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White, Timothy D
Carlisle, Aaron B
Kroodsma, David A
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Assessing the effectiveness of a large marine protected area for reef shark conservation

Timothy D. White [a,*], Aaron B. Carlisle [a], David A. Kroodsma [b], Barbara A. Block [a], Renato Casagrandi [c], Giulio A. De Leo [a], Marino Gatto [c], Fiorenza Micheli [a], Douglas J. McCauley [d]

[a] Hopkins Marine Station, Stanford University, Pacific Grove, California, USA
[b] SkyTruth, Shepherdstown, West Virginia, USA
[c] Dipartimento di Elettronica, Informazione, e Bioingegneria, Politecnico di Milano, Milano, Italy
[d] Marine Science Institute and Department of Ecology, Evolution, and Marine Biology, University of California at Santa Barbara, Santa Barbara, California, USA

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ABSTRACT

Large marine protected areas (MPAs) have recently been established throughout the world at an unprecedented pace, yet the value of these reserves for mobile species conservation remains unclear. Reef shark populations continue to decline even within some of the largest MPAs, fueling unresolved debates over the ability of protected areas to aid mobile species that transit beyond MPA boundaries. We assessed the capacity of a large MPA to conserve grey reef sharks - a Near Threatened species with a widespread distribution and poorly understood offshore movement patterns - using a combination of conventional tags, satellite tags, and an emerging vessel tracking technology. We found that the 54,000 km^2 U.S. Palmyra Atoll National Wildlife Refuge in the central Pacific Ocean provides substantial protection for grey reef sharks, as two-thirds of satellite-tracked sharks remained within MPA boundaries for the entire study duration. Additionally, our analysis of >0.5 million satellite detections of commercial fishing vessels identified virtually no fishing effort within the refuge and significant effort beyond the MPA perimeter, suggesting that large MPAs can effectively benefit reef sharks and other mobile species if properly enforced. However, our results also highlight limitations of place-based conservation as some of these reef-associated sharks moved surprising distances into pelagic waters (up to 926 km from Palmyra Atoll, 810 km beyond MPA boundaries). Small-scale fishermen operating beyond MPA boundaries (up to 366 km from Palmyra) captured 2% of sharks that were initially tagged at Palmyra, indicating that large MPAs provide substantial, though incomplete, protection for reef sharks.

1. Introduction

Marine protected areas (MPAs), which restrict fishing in order to aid conservation and fishery production, have become increasingly common in coastal waters over the last several decades (Lubchenco et al., 2003; Gaines et al., 2010; McCauley et al., 2015). A new pattern of MPA design has recently emerged: the creation of large, remote, pelagic MPAs (Lubchenco and Grorud-Colvert, 2015). The rapid establishment of these large MPAs, some spanning over one million km^2, has nearly doubled the total area of protected ocean on Earth in just five years (McCauley, 2014). Surrounding this unprecedented and fast-moving trend in global ocean management, there is considerable uncertainty about which species will benefit from MPAs of this size (De Santo, 2013; Pala, 2013).

The advantages of large MPAs for highly mobile species are particularly unclear, as the movements of many marine mammals, turtles, sharks, tunas, and other pelagic fish can dwarf even the largest MPAs (Game et al., 2009; Block et al., 2011; Sibert et al., 2012; Dueri and Maury, 2013). The presumed ecological importance of large and more mobile marine predators to marine ecosystem functioning (Bouchard and Bjorndal, 2000; Ferretti et al., 2010; Estes et al., 2011; McCauley et al., 2015) makes it essential to determine their relationship to large MPAs. To assess the benefits of large MPAs for mobile species, it is critical to determine both the proportion of time that individuals spend outside MPA boundaries, and the severity of mortality risks that occur beyond these boundaries (Graham et al., 2012; Rosenbaum et al., 2014). While spillover of populations from MPAs to adjacent waters may benefit nearby fisheries (Roberts et al., 2001; Halpern et al., 2009), under some conditions anthropogenic impacts outside an MPA can outpace reproduction and recruitment inside an MPA, resulting in population declines (Moffitt et al., 2009). Incomplete protection of an individual's activity space may be especially detrimental to shark

* Corresponding author.
E-mail address: timwhite@stanford.edu (T.D. White).

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species due to their low fecundity, late age at sexual maturity, and high susceptibility to fishing pressure (Cortés, 2000; Dulvy et al., 2014). Recent shark population declines within some large MPAs have fueled uncertainty about the efficacy of these reserves for mobile species and the ability of nations to reduce fishing effort across such vast regions (Graham et al., 2010; White et al., 2015).

Despite the fact that reef shark conservation is an explicit goal of many large MPAs (Koldewey et al., 2010; Davidson, 2012; Dulvy, 2013), the offshore movement patterns of some species are not well resolved and anthropogenic impacts surrounding large MPAs are rarely quantified, so it remains unclear how much protection they will truly receive from these measures. Here, we assessed the effectiveness of a large MPA for conserving one of the most historically abundant sharks in Indo-Pacific coral reef ecosystems: the grey reef shark (*Carcharhinus amblyrhynchos*). Grey reef sharks can comprise up to 46% of upper trophic level biomass in unfished reef ecosystems (Stevenson et al., 2007; Friedlander et al., 2014). However, grey reef sharks have experienced severe population declines across some of their Indo-Pacific distribution and are listed as Near Threatened in the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (Robbins et al., 2006; IUCN, 2015). Grey reef shark movements have been studied within individual atolls and coastal regions using acoustic telemetry (McKibben and Nelson, 1986; Heupel et al., 2010; Barnett et al., 2012; Espinoza et al., 2015a; Espinoza et al., 2015b) - a method that records the presence of tagged individuals when they approach nearshore acoustic receivers - but their broader, offshore movements when away from stationary receivers remain poorly understood. Stable isotope analysis of grey reef shark tissue has revealed heavy reliance on pelagic prey (McCauley et al., 2012), but it is unclear if this putative trophic subsidy reflects the movements of the sharks to pelagic habitats or movement of pelagic prey into nearshore habitats.

