



# Pelagic marine protected areas protect foraging habitat for multiple breeding seabirds in the central Pacific



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## ABSTRACT

Despite many biotic, physical, and political challenges for place-based conservation in open ocean environments, conservation of discrete oceanic regions by designating pelagic marine protected areas (PMPAs) has gained considerable traction. In the oligotrophic central Pacific, a patchy and dynamic ecosystem, a robust network of PMPAs has recently been established. However, evaluations of PMPA efficacy in providing appropriate habitat coverage for pelagic species are lacking, particularly in the tropics. Here, we used high resolution GPS tracking and home range analyses of tropical boobies to determine the distribution and foraging habitat use of three sympatric species (*Sula sula*, *Sula dactylatra*, and *Sula leucogaster*) in two PMPAs that varied substantially in size and shape. At each site we characterized the extent and use of foraging habitat inside and outside the PMPA that surrounded each breeding colony. We found profound variation within and among species in foraging behavior and habitat use across the two sites; this was partially explained by variation in bathymetry. Yet, despite variation both in PMPA size and shape, and in foraging behavior of the birds, we determined that the PMPAs each encapsulated more than 85% ( $n = 216$  trips) of foraging habitat for each species, indicating that these PMPAs provided important habitat coverage for highly mobile tropical species. While this study highlights the challenges in effectively designing PMPAs even for relatively well-studied, central place foragers, given strong variation in foraging ecologies across sites, it also suggests that PMPAs do provide meaningful habitat coverage for at least some pelagic species.

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## 1. Introduction

Many studies have demonstrated the efficacy of marine protected areas (MPAs) for conserving habitats and species; however, these studies have typically focused on small-scale MPAs and their effects on fish in coastal, habitat-specific systems (e.g. coral reefs) (Lester et al., 2009; Gaines et al., 2010; Lotze et al., 2011). Small-scale MPAs are increasingly recognized as insufficient to address conservation and habitat needs of a wide swath of pelagic species (Game et al., 2009; Agardy et al., 2011), despite the fact that conservation of such mobile predatory species is a major goal of many MPAs (Ballard et al., 2012). Recently, large-scale, pelagic MPAs (PMPAs) have also been created, in part to protect these more oceanic species (Hyrenbach et al., 2000; Norse, 2005; Alpine and

Hobday, 2007; Game et al., 2009; Sheppard et al., 2012; Maxwell et al., 2014). However, the efficacy of PMPAs for protecting species remains largely unclear because pelagic environments are dynamic and ephemeral compared with coastal ecosystems. Pelagic species often occupy massive home ranges, and the ecology and habitat requirements of these species are poorly understood (Block et al., 2011; Witt et al., 2011; Rosenbaum et al., 2014). Yet many pelagic species have more spatially limited, and predictable, movements during key life history phases, such as when breeding (Itano and Holland, 2000; Louzao et al., 2006; Shillinger et al., 2008; Hooker et al., 2011; Louzao et al., 2011; Maxwell et al., 2011).

Although seabirds are among the most conspicuous of pelagic predators, only recently have any efforts been made to evaluate the efficacy of MPAs in protecting relevant foraging habitat for seabirds (Garthe et al., 2012; Lascelles et al., 2012). Although PMPAs can effectively incorporate seabird habitat (Hyrenbach et al., 2006; Maxwell et al., 2013), work to date has focused largely on

