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ARTICLES

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Ecology and Conservation of Marine Turtles in a Central Pacific Foraging Ground

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Abstract. – Foraging grounds are critical to the survival of marine turtles, yet studies of these areas lag behind those of nesting sites. Our study represents the first data and discussion on marine turtle distribution, abundance, and health at a marine turtle foraging ground in the central Pacific, Palmyra Atoll National Wildlife Refuge, which constitutes a regionally important mixed-size-class foraging ground for green turtles (*Chelonia mydas*) and, to a lesser extent, for hawksbill turtles (*Eretmochelys imbricata*). Surveys and anecdotal reports suggest that nesting activity is rare, and we have confirmed the presence of limited suitable nesting habitat. During in-water activities from 2008 to 2011, we caught 211 green turtles ranging from postpelagic juveniles to adults (weight: mean = 44.6 kg, range = 7.2–146.3 kg; curved carapace length (CCL): mean = 69.7 cm, range = 41.0–113.6 cm) and 2 juvenile hawksbills ($weight_{2009}$ = 16.3 kg, CCL_{2009} = 57.0; $weight_{2011}$ = 11.2 kg, CCL_{2011} = 50.5 cm). Body condition indices did not significantly differ by year of capture. These indices, along with the absence of observed fibropapilloma tumors, indicated that turtles at Palmyra Atoll were on average in very good condition. We also conducted 11 relative abundance surveys from 2005 to 2011, a subset of which revealed an uneven distribution of turtles around Palmyra Atoll with 3 hot spots of turtle abundance off the flats to the north, south, and east. By linking several aspects of our research program with similar efforts at foraging grounds throughout the Pacific Basin, we can further our understanding of poorly known regional migratory connectivity.

Key Words. – Reptilia; Testudines; *Chelonia mydas*; *Eretmochelys imbricata*; Eastern Pacific green turtle; hawksbill turtle; Palmyra Atoll; foraging; conservation threats; body condition; relative abundance

Marine turtles, many of which are endangered or threatened around the world (International Union for Conservation of Nature [IUCN] 2012), are key members of diverse ecosystems including estuaries, coasts, and open oceans. Although their ecological function remains insufficiently understood, marine turtles serve as prey for some species such as sharks, as consumers and habitat modifiers, and as nutrient transporters (Bjorndal and Jackson 2003). They may also serve as sentinel species with respect to the health of coastal environments (Aguirre and Lutz 2004). As juveniles, green turtles recruit to feeding grounds in coastal regions (Musick and Limpus 1997). Research on these in-water habitats occurs less frequently than at more accessible nesting beaches, as it is usually more difficult to undertake. Even so, studies of foraging areas indicate variation in green sea turtle diet across stage classes (Reich et al. 2007) and space (Parker et al. 2011). While it is widely accepted that adult green sea turtles are largely herbivorous in neritic habitat (Bjorndal 1980; Forbes 1994; Seminoff et al. 2002), significant variation in foraging habits among animals residing at different foraging grounds also exists (Senko et al. 2010). Neritic foraging grounds represent one of the most important habitats for green turtles, as they can spend over 20 yrs in these areas (Nichols 2003; Senko et al. 2010). Research on foraging populations is essential for providing suitable population assessments (Balazs et al. 1987; National Research Council 2010), as feeding grounds are often composed of genetically ''mixed stocks'' drawn from different natal sources. Demographic data from foraging areas can help to substantiate information on the transition from the pelagic to coastal feeding grounds, migrations among feeding grounds, and other information critical for developing effective conservation strategies (National Research Council 2010). A recent article summarizing ''resource management units (RMUs)'' for marine turtles points to the importance of developing conservation units using diverse data sources and recognizes that a next step in turtle conservation will be to incorporate foraging areas into RMU definitions (Wallace et al. 2010a).

Marine turtles face a number of anthropogenic threats across their foraging grounds, including harvest, entanglement in fishing gear, habitat loss, pollution, climate change, and disease (Seminoff 2004; IUCN 2012). Fibropapilloma disease can cause tumors and high rates of stranding, especially in green turtles (Herbst and Jacobson 2003; Baboulin 2008; Chaloupka et al. 2009). Green turtles are considered endangered globally (Seminoff 2004) and, with the exception of Florida's breeding colonies, are listed as threatened under the US Endangered Species Act (ESA) throughout the coastal United States. Green turtles nesting on the Pacific coast of Mexico are also listed as Endangered under the US ESA. In other Pacific regions, listings and levels of protection vary. In Oceania some countries grant green turtles full protection, while in others harvest is allowed or there is no specific protective legislation (Maison et al. 2010). In Australia, for example, where the species is listed as vulnerable, full protection is granted, but indigenous and subsistence harvest is allowed (Maison et al. 2010). Protection in Asia is also varied, and the Turtle Islands Heritage Protected Area of the Philippines and Malaysia is a well-known transboundary protected area established to conserve the species. Marine turtle populations have experienced declines in the Pacific and the other oceans and seas, though recent data point to recovery of some stocks (Balazs and Chaloupka 2004; Broderick et al. 2006; Chaloupka et al. 2007). For example, while several Eastern Pacific green turtle populations (green turtles of darker coloration also known as ''black turtles,'' *Chelonia agassizii*, or *Chelonia mydas agassizii*; Pritchard 1997; Parker et al. 2011) have declined over the past 3 decades (National Marine Fisheries Service and US Fish and Wildlife Service [NMFS and USFWS] 1998c; Seminoff et al. 2003a; Chassin-Noria et al. 2004; Seminoff 2004), there are signs of recovery (Seminoff 2004; Delgado-Trejo and Diaz 2012).

The central Pacific supports several marine turtle stocks (Wallace et al. 2010b), many of which are poorly studied with little known about their current or historical ecology and status (Balazs 1995; Chaloupka et al. 2004). There are significant demographic data of green turtles from foraging grounds in a few regions in the Pacific, including Hawaii, the eastern Pacific (Green and Ortiz 1982; NMFS and USFWS 1998c), and the southern Great Barrier Reef, but vast regions of the central Pacific are understudied. One of the lesser-known areas, the Palmyra Atoll National Wildlife Refuge (PANWR) located within the Pacific Remote Islands Marine National Monument (Fig. 1), is a feeding ground for green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles (Fefer 1987; Depkin 2002; this study). Palmyra Atoll is presently uninhabited except for periodic occupation by a small number of management and research personnel from the USFWS, The Nature Conservancy, and other members of the multi-institutional Palmyra Atoll Research Consortium (PARC). Although Palmyra Atoll is currently free from intensive anthropogenic impacts, the US military altered the atoll over the course of its occupation during World War II. Extensive dredging, connection, and expansion of the islets significantly changed its hydrological and oceanographic features (Collen et al. 2009), but no large-scale manipulation of the atoll's landmasses or water flow occurred after the war. The USFWS is currently reviewing proposals to restore the hydrodynamic flow within Palmyra Atoll's lagoon system to its prewar state. Some restoration activities might, in the short term, create toxic plumes from pollutants left by the military and load large amounts of sediment into the marine environment (Collen et al. 2009), potentially negatively impacting lagoon and reef flat habitats, including those used by marine turtles foraging on algae and other food sources.

