



Marine protected areas and migratory species: residency of green turtles at Palmyra Atoll, Central Pacific

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ABSTRACT: Protected areas are a cornerstone of conservation strategies globally, yet questions remain about their impacts, including on highly migratory species. The Palmyra Atoll National Wildlife Refuge, one of the Northern Line Islands in the Central Pacific, contains a regionally significant green turtle *Chelonia mydas* foraging ground. Residency patterns of this species were investigated through satellite telemetry (n = 15 males, 1 female, 2 subadults) and flipper tagging (n = 555) between 2008 and 2013. Almost every captured turtle was flipper-tagged, but telemetry efforts focused primarily on adult males, which have been studied infrequently. Overall, the turtles tracked during 4076 transmission days (mean = 227, range = 37 to 633) had high site fidelity and small home ranges, and remained close to their capture sites in waters ≤50 m deep. Five turtles were tracked for >1 yr, but none left Palmyra on annual breeding migrations. Only one satellite-tracked turtle departed the atoll, covering a total distance of ~5600 km in a near-circular loop. Similarly, flipper tag recaptures on the atoll (n = 67) occurred near the original capture site. However, additional tags were recovered from 1 female in Kiritimati, Northern Line Islands, and from 1 subadult in Kosrae, Micronesia, ~690 and 3800 km away from Palmyra, respectively. Such extended, spatially restricted residency with low turnover is expected in small, high-quality habitats. The study highlights the importance of this protected area, which harbors regionally endangered turtles whose movements over several years are almost entirely encompassed within its established boundaries.

KEY WORDS: Marine protected area · Satellite tracking · Site fidelity · Home range · Hexagon grid · Kernel density · T-LoCoH · Utilization distribution overlap index

INTRODUCTION

Marine protected areas (MPAs) are proving to be an important tool for countering threats such as habitat alteration, overexploitation, and climate change (Scott et al. 2012, Simard et al. 2016). The International Union for Conservation of Nature (IUCN, <https://www.iucn.org/theme/protected-areas/about>) defines a protected area as 'a clearly defined geo-

graphical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values'. However, reserves do not automatically achieve conservation outcomes. Globally, only ~3.7% of the world's oceans are protected in actively managed MPAs, with as little as ~2% considered to be strongly protected in no-take reserves (MCI 2018). Existing MPAs may fail to pro-

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vide optimal habitat, and migratory megafauna, like marine turtles, benefit only partially from reserves due to limited protection measures or spatial coverage of their wide ranges, underscoring the importance of understanding a species' spatial ecology with respect to protected areas (McClellan & Read 2009, Scott et al. 2012, Shimada et al. 2017).

The Palmyra Atoll National Wildlife Refuge (hereafter, 'Palmyra') is one of 7 reserves encompassed by the Pacific Remote Islands Marine National Monument (see Fig. 1). Palmyra is located within the Northern Line Islands, which span a gradient of human influence. The uninhabited US naval defense area of Kingman Reef lies to the north, and there are 3 increasingly populated islands of the Republic of Kiribati to the south (see Fig. 1). The remaining Central and Southern Line Islands are uninhabited. Access to Palmyra is currently restricted to research and management staff, but the atoll was occupied by the United States military during World War II. Significant structural changes were made then, such as connecting the islets and building an airstrip, although the reef flats were left largely intact (Papastamatiou et al. 2010). Palmyra was designated a US National Wildlife Refuge in 2001 and a Ramsar Wetland of International Importance in 2009. The atoll now contains relatively undisturbed coral reef and algal communities with robust marine turtle, shark, and manta ray populations (Braun et al. 2008, Sandin et al. 2008, Papastamatiou et al. 2010, 2012, Sterling et al. 2013, Williams et al. 2013, McFadden et al. 2014). Such small, high-quality habitats can be predictors of small home ranges, low turnover, and extended residency for many animals (Winker et al. 1995, Griffen & Drake 2008).

Megafauna, including marine turtles, play key roles in maintaining ecosystem structure and function (Bjorndal & Jackson 2003). Palmyra contains a regionally significant foraging ground for green turtles *Chelonia mydas* and Critically Endangered hawksbills *Eretmochelys imbricata* (Sterling et al. 2013). Green turtles are the dominant marine chelonian, and juveniles are the most frequent life stage encountered, with adult males and females each constituting about one-tenth of the population (Sterling et al. 2013). Palmyra's green turtles are generally very healthy (Sterling et al. 2013, McFadden et al. 2014). Further, none have yet been observed with fibropapillomatosis (Sterling et al. 2013, McFadden et al. 2014), a tumor-producing viral disease that has become common and often severe in some coastal foraging pastures such as those found in Hawai'i (Hargrove et al. 2016). Green turtles at Palmyra fall

within the Central South Pacific Distinct Population Segment, a discrete grouping that was listed as endangered under the US Endangered Species Act in 2016 (NOAA, https://www.fpir.noaa.gov/PRD/prd_green_sea_turtle.html). On a global scale, the IUCN also considers the species Endangered (Seminoff 2004). However, at Palmyra green turtles face few threats and forage in an environment free from pervasive human influence. Typical threats to marine turtles such as fishing and habitat alterations are currently prohibited there, and the human population is limited to refuge staff and researchers, although there is natural predation by sharks (Sterling et al. 2013). A beach suitable for nesting formed at Palmyra following habitat modification and sediment accumulation in the 1940s but nesting is still rare (Maison et al. 2010, Sterling et al. 2013).

All marine turtles hatch from eggs on nesting beaches, where incubation temperature determines hatchling sex (Ackerman 1997). After a pelagic phase, green turtles generally recruit as juveniles to coastal foraging grounds, where they feed mostly on algae or seagrasses and smaller amounts of animal food items (Musick & Limpus 1997, Russell et al. 2011). Adults undergo breeding migrations between often distant nesting and feeding habitats, although there are non-migratory groups (Godley et al. 2008, Whiting et al. 2008, Hart et al. 2013). Green turtles foraging throughout Hawai'i, for example, nest only within that archipelago and mainly at French Frigate Shoals, where females breed about every 4 yr (Balazs et al. 2015, 2017). Male marine turtles are less studied than the more accessible nesting females. In most marine turtle species, including green turtles, males are reported to reproduce more frequently than females, and some are capable of annual breeding (Wibbels et al. 1990, Limpus 1993, James et al. 2005, Van Dam et al. 2008, Hays et al. 2010, Wright et al. 2012, Nurzia Humburg & Balazs 2014). Mating may occur offshore of, on the way to, or distant from the nesting beach (Limpus 1993, Plotkin 2003). Green turtles display natal homing behavior and often return to the rookery or region of their birth to breed (Meylan et al. 1990). Once reproductive activities are concluded, green turtles generally go back to their resident foraging grounds (Limpus et al. 1992, Limpus 1993, Plotkin 2003).

Foraging grounds are where turtles spend most of their lives and are more difficult to assess than nesting beaches. Mark-recapture, satellite tracking, and genetic research have revealed that foraging populations are usually 'mixed stocks' whose natal origins can be traced to multiple nesting beaches (Bowen &

Karl 2007). Green turtles foraging at Palmyra have been genetically traced to a mix of South-Central and West-Central Pacific Regional Management Units, an area which includes Micronesia (Naro-Maciel et al. 2014). As with other hard-shelled marine turtles, green turtle adult migrations and movements can be typified as targeted or direct, shuttling seasonally along coasts, pelagic living, or residing locally (Godley et al. 2008).

With respect to residency or inhabiting a restricted geographic area over an extended time, green turtles may temporarily, seasonally, or permanently live at a foraging ground when not migrating. Short-term tracking of green turtles has revealed areas of core use for routine purposes outside of migrations, such as preferred foraging or resting spots, within larger home ranges (Hart & Fujisaki 2010). At Palmyra, for example, 4 hot spots or high-use zones were identified in the atoll's Southern and Northern Flats, as well as the Western and Central Lagoon and Flats, and Eastern Lagoon and Flats (Sterling et al. 2013) (see Fig. 1). Satellite tracking of immature turtles at their foraging grounds (Godley et al. 2003, McClellan & Read 2009, Hart & Fujisaki 2010, González Carman et al. 2012, Fukuoka et al. 2015, Williard et al. 2017) and of post-nesting females reaching these areas (Cheng 2000, Chan et al. 2003, Trøeng et al. 2005, Hatase et al. 2006, Broderick et al. 2007, Seminoff et al. 2008, Scott et al. 2012, Balazs et al. 2015, Baudouin et al. 2015, Parker et al. 2015) emphasize residency close to food resources, as well as site fidelity, in which turtles return to the same foraging area (Godley et al. 2008, Balazs et al. 2015, Shimada et al. 2016). Further, adult green turtle satellite tracks substantially overlap with large and well-established MPAs (Scott et al. 2012).