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coastal regions and in temperate systems (Ludynia et al., 2012; Péron et al., 2013). Tropical seabird conservation has often been cited as an objective in the designation of tropical PMPAs (Kenyon et al., 2012; Sheppard et al., 2012); yet the efficacy of PMPAs in protecting important foraging grounds for these species is far less clear than for temperate or coastal species. Although seabirds are central place foragers when breeding, they are also highly mobile predators, and frequently depend on ephemeral, patchily distributed resources in pelagic environments (Ricklefs, 1990; Le Corre et al., 2003; Weimerskirch et al., 2005; Weimerskirch, 2007). Unlike temperate seabirds, tropical species generally lack deep diving capabilities and thus depend on associations with other large, highly mobile, groups of subsurface predators (e.g. sharks, cetaceans, tuna), using subsurface predator facilitated foraging behavior (SPFF) (Harrison et al., 1983; Au and Pitman, 1986; Maxwell and Morgan, 2013). Many, although not all, of these subsurface predators are in decline (Myers and Worm, 2003; Ward and Myers, 2005; Ferretti et al., 2010) with strong net declines in biomass of large pelagic predatory species reported (Myers and Worm, 2003; Ward and Myers, 2005; Ferretti et al., 2010); this is likely to result in reduced foraging opportunities for tropical seabirds who rely on SPFF (Ashmole and Ashmole, 1967; Spear et al., 2007; Maxwell and Morgan, 2013). Consequently, tropical seabirds would appear to pose particular challenges to fixed protected area approaches given the mobility of subsurface predators that potentially move in and out of protected areas. Given ongoing global declines in tropical seabird populations (Croxall et al., 2012), and particularly given concerns about future declines in response to effects of climate change and fishing pressures on SPFF activity (Maxwell and Morgan, 2013), there is a great need for identifying the efficacy of PMPAs as a tool for the conservation of tropical seabirds.

Two of the largest and most recently created MPAs – the Pacific Remote Islands Marine National Monument (PRIMNM) and the Papahānaumokuākea Marine National Monument (PMNM; previously called Northwestern Hawaiian Islands Marine National Monument) – were created in 2006 (PNMN) and 2009 (PRIMNM) (Federal Register, 2006, 2009), and are part of an expansive network of PMPAs in the tropical and sub-tropical Pacific. Together they cover more than 1.6 million km<sup>2</sup> (~360,000 km<sup>2</sup> PMNM, ~1.3 million km<sup>2</sup> PRIMNM) (Fig. 1) and provide habitat for more than 18 million nesting seabirds from 22 species. Populations of large vagile fish are thought to be in relatively good condition in these parts of the Pacific (Cox et al., 2002; Langley et al., 2009, but see Polovina et al., 2009). While the monuments were not explicitly created for protection of pelagic species (Federal Register, 2006, 2009), they can facilitate such protection given their large size and extensive pelagic coverage.

We measured the extent to which these two central Pacific PMPAs encompass the foraging habitat of three sympatric sulid seabird species that breed in these remote tropical (e.g. PRIMNM) and subtropical (e.g. PMNM) waters. While characterizing habitat use and spatial coverage by the PMPA clearly is not equivalent to demonstrating efficacy in providing long-term population level significance of PMPAs for these species, it is a first critical step in evaluating protection potential. We studied red-footed (*Sula sula*, RFBO), masked (*Sula dactylatra*, MABO), and brown (*Sula leucogaster*, BRBO) boobies because they breed sympatrically, are known to partition habitat (Anderson and Ricklefs, 1987; Young et al., 2010a; Kappes et al., 2011), and vary greatly in body size, foraging parameters (Young et al., 2010a; Kappes et al., 2011), and energetic costs of flight (Table 2 in Maxwell and Morgan, 2013). In many ways these sympatric boobies typify the challenges posed for protecting tropical seabirds using PMPAs, because their foraging is dynamic, with large variation on daily, seasonal, and annual scales (Weimerskirch et al., 2005; Young et al., 2010b). Tropical and

sub-tropical boobies rely on SPFF foraging behaviors yet their habitat has a higher likelihood of being effectively protected by PMPAs because their foraging ranges are relatively small for tropical seabirds (Maxwell and Morgan, 2013). Although no tropical sulids are currently considered threatened or endangered, all species are of moderate conservation concern in some regions; globally populations of all species are declining (Croxall et al., 2012) and changes in climate combined with changes in the abundance of subsurface predators due to fishing pressure may be threats to the long term viability of tropical seabird populations (Maxwell and Morgan, 2013).