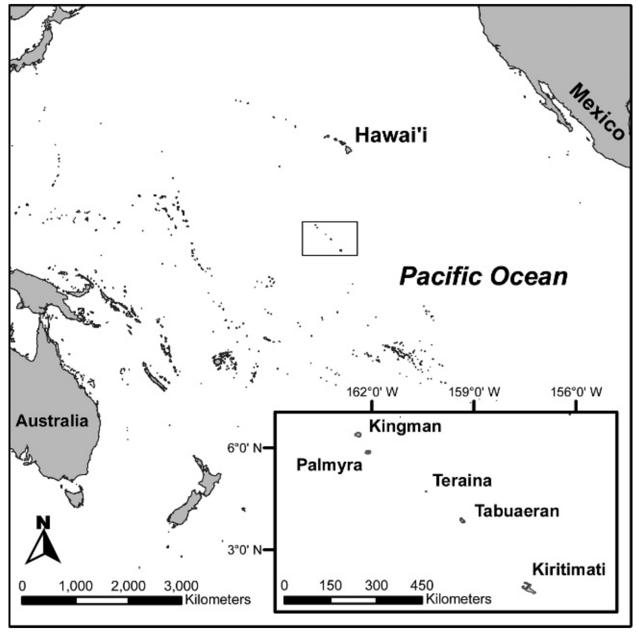

Figure 1. Location of the Northern Line Islands, including Palmyra Atoll, central Pacific Ocean.

Assessing the current abundance, distribution, and habitat usage of marine turtles is a critical component of efforts to understand how restoration activities may impact the marine communities of Palmyra Atoll and to comprehensively manage and conserve these species and their habitats. This information will also significantly contribute to a comprehensive management plan for marine turtles throughout the central Pacific Basin. In 2005, we initiated a multiyear conservation research and management program for the 2 marine turtle species found on the atoll, focusing on their distribution, abundance, health, and threats. We designed our research strategies to gather data called for by recovery plans for US Pacific green and hawksbill turtles (NMFS and USFWS 1998a, 1998b). This includes identifying and protecting important feeding grounds and determining distribution, abundance, and status of populations at feeding grounds (NMFS and USFWS 1998a, 1998b). We began relative abundance surveys in 2005 and started a second phase of research in 2008 that involved in-water captures for health and ecological studies needed to assess the conservation status of this population. Our findings represent the first data and discussion on the distribution, abundance, and health status of Palmyra Atoll's marine turtles.

METHODS

Study Area. — The PANWR, located in the central Pacific Ocean near the Equator (5°53′N, 162°05′W; Fig. 1), consists of multiple small, heavily vegetated, connected islets and a variety of reef structures and lagoons of varying depth and size. At present, the atoll comprises 2.5 km^2 of emergent land and approximately 155 km^2 of coral reefs and lagoons (Collen et al. 2009). Reef habitat varies but is generally made up of wide, shallow, algae-rich reef flats and patch reefs. These lead out to a steeply sloped fore reef to the north and south and a gradually sloped reef to the east and west. Palmyra Atoll coastal vegetation is mainly *Pisonia grandis* and coconut palms. No mangroves or seagrass beds exist within the refuge. The atoll's algal communities vary in composition but generally are made up of turf algae such as *Jania*, *Cladophora*, and *Spyridia* species that dominate the reef flats and macroalgal communities including *Bryopsis*, *Turbinaria*, and *Avrainvillea* species along the reef break and fore-reef areas (McFadden et al. 2010).

Marine Turtle Capture, Handling, and Analyses. — We captured turtles following standard protocols (NMFS 2008) using a scoop net (Sterling Brand, Super Sport Model), by hand, or using tangle nets (18-gauge twisted nylon nets with mesh size of approximately 35 cm) in August 2008, August–September 2009, July 2010, and July–August 2011. Nets, ranging from 45 to 120 m and set at 0.5–1.5-m depth, were continuously monitored during deployment.

The team visually examined captured turtles to determine species, sex (if apparent), body condition, and general health. Following standardized protocols, we measured straight carapace length (SCL), curved carapace length (CCL), and tail length on captured turtles, rounding to the nearest 0.1 cm. We recorded weight of animals processed on land to the nearest 0.1 kg using a digital scale (Pelouze, model 4040) and of animals processed on a boat platform using a hanging scale (Detecto Co., model 400H). Following Chaloupka et al. (2004) and Chaloupka and Limpus (2005), we divided turtles into 3 size categories based on CCL: 1) juvenile, less than 65 cm CCL; 2) subadult, 65–84.9 cm; and 3) adult, over 85 cm. We used conservative morphological estimates to define mature animals and assign sex. Turtles over 85 cm CCL and with a minimum tail length ≥ 30 cm were considered males (Hamann et al. 2003, 2006; Wibbels 2003), and we tentatively assigned as females those over 85 cm CCL with tails ≤ 21 cm long, with the understanding that without determinative techniques, the sex was not definitive (Limpus and Reed 1985; Limpus et al. 1994; Hamann et al. 2003, 2006).

The research team examined all turtles for existing conventional and passive integrated transponder (PIT) tags. When no tags were found, we applied 1 uniquely numbered Inconel flipper tag to the trailing edge of each front flipper on turtles over 45 cm SCL (National Band and Tag Co., model 1005-681). We injected 1 PIT tag (Biomark, Inc.) under the epidermal layer of each of the rear flippers where possible. We lightly scored identifying numbers using a Dremel moto-tool on dorsal scutes and/or painted temporary numbers (Balazs 1980). This served as a short-term, within-season visual recognition tool for tagged turtles after their release.

We examined all turtles for evidence of lesions, FP tumors, epibiont load, missing or damaged limbs, skin and carapace abnormalities, and other health-related issues. All injuries were photographed, and any crescent-shaped damage to the carapace ≥ 10 cm long was tentatively attributed to shark attack following Norem (2005). We used a commonly used body condition index (CI) based on Fulton's K ($CI = [mass/SCL^3] \times 10^4$; Ricker 1975; Bjorndal and Bolten 2010). In order to provide context for the CI scores, we calculated the mean and range of CIs for turtles from Palmyra Atoll and compared them to body condition categorization criteria developed for green turtles in Queensland, Australia, by Flint et al. (2009). We considered animals with CIs over 1.20 to be in ''very good'' condition, those with CIs between 1.11 and 1.19 to be in ''good'' condition, those between 1.00 and 1.10 as ''average,'' and those under 1.00 as ''poor.''

We grouped marine turtle capture data into 4 broad geographical regions along the atoll: the northern reef flats, the southern reef flats, the eastern lagoon and flats, and the western and central lagoons and flats (Fig. 2A). The flats are composed of shallow-water reef rubble, and the lagoons typically encompass deeper waters and sandy substrate.