We conducted our investigation of large MPA effectiveness on the northern Line Islands archipelago in the central Pacific Ocean. Within this archipelago, the U.S.-managed Palmyra Atoll National Wildlife Refuge (approximately 54,000 km^2, fishing fully prohibited) is located several hundred kilometers from three inhabited and fished atolls that partially comprise the nation of Kiribati (Fig. 1). Protected reefs in this region host large populations of grey reef sharks and other mobile predators, while the fished reefs of Kiribati host dramatically lower predator densities (Sandin et al., 2008). The boundaries of the protected area at Palmyra Atoll have been expanded multiple times since 2001, and similarly the boundaries of the Papahānaumokuākea Marine National Monument in the Northwestern Hawaiian Islands were substantially expanded in August 2016, making discussions of reserve design in this area relevant and timely.

The specific goals of this study were to 1) determine the amount of time that grey reef sharks spend outside of historical and contemporary MPA boundaries by deploying conventional tags and satellite tags on this species at Palmyra Atoll, 2) assess the interaction dynamics between grey reef sharks and both commercial and small-scale fishermen by recovering conventional tags from fishermen and quantifying commercial fishing effort via recently-developed remote sensing capabilities, and 3) evaluate how locally relevant changes in MPA size may shape a species' exposure to risk. The combination of both satellite telemetry and conventional tagging provides us with unique insight into the oceanic movements and potential conservation strategies for this key species.

An important additional aim of this work was to demonstrate the value of cross-evaluating data on the spatial ecology of large marine predators obtained via animal tracking with newly available data on the spatial ecology of human predators (i.e. fishermen) obtained via vessel tracking. Historically, such comparisons have been limited as high-resolution fishing vessel data have either not been available or have been kept private by regional management authorities (but see Queiroz et al., 2016). The recent release of publically accessible data on fishing vessel activity and the development of new behavioral filtering algorithms to interpret these vessel tracks (McCauley et al., 2016) opens the door to novel analytical opportunities. Using information derived from the Automatic Identification System (AIS), a globally abundant vessel transmitting system, we generated a spatially explicit quantification of industrial fishing effort throughout the region where we tracked grey reef sharks. We evaluated how fishing effort density related to the boundaries of the focal MPA in our study region and examined interactions between shark behavior and the behavior of fishermen. Collectively these diverse forms of insight into how coastal sharks use space, combined with spatially explicit views of how fishermen use some of the same ocean space, empowers us to make much more informed decisions about how best to tailor marine management tools to meet conservation objectives.

2. Materials and methods

2.1. Study area

We tracked the movements of grey reef sharks and fishermen in relation to an MPA in the central Pacific Ocean (1–11°N, 152–167°W). This study focused on four atolls within the northern Line Islands. Palmyra Atoll is located within a large, no-take marine protected area (54,126 km^2) that is federally managed by the U.S. Fish and Wildlife Service, while Teraina, Tabuaeran, and Kiritimati are fished islands within the Republic of Kiribati (Fig. 1). Palmyra Atoll is uninhabited except for a small number (<20) of visiting researchers, research station staff, and wildlife refuge employees. The area within a 12 nautical mile (NM; 22.2 km) radius of Palmyra Atoll was first established as a National Wildlife Refuge (NWR) in 2001. In 2009, the boundaries of Palmyra Atoll NWR were expanded to 50 NM (92.6 km) through the establishment of the Pacific Remote Islands Marine National Monument (PRIMNM). PRIMNM consists of Palmyra Atoll and 6 other remote atolls, all protected out to 50 NM from fishing and other extractive activities. In 2014, the MPA boundaries were expanded out to 200 NM (370.4 km) at 3 of those 7 atolls (Jarvis and Wake Island and Johnston Atoll), bringing the total protected area to nearly 1.3 million km^2. Though Palmyra's boundaries were considered for an extension to 200 NM, its boundaries remained fixed at 50 NM. This 200 NM boundary is the extent of the U.S. exclusive economic zone (EEZ), and as such it is the maximum MPA limit that any nation can independently manage under current international law. Expansions of this scale are currently underway at other locations in the Pacific Ocean; the August 2016 expansion of the Papahānaumokuākea Marine National Monument's boundaries from 50 NM to 200 NM brought its total protected area to over 1.5 million km^2, making it the world's largest MPA at the time.