The primary goal of our study was to evaluate how effectively these two PMPAs cover foraging habitat of the three tropical seabird species studied. We thus (1) characterize foraging patterns of these seabirds during the breeding cycle, and identify the importance of species, sex and other factors that influence the variation in their habitat use, (2) delineate important habitats for each species and site by examining correlations with bathymetry, and (3) quantify the extent to which the PMPAs encapsulate foraging habitat for these seabirds among species and sites.

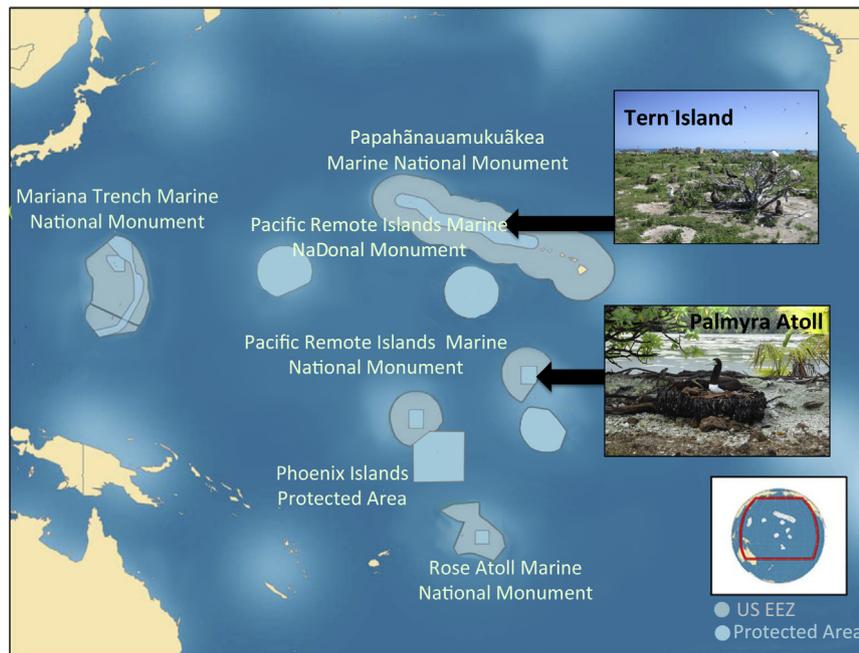
## 2. Methods

### 2.1. Study sites

Work for this project was conducted at two localities: (1) Palmyra Atoll in the Line Islands chain in PRIMNM (5°52'N, 162°04'W), and (2) Tern Island in French Frigate Shoals in PMNM (23°52'N, 166°17'W). Each monument varies substantially in both size and shape (Fig. 1); the PRIMNM monument is composed of a series of square monuments each focused around a single islet while the PMNM monument is a single polygon stretching across an island chain. However, the shortest distance between the colony and the National Monument boundary is similar at both of these sites (95 km at Palmyra, and 97 km at Tern Island). Surface waters at both sites is relatively warm (>25 °C at Palmyra Atoll and >20 °C at Tern Island and) and oligotrophic (<0.2 mg m<sup>-3</sup> at Palmyra and <0.3 mg m<sup>-3</sup> at Tern), but with significant latitudinal differences among sites. Palmyra Atoll is situated on the boundary of the Intertropical Convergence Zone and Tern Island is located in the center of the North Pacific Subtropical Gyre. While boobies nest year round at Palmyra, at the higher latitudes of Tern Island, the birds show more seasonality with defined breeding phenologies that occur between March and June. Population estimates for nesting sulids at Palmyra are between 200 and 600 for BRBO, between 8000 and 25,000 for RFBO, and approximately 50 for MABO (Depkin, 2002, Young unpublished data). At Tern, the estimates are between 3000 and 5000 nesting pairs for RFBO and approximately 200 for MABO (Hartzell et al., 2012).