Data were analyzed using nonparametric tests after confirming that the data did not meet the assumptions required for parametric statistics. The CCL of turtles caught using the 2 main capture methods were compared using a Wilcoxon Mann-Whitney test. Differences in CCL, weight, and body condition across these 4 regions were examined using Kruskal-Wallis tests, and Bonferroni corrections were used to assess post hoc independence between pairings. All statistical analyses were performed in R (R Development Core Team 2011) and were considered significant at the $p < 0.05$ level.

Marine Turtle Surveys and Nesting. — We conducted standardized relative abundance surveys at least once a year, usually between June and September, from 2005 to 2011 ($n = 11$ surveys) using a belt-transect approach modified to work within various logistical constraints. In an attempt to reduce interobserver variation, all participants were trained in survey techniques and turtle size categorization before each survey. For consistency,

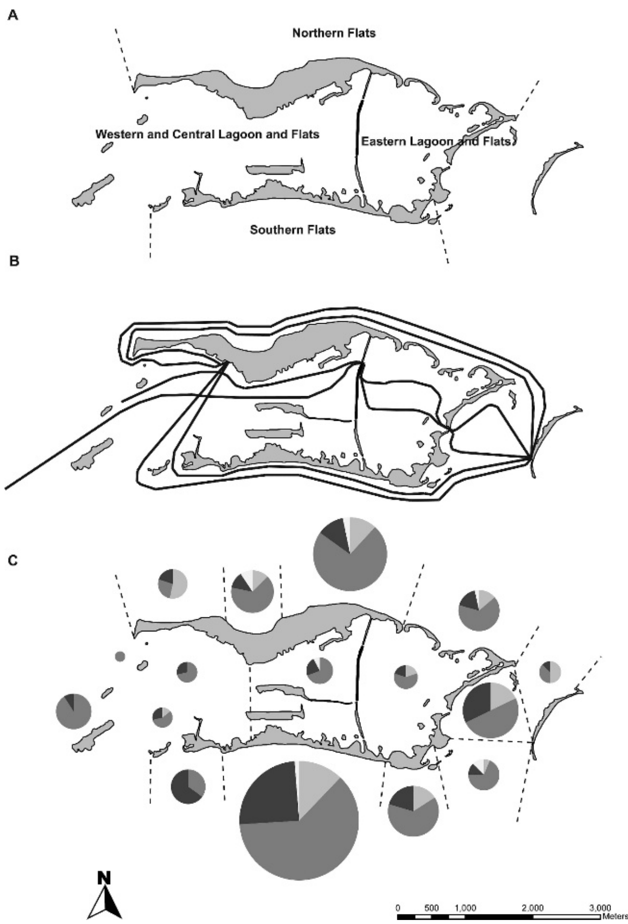

Figure 2. (A) Islands of Palmyra Atoll (gray masses) and the 4 major regions where sea turtles were captured. (B) Transects followed by observers during sea turtle relative abundance surveys. Solid lines depict transects traveled by kayaks (2 across the northern area and 2 across the southern area) and motor boats (1 along the northern edge of the lagoons and 1 along the southern edge of the lagoons). Boat travel between the lagoon systems requires passing through a narrow break in the man-made north-south causeway. (C) Relative abundance of sea turtles observed over 7 atoll-wide surveys conducted from 2008 to 2011. Zones are demarcated by dotted lines, and the size of each pie chart reflects the relative mean number of turtles seen in each zone by the 14 northern, 14 lagoon, and 13 southern boat surveys. Each pie is divided up into the mean number of small (~ 30–60 cm curved carapace length [CCL], light gray), medium (~ 61–90 cm CCL, medium gray), large (> 91 cm CCL, dark gray), and unknown (off-white) sized turtles seen in that zone.

surveys were conducted at midday high tides on days with good weather conditions and visibility. All observers (generally 6–10 individuals in 4 kayaks and 2 motor boats) began the count at a single point in the eastern atoll, with each boat independently traveling along 1 of 6 transects (Fig. 2B). Observers traveling along the shallow-water northern and southern reef flats used kayaks, and observers traveling in the lagoons used small motor boats. The stratification was based on logistical constraints (such as shallow-water areas that prohibited the use of motor boats and available number of kayaks) rather than on ecological factors. Transects were paired so that during each survey, 2 boats traveled across each of the northern, lagoon, and southern areas (Fig. 2B). One exception occurred during the September 2008 survey, when only 1 transect was conducted across the southern area.

All teams in similar equipment (motor boats or kayaks) attempted to move at approximately similar and constant speeds along the predetermined paths. The complete surveys took approximately 2–3 hrs, with kayaks taking longer than motor boats. Over the research period, we improved survey methodology to include a breakdown of the atoll by several zones within each region so that we could identify hot spots of turtle presence (Fig. 2C). During surveys conducted from 2008 to 2011, observers recorded the location of each turtle among these zones using terrestrial land formations as zone markers or waypoints. Researchers recorded each turtle they encountered and assigned a visually based qualitative carapace size ranking (small: ~ 30–60 cm; medium: ~ 61–90 cm; large: > 91) to the best of their ability under the conditions. In cases where observers were unable to assign a turtle to a size class, they still noted the observation and gave it an ''unknown/unassigned'' designation. For the analysis, we assumed that all turtles were green turtles because, although species verification was often impossible due to visibility conditions, hawksbills are rarely observed along the atoll.

We calculated the average number of turtles sighted (± SD) across the surveys in each zone. Because logistical constraints led to different methods being used to survey the outer flats (kayaks) versus lagoons (motor boats) and the number of transects run and observers involved fluctuated between survey events, overall observation efforts between the transects were not equal. Therefore, data of turtle sightings from across the entire atoll could not be compared statistically in a spatial analysis. Similarly, because effort level, weather, and visibility conditions could not be kept constant between years, temporal comparisons could not be performed. However, during each individual survey, the technique (kayak or motor boat) and number of observers were kept constant within each of the 3 paired transects (northern, lagoon, and southern), so the mean number of turtles observed in each zone can be used to reveal patterns of turtle densities allowing for the multiple transects across survey events to serve as replicates. At least once a week during field seasons, researchers walked the sandy beaches or, where walking is restricted, kayaked along shores looking for evidence of nesting.