Priority questions that guide marine turtle research (Hamann et al. 2010, Rees et al. 2016) remain largely unanswered with respect to the remote Central Pacific region, and male turtles in general (Godley et al. 2008). In this study, green turtles at Palmyra were flipper-tagged and satellite-tracked to evaluate residency in and spatial use of the Palmyra MPA and to inform management recommendations.

MATERIALS AND METHODS

Study site

The Palmyra Atoll National Wildlife Refuge (5° 53' N, 162° 05' W; Fig. 1) consists of ~2.5 km² of emergent land divided among several islets and ~155 km² of

coral reefs, flats, and lagoons (Collen et al. 2009). The lagoons are connected by small channels and shallow areas with a maximum depth of ~50 m in the Western Lagoon (Papastamatiou et al. 2010). There are steeply sloped fore-reefs to the north and south and gradually sloped reefs to the east and west. Directly off the atoll, there are steep plunges to initial depths of 200 to 2000 m. The atoll's fish biomass including apex predators is substantial (Sandin et al. 2008, Williams et al. 2013, Smith et al. 2016). Reef habitat is comprised of wide, shallow, algae-rich reef flats and patch reefs also containing stony coral and crustose coralline algae. Turf algae, including green turtle forage species of *Jania*, *Cladophora*, and *Spyridia*, and macroalgae such as *Bryopsis* and *Turbina-ria*, are abundant along the reef break and fore-reef (McFadden et al. 2010). Macroalgae-dominated communities are common around the atoll including species of *Halimeda* (calcareous green algae), *Lobophora* (brown algae), *Dictyosphaeria* (green algae), and *Galaxaura* and *Dichotomaria* (red algae) (Braun et al. 2008).

Green turtle capture and tagging

We captured green turtles at Palmyra for scientific research following permitted procedures (Sterling et al. 2013). Capture methods included using a scoop net, rodeo technique, or tangle nets, and took place in August 2008, August to September 2009, July 2010, July and August 2011, June to July 2012, and June to July 2013 (Sterling et al. 2013). Capture location by GPS coordinates and Palmyra zone designation (Fig. 1; Sterling et al. 2013) were noted for each turtle. Local time at Palmyra (GMT-10) was used for all analyses. Captured turtles were visually examined to determine species, sex (if apparent), body condition, and general health. We measured curved carapace length (CCL), curved carapace width (CCW), and tail length. We divided turtles into 3 size categories based on CCL: (1) juvenile (<65 cm); (2) subadult (65 to 84.9 cm); and (3) adult (>85 cm) (Sterling et al. 2013). Turtles ≥85 cm CCL with tails ≥30 cm were classified as males, with the caveat that sex was not determined laparoscopically and testes maturity could not be discerned (Hamann et al. 2003, Sterling et al. 2013). However, due to tail size, 1 satellite-tracked individual (23513) and 4 flipper-tagged turtles were classified as male despite having <85 cm CCL and being categorized as subadults. All captured animals were tagged with numbered Inconel flipper tags on the front flippers and subcutaneous

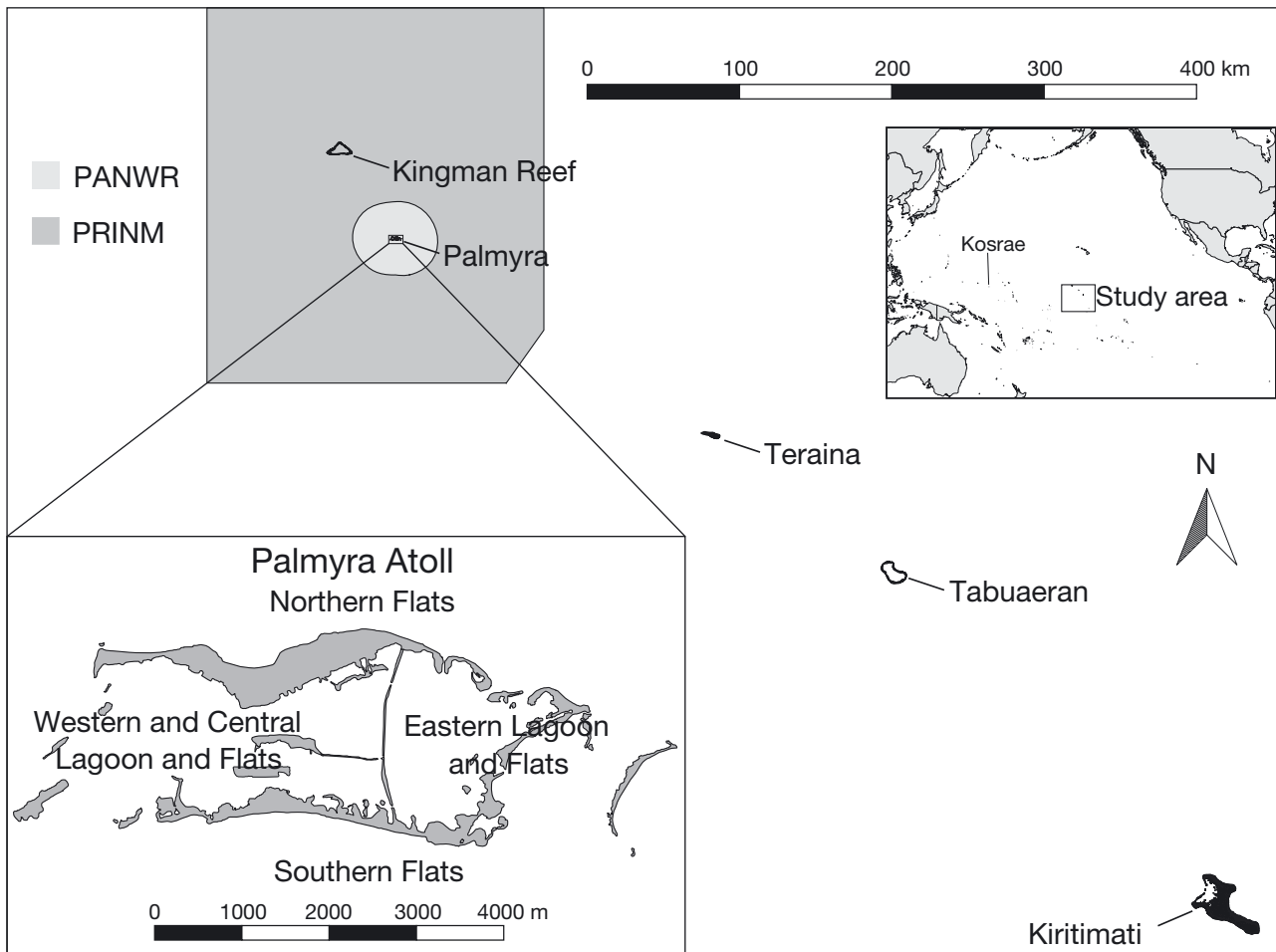


Fig. 1. Palmyra Atoll, Northern Line Islands, USA; study site is shown with respect to boundaries of the Palmyra Atoll National Wildlife Refuge (PANWR) and as part of the Pacific Remote Island National Monument (PRINM) in the Central Pacific Ocean. Also shown are the sites of 2 green turtle flipper-tag recoveries, one at Kiritimati (Northern Line Islands, Republic of Kiribati), where there is a small green turtle rookery, and one in Kosrae, Micronesia, where nesting has not been documented (Maison et al. 2010, Trevor 2010). Lower inset: 4 major zones where green turtles were captured at Palmyra: Northern Flats, Southern Flats, Western and Central Lagoon and Flats, and Eastern Lagoon and Flats

passive integrated transponder (PIT) tags on the hind flippers, photographed, and released at or near the capture site (Sterling et al. 2013). Mortality events, when observed, were recorded by refuge staff or researchers.