### 2.2. Field work

Tracking spanned five years total (2007–2012) and included 140 birds, with multiple years of data for each species and each site (Palmyra tracks from 2007, 2008, and 2010; Tern tracks from 2009, 2010, 2012). All individuals were captured at their nests at dawn or dusk. Birds were equipped with a GPS logger on first capture (either Technosmart GiPSY-2 logger, E&O Technologies MiniGPSlog, or an iGotU GT-120, Mobile Action Technology Inc.). Total mass of loggers and attachment materials varied from ~18 g to about ~25 g based on tag type, which represented between 0.1% and 2.3% of bird body mass depending on the species and logger type used. Tags were encapsulated in waterproof plastic, and then attached to 3–4 central tail feathers using TESA cloth tape. Loggers recorded GPS positions every 10–60 s (depending on tag type) with



**Fig. 1.** The two study sites, Palmyra Atoll and Tern Island are located within two of the largest pelagic marine protected areas in the world, the Papahānaumokuākea Marine National Monument and the Pacific Remote Islands Marine National Monument. These two monuments are also situated within a complex of large Pelagic Marine Protected Areas in the central Pacific including the Marianas Trench Marine National Monument, the Rose Atoll Marine National Monument, and the Phoenix Island Protected Area. This refuge complex provides habitat to many millions of seabirds including multiple species of sulids. Figure is modified with permission from NOAA Fisheries Pacific Islands Region.

**Table 1**  
Foraging parameters by species and site.

Site	Species	# Tracks	Individuals (male/female)	Nest status (egg/chick)	Time at sea (min)	Max Range (km)	Distance travelled (km)	Average speed (km/h)	Average size of individual core (50% gridded UD (km <sup>2</sup> ))	Average area of individual minimum convex polygon (km <sup>2</sup> )
Palmyra	BRBO	30	9 (5/4)	6/3	219.8 ± 143.5	37.3 ± 19.6	98.5 ± 52.9	32.9 ± 3.1	274.5 ± 197.3	610 ± 1011
Palmyra	MABO	55	22 (9/13)	8/14	194.7 ± 134.9	33.6 ± 14.0	93.7 ± 39.1	36.8 ± 6.2	164.0 ± 90.7	171 ± 204
Tern	MABO	49	44 (22/22)	44/0	427.7 ± 224.8	84.1 ± 48.9	239.0 ± 127.8	41.6 ± 5.5	229.3 ± 134.0	1133 ± 1328
Palmyra	RFBO	49	34 (19/15)	32/2	470.9 ± 295.9	61.0 ± 45.5	182.6 ± 127.8	30.9 ± 5.7	233.3 ± 161.1	1563 ± 2604
Tern	RFBO	33	31 (16/15)	29/2	808.8 ± 373.9	104.5 ± 42.2	323.0 ± 141.1	33.5 ± 4.5	286.6 ± 131.0	2126 ± 2016
Total		216	140 (71/69)	119/21						

a spatial accuracy of 3–20 m depending on tag type. Tags were typically recovered within 24–72 h after initial deployment. Both nest status (egg or chick) and sex were recorded for each nest. In total, we analyzed 30 tracks from BRBOs (9 birds), 82 tracks from RFBOs (65 birds) and 104 tracks from MABOs (66 birds; see Table 1 for breakdown by species, site, year). Only complete tracks were used. For each species and site, the number of tracks was similar among sexes (Table 1). Most (>80%) individuals of every species were incubating eggs, with the remainder rearing small chicks. Upon recapture, approximately 1 mL of blood was collected from a brachial vessel using aseptic methods. For RFBOs in particular, which can be difficult to sex externally and by morphometrics, blood samples were used to confirm field sex identification for a subset of individuals (Young et al., 2010b).