RESULTS

Marine Turtle Capture, Handling, and Analyses. — In total, we captured 211 individual green turtles (excluding recaptures; $n_{2008} = 41$; $n_{2009} = 49$; $n_{2010} = 43$; $n_{2011} = 78$) and 2 hawksbill turtles ($n_{2009} = 1$, $n_{2011} = 1$) over the course of this study. Three green turtles captured in 2009 exhibited a tear-shaped carapace and darker carapace coloration, as has been described for Eastern Pacific turtles (Pritchard 1999) and turtles caught in regional fisheries

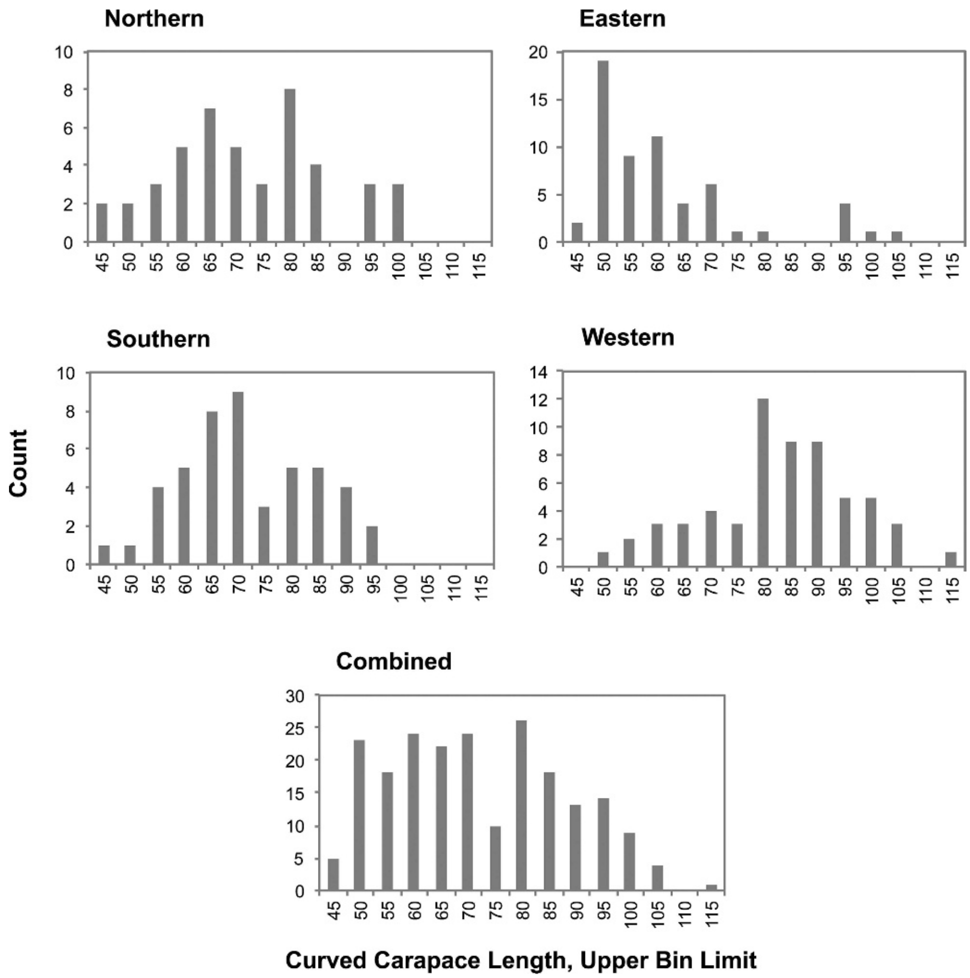

Figure 3. Frequency distributions of curved carapace lengths (CCL) of green turtles (*Chelonia mydas*) captured across 4 regions of Palmyra Atoll (the northern reef flats, the southern reef flats, the eastern lagoon and flats, and the central and western lagoons and flats) and among all regions combined from 2008 to 2011 (n = 45, 59, 47, 60, and 211 for northern, eastern, southern, western, and combined, respectively).

(Parker et al. 2011). Excluding recaptures, green turtles ranged from 41.0 to 113.6 cm CCL ($n = 211$, mean 69.7 ± 16.1 cm). The mean weight (± SD) for green turtles was 44.6 (± 29.7 kg), and weight ranged from 7.2 to 146.3 kg ($n = 204$; some individuals were excluded due to mechanical difficulties with scales). No captured individuals carried flipper or PIT tags applied prior to this study. We recaptured or resighted no turtles in 2008, had 3 within-season resightings in 2009, and had 4 recaptures in 2010 (1 from 2008, 2 from 2009, and 1 within-season recapture). In 2011, there were 7 recaptures (2 from 2008, 1 from 2009, 3 from 2010, and 1 within-season recapture) and 3 within-season resightings.

A total of 42 turtles (20% of the total green turtle capture) had a CCL 85 cm or greater, with 22 being identified as adult males using pronounced tail length ($\geq$ 30 cm) combined with CCL and 11 likely adult females (tail length $\leq$ 21 cm) with the caveat that laparoscopies were not used to confirm sex. Eighty (38%) of the green turtles fell in the subadult range (65–84.9 cm CCL), and 42% were assigned as juveniles ($<$ 65 cm CCL, $n = 89$). The majority of the turtles fell within CCL length intervals of 55–84.9 cm ($n = 123$; Fig. 3). The size of the captured turtles did not differ between the 2 main capture methods: hand and tangle net (mean $CCL_{hand} = 71.7$ cm, $n_{hand} = 105$; mean $CCL_{tangle} = 67.9$ cm, $n_{tangle} = 105$; Wilcoxon Mann-Whitney test, W = 6080, $p = 0.1978$). A single turtle with a CCL of 59.0 cm was caught using a scoop net.

Captured turtles' CCLs varied significantly among the 4 regions on the atoll (the northern reef flats, the southern reef flats, the eastern lagoon and flats, and the western and central lagoons and flats; Fig. 2A; Kruskal-Wallis $\chi^2_3 = 57.29$, $p < 0.001$; Fig. 3). Overall, captures showed a bimodal size-class distribution with individuals captured from the eastern region showing the most pronounced groupings of very small turtles and from the west of very large turtles (Fig. 3). A Kruskal-Wallis test indicated CCL varied by region ($\chi^2_3 = 57.29$, $p < 0.001$). A Bonferroni post hoc test indicated that turtles captured in the east had significantly smaller CCL measures than those found in the north or south

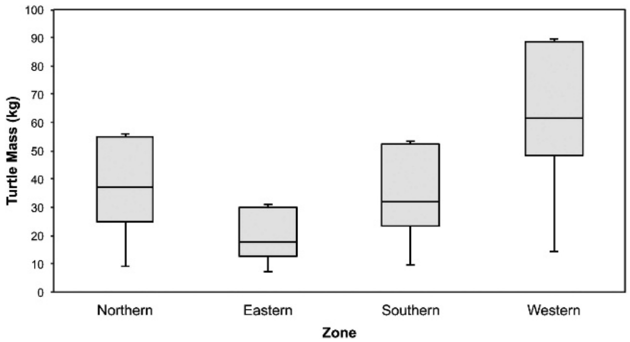

Figure 4. Body mass of green sea turtles (*Chelonia mydas*) captured from different regions within Palmyra Atoll (the northern reef flats, the southern reef flats, the eastern lagoon and flats, and the western and central lagoons and flats) from 2008 to 2011 represented in box plots. For each region, the box extremes reflect the upper and lower quartiles, the middle band denotes the median, and the error bars reflect 1 standard deviation from the mean for that population (n = 42, 59, 45, and 58, respectively).