To provide a general baseline on movements, data-archiving satellite transmitters set to an active duty cycle of 24 h were attached using epoxy to a subset of turtles captured in 2008 (3 males, 1 female, 2 subadults) (Table 1). Of these, 1 subadult (85945) and 1 male (85946) received highly precise MK10-AFB Fastloc GPS tags (Table S1 in the Supplement at www.int-res.com/articles/suppl/n037p165_supp.pdf). From 2009 to 2013 the study shifted entirely to turtles identified as males ($n = 12$; Table 1), since comparatively little was known

about their movements (Godley et al. 2008), and males tend to depart on breeding migrations more frequently than females (Limpus 1993, Hays et al. 2010).

Satellite tracking and data filtering

The Argos-CLS data were stored and filtered for location quality using the Satellite Tracking and Analysis Tool (STAT) program available at www.seaturtle.org (Coyne & Godley 2005). Argos provided the positional data accuracy specified as location classes (LCs) 3, 2, 1, 0, A, B, and Z (Table S1 in the Supplement). LCs A and B have no accuracy estimates supplied by Argos, but LC A accuracy

Table 1. Data on satellite-tracked green turtles at Palmyra Atoll. Included are the Argos transmitter identification number, Palmyra capture and release zone, sex (M = male, F = female, U = unknown), curved carapace length (CCL) and width (CCW), and mass, with mean and standard deviation (SD). Release, recapture (if applicable), and final transmission dates are given (in MM/DD/YY), along with transmission duration. The capture and release zone is labeled as per Fig. 1. Residency areas on the Atoll of the individual or grouped (all turtles, all males, or by field year) satellite-tracked turtles were calculated from best daily locations using location classes (LC) 1, 2, or 3 Argos data, or from earliest daily locations for Fastloc GPS data. Calculations were based on minimum convex polygon (MCP), kernel density (KDE), grid density estimation (Hexagon grid), and time-local convex hulls (T-LoCoh), except for turtles 93344, 93341, 54162, and 106302 that lacked in sufficient fine-scale data

Argos ID	Palmyra zone	Sex	Turtle data					Transmissions		Residency (km ²)							
			CCL (cm)	CCW (cm)	Mass (kg)	Release date	Recap. date	Final date	Total days	MCP	KDE (%)		T-locoh (%)		Hexagon grid		
2008																	
85923	Western	U	73.0	67.5	46.8	08/10/08		02/24/09	197	1.4	0.1	1.3	0.0	0.4	0.2	1.1	
23513	Southern	M	75.2	69.2	56.8	08/13/08		05/07/09	267	8.5	1.4	4.8	0.3	2.6	0.2	3.2	
85924	Southern	M	87.0	80.5	71.8	08/13/08		05/09/10	633	109.4	2.1	14.9	1.6	10.2	0.3	12.4	
85946	Western	M	94.5	85.0	94.2	08/14/08		10/23/08	68	0.5	0.2	1.5	0.0	0.1	0.2	0.9	
85945	Northern	U	81.0	72.2	52.8	08/20/08		11/12/08	84	7.7	0.2	3.6	0.1	1.8	0.2	2.3	
85922	Western	F	85.5	78.0	66.9	08/23/08	06/21/13	10/13/08	51	0.4	0.1	0.3			0.0	0.5	
2009																	
85921	Eastern	M	96.0	86.5	107.3	08/25/09		09/25/10	396	80.3	5.4	20.6	5.0	33.0	0.3	12.7	
85920	Southern	M	88.7	80.9	74.4	08/26/09	07/19/10	02/07/11	530	15.7	1.2	6.6	1.1	7.2	0.3	3.6	
on atoll																	
93344	Southern	M	85.0	78.5	80.0	08/28/09		10/31/09	64	–	–	–	–	–	–	–	
93342	Northern	M	96.5	96.2	101.0	08/31/09		12/08/09	98	0.7	0.1	0.3	–	–	0.0	0.6	
93343	Northern	M	96.2	86.3	97.5	08/31/09		11/04/09	64	1.4	0.3	0.8	0.1	0.6	0.2	0.8	
93341	Western	M	91.8	87.5	86.0	09/02/09		05/04/10	243	–	–	–	–	–	–	–	
2010																	
54162	Western	M	85.3	85.0	89.0	07/18/10		08/31/10	43	–	–	–	–	–	–	–	
2011																	
54158	Western	M	94.1	91.2	98.6	07/24/11		02/05/13	561	16.3	1.4	5.4	1.5	10.4	0.2	4.2	
106301	Western	M	99.6	90.4	119.4	07/24/11		10/07/12	440	14.2	2.1	4.4	1.0	7.0	0.2	3.4	
106300	Northern	M	94.0	83.3	83.8	07/26/11		09/02/11	37	4.1	0.5	0.8	0.4	2.7	0.0	1.1	
106302	Western	M	89.1	80.6	81.2	08/12/11		11/05/11	84	–	–	–	–	–	–	–	
2012																	
36501	Eastern	M	90.0	78.2	77.8	07/10/12	06/28/13	02/12/13	216	3.5	0.5	1.1	1.1	1.7	0.9	0.2	
Totals																	
08/08–07/09										54.8	3.3	17.6	6.3	16.1	0.5	11.4	
08/09–07/10										146.0	3.7	26.6	6.9	50.8	0.2	17.4	
08/10–07/11										12.4	1.3	2.3	4.4	9.8	0.2	2.5	
08/11–07/12										38.4	4.3	10.9	4.3	22.2	0.3	7.4	
All males										3744	186.4	5.7	44.4	8.1	55.8	0.5	32.4
Mean			90.9	84.0	87.9						249.6						
SD			6.2	6.5	15.6						210.8						
All turtles										4076	186.4	6.0	44.8	8.3	55.7	0.5	33.5
Mean			89.0	82.1	82.5						226.4						
SD			7.3	7.5	19.2						200.3						

is reportedly lower than LC 1 (Hazel 2009, Hoenner et al. 2012). Argos positions were filtered and excluded if swim speed exceeded 5 km h⁻¹ or if the LC was Z (Table S1 in the Supplement). The Wildlife Computers online portal was used for the 2 MK10-AFB Fastloc GPS tagged turtles (Table S1 in the Supplement). Fastloc GPS positions are reportedly accurate to between 20 and 75 m, although the linear error can exceed 75 m (Hazel 2009, Dujon et al. 2014).

Spatial analysis

Residency calculations were carried out using 4 different methods in R (R Core Team 2016) and spatial analysis tools in QGIS 2.16 (QGIS 2016). For these fine-scale analyses, Argos data were additionally filtered to include only the most accurate, or LC 1, 2, and 3 classes of positions, that fell on water. To avoid spatial autocorrelation, the single best daily location of highest LC quality was used (Doherty et

al. 2017). For the Fastloc-tagged turtles, on days with multiple locations, only the earliest known position for each day was considered (Table S1 in the Supplement). The mapped locations in STAT provided sea surface temperature (SST) and estimated turtle displacement, which was calculated from the summed straight-line distance between accepted positions.

For comparison to past studies, the minimum convex polygon (MCP), also considered to be the home range (Burt 1943), was calculated. In addition, high-use areas were characterized through widely employed kernel density estimations (KDEs). KDEs encompassing 50 and 95% of the positional data were used to calculate core-use and home range areas, respectively (Hart & Fujisaki 2010). KDE point densities were determined per 0.25 km² unit and densities were classified under 4 classes of different quantiles. The bandwidth, which smooths and determines the kernel size (Gitzen et al. 2006), was the same as the resolution of the cell size (0.25 km²). The third method, a hexagon sampling grid, was used to map the proportional use of each hexagon. Hexagons were 0.154 km² in area and covered the larger Palmyra Atoll site. Hexagon size was determined by applying the same hexagon grid across all turtle ranges using 8000 hexagons to fill the study area. Fourth, through local convex hull (LCH) procedures, local MCPs were aggregated, sorted, and combined to make isopleths using the R package T-LoCoH (Lyons et al. 2013). LCH uses an optimal number of nearest neighbors determined through reducing errors of commission and omission.