### 2.3. Track analyses

As foraging strategies of all three species is dominated by plunge diving, we were able to estimate foraging activity by finding locations along the track where travel speeds dropped below 5 km hr<sup>-1</sup> – speeds that indicate time on water either during or after a plunge (Weimerskirch et al., 2005; Young et al., 2010b; Zavalaga et al., 2010). All trips less than 1 km from the nest were excluded from

analyses and all departure and return times were based on travel outside the 1 km buffer. Trip duration was measured as the total hours away from the colony, and trip distance as the total distance travelled by a bird while away from the colony. Travel rate was estimated as the distance flown per unit time. Maximum range from the colony was calculated as the distance of the farthest location travelled by a bird from its nest during a single trip to sea. To estimate at-sea activity, we also calculated the total time, total distance travelled, and number of landings made both inside and outside monument waters at each site. All analyses were determined with custom routines created in MATLAB (The Mathworks, Natick, MA).

### 2.4. Spatial analyses

We used three different techniques to measure various aspects of habitat utilization. First, total home range of each individual was calculated using a minimum convex polygon (MCP) function (*convhull*) in MATLAB (The Mathworks, Natick, MA). The MCP encompasses the total area (in km<sup>2</sup>) covered while at sea by each individual or for all individuals combined of a species at each site. This technique is commonly used in other studies, allowing for easy comparison among studies, and is a conservative estimate

of home range as it encompasses the minimum convex hull around all points (Kernohan et al., 2001).

Second, to delineate important individual habitat (individual core area) from total habitat covered (i.e. MCP), and as a more conservative estimate of home range, we used a gridded utilization distribution (gridded UD) technique (Maxwell et al., 2011). This measurement is based on the relative frequency of occurrence by individuals to a specific cell of a given spatial size (SI Fig. 1) (Keating and Cherry, 2009). The gridded UD approach allows for more refined discrimination of animal habitat use by reducing oversmoothing of data that is common with other techniques (Fieberg, 2007) allowing for robust comparison between home range size and core areas for individual birds (Maxwell et al., 2011). Following Maxwell et al. (2011), we used a grid cell size of  $0.1^\circ$ , and defined core areas as utilization distributions of 50% or less (denoted as 'core gridded UD' from here forward; Maxwell et al., 2011). The core gridded UD (50% UD) was calculated for each individual.

Finally, we also calculated utilization distribution for all birds of each species from each colony using the fixed kernel density (KD) estimation that is part of the adehabitat HR package in R (number of grid intervals = 150, cell size =  $0.0115^\circ$ , bandwidth =  $0.03^\circ$ ) to visualize the overall home range for each species (Silverman, 1986; Kernohan et al., 2001; Calenge, 2007). Kernel density home ranges were used to determine the overall UD (95% or 'full kernel UD') and the core UD (50% or 'core kernel UD') within the PMPAs for the entire tagged population for each species. Kernel density approaches offer the advantages of being widely used, and capable of identifying population-level core habitat areas.

For both MCP and kernel UD, we estimated the overlaps of each species home range with their respective PMPA to determine area ( $\text{km}^2$ ) coverage inside and outside protected waters. The percent area covered by monument waters was determined by subtracting the total area outside a PMPA and dividing the remainder by the total area of the MCP or kernel UD that overlapped the PMPA. These analyses were determined using functions in MATLAB or R, respectively.

## 2.5. Bathymetry

To characterize differences in habitat type utilized by each species, the bathymetry underlying each track was obtained for all tracks using xtractomatic (<http://coastwatch.pfel.noaa.gov/xtracto>) sourced from ETOPO2 bathymetric relief (U.S. National Geophysical Data Center, 2006). Bathymetry was separated for transiting and foraging locations for each species at each location.