In contrast with the protected areas of PRIMNM, the islands of Teraina, Tabuaeran, and Kiritimati are respectively inhabited by 1690, 1960, and 5586 people (Tekaieti, 2012). Teraina, Tabuaeran, and Kiritimati are located a distance of 223 km, 366 km, and 665 km from Palmyra Atoll (113 km, 255 km, and 548 km from the MPA boundary). The residents of these islands are heavily dependent upon fishing for subsistence and economic opportunity (Tekaieti, 2012). Small-scale shark fisheries and the shark fin trade operate on all three of these islands, though the origins and biomass of sharks that are captured in these fisheries are currently unknown. Line Islands small-scale fishermen primarily operate out of 4–5 m aluminum skiffs and wooden canoes. Since Kiribati fishermen generally do not leave sight of their islands due to a lack of navigational equipment and limitations in gasoline availability, these fishermen do not have the range to make the 446 km to 1330 km round-trip journey to illegally fish at Palmyra Atoll.

2.2. Conventional tagging and small-scale fisheries mortality

In order to measure the movements and observe mortality of grey reef sharks from Palmyra NWR to the small-scale fisheries operating beyond the MPA boundary, we deployed 262 numbered dorsal fin tags

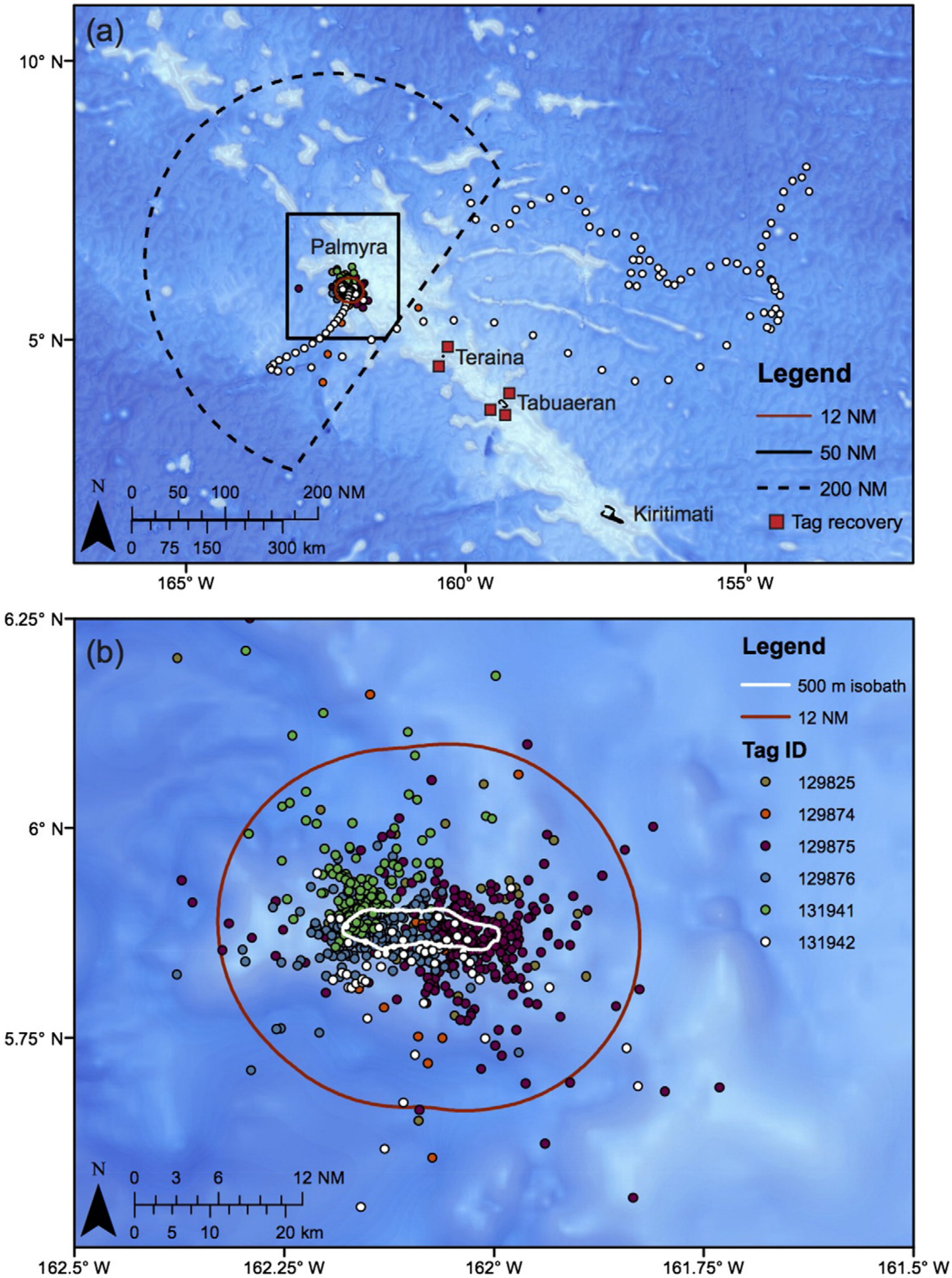

Fig. 1. (a) The state-space modeled daily position estimates for 6 grey reef sharks (*Carcharhinus amblyrhynchos*) fitted with satellite tags at Palmyra Atoll and (b) the subset of those positions surrounding Palmyra Atoll.

(Dalton Rototags, Newark, United Kingdom) on grey reef sharks during October 2006 to July 2009. Each of these conventional tags was imprinted with a unique identification number. We captured sharks on the forereef of Palmyra Atoll using barbless hooks and handlines. We recorded sex and total length (TL) before releasing the animals. All tagging work was conducted under U.S. Fish and Wildlife Service permit # 13810.