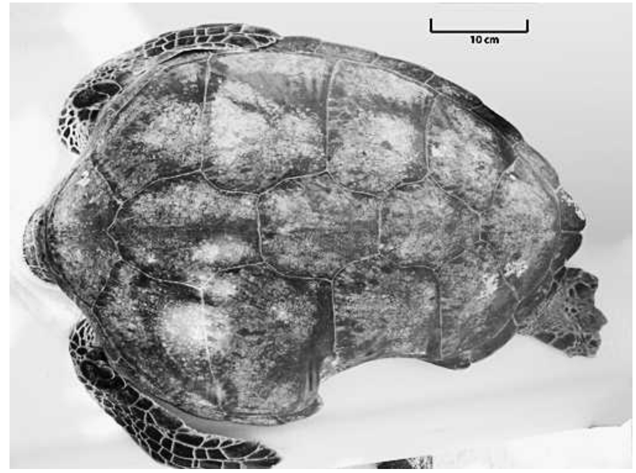

Plate 1. Green turtle captured in 2008 with large portion of carapace and plastron missing (photo by F. Arengo).

($p < 0.001$) and that those in the west were larger than all other regions ($p < 0.001$). Captured turtles' weights also varied significantly among the 4 regions on the atoll, with on average lighter turtles found in the east and heavier turtles in the west ($\chi^2_3 = 61.26$, $p < 0.001$; Fig. 4).

The mean body condition index for green turtles was 1.38 ± 0.16 (range: 0.69–2.22, $n = 204$). Ninety-two percent of all turtles had a CI value greater than 1.20, reflecting a ''very good'' body condition (Flint et al. 2009). Body condition did not significantly vary among years (Kruskal-Wallis $\chi^2_3 = 6.50$, $p = 0.09$) but it did vary among regions (Kruskal-Wallis $\chi^2_3 = 13.24$, $p = 0.004$). A Bonferroni post hoc test indicated that only western-caught turtles were in significantly better condition than southern-caught turtles at a $p < 0.05$. Even so, turtles captured from all regions were, on average, in very good condition with mean CI values above 1.2 ($BCI_N = 1.36$; $BCI_S = 1.32$; $BCI_W = 1.44$; $BCI_E = 1.37$). No turtle showed evidence of tumors. However several turtles showed a variety of healed injuries including missing flippers ($n = 9$) and carapace damage suggesting predator attack ($n = 8$; Plate 1).

Both hawksbill turtles captured were juveniles of unknown sex. The hawksbill turtle we captured in 2009 weighed 16.3 kg and measured 57.0 cm CCL, and the juvenile we captured in 2011 weighed 11.2 kg and measured 50.5 cm CCL.

Marine Turtle Surveys and Nesting. — The average number of turtles (± SD) counted over 11 atoll-wide surveys conducted from 2005 to 2011 was 87.9 ± 28.5 (range: 41–125). Over the research period, we improved survey methodology to include a breakdown of the atoll into smaller zones so we could identify hot spots of turtle presence (Fig. 2C). The 7 surveys conducted from 2008 to 2011 revealed population distributions along the 3 major transect pairings (northern, lagoon, and southern; Fig. 2C). Across the northern transects, turtles were most commonly sighted in the central zone of the north (mean = 6.6 ± 7.7, $n = 14$ transects over 7 surveys); across the lagoon transects, turtles were most commonly sighted in the eastern flats (mean 4.0 ± 3.1, $n = 14$ transects over 7 surveys); and across the southern transects, turtles were most commonly sighted in the central zone of the south (mean = 18.4 ± 8.0, $n = 13$ transects over 7 surveys; Fig. 2C). Overall, including data collected from all 11 surveys, the most commonly sighted size class was medium-size turtles (~ 61–90 cm CCL; mean = 50.1 ± 18.5), followed by large (> 91 cm CCL; 20.3 ± 5.8) and then small (~ 30–60 cm CCL; 13.0 ± 8.8) turtles. That trend is also visible at each of the 3 main hot spots with sightings of medium-size turtles dominating (Fig. 2C). No signs of nesting or crawls were found on any of the walk or kayak surveys of beaches in this study.

DISCUSSION

The PANWR is among the most isolated and relatively intact extant marine turtle foraging grounds. While historically the lagoon systems were altered during the US military's occupation, Palmyra Atoll's remote nature and protection from many of the more common modern-day anthropogenic impacts over the past 70 yrs make it a rare and increasingly important place of study. Yet the conservation status of the marine turtles at Palmyra Atoll had not been documented prior to this study. Our results reveal the area to be a mixed-species and mixed-size class assemblage where turtles are in generally good health. The area is likely an important foraging ground for green turtles in the Pacific.

Mixed Species and Size-Class Assemblages. — Both green and hawksbill turtles occur at Palmyra, with green turtles being considerably more abundant as indicated by capture data, survey data, and ad hoc observations.

Previous studies at other feeding grounds where green turtles forage indicate that both single-species (Kolinski et al. 2006) and mixed-species assemblages occur. For example, in the Pacific, foraging habitats throughout the Hawaiian Islands (Balazs 1995) and in Baja California (Seminoff et al. 2003b) also support mixed-species groups of green and hawksbill turtles.

Palmyra Atoll is a mixed-size-class foraging ground for green turtles where individuals ranging from post-pelagic juveniles to adults of breeding size were observed and captured. Co-occurrence of different size classes, including small juveniles and very large mature adults, has been reported elsewhere in the Pacific basin (Limpus and Reed 1985; Limpus et al. 1994; Balazs et al. 2005). Long-term studies in Australia, for example, indicate the presence of variable proportions of adults and juveniles at resident feeding grounds, the latter usually being observed more frequently (Limpus and Reed 1985; Limpus 2008). In contrast, Bermuda (Meylan et al. 2011), as well as Ubatuba and Espírito Santo, Brazil, are examples of developmental habitats used mainly by juveniles (Gallo et al. 2006; Torezani et al. 2010). While Palmyra clearly supports a wide range of size classes, the findings that turtles caught in the western flats were significantly larger, and that there was a bimodal size class distribution among turtles in the eastern lagoon and flats could indicate size-specific preferences in habitat utilization (Fig. 3).

There may be several reasons why certain size classes are more prevalent in different regions of the atoll. Although future analyses of algal community structure as it relates to fine-scale behavioral movements (as detected by acoustic telemetry) are pending, in the far eastern flats, where on average turtles are smaller, the habitat contains both macroalgal and turf algal communities in relatively shallow areas where few tiger sharks (*Galeocerdo cuvier*) have been reported. In contrast, the western area, where on average the turtles are significantly larger in size, is linked directly to the open ocean via deeper reefs and a channel. This area hypothetically may harbor more diverse prey because it is composed of both reef rubble in shallow-water flats (where turf algae is dominant) and deeper and larger coral formations, providing more complex and varied niche space and prey base.

Of the sites reported from the literature, only San Diego, Australia, the Northern Mariana Islands, and Palmyra Atoll harbored individuals of all size classes, with the broadest ranges found in Palmyra Atoll and Australia (Table 1). These areas also had the largest sample sizes, and if more animals were caught in the other locations, perhaps in deeper waters, the reported size ranges might expand. In the case of Palmyra Atoll, this breadth may be due in part to the availability of different habitats that support all stages of marine turtle development, ranging from shallow-water sites that provide protection and rich algal foraging grounds (McFadden et al. 2010) to atoll shelves extending to pelagic zones.