## 2.6. Statistical analyses

To test for differences in foraging parameters (time at sea, distance travelled, max range, landing rates, and average travel speed) among species and sites, we used linear mixed effect models. Individual bird identity was used as a random factor and species and site (nested within species) were fixed factors. For time at sea, distance travelled, and maximum range travelled, we  $\log_{10}$  transformed response variables prior to analysis to meet assumptions

of normality. Prior to mixed model analyses, we tested the effects of nest status (egg vs. chick), sex (within species), and year (within species, for RFBO and MABO only) for each site; because we found no significant effects for any of these parameters (as in previous analysis (Young et al., 2010b)) these parameters were not included in final mixed effects models. To test for differences in habitat usage between species and site, individual level home range, (MCP) and core gridded UD areas (50% UD) were used in a mixed effects model approach identical as described above, except there was no random effect of individual as data was calculated on a per bird (rather than per trip) basis. For analysis of the number of trips taken outside monument boundaries, we used multiple chi square tests to look for effects of species, site, and species within the site. We used a Bonferonni corrected alpha of 0.01 to address concerns of Type II error from multiple tests. For the subset of trips ( $n = 27$ ) that were conducted outside of the PMPAs we used generalized linear models with a negative binomial distribution to examine the effects of species and site (within species) on the proportion of time, distance, and landings conducted outside of monument waters. Because only one individual conducted multiple trips (two) outside of the monument, that individual was not included as a random factor.

We examined differences in bathymetric habitat across species at each location, using Welch's *t*-tests to account for unequal variances. Due to autocorrelation between points along the track increasing the likelihood of Type I error, we determined the effective sample size for bathymetry across foraging and transiting for species by using the correlation coefficient (first order autocorrelation model) to adjust for sample size following (Dawdy and Matalas, 1964).

All figures and tables depict untransformed data unless otherwise noted. Statistical analyses were performed in JMP 11 (SAS Institute) and R.v.2.14.2 (R Development Core Team, 2012).

## 3. Results

### 3.1. Variation in seabird foraging parameters

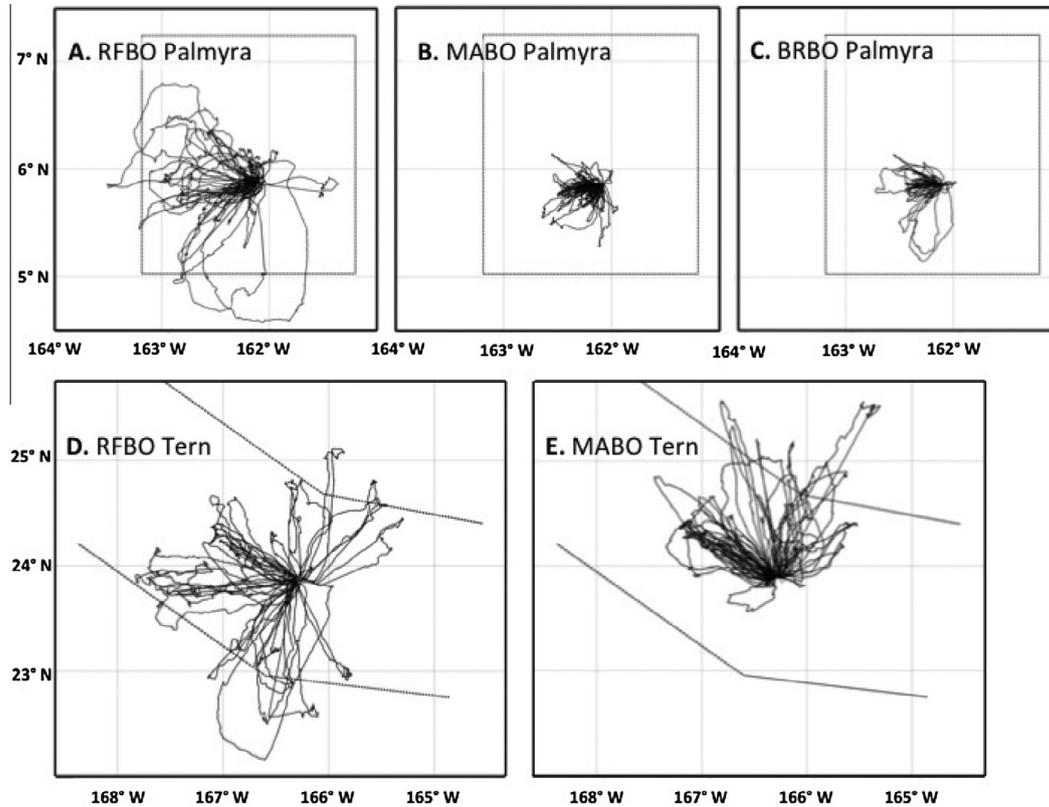
We recorded a total of 216 complete trips, with an average of 1.5 trips per bird (Table 1).