Comparisons of space-use were made using the utilization distribution overlap index (UDOI) for all turtle pairs through the R package adehabitatHR (Calenge 2006). UDOI describes the space-use comparison between 2 utilization distributions of individuals where kernel densities are estimated, and density grids are compared across the usable space. Values can range from 0 (no overlap) to 1 (entire overlap, and identical distributions). Values >1 are observed when the overlap is higher than uniform space-use overlap (Fieberg & Kochanny 2005). Lastly, space-use was measured by comparing the true track of an individual to 1000 random tracks and tested for significance as determined by the sum of least-squares p-values in the R package adehabitatLT (Calenge 2006). Random tracks were generated for each turtle beginning at its starting position and randomizing the angles between occurrences (source code available at https://github.com/dnbucklin/r_movement_homerange/blob/master/site_fidelity_test.r). Since turtles rarely left the vicinity of Pal-

myra Atoll, the tracks were constrained to an area of 10 km around the atoll. The tracks were randomized such that the random track's distance was equal to that of each turtle's true track.

RESULTS

Green turtle flipper-tagging

We flipper-tagged 555 green turtles with Inconel and PIT tags from 2008 to 2013. Of the 555 turtles captured, we had CCL measurements for 554, and the average CCL was 69.86 cm (range = 40.3 to 113.6 cm). Following Sterling et al. (2013), a total of 123 (22.2%) were classified as adults (CCL ≥ 85 cm), with 45 assigned as male, 32 as female, and the remainder of unknown sex. Further, 193 turtles (34.8%) were considered to be subadults and 43% were juveniles. Of these, 59 individuals were recaptured on site, with 4 turtles recaptured twice, and 2 turtles recaptured 3 times for a total of 67 flipper-tag recaptures (Table 2). Four individuals flipper-tagged in 2008, including the satellite-tracked female (85922), were recaptured at Palmyra in 2013. Of the recaptures, 81% occurred in the zone where the turtle was originally tagged. No turtles tagged elsewhere were recaptured on the atoll.

Two turtles with Inconel flipper tags were recovered away from Palmyra (Fig. 1); one at Kiritimati (Northern Line Islands), where there is a small green turtle rookery, and one in Kosrae, Micronesia, where nesting has not been documented (Maison et al. 2010, Trevor 2010). The individual captured in Kiritimati had been classified as female based on tail length (<30 cm) and carapace measurements (CCL ≥ 85 cm) when tagged at Palmyra in 2011. The tag recovery was reported in 2015 but the date of recovery is uncertain and occurred when the turtle was captured for food. Similarly, the individual captured in Kosrae was offered for sale in 2017. When captured on Palmyra in 2009, this subadult had front flipper damage, with both flippers missing above the claw. This study's tally of observed green turtle mortality consists of these 2 flipper-tagged turtles, and 9 carcasses without flipper tags recorded at Palmyra since 2006.

Satellite tracking and analysis

The turtles fitted with satellite transmitters ranged from 73.0 to 99.6 cm CCL (mean = 88.7 cm; Table 1).

Table 2. Mark-recapture data from green turtles marked with Inconel and PIT tags at Palmyra Atoll. The number of turtles (males, females, and juveniles/subadults) tagged and recaptured in each of the 4 zones on Palmyra during the 2008–2013 study is given. No turtles were recaptured in 2008 or 2009. Recapture numbers in parentheses are individuals that were caught in a different zone than the one in which they were originally captured and tagged; zones are labeled as per Fig. 1 — N: Northern Flats; S: Southern Flats; W: Western and Central Lagoon and Flats; E: Eastern Lagoon and Flats

Stage/ sex	Zone	2008	2009	2010		2011		2012		2013	
		No. tagged	No. tagged	No. tagged	Recaptured	No. tagged	Recaptured	No. tagged	Recaptured	No. tagged	Recaptured
Adult males	N	0	2	1	0	1	0	2	0	1	(1)
	S	5	2	1	1	0	0	1	0	0	(1)
	E	0	1	1	0	0	0	4	0	2	1 (1)
	W	1	2	3	0	4	0	5	0	7	0
Adult females	N	0	2	1	0	0	0	1	1 (1)	3	1
	S	0	0	0	0	0	0	0	0	2	0
	E	0	1	3	0	0	0	0	0	1	2
	W	1	6	2	0	2	0	19	2 (1)	15	7 (1)
Juveniles/ subadults (sex unknown)	N	16	7	3	0	13	1	29	0	16	4
	S	5	8	11	1	15	2	12	0	20	3 (1)
	E	7	9	15	2	22	3	66	4 (1)	61	12 (4)
	W	6	9	2	0	21	1	30	0	47	6 (1)
Total		41	49	43	4	78	7	169	10	175	46

In total, 7586 Argos locations were obtained from the complete range of accepted LCs, in addition to 173 Fastloc GPS positions (Tables 1 & S1). Tracking duration for all turtles (including 2 subadults and 1 female; $n = 18$), as well as for males only ($n = 15$), ranged from 37 to 633 d, with a mean of 227 d for all turtles and 250 d for males. The Fastloc GPS technology provided significantly more high-quality locations but lasted for shorter periods (Tables 1 & S1).

With the exception of 1 male, all of the satellite-tracked turtles remained within refuge boundaries for the entire tracking duration. Five turtles visually identified as males were tracked for over 1 yr (Table 1). Three of the 18 satellite-tracked turtles were recaptured at Palmyra: male 85920 before leaving the atoll, as well as male 36501 and female 85922 in 2013 after transmissions ended (Table 1).

After the second round of fine-scale filtering described above, residency patterns were estimated for 14 turtles, of which 11 were male (Table 1). These turtles stayed close to capture and release sites (~2 km displacement, range = 0.8 to 3.6 km), near-shore (mean = 0.75 km, range = 0.70 m to 20 km distance from shore), and within a narrow SST range (24.5 to 30.8°C, mean = 27.8°C). They generally remained in shallow waters, although a few off-atoll positions were in the vicinity of sharp drop-offs. High-use areas were detected along the Southern, Northern, and Eastern Lagoon and Flats, as well as the Western and Central Lagoon and Flats, where higher concentrations of larger and heavier turtles had been previously noted (Sterling et al. 2013).

Within these zones, spatial and temporal overlap of tracks was evident, and spatial overlap between adjacent zones was observed (Figs. 2, 3, & S1–S6 in the Supplement).

The UDOI for all pairwise turtle comparisons ranged from 0.000 to 1.210 (mean = 0.173, SD = 0.220). The lowest UDOI was from turtles with tags 54158 and 36501, which had completely non-overlapping MCPs and KDEs concentrated on the Western (54158) and Southern (36501) portions of the Atoll (Figs. 2A & S2). In contrast, the highest UDOI was from turtles with tags 23513 and 85924, which had overlapping MCPs and similar KDEs indicating high congruence of these individuals in their range utilization. Of the 14 turtles from which we collected data, 12 turtles' space-use was more likely to be near the initial position as revealed by sum of least-squares p -values of <0.001, with the sums of least squares being lower than in the random walk. Two males with tags 106300 and 93342, despite spatially restricted positions close to the atoll, were not more likely to be found near their initial position but had very few overall positions. All other turtles showed high site fidelity as revealed by sum of least-squares p -values of <0.001, with the sums of least squares being lower than in the random walk.

One turtle, male 85920, remained at Palmyra for over 1 yr (~388 d) and then departed in September 2010 for a total distance traveled of 5614 km (Fig. 4). This track revealed continuous movement within a narrow SST range (24.5 to 28.9°C, mean = 26.4°C) and over deep water. The circular loop's clockwise