We calculated the percentage of tags that were recovered by Kiribati fishermen as a minimum estimate of interisland movements and small-scale fisheries mortality. We actively searched for tags recovered by fishermen on the islands of Teraina, Tabuaeran, and Kiritimati in 2007, 2009, and 2013 (197 days total). In addition, we raised awareness of the tagging program through posted notices and public discussions at village halls, radio interviews, and direct conversations with regional Kiribati fisheries officers, local fishermen, and shark fin retailers. Local fisheries agents based on each island were contracted to collect and report tags that were recovered while we were not present. We physically retrieved all reported tags in order to verify their authenticity and to record the recovery location and date from fishermen.

Table 1
The percentage of state-space modeled daily location estimates and maximum distance beyond the previous (12 nautical mile, NM), current (50 NM), and maximum potential (200 NM) boundaries for Palmyra Atoll National Wildlife Refuge. The percentage of pelagic detections refers to positions beyond a 500 m isobath surrounding Palmyra Atoll.

						Positions beyond MPA boundary (%)			Maximum distance beyond boundary (km)			
Tag ID	Sex	Total length (cm)	Days at liberty	Detections (n)	Detections in pelagic waters (%)	12 NM	50 NM	200 NM	Palmyra Atoll 500 m isobath	12 NM	50 NM	200 NM
129825	M	148	40	51	24	4.8	0.0	0.0	40.4	22.1	–	–
129874	M	143	204	32	44	18.8	9.4	3.1	182.1	166.0	88.1	19.1
129875	M	156	390	179	13	4.6	0.0	0.0	88.6	72.0	–	–
129876	M	143	466	154	6	0.8	0.0	0.0	18.7	6.3	–	–
131941	M	150	139	89	31	4.3	0.0	0.0	43.8	22.0	–	–
131942	M	151	237	375	97	63.8	57.0	46.3	926.3	907.7	809.7	617.6
Median	–	149.0	220.5	121.5	27.5	4.7	0.0	0.0	66.2	–	–	–

2.3. Satellite tagging and kernel utilization distribution analysis

In order to gain a higher resolution understanding of large-scale shark movements, we deployed 11 fin-mounted satellite tags on adult grey reef sharks at Palmyra Atoll NWR in May and August 2013 (Table 1). Sharks were captured on handlines as described above. We used position-only SPOT tags (SPOT5, Wildlife Computers, Seattle, Washington, USA). The tags were not programmed to record temperature because this reduces battery life, and our primary objective was to record movements with respect to MPA boundaries for as long as possible. SPOT tags transmit a location and accuracy estimate when the dorsal fin breaks the surface of the water, which is a behavior that has been observed during grey reef shark feeding events on pelagic prey at Palmyra Atoll (McCauley et al., 2012). To estimate the frequency with which sharks left the atoll for pelagic habitats, we used ArcGIS 10.0 to calculate the percentage of these hits that fell outside a 500 m isobath surrounding Palmyra Atoll. We used Argos detections to assess movements away from the atoll and not daily position estimates (see Section 2.4) because they have the greatest spatial resolution and therefore are most appropriate for atoll-scale calculations (Papastamatiou et al., 2010). Additionally, we calculated kernel utilization distributions (KUD) using Argos detections through the Geospatial Modeling Environment version 0.7.3.0 (www.spatialecology.com/gme) in order to measure the activity space (95% KUD) and core area (50% KUD) of individual animals (Papastamatiou et al., 2010; Olson et al., 2012; Carlson et al., 2014). To avoid bias that may result from differences in detection frequency, we first filtered detections to one point per day of data by calculating the daily median position (Olson et al., 2012; Carlson et al., 2014).

2.4. Analysis of shark movements across management boundaries

The error radius of a SPOT tag detection is determined by the orientation of Argos receiving satellites at the time of transmission. Satellite detections fall into 7 different location classes (LC) of varying accuracy (3, 2, 1, 0, A, B, Z). For our analyses, we accepted locations from LC3 to LCB. LC3–LC1 have error estimates ranging from 250 m to 1500 m as reported by Argos, and error estimates for LC0–LCB were based on peer-reviewed, empirical estimates that range from 4180 m to 10,280 m (Costa et al., 2010).

In order to determine the amount of time that sharks spent outside of historical and contemporary MPA boundaries, we estimated daily shark positions and 95% credible intervals using a Bayesian state-space model (SSM) that explicitly accounted for uncertainty in satellite detections and the uneven distribution of detections over time (Jonsen et al., 2005). The SSM that we applied is fully described in Block et al., 2011 and has been previously shown to produce robust estimates of the movements of shark species and other taxa (Block et al., 2011; Winship et al., 2012). This SSM interpolated across gaps in the satellite detections that were ≤20 days (Bailey et al., 2008; Block et al., 2011). We did not attempt to estimate changes in animal behavioral modes via a switching model, as our primary objective was to determine the movements of the tagged animals in relation to MPA boundaries. The relevant MPA boundaries considered were the 12 NM limit (the boundary of Palmyra NWR from 2001 to 2009), 50 NM limit (the boundary of Palmyra NWR from 2009 to present), and 200 NM limit (U.S. EEZ; the current boundaries of other large MPAs in PRIMNM and the maximum potential boundary for Palmyra NWR or other national jurisdictions). Sharks were considered to be outside an MPA boundary if their mean position estimate (and correspondingly, over 50% of the uncertainty estimate) fell outside of that limit.