Our transect survey results generally concur with the capture data in revealing that Palmyra supports a range of size classes for green turtles (ranging from small juveniles to adults) with medium-size turtles being the most frequently sighted size class. While capture data show that, on average, smaller turtles are caught in the east of the atoll and larger turtles in the west (Fig. 3), relative abundance data did not suggest such differences. This could be because estimates of body size by observers at a distance may be inaccurate and should be interpreted with caution. Another potential source of error in the visual survey is that observers do not detect the entire portion of the turtle population present in the survey area because some turtles remain submerged and are not easily spotted.

Relative Abundance Within the Atoll. — Our surveys revealed that green turtles were less abundant in the lagoons than on the shallow reef flats, where researchers often observed them foraging on algae such as *Bryopsis*, *Turbinaria*, and *Cladophora* species, or mixed assemblages of turf algae (McFadden et al. 2010). Both algal species diversity and biomass are higher on the reef flats compared to the lagoon systems (McFadden et al. 2010), and these rich algal communities appear to provide important foraging grounds for Palmyra Atoll's green turtles. Several additional factors are likely to contribute to the high densities of turtles found along shallow-water reef flats in comparison with lagoons. The lagoons, which were extensively modified by the military, can be highly turbid such that the deeper areas have poor visibility. Further, they are frequented by tiger sharks known to commonly prey on marine turtles (Witzell 1987; Cliff and Dudley 1991; Fergusson et al. 2000; Papastamatiou et al. 2006), possibly making them poor turtle habitat and explaining the lower number of turtles.

Population Size. — Individuals captured or counted may represent only a small portion of the population, many of which may be moving back and forth between nearshore and deeper-water zones (Seminoff et al. 2002). A small number of recaptures indicate that some turtles do move across regions within the atoll, although most were caught in the original region. Alternately, observed low recapture rates between seasons may be the result of the sample sizes obtained in the capture work or our survey methods. However, while some double counting of turtles moving during the survey is possible, it is more likely that our counts greatly underestimate the total number of turtles, particularly given the deeper-water habitats that cannot be covered with this survey method. Further work on surveys, recaptures, and tracking will help determine estimates of green turtle population size and whether the population is open, with different turtles coming and going between seasons. This work will also help elucidate why we experienced low recapture rates in comparison with other mark–recapture studies of marine turtles (Bjorndal et al. 2005; Koch et al. 2007; Bjorndal and Bolten 2010).

Table 1. Reported mean, minimum (min), and maximum (max) curved carapace length (CCL), and straight carapace length (SCL) measured in centimeters for Pacific green turtle foraging populations.

Site	Mean	Min	Max	Max – Min	*N*	Source
			CCL			
Palmyra Atoll, USA	69.7	41.0	113.6	72.6	211	This report
Baja California, Mexico	80.9	48.5	104.3	55.8	200	Seminoff et al. (2003a)
Galapagos Islands, Ecuador					65	Carrión-Cortez et al. (2010)
Bahia Elizabeth	81.0	46.0	74.0	28.0		
Caleta Derek	66.8	46.0	74.0	28.0		
Punta Nunez	59.1	74.0	95.0	21.0		
Kawela Bay, Hawaii	61.5	40.0	81.0	41.0	35	Balazs et al. (1987)
Johnston Atoll, USA	89.8	63.0	107.8	44.8	21	Balazs (1985)
Mantanani, Malaysia	47.4	38.0	79.9	41.9	75	Pilcher (2010)
Olimarao Atoll, Yap	104.0	93.0	117.0	24.0	27	Kolinski (1991)
Gulf of Carpentaria, Australia		36.0	113.5	77.5	107	Hamann et al. (2006)
S. Great Barrier Reef, Australia		40.0	120.0	80.0	954	Chaloupka and Limpus (2001)
S. Great Barrier Reef, Australia		39.0	116.0	77.0	537	Chaloupka and Limpus (2005)
			SCL			
Palmyra Atoll, USA	65.2	39.2	105.5	66.3	211	This report
Bahia Magdalena, Mexico	54.6	43.0	73.0	30.0	125	Koch et al. (2007)
Hawaiian Islands, USA		35.0	74.9	39.9	191	Arthur and Balazs (2008)
Kaneohe Bay, Hawaii, USA	45.3	37.5	55.2	17.7	53	Aguirre and Balazs (2000)
Kiholo and Kona, Hawaii, USA	47.7	38.5	62.0	23.5	37	Aguirre and Balazs (2000)
Pala'au, Hawaii, USA	51.9	32.6	72.9	40.3	54	Work and Balazs (1999)
Rota Island, Commonwealth of the Northern Mariana Islands		< 40	> 100			Kolinski et al. (2006)
San Diego Bay, California, USA	85.0	44.0	110.4	66.4	96	Eguchi et al. (2010)

Green Turtle Body Condition and Health. — While potentially contributing to population growth and size, the body condition of wild animals can reflect an individual's likely reproductive success and potential survival (Caughley 1997) and provide valuable information concerning population health. Both our anecdotal observations and the Palmyra Atoll population's high mean body condition index indicate that, on average, Palmyra Atoll's marine turtles are in very good condition. With the exception of 1 captured individual that was emaciated (CI = 0.69), the range of CI values for Palmyra's turtles is within the range of CI values reported for green turtles in other studies in both the Caribbean and the Pacific Ocean (Bjorndal et al. 2000; Koch et al. 2007).

We observed no FP tumors despite the fact that this disease is generally readily observable elsewhere (Baboulin 2008), for example, in parts of Hawaii and Florida (Herbst and Jacobson 2003; Chaloupka et al. 2009). FP is considered to be transmitted by a herpesvirus (Herbst 1994; Herbst et al. 1995; Casey et al. 1997; Quackenbush et al. 1998; Lu et al. 2000; Greenblatt et al. 2004; Work et al. 2009), and occurrence of the disease may be linked to environmental, ecological (Herbst et al. 2004), and anthropogenic factors, such as pollution (Herbst and Jacobson 2003). FP could also be related to turtle size, land use, nitrogen footprints, and foraging ecology (Chaloupka et al. 2009; Van Houtan et al. 2010). For the FP disease to be present in the foraging population at PANWR, the turtles must be exposed to the virus and, possibly, also be affected by external stressors that cause the tumors to proliferate (Aguirre and Lutz 2004). The lack of evidence of FP at Palmyra Atoll suggests that these green turtles may not interact with infected turtles from other areas, and the virus has therefore not reached the atoll. Alternately, even if infected, the turtles may remain tumor free in the absence of environmental stressors. It is also possible that older turtles are able to suppress the disease or that younger turtles with tumors may perish prior to reaching Palmyra during their migratory journeys.