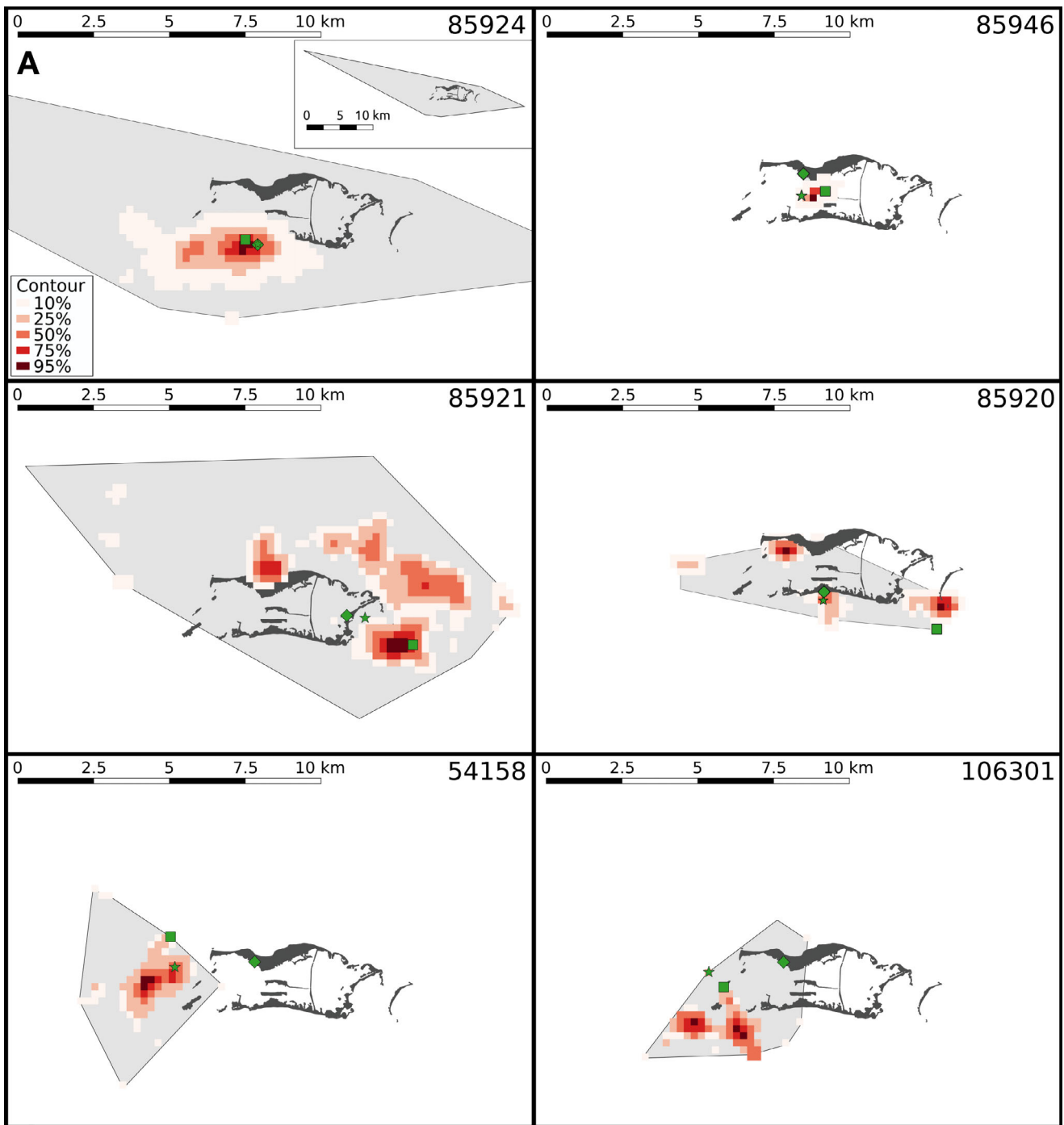


Fig. 2. Residency patterns of select satellite-tracked male green turtles, with contour percentages. (A) Minimum convex polygon (gray) and kernel density (MCP/KDE), (B) grid density estimation (hexagon grid), and (C) time-local convex hulls (T-LoCoh) maps are shown for turtles 85924, 85946 (Fastloc GPS), 85921, 85920 (on atoll), 54158, and 106301, which were the turtles with most data (Table 1). The remaining individuals are depicted in Figs. S1–S6 in the Supplement. Green symbols in Fig. 2A represent capture (star), release (diamond), and final transmission (square) sites

Fig. 2 continued on p 9 + 10

direction appeared to match prevailing surface currents. There were no extended stops near nesting beaches nor courtship areas where mating might

occur. The turtle did approach Tabuaeran (Northern Line Islands, Fig. 4), where marine turtle nesting has been recorded (Maison et al. 2010).

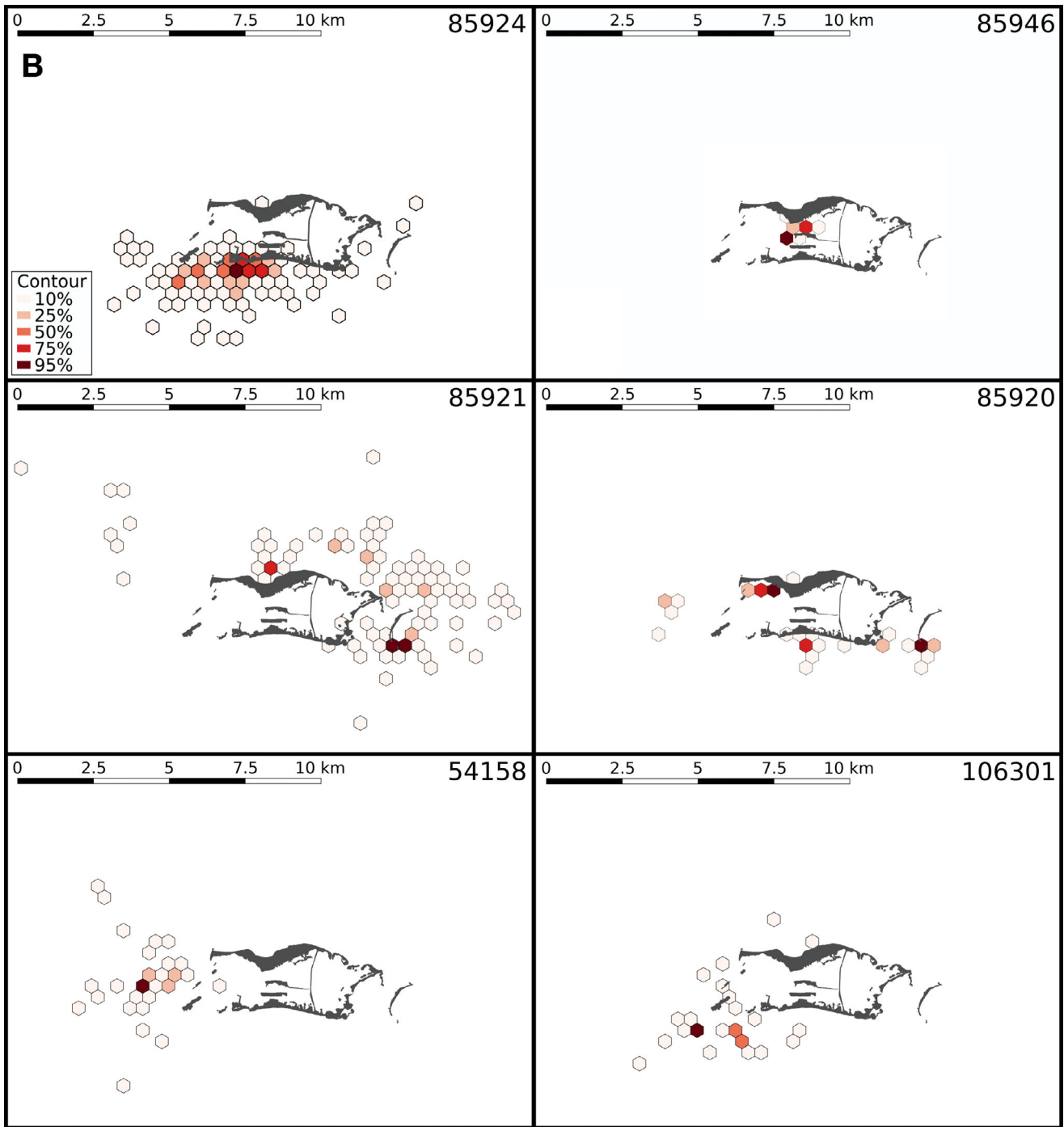


Fig. 2 (continued)

DISCUSSION

This study on residency of regionally endangered green turtles foraging at the Palmyra Atoll National Wildlife Refuge highlights the importance of this remote, well-protected area, which provides within

its boundaries respite from fishing and other pervasive human influence. Key knowledge gaps were bridged by focusing on the under-characterized Central Pacific region, as well as very rarely tracked male marine turtles (Godley et al. 2008). Green turtle movements were revealed to be almost fully con-

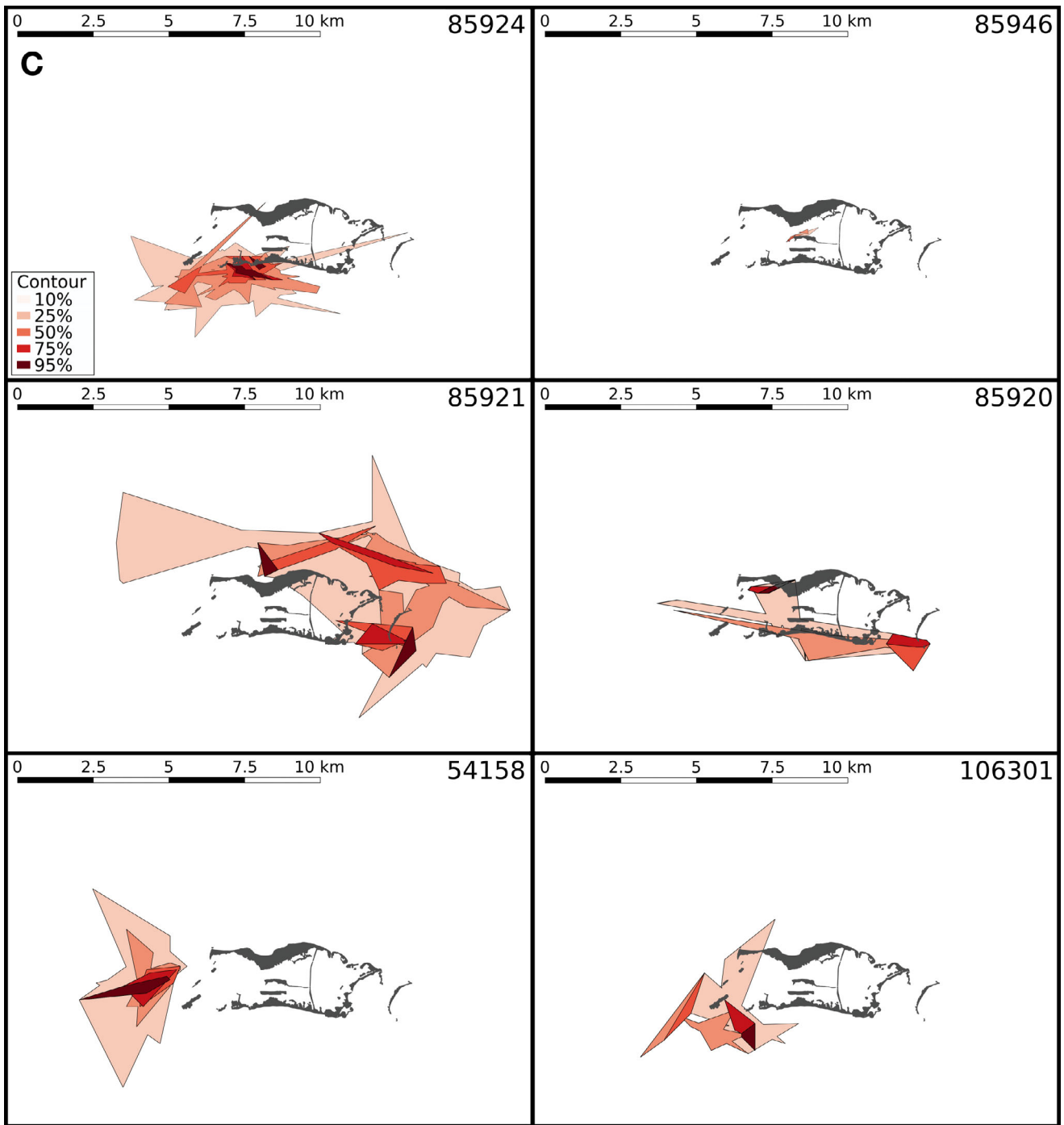


Fig. 2 (continued)

tained within the refuge, close to food resources and the shore, supporting the idea of long-term residency and site fidelity. Further, males tracked for more than 1 yr did not undertake annual breeding migrations. The study did, however, document 3 departures from the Palmyra Atoll National Wildlife Refuge, support-

ing previously noted links to Micronesia (Naro-Maciel et al. 2014) while uncovering new connectivity to the Northern Line Islands. Priority research questions were thus addressed, underscoring the broader utility of reserves as marine conservation cornerstones.

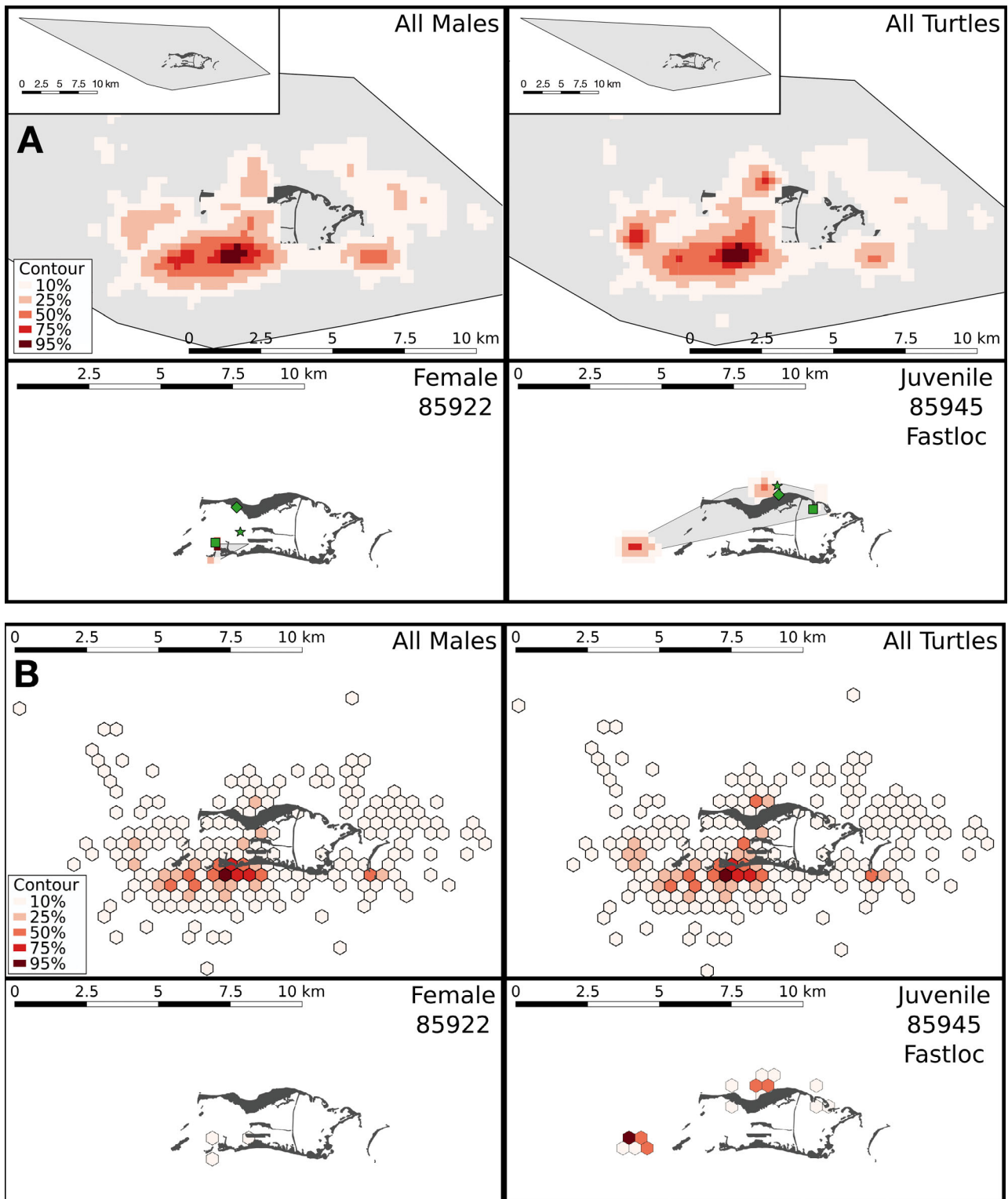


Fig. 3. Residency patterns of satellite-tracked green turtles. (A) Minimum convex polygon (gray) and kernel density (MCP/KDE), (B) grid density estimation (hexagon grid), and (C) time-local convex hull analysis (T-LoCoh), are shown for turtles as follows: all males, all turtles, female 85922 (there was insufficient data for T-LoCoh estimates), and subadult 85945 (Fastloc GPS). Insets in Fig. 3A: MCP estimates at a greater distance. Green symbols in Fig. 3A represent capture (star), release (diamond), and final transmission (square) sites