2.5. Automatic identification system (AIS) analysis of commercial fishing pressure

We determined patterns of international commercial fishing effort near the Line Islands by analyzing satellite detections of vessel AIS transmissions. We analyzed the tracks of registered longline and purse seine fishing vessels that entered our study region (1–11°N, 152–167°W) from 1 January 2013 to 31 December 2014. Fishing events were identified using a machine learning algorithm that used frequency of vessel course changes and vessel speed to calculate a “fishing score,” or the likelihood that observed vessel tracks are indicative of distinctive fishing behaviors (McCauley et al., 2016). Fishing scores range from 0 to 1, where 0 is a vessel that is least likely to be fishing, and 1 is a vessel that is very likely fishing. A linear regression analysis has previously demonstrated that algorithm-estimated fishing effort is highly correlated with effort estimates derived from fisheries reporting agencies (McCauley et al., 2016). A shared limitation of AIS and traditional vessel tracking technologies is that illegal fishing vessels will not be detected if they do not transmit signals. Additionally, smaller vessels are not required to transmit AIS so satellite analysis of AIS data primarily focuses on larger, industrial vessels; an estimated 71% of large fishing vessels (>24 m) regularly transmit AIS (McCauley et al., 2016). We aggregated “likely fishing days,” defined as fishing score ≥ 0.5, into 0.25° by 0.25° grid cells. Fishing days detected within three nautical miles of land were discarded since vessels exhibit more frequent changes in speed and course when navigating coastal waters and ports.

3. Results

3.1. Tags recovered beyond the MPA from small-scale fisheries

We deployed 262 conventional tags at Palmyra Atoll on grey reef sharks that ranged from 90 to 175 cm in total length (TL). Five of our 262 conventional tags deployed within Palmyra NWR were recovered from small-scale, nearshore shark fishermen in Kiribati (Fig. 1; Table 2). These sharks were reported to have been caught on the forereef of Tabuaeran (3 tags; 366 km from Palmyra tagging site) and Teraina (2 tags; 223 km from Palmyra tagging site). No tags were recovered on Kiritimati during this study. Eighty-five percent of the 262

Table 2
Coastal fishermen operating beyond the Palmyra Atoll National Wildlife Refuge's boundaries captured 5 of 262 grey reef sharks that were initially tagged within the MPA, indicating shark movements of up to 366 km.

Days at liberty	Sex	Total length (cm)	Recapture location	Distance shark traveled (km)
68	F	130	Teraina	223
152	F	154	Tabuaeran	366
461	F	155	Tabuaeran	366
834	F	133	Tabuaeran	366
1420	F	144	Teraina	223

Table 3
Core areas (50% kernel utilization distribution, or KUD) and activity space (95% KUD) of six grey reef sharks that were satellite-tagged at Palmyra Atoll.

Tag ID	Sex	Total length (cm)	50% KUD (km^2)	95% KUD (km^2)
129825	M	148	192	950
129874	M	143	757	5442
129875	M	156	116	915
129876	M	143	24	217
131941	M	150	104	857
131942	M	151	106,049	412,189
Median	–	149	154	933

conventionally tagged sharks were female and all 5 of the recovered tags were from female sharks (Table 2). Tagged sharks were at liberty for a mean of 587 (SE 247) days prior to capture. These 5 sharks were all captured with single-hook handlines aboard 4–5 m aluminum skiffs.

3.2. Reef shark movements in pelagic waters

Eleven SPOT tags were deployed on grey reef sharks that ranged from 143 cm to 159 cm in TL. From these deployments we obtained a total of 1280 satellite detections from 6 tagged sharks and analyzed 880 detections that were LC3–LCB (Table 1). All 6 sharks were detected in pelagic waters away from the atoll; the median percentage of detections per animal beyond the 500 m isobath was 28%, with values for individual animals ranging from 6% to 97% (Table 1). Three of our 11 satellite tags failed to transmit any data and 2 tags reported data for 3 or less days, so these tags were not included in analyses. The 6 successful SPOT tags transmitted for an average of 246 (SE 65) days (Table 1). Although we tagged 4 female and 7 male sharks, all 6 of the successful tracks came from male sharks.

3.3. Percentage of time and maximum distance beyond MPA boundaries

The SSM analysis produced a total of 919 daily position estimates for the 6 SPOT-tagged sharks, with a mean of 153 (SE 45) daily position estimates per animal (Fig. 1). A relatively small percentage of daily positions beyond MPA boundaries had error estimates that overlapped with MPA boundaries (24% for 12 NM, 14% for 50 NM, and 3% for 200 NM); in these cases positions were considered outside the MPA boundary if the mean position estimate fell beyond the boundary. Based on these position estimates, 4 of the 6 SPOT-tagged sharks remained inside Palmyra MPA's current 50 NM boundaries for the entire study duration, while 2 sharks ventured outside for 9% and 57% of their daily position estimates (Table 1). All 6 sharks transited beyond the historical 12 NM boundaries of Palmyra NWR for a median of 5% of their daily position estimates (range: 1% to 64%). Two sharks were detected outside of the 200 NM limit (the U.S. EEZ boundary) for 3% and 46% of their daily location estimates. The median maximum linear distance from Palmyra Atoll's 500 m isobath for these 6 sharks was 66 km, with a range of 19 to 926 km. The shark that traveled the furthest reached a maximum linear distance of 908 km from the previous 12 NM MPA boundary surrounding Palmyra Atoll, 810 km from the current 50 NM MPA boundary, and 618 km from the 200 NM boundary (Table 1).

3.4. Activity spaces and core areas

Activity space (95% KUD) and core area (50% KUD) estimates for SPOT-tagged grey reef sharks were highly variable across individuals. The median activity space was 933 km^2 and median core area observed was 154 km^2 (Table 3). Four activity spaces were fully contained within the current MPA boundaries, while 2 activity spaces included pelagic waters outside the current MPA and U.S. EEZ. The most mobile shark that we observed had an activity space of 412,189 km^2 and a core area of 106,049 km^2.

3.5. Overlap of shark habitat with commercial fisheries

Within the study region, we analyzed 593,807 AIS detections with behavioral algorithms (McCauley et al., 2016) that identified 6752 total days of fishing activity exhibited by 151 unique longliners and 42 unique purse seiners in 2013–2014. Virtually no fishing pressure was observed within Palmyra NWR (1 fishing day over two years) and negligible effort was observed in the U.S. EEZ (6 fishing days) (Fig. 2). A hotspot of likely fishing days (up to 51 fishing days in a 0.25° grid cell) was recorded directly outside the MPA's southeastern border and the U.S. EEZ. The AIS devices of the 193 detected fishing vessels were registered to 12 different nations distributed across Asia, Oceania, Europe, North America, Central America, and South America (Fig. 3). South Korean ships comprised 62% of detected fishing vessels (103 longliners and 16 purse seiners).

4. Discussion

Our results demonstrate that large MPAs like the U.S. Pacific Remote Islands Marine National Monument provide substantial, though incomplete, protection for grey reef sharks. We analyzed the satellite tracks of grey reef sharks and found that the majority of tag detections occurred within Palmyra Atoll National Wildlife Refuge (Fig. 1; Table 1). Two thirds of the satellite-tagged sharks were exclusively detected within this MPA, for up to 1.27 years post-release. Activity spaces (95% KUD) and core areas (50% KUD) of habitat utilization for these sharks were centered on Palmyra Atoll and the surrounding pelagic waters, well within MPA boundaries. The median activity space of all tagged sharks was 933 km^2, <2% of Palmyra NWR's 54,126 km^2 of protected area (Table 3). These results offer support for the conclusion that large MPAs can offer meaningful amounts of protection for mobile species with patterns of space use like grey reef sharks.

Importantly, we also found that grey reef sharks displayed a surprising diversity of movement patterns with some individuals swimming great distances that took them well beyond the boundaries of this focal large MPA. For an animal that is believed, as is eponymously implied, to be a quintessential reef-associated species (Compagno, 2001; Randall, 2007) it is indeed surprising that up to 97% of satellite detections for one tagged individual occurred in the pelagic environment (Table 1). We recorded the largest known movement of a grey reef shark; a SPOT-tagged shark swam across 926 km of pelagic waters, reaching a maximum linear displacement of 810 km beyond the MPA boundary (Fig. 1; Table 1). To our knowledge, the maximum-recorded movement of a grey reef shark, measured via stationary acoustic telemetry stations near the Great Barrier Reef, is 134 km (Heupel et al., 2010). Our satellite-derived value of 926 km increases the upper bound of observed mobility by sevenfold.

Approximately half of the daily location estimates for the farthest travelling individual in this study occurred outside the MPA, and portions of its activity space and core area were located over 900 km from Palmyra Atoll. A second shark was detected 182 km from Palmyra Atoll (88 km beyond the current MPA boundary). These offshore movements, considered alongside previous isotopic analysis, support the

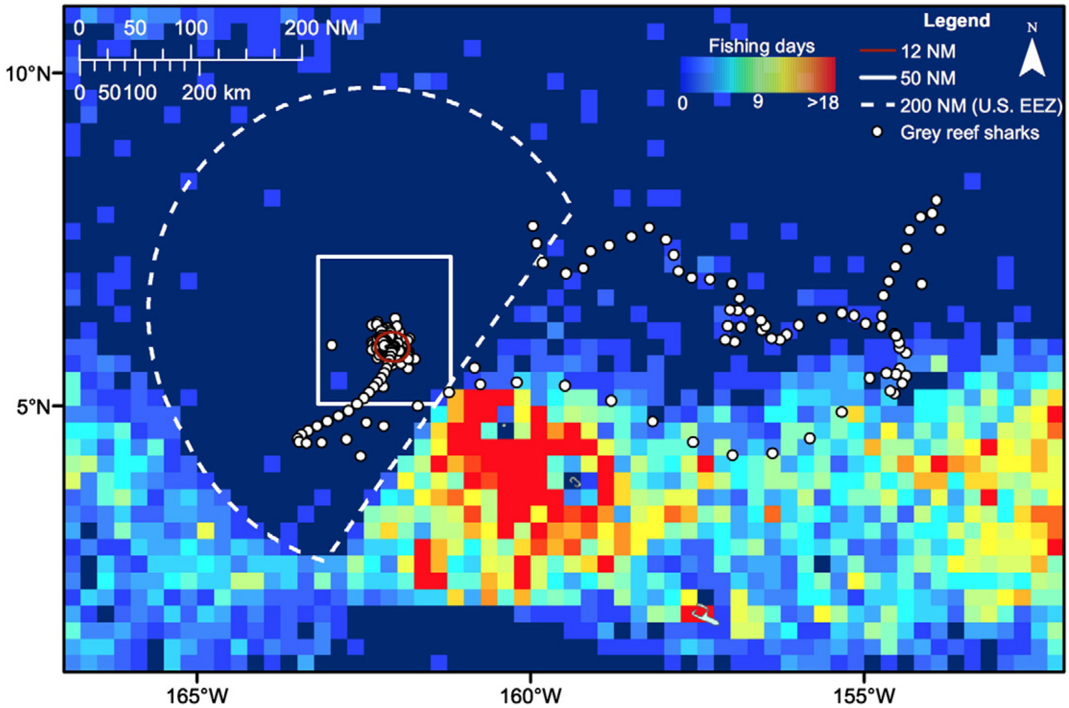

Fig. 2. A fishing effort density map for 193 commercial fishing vessels as determined through remote sensing of vessel Automatic Identification System (AIS) transmissions. Grid size is 0.25°.