Foraging parameters varied dramatically among species and sites (Tables 1 and 2, Fig. 2). For all four parameters examined (time at sea, distance travelled, max range, and average travel speed), there were significant overall differences by both species and site (Table 2). BRBOs had shorter foraging trips compared to RFBOs, but no significant differences in average travel speed. MABOs had overall faster travelling speed than RFBOs, but no significant differences in travel duration, distance, or range. For the two species that occurred at both sites (MABO and RFBO), there were significant species-specific differences in foraging behavior between sites. Both species ranged further (155% for MABO, and 77% for RFBO), travelled faster (13% for MABO and 8% for RFBO), and spent longer times at sea (119% for MABO, and 72% for RFBO) at Tern Island than at Palmyra Atoll. The area of each minimum convex polygon varied by species and site (Fig. 3). At both sites, RFBO had the largest individual home range areas (using individual MCPs), with MABO having smaller MCPs and BRBOs (at Palmyra

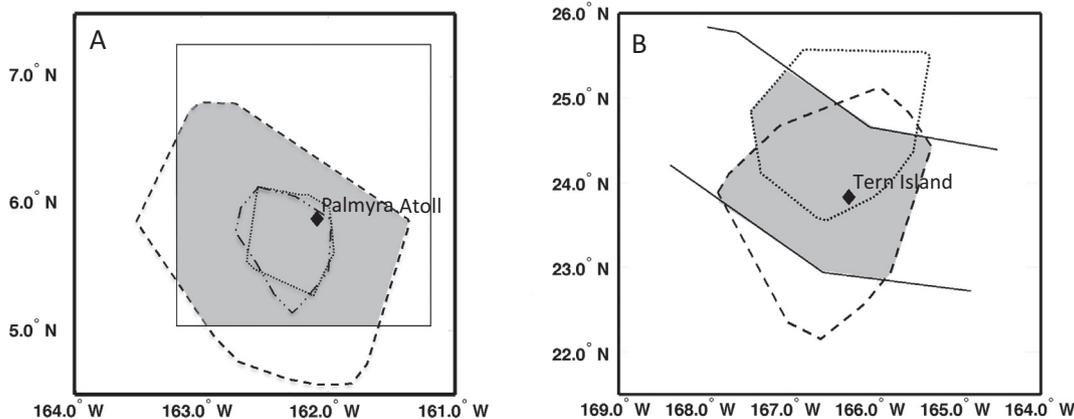
**Table 2**

Effects of species and site (within species) on foraging parameter (parameter coefficient  $\pm$  SD provided). All response variables, except average speed are log transformed prior to model analysis to meet assumptions of normality. For species comparisons, RFBO and BRBO are compared to MABO, the largest of the three species.

