharlamenko et al., 2001; Orth et al., 1984), it is likely that conservation of this habitat type would have broader value for many different species in addition to green turtles.

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