hypothesis that grey reef sharks may play an ecologically important role in maintaining ecosystem connectivity between reefs and pelagic environments (McCauley et al., 2012). While the majority of grey reef sharks remain inside the MPA and receive substantial protection, these observations also highlight the possible limitations of the protection that large MPAs can provide to highly mobile species. As satellite tracking and large MPA establishment both continue to advance, we must consider that additional reef or coastal species may in fact make large-scale movements, which may compromise large MPA effectiveness for some species depending on the scale of movements and fishing pressure outside the MPA. Acoustic tracking of grey reef shark movements has suggested that relatively small MPAs (e.g., 15 km^2) may be beneficial to grey reef shark populations (Barnett et al., 2012), while the satellite and conventional tag data presented here suggest that much larger MPAs are ideal. Continued tagging efforts and analyses of fishing effort will bring an improved understanding of which species may or may not be likely to benefit from large MPAs.

While the observation of pelagic movement patterns in grey reef sharks via satellite telemetry and conventional tagging improves our understanding of reef shark ecology and conservation, we caution that

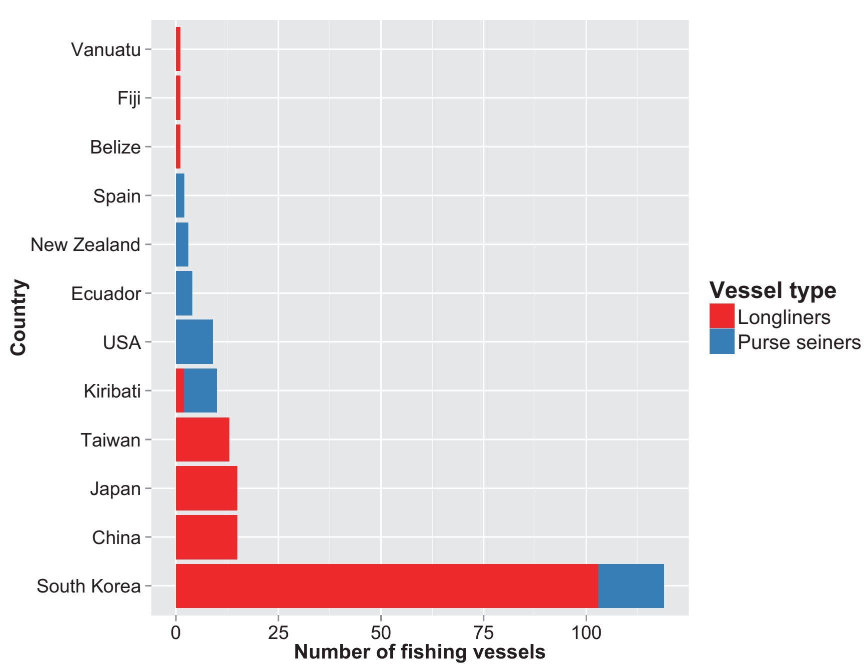

Fig. 3. The nationality and fishing method used by the 193 fishing vessels that we observed in our study region.

the interpretations of spatial ecology that we report are derived from a relatively low sample size (n = 262 conventional tags sharks, n = 6 successful satellite tags). All methods for tracking animal movements provide a limited view of dynamic behavior; for example, acoustic telemetry may lead to underestimates of activity space size since it does not capture offshore movements away from coastal receivers, the density of satellite telemetry data is often limited by the time that tagged animals spend near the surface, and both methods are temporally restricted by the battery life of electronic tags. Our estimates of grey reef shark movements may be larger if individuals could be studied on time scales longer than our 8.1 month mean tag life. Additionally, since SPOT tags transmit location when the tag breaks the water surface, it is very possible that activity spaces are larger than recorded since individuals may have undertaken additional movements in deeper waters. More will certainly be learned by replicating this work on a larger number of individuals and examining potential for geographic and environmental variability in space use by this species.

The recovery of 5 conventional tags (initially deployed at Palmyra Atoll) by Kiribati fishermen on islands that are 223 km and 366 km from Palmyra provides two additional insights. All 5 of the recovered conventional tags were from female sharks, and all successful satellite tracks came from male sharks. Combining both tagging results therefore indicates that both male and female grey reef sharks undertake interisland transit and substantial pelagic movements. The infrequent detections of satellite-tracked females deserve further exploration but may be the result of behavioral differences between sexes, stochasticity, or reduced Argos satellite coverage across tropical latitudes (Breed et al., 2012). Additionally, the recovery of conventional tags from shark fishermen underscores the importance of aligning the scales of marine policy and spatial ecology of conservation targets. The 2% rate of tag recovery from Kiribati (5 out of 262 tags) should be taken as a minimum estimate of grey reef shark mortality from small-scale fishermen in Kiribati, as some animals may have shed tags over time, and we are unlikely to have received 100% of recovered tags given the remoteness of Kiribati and the associated challenges in communication. The overall rate of fishing mortality for grey reef sharks tagged at Palmyra Atoll is likely higher than 2% because international fishing vessels may have recovered additional tags that went unreported.