Fig. 3 continued on next page

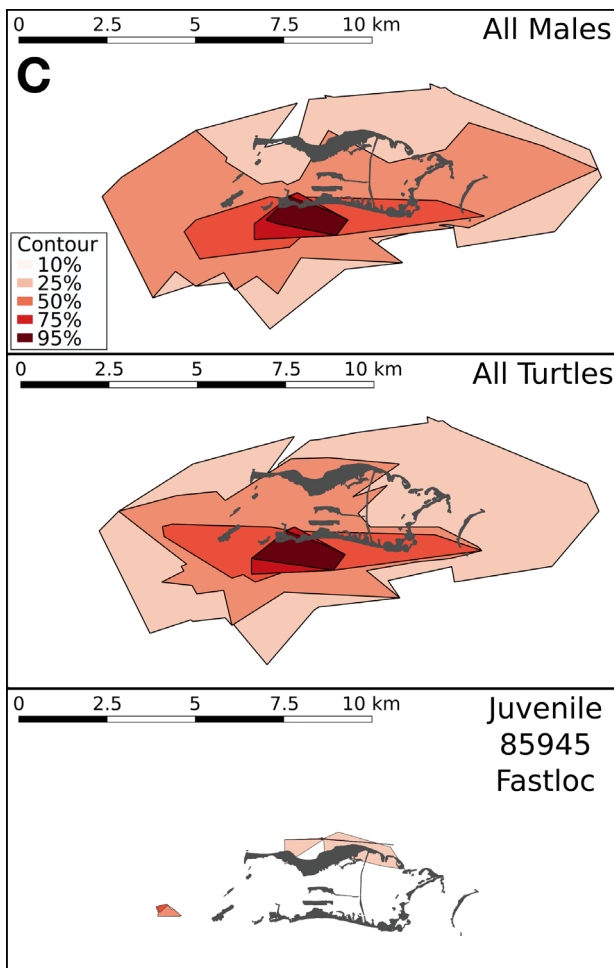


Fig. 3 (continued)

Green turtle residency at Palmyra, with a focus on males

High-quality habitats, where energy expenditure to gain resources or avoid threats is minimized, are predictors of extended residency, small home ranges, and low turnover for many animals (Winker et al. 1995, Griffen & Drake 2008). These patterns are also consistent with marine megafaunal behavior in remote, spatially restricted areas such as Palmyra that contain substantive food and other resources (Karczmarski et al. 2005, Papastamatiou et al. 2010, 2012, Barnett et al. 2012). The small atoll is considered a quality habitat for green turtles (Sterling et al. 2013) and other marine vertebrates (Papastamatiou et al. 2010, 2012). Green turtles are among the animal species predicted to aggregate in high-quality, low-threat areas including large reserves with strict measures such as Palmyra (Scott

et al. 2012, Sterling et al. 2013, Doherty et al. 2017). Local residency constitutes 1 of 4 general patterns observed in marine turtle satellite tracking studies (Plotkin et al. 1996, Hays et al. 2001, Shaver et al. 2005, Godley et al. 2008), and extended residence at foraging sites can enhance survival and reproduction through consistent access to food combined with predator familiarity and avoidance (Shimada et al. 2016).

Spatial isolation and lack of human impact likely contribute to the habitat quality observed at Palmyra, along with environmental factors. For green turtles, seasonal movements generally occur when temperature differences are more pronounced and may lead to dangerous cold-stunning events (Shimada et al. 2016). In contrast, temperatures at the near-equatorial Palmyra fall within a narrow range suitable for this species and well above the 15°C approximate threshold for dormancy or migration (Williard et al. 2017). Palmyra further offers abundant algal resources, including common components of green turtle diets, although the extent of competition for these remains to be determined (McFadden et al. 2010). With respect to threats, the atoll's green turtles are free of fibropapillomatosis disease and are protected from fishery activity or habitat alteration prohibited within the refuge (Sterling et al. 2013).

In contrast, sharks are common predators at Palmyra, also preying on green turtles, as revealed by missing flippers and bite-shaped carapace damage (Sterling et al. 2013). Given the relatively low mark-recapture rate, unobserved mortality by natural predators cannot be excluded. There was also evidence of recovery from shark attacks. For example, satellite-tracked female 85922 had a large, healed shark bite when first caught in 2008 and was still in an otherwise healthy condition when recaptured in 2013. Shark predation decreases as turtles become larger and less vulnerable, and there is plentiful alternate prey for sharks on Palmyra.

This study represents one of the largest single data sets on satellite-tracked male green turtles and complements substantive conventional tagging efforts to reveal restricted residency at Palmyra. With the caveat that sex and reproductive maturity were not determined laparoscopically, the presumed male green turtles that we tracked used most of the atoll (Figs. 3 & S1–S6), including previously noted high-use areas (Sterling et al. 2013), with a concentration on the Southern Flats. Displacement of individual turtles, however, was generally restricted and constrained mostly to shallow waters that were close to

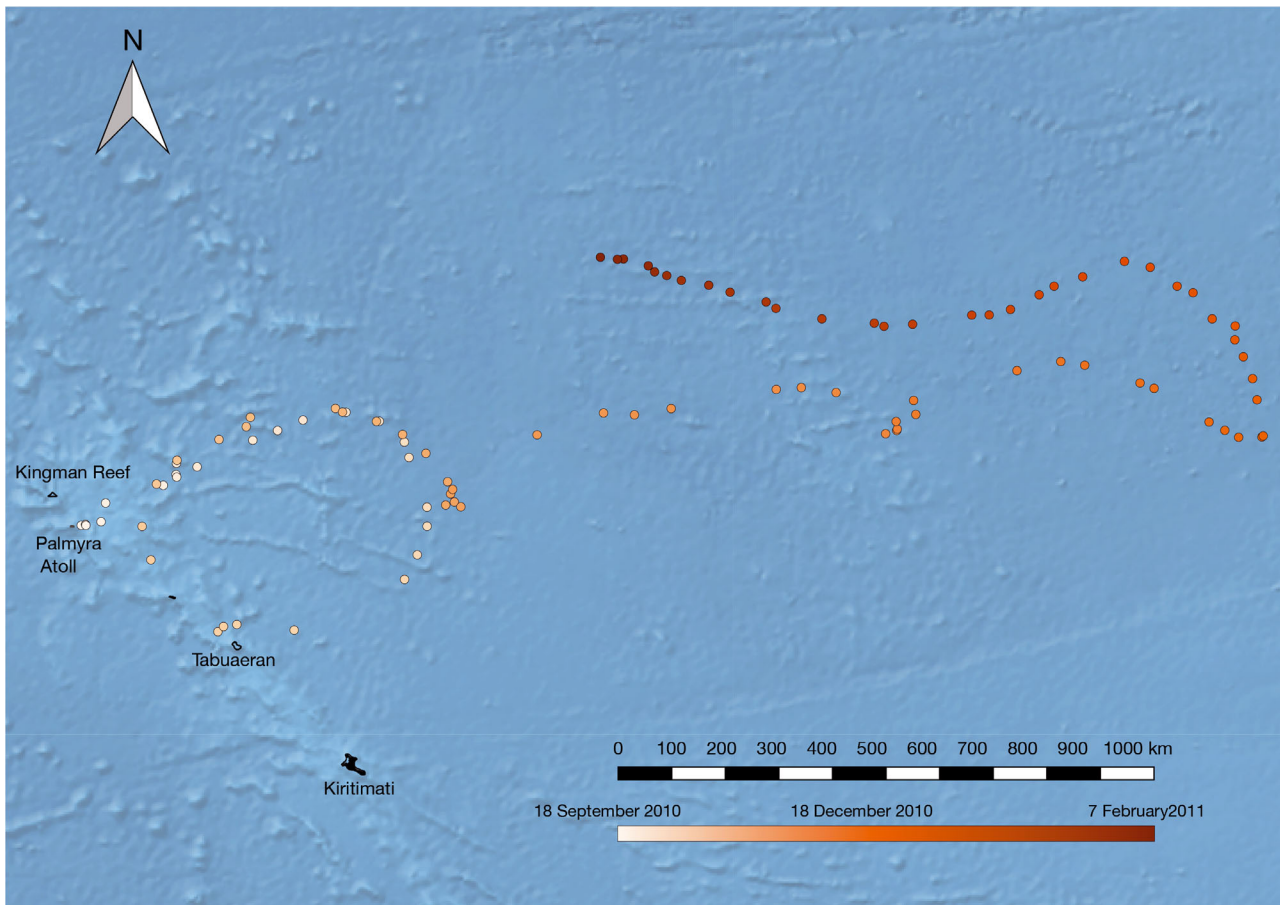


Fig. 4. Satellite telemetry of male green turtle 85920 after leaving Palmyra Atoll until transmissions ceased 141 d later. Locations are shown with respect to the Northern Line Islands of Kiritimati and Tabuaeran, where there are green turtle rookeries. Bathymetry relief is indicated and tracking dates are coded as a gradient, with lighter colors representing earlier dates. The sum distance of each location indicates this turtle traveled ~5600 km. Made with Natural Earth. Free vector and raster map data at naturalearthdata.com