Eastern Pacific Green Turtles. — The capture of 3 turtles whose coloration and carapace shape were consistent with turtles of eastern Pacific origin (Pritchard 1999; Parker et al. 2011) is notable in that Palmyra is far to the west of prior published occurrence localities for these turtles, which include coastal waters and beaches from Baja California south to Chile, north to British Columbia, and west to the Galapagos Islands (Green and Ortiz 1982; NMFS and USFWS 1998c; Seminoff et al. 2003a; Chassin-Noria et al. 2004; Seminoff 2004; Senko et al. 2010). However, given wide variation in this group, coloration and other characteristics may not be unique to geographic locations or groups (Karl and Bowen 1999), and genetic characteristics of these 3 turtles are being investigated to further explore their origins (E.N.-M., *pers. obs.*). On the other hand, the foraging grounds for Eastern Pacific green turtles are not clearly delimited, especially outside of Mexico and Central and South America (NMFS and USFWS 1998c; Seminoff 2004). Further, long-line fisheries data from Hawaii reveal catches of Eastern Pacific greens near Palmyra (Parker and Balazs 2008), and other research indicates that the range of Eastern Pacific green turtles is wider than previously believed (Okamoto et al. 2010; Godoy et al., in press). Neritic foraging areas less than 200 m deep, such as those found around Palmyra, are critical habitat in the life cycle of Eastern Pacific green turtles (Senko et al. 2010). Our ongoing work at Palmyra Atoll can help ascertain the extent to which central Pacific foraging areas are transitory stopover locations for Eastern Pacific green turtles or habitat where individuals spend a longer time foraging. This information will be helpful for conservation and management efforts at PANWR and across the Pacific Basin.

Hawksbill Turtles. — We captured 2 hawksbill turtles at Palmyra Atoll during this study, yet individual hawksbills have been sighted on most of the research team's annual trips to the atoll. Still, hawksbills are clearly less abundant than green turtles at Palmyra. Hawksbill turtles are considered critically endangered by the IUCN (2012) and listed as endangered under the US Endangered Species Act and are generally less abundant than green turtles in other locations as well, as reflected by their IUCN classifications. Globally, hawksbill turtles have been exploited throughout their range for eggs, meat, parts, and tortoiseshell. While turtles at Palmyra Atoll are protected within the wildlife refuge, these individuals may well face threats elsewhere, as they may breed in areas of the Pacific where hunting and other threats persist.

Nesting. — Evidence from this study, in combination with previous reports (Fefer 1987; Depkin 2002), points to Palmyra Atoll not being a substantial nesting site for turtles. No nests or crawls were observed during this study. In addition, team members collected ad hoc observations from other scientists and specialists living on the atoll and reviewed government agency reports for evidence of nesting activity. Researchers found minor evidence of nesting from a literature review as well as in discussions with other scientists working at Palmyra Atoll. In 1987, eggs were found in the 1 nest on North Beach that was excavated (Fefer 1987), and 2 other probable nests and 1 other possible nest were encountered (Fefer 1987). On-site naturalists familiar with turtle breeding activities observed few signs of nesting in the 1990s and early 2000s (E. Lange, *pers. comm.,* October 2006). In June–August 2001 and 2002, USFWS surveys of possible nesting areas detected 7 crawls, all of them at North Beach. Eggs or hatchlings were subsequently observed at North Beach (Depkin 2002). In June 2006, scientists observed a single pair of tracks consistent with a nesting attempt at the east end of North Beach. The tracks terminated near the vegetation line, but there was no clear indication of digging at a nest site, suggesting that this may have been a false crawl and did not result in nesting (D. McCauley, *pers. comm.,* September 2008).

Similar to some other Pacific locations within the Line Islands (i.e., Christmas, Jarvis, Fanning Islands), where low levels of nesting takes place (Balazs 1982, 1995; Pritchard 1997), Palmyra Atoll is currently not a significant nesting site for marine turtles (Maison et al. 2010). Although suitable nesting habitat exists on the north shore of the atoll, it appears there is only rare reproductive activity (Fefer 1987; Depkin 2002; this study). This may be due to high hatchling predation or stranding of breeding females on the surrounding reef or a lack of recolonization following past extirpation. Efforts to understand and model the premilitary occupation state of Palmyra's land habitats may reveal if there were beaches suitable for nesting prior to the base's development. Continued monitoring for nesting activity on appropriate beaches would be useful to determine the extent to which nesting may occur into the future.

Future Research Directions. — The findings presented here represent a first step toward characterizing marine turtles of the remote PANWR. We are also pursuing several studies to build on our understanding of the role of Palmyra Atoll as a foraging ground by exploring the connectivity of foraging sites throughout the Pacific Basin. Like other researchers (Reisser et al. 2008; Jean et al. 2010), we are able to use facial profile photographs of green turtles to identify and resight individuals. By analyzing and coding the position and shapes of the scutes located posterior to the eye, we can create unique identifiers for each turtle, and we are reaching out to other researchers in the central Pacific to develop a basinwide database that would allow us to track connectivity between locations. This work will help us to expand our data on turtles at Palmyra Atoll, through inclusion of observations in deeper water and other areas outside of the reef flats that have been the focus of our work. At the Pacific scale, it would generate additional connectivity data with the possibility that snorkelers or divers in other areas of the Pacific may photograph turtles captured on Palmyra Atoll. We will use hatchling movement modeling in combination with genetics to study connectivity and explore how oceanographic conditions might affect recruitment to Palmyra Atoll and other locations. This analysis can be supplemented by the use of satellite telemetry to better understand movements and comparative stable isotope analyses to determine foraging patterns of turtles at Palmyra Atoll with respect to other areas. By linking our research program with similar efforts at foraging grounds throughout the region, we can further understanding of poorly known migratory connections with conservation applications.

Conservation Threats. — Due to low human population density and a mandated low impact on wildlife, Palmyra Atoll's turtles are not under extreme threat within the refuge. However, efforts to restore the lagoon system previously modified by US military activity have the potential to negatively impact marine turtles on the atoll. The lagoon system currently experiences relatively long water retention times, low flow from outer reef systems, generally high turbidity, and low coral formation, though continued natural erosion of the causeways and fill between islets increase water flow and modify these conditions (Collen et al. 2009). Proposed projects to restore the original hydrodynamic flow could involve breaching the north–south causeway built by the military (Fig. 2A). While significantly improving the hydrodynamic flow, this could also cause a pulse of sediments and pollutants left by military occupation to be released into the marine environment, potentially negatively impacting turtle feeding grounds and other habitats. These modifications could cause a sudden change to the nature, distribution, and abundance of the algal food sources for turtles in the lagoon and possibly also the outer reef flats area. Alternately, in the long run, a clearer lagoon with coral growth may provide quality habitat for turtles, particularly hawksbills. Clearly, a better understanding of how marine turtles use the various habitats on the atoll, along with accurate predictions of the probable sediment load, sedimentation patterns, and time scale of release, can inform these restoration efforts and is a focus of ongoing research.