Our capacity, for the first time, to summarize publically accessible data on fishing activity along the perimeter of large MPAs, like Palmyra, provides an exciting and sobering view of the significance of the observed movements of grey reef sharks beyond MPA boundaries. By behaviorally processing AIS location data we detected 6752 likely fishing days displayed by 193 fishing vessels in the region of this particular large MPA over the course of two years (Fig. 2). This level of fishing effort is quite remarkable given the extreme remoteness of this region of the Pacific (McCauley et al., 2013). It is important to recall that this represents a lower bound estimate of total fishing effort near this large MPA since smaller vessels do not transmit AIS and some vessels do not properly use this tracking system (McCauley et al., 2016).

We see in these outputs virtually no fishing pressure inside both the Palmyra Atoll NWR and the U.S. EEZ, suggesting that large-scale spatial management can effectively reduce fishing pressure on mobile species if enforcement is adequate. Fishing vessels from Asia, Oceania, Europe, North America, Central America, and South America were active in our study region, underscoring the globalized nature of addressing management for mobile species, like grey reef sharks (Fig. 3.). The majority of the detected vessels were from East Asian nations, which could prove problematic for shark conservation since the region is a major driver of the shark fin trade. These kinds of new observations highlight the value of using emerging data sources on vessel activity to examine overlap between the spatial ecology of marine apex predators and human predators – and the role of MPAs in mediating these interactions. Future work that engages AIS data can be put to work for myriad allied applications, such as examining competition between fish and fishermen for forage fish, examining the spatial dynamics of human-marine predator interactions, and generating views of bycatch risk that are independent of fisheries reporting data.

Our simple analysis of historical and potential MPA expansion scenarios suggest that enlargement of this MPA has and would, respectively, decrease the amount of time grey reef sharks spend outside protected areas. Every satellite-tagged shark left the historical, 12 NM boundaries of Palmyra Atoll NWR, while only 2 sharks swam beyond the maximum potential 200 NM limit (Table 1). Through the analysis of AIS detections, we observe minimal differences in fishing effort within the MPA compared with EEZ waters. The U.S. EEZ appears to be functioning as a de facto region of reduced fishing effort, though smaller vessels that do not transmit AIS may be fishing in this region. In this case, expanding large MPAs may prevent future spatial expansion of fishing, while addressing additional stressors besides fishing. For instance, deep-ocean mining is emerging as a major threat to slow-growing ecosystems across much of the planet (Mengerink et al., 2014), and the recent expansion of PRIMNM and the Papahānaumokuākea Marine National Monument directly ensure that mining contracts will not be granted throughout these immense protected regions.

In more heavily fished EEZs, expansions of large MPA boundaries – if properly enforced – would decrease the amount of time grey reef sharks and other mobile organisms spend exposed to elevated risk of fishing mortality. Future work should explicitly explore what this added protection means to the population dynamics and persistence of this and other at-risk species, but for shark species with low reproductive rates and high sensitivity to fishing pressure, increases in protection of this magnitude may confer meaningful benefits. These results parallel observations in the central Pacific that showed that seabirds, another ecologically important class of marine predator, travel and forage beyond large MPA boundaries (e.g. red-footed boobies at Palmyra NWR spent 33% of their at-sea time outside of the MPA boundaries; Young et al., 2015) and that sea turtle populations maintain connectivity across protected and fished regions (Naro-Maciel et al., 2014). While it is clear that large MPAs offer crucial protection for many highly vagile and threatened species, these results also make it equally clear that it would be prudent to develop diverse portfolios of conservation measures. Many large marine vertebrates (mammal, reptile, and fish) are likely to be similar to grey reef sharks in that some proportion of their ecology will spill out beyond the boundaries of even the largest politically tenable MPAs. Consequently, large MPAs will become much more effective if they are matched with other non-place-based conservation strategies such as gear restrictions, catch limits, and dynamic, temporal closures (Maxwell et al., 2015).

4.1. Conclusions

The establishment of very large MPAs in the last five years has far outpaced research on the ecological effectiveness of these MPAs. Reviews and commentaries have highlighted both the potential benefits of large MPAs (Koldewey et al., 2010; Lubchenco and Grorud-Colvert, 2015) and skepticism of their utility (Dulvy, 2013; Hilborn, 2015). Here we show how uniting the insight of new satellite tracking data for marine species with emerging datasets on fishing effort can help resolve the value of large MPAs. In the case of grey reef sharks, large MPAs unambiguously confer substantial protection to this at-risk species, though this protection is not complete for particularly mobile individuals. Recent expansions of this MPA's boundaries have reduced the potential for sharks to overlap with industrial fisheries, but some grey reef sharks transit beyond the 200 NM maximum potential limit of a MPA and in so doing interact with small-scale and industrial fisheries. The process of drawing out these conclusions provides a valuable model for strategically assessing the effectiveness of large MPAs for other mobile species across the burgeoning number of marine regions where large MPAs are being established.

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Appendix A. Supplementary data

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