food resources and the shore. The only other study known to us that includes adult green males at foraging grounds (Shimada et al. 2016) confirms mark-recapture findings of long-term site fidelity and spatially restricted residency, outside of seasonal or breeding migrations (Limpus et al. 1992, Limpus 1993, Craig et al. 2004). Although these males, tracked in Australia, ceased transmission sooner than those in our study, no significant differences were detected between male and female residency patterns except that males bred more frequently than females, supporting previous findings (Limpus 1993, Godley et al. 2008). However, this rare documentation of 5 male tracks lasting over a year does not support male annual breeding migrations observed elsewhere (Limpus 1993, Hays et al. 2010), and suggests that Palmyra males may depart less frequently on breeding migrations, or perhaps mate at the refuge itself.

Evidence has been found that male green turtles in Cyprus also do not exhibit annual breeding behaviors (Wright et al. 2012).

The Palmyra tagging and tracking data confirmed limited movements of juveniles, subadults, and females, in addition to males. Most recaptures occurred in the original or adjacent capture/release zone, regardless of tagging or tracking year and duration (Sterling et al. 2013, our Table 2). Satellite telemetry of 1 female and 2 subadults showed similar patterns to the tracked males, with greatly enhanced resolution provided by Fastloc GPS technology for subadult 85946 (Fig. 3). Limited movements have also been reported for many satellite-tracked females and immature turtles at foraging grounds around the world (Godley et al. 2003, Troëng et al. 2005, Broderick et al. 2007, McClellan & Read 2009, Hart & Fujisaki 2010, Shimada et al. 2016). At Palmyra, how-

ever, home range and core-use areas were smaller and less varied than those of most immature turtles or females tracked along more extensive coastlines. High-use areas were mostly concentrated within the capture/release or adjacent zone and were substantially smaller than the estimated 155 km² of available lagoon and reef habitat. Displacement at Palmyra was further limited by an apparent lack of seasonal migrations. Low temperature variation in the region (Hijmans et al. 2005) likely greatly reduces the need for seasonal movement, which also carries energetic costs for capital breeders (Jonsson 1997).

Departures from Palmyra

Palmyra male green turtles displayed extended residency and sparse evidence of movements beyond the atoll. Two of the 3 known departures revealed previously unknown connectivity with the nearby Northern Line Islands, in the Kiribati rookery group (Balazs 1981, Maison et al. 2010). The flipper tag return came from a female, and Palmyra's females are believed to depart for breeding as there is very little nesting on Palmyra (Sterling et al. 2013). Indeed, the natal origins of Palmyra's green turtles were genetically traced to rookeries in the South-Central and West-Central Pacific Regional Management Units (Naro-Maciel et al. 2014). The genetic findings are supported by the second flipper tag return in Kosrae of a turtle identified as a subadult when tagged 8 yr earlier on Palmyra. Although rookery coverage in the genetic study was comprehensive, no genetic samples from Kiribati were available. There may be additional, uncharacterized source rookeries in the Phoenix Islands, Kiribati, with nesting grounds reported on Canton (Kanton) and Enderbury Islands (Balazs 1975, Maison et al. 2010). The remote Central Pacific remains a poorly studied region for marine turtles (Balazs 1981, Craig et al. 2004, Godley et al. 2008). Thus, additional region-wide mark-recapture, satellite, and genetic data are needed to better discern the migratory behavior of all Palmyra turtles.

Contrary to green turtles elsewhere, Palmyra's male turtles, like those of Cyprus (Wright et al. 2012), showed no evidence of annual migration and underscore the persistent knowledge gap surrounding this marine chelonian sex (Limpus 1993, Hays et al. 2010, Balazs et al. 2015). Male 85920 provided a tantalizing glimmer of information through the rarely documented, near-circular pelagic track, also observed in a hawksbill in the Phoenix Islands

(Jayne & Solomona 2007). Circular loops among post-nesting green turtles in Costa Rica were attributed to *Sargassum* foraging (Troëng et al. 2005). Those females made counterclockwise movements matching surface currents, and 85920 moved clockwise also with an apparent relationship to ocean currents. The normal behavior for post-pelagic green turtles was thought to be neritic feeding, but other studies have begun to document post-recruitment pelagic foraging or movements (Hatase et al. 2006, Parker et al. 2015, Williard et al. 2017). This track also coincided with the regional peak nesting season of October–November (Balazs 1981, Maison et al. 2010), and approached Northern Line Islands rookeries (Fig. 4). Even so, the telemetry data do not reveal male reproductive behavior such as remaining in a courtship area for about 2 mo. On the other hand, the track could indicate a mate search, possibly reflecting an Allee effect; the small population size and wide dispersion of females nesting all year across Kiribati's Islands could affect the success of mating encounters. Therefore, neither explanation for this loop— foraging versus breeding migrations— could be dismissed.

Another hypothesis proposed for future testing is that mating occurs at Palmyra and that most breeding migrations are undertaken by females inseminated at the refuge, as reported in Australia (Limpus 1993), saving males the energetic costs of migration (Arendt et al. 2012). Mating activity has not been frequently recorded at Palmyra, but during fieldwork within the refuge's boundaries (Fig. 1), several males were observed with extruding reproductive organs, possibly indicating sexual activity, and behavior consistent with mating was photographed. The lack of continuous monitoring paired with the temporal and spatial dispersion of mating turtles could hinder observation of this behavior at the remote site.

Management recommendations

This study demonstrates the importance of high-quality MPAs such as Palmyra for regional conservation including migratory species, and our main recommendation is to keep this reserve well-protected. The high site fidelity to foraging grounds of hard-shelled marine turtles in general means that they will continue to return to and use protected areas, underscoring the fundamental importance of these areas for marine conservation. As shown in this study, and supported by a global analysis, reserves that are large and well-established are widely used by green

turtles (Scott et al. 2012). Providing optimal and highly protected habitat that spatially encompasses most focal organisms' movements, as achieved at Palmyra, is key to protected area effectiveness (McClellan & Read 2009, Scott et al. 2012, Shimada et al. 2016). Such permanent areas may be particularly important in achieving conservation goals and improving the metrics of marine reserves recognized to be effective (Simard et al. 2016).

In the most successful marine protected areas, protection measures closely match the needs of key organisms, including marine turtles (Scott et al. 2012, Shimada et al. 2016). The present study highlights an unusual situation in which areas heavily used by migratory organisms were completely contained within refuge boundaries. Marine turtles and other migratory megafauna may depart reserve boundaries and thus gain only partially from protection, due to limited spatial overlap or insufficient conservation levels (McClellan & Read 2009, Scott et al. 2012, Shimada et al. 2016). The extended residency patterns revealed herein confirm that Palmyra stands out among protected areas, as it sustains and effectively shields endangered green turtles that spend most of their lives within its borders. The high-quality habitat shelters large juvenile, subadult, and adult turtles, the stages known to most impact population growth (Crouse et al. 1987).

The Palmyra green turtle population is genetically distinct from others in the region (Naro-Maciel et al. 2014) and forages in a unique and relatively undisturbed habitat (McFadden et al. 2010, 2014, Sterling et al. 2013). Healthy marine turtles play important roles in the ecosystem, for example through nutrient transport and predator-prey interactions (Bjorndal & Jackson 2003). With highly migratory megafauna, these ecosystem services often extend across different nations and these ties can foster or require international cooperation for research and conservation initiatives. Indeed, threat levels and legislative measures in the Central Pacific vary widely (Maison et al. 2010, Sterling et al. 2013). The main recommendation of this study is, therefore, to maintain or expand the protective measures at Palmyra and other protected areas including the Pacific Remote Islands Marine National Monument, within which it is contained.

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