Palmyra Atoll and nearby Kingman Reef support nearly 3 times the number of coral species as Hawaii (Maragos and Williams 2011). A fundamental threat to hawksbill turtles is alteration in their coral reef foraging habitat due to climate change (Mortimer and Donnelly 2008). Coral bleaching events have been documented at Palmyra as recently as 2009 (Williams et al. 2010), and this phenomenon is predicted to become more intense and frequent in the coming decades around the world (Donner et al. 2005). Stress from coral bleaching is known to cause coral mortality (McClanahan 2004), reduced reef productivity (Glynn 1993), coral disease outbreaks (Whelan et al. 2007), and invasion and overgrowth of certain algal species (Diaz-Pulido and McCook 2002). Some areas within Palmyra Atoll may be more susceptible to bleaching because modifications made to the atoll during World War II may still be impacting the reefs via shoreline sediment redistribution and increased turbidity (Williams et al. 2010).

Natural predation is likely to be an important driver of Palmyra Atoll's turtle population structure. The density of sharks at this small atoll is one of the highest in the world (DeMartini et al. 2008; Sandin et al. 2008). Tiger sharks are the most common natural predators of adult marine turtles globally (Witzell 1987; Cliff and Dudley 1991; Fergusson et al. 2000; Papastamatiou et al. 2006). They probably pose the greatest threat to turtles on the atoll, but insufficient information exists on tiger shark populations at this location. Researchers at Palmyra Atoll observe tiger sharks (*pers. obs.*) within both the lagoon and fore-reef waters, and clear evidence of shark attack on turtles has been documented, though where those attacks took place is unknown (Plate 1). Shark predation may influence turtle behavior and population density. Heithaus et al. (2007, 2008), for example, argue that risk of predation may be as important as reproduction and foraging in affecting movement and habitat use patterns in green turtles. While predation pressure on turtles at Palmyra Atoll may serve as a source of mortality, it is also possible that it influences the overall health status of the green turtles there, as less healthy turtles may be more susceptible to predation. By lowering population numbers, sharks may also be reducing the strength of density dependence, a mechanism known to regulate green turtle population sizes in the Atlantic (Bjorndal et al. 2000; Tiwari et al. 2006).

The possibility that turtles feeding at Palmyra Atoll may be linked to populations declining regionally elsewhere is of serious conservation concern. Turtles that forage at Palmyra Atoll may move to breeding or feeding areas that face common marine turtle threats, including egg harvest from nesting beaches, hunting of juveniles and adults, habitat loss, disease (Seminoff 2004), entanglement in marine debris, coastal development (Witherington 1992), mortality due to vessel strike (Hazel et al. 2007), and incidental bycatch in fisheries (Seminoff 2004; Wallace et al. 2010b). While fishing is not allowed within the wildlife refuge or the national monument, long-line fisheries data from Hawaii reveal catches of Eastern Pacific greens near Palmyra Atoll (Parker and Balazs 2008), which could represent a threat to turtles moving to and from the atoll. Further, a report by the Secretariat of the South Pacific Regional Environment Program (2001) indicated annual mortality estimated between 500 and 600 turtles per year in the long-line fishery in the Oceania region. This report identified green and hawksbills among the turtles caught as bycatch, although they are not the species most affected by fishery interactions in the Pacific (Bolten et al. 1996; Crowder and Meyers 2001). More recent reports estimate a mean annual catch by long-line fisheries of 918 turtles per year, with the highest rates of mortality from the tropical deep long-line fishery (Molony 2005). By determining the linkages between turtles found at Palmyra Atoll and other regional breeding or feeding sites, it will be possible to better understand the distributional range of turtles occurring at Palmyra Atoll, identify regional management partners, and determine conservation priorities.

All of these threats exacerbate low population growth rates due to life history traits that include delayed maturation and low annual recruitment; these life history traits lead to populations that can be slow to recover from even low levels of disturbance. Marine turtles have been referred to as ecosystem sentinels (Aguirre and Lutz 2004), and trends in their abundance and distribution may shed light on the overall health of Palmyra Atoll as both a wildlife refuge that supports numerous marine organisms (Maragos et al. 2008) and a feeding ground for marine turtles. In addition, trends in growth patterns, abundance, and health of turtles at Palmyra Atoll may serve as an independent comparison of these ecological factors relative to areas with greater human influences. Palmyra Atoll has been described as an atoll with unparalleled diversity and ecosystem health—one that, despite its history, has not suffered such drastic human influences as most of the other populated areas within the Pacific. For this reason, Palmyra Atoll is a protected microcosm that can serve as a baseline for restoration and management of other more anthropogenically influenced areas.

We believe that Palmyra Atoll is an important foraging area for green turtles given that it is removed from pervasive human influence and individuals appear to be in remarkably good body condition and health and, particularly, free of tumors. Further, its isolation in the central Pacific may mean it could serve as a stopover point for turtles migrating over long distances. Research at the PANWR is coordinated by the PARC. This collaborative partnership of institutions provides infrastructure for long-term studies of sea turtles, which is a unique opportunity to research population dynamics in an understudied area of the Pacific. It is also an exceptional opportunity to learn about turtle ecology and behavior in the context of well-studied predator and prey populations. Given Palmyra Atoll's remote location and the relative health of this turtle population, understanding of these dynamics could help in restoration efforts of degraded areas elsewhere. Like other green turtle foraging grounds in the Pacific, such as Hawaii (Balazs et al. 1987) and the Gulf of California, Mexico (Seminoff et al. 2002), algal communities are a critical component of the Palmyra Atoll for turtles. Off the coast of Baja California (Mexico), green turtle diet is primarily seagrass and algae (López-Mendilaharsu et al. 2005). In other regions, such as the Galapagos (Green and Ortiz 1982), the Pacific coast of Honduras (Carr 1952), and Peru (Márquez 1990), green turtles are known to include invertebrates in their diet (Carrión-Cortez et al. 2010). We hypothesize that the combination of a diverse prey base (including coral-based microhabitat that supports algal and invertebrate communities) along with habitat protected from predators and a lack of direct anthropogenic stressors makes Palmyra Atoll one of the more productive foraging grounds in the central Pacific. Palmyra Atoll's strong ecological integrity as a foraging ground for sea turtles is supported by the ''very good'' body condition of the majority of sea turtles. Other aspects of the ecosystem also appear to be thriving: top predators and reef-building organisms dominate Palmyra Atoll, while smaller fish, more coral disease, and lower coral recruitment characterize more populated islands in the Northern Line Islands (Sandin et al. 2008).

If a key goal for conservation management is to protect a large, healthy, and vibrant sea turtle foraging ground, then managers should focus on the following: 1) keeping anthropogenic influences to a minimum at Palmyra, including those influences such as illegal fishing outside the waters of Palmyra Atoll; 2) minimizing the potential introduction of marine invasive species; 3) continuing to monitor and research this understudied population to better understand its habitat requirements, population trends, full life cycle, and range, including expanding research from the reef flats to the fore reef and (to the extent possible) nearby benthic areas; 4) monitoring the effect of global conservation threats such as ocean acidification and increasing sea level temperatures on coral reef integrity and the corresponding influence this may have on sea turtle foraging habitat; and 5) planning for future restoration efforts on Palmyra Atoll that consider the potential effects of sedimentation on areas with high turtle densities such as the eastern flats. This study represents an important first step in advancing scientific understanding of these populations, with valuable applications for conservation and management of this unique ecosystem.

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