	Species	Site [species]	Species [RFBO]	Species [BRBO]	Site (MABO)	Site (RFBO)
Time at Sea (min)	19.1 ( $P < 0.001$ )	14.6 ( $P \ll 0.001$ )	$0.26 \pm 0.05$ ( $P < 0.001$ )	$-0.19 \pm 0.06$ ( $P < 0.010$ )	$-0.14 \pm 0.04$ ( $P < 0.010$ )	$-0.31 \pm 0.10$ ( $P \ll 0.001$ )
Distance travelled (km)	13.1 ( $P \ll 0.001$ )	21.8 ( $P \ll 0.001$ )	$0.44 \pm 0.09$ ( $P < 0.001$ )	$-0.44 \pm 0.12$ ( $P < 0.001$ )	$-0.42 \pm 0.08$ ( $P \ll 0.001$ )	$-0.34 \pm 0.08$ ( $P \ll 0.001$ )
Maximum Range (km)	7.8 ( $P < 0.001$ )	19.8 ( $P \ll 0.001$ )	$0.15 \pm 0.04$ ( $P < 0.001$ )	$-0.15 \pm 0.04$ ( $P = 0.010$ )	$-0.17 \pm 0.04$ ( $P \ll 0.001$ )	$-0.15 \pm 0.04$ ( $P \ll 0.001$ )
Average speed (km/hr)	27.9 ( $P \ll 0.001$ )	9.5 ( $P \ll 0.001$ )	$-2.28 \pm 0.68$ ( $P < 0.010$ )	$-1.91 \pm 1.01$ ( $P = 0.060$ )	$-2.44 \pm 0.62$ ( $P \ll 0.001$ )	$-1.21 \pm 0.65$ ( $P = 0.070$ )
Area of MCP ( $\text{km}^2$ )	9.7 ( $P < 0.001$ )	11.8 ( $P \ll 0.001$ )	$-0.38 \pm 0.20$ ( $P = 0.070$ )	$-0.44 \pm 0.30$ ( $P = 0.140$ )	$-0.78 \pm 0.20$ ( $P < 0.001$ )	$-0.57 \pm 0.21$ ( $P < 0.010$ )



**Fig. 2.** All tracks for each species tracked at both Palmyra Atoll (A – RFBO, B – MABO, C = BRBO) and Tern Island (D – RFBO, E – MABO). Monument boundaries are shown in dotted gray line. Scale is identical on all panels.



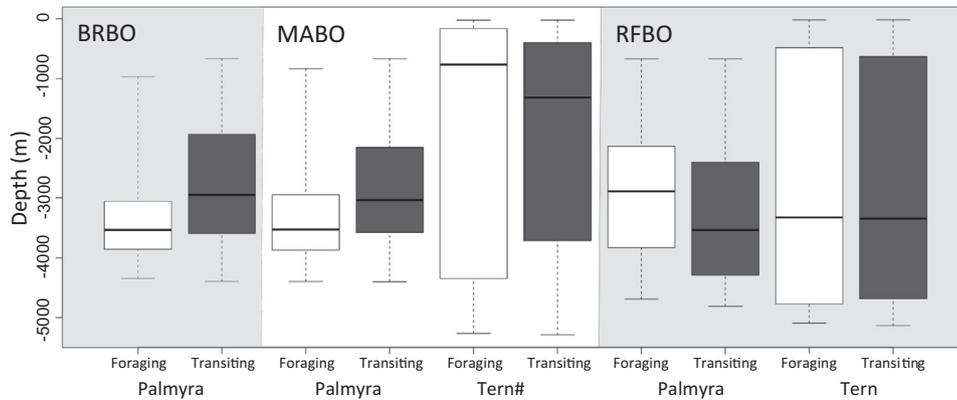
**Fig. 3.** Minimum convex polygons (MCP) for all species at (A) Palmyra Atoll and (B) Tern Island. National Monument boundaries are shown in solid black line in each panel. Species specific polygons are delimited by dashed lines for RFBO, dotted lines for MABO, and dash-dot lines (BRBO, Palmyra only). Overlap between minimum convex polygons and PMPA boundaries are shaded in light grey. Absolute area of polygons for Palmyra and Tern, respectively, are as follows: 5854 km<sup>2</sup> for BRBO (Palmyra only); 5311 km<sup>2</sup> and 35,595 km<sup>2</sup> for MABO; 37,789 km<sup>2</sup> and 52,089 km<sup>2</sup> for RFBO; and 53,927 km<sup>2</sup> and 36,1584 km<sup>2</sup> for all species combined.

only) having intermediate MCP areas (Table 1). The magnitude of the differences in MCP between MABO and RFBO was greater (813%) at Palmyra than at Tern (89%). Individual core gridded UD areas (50% UDs) also varied significantly among species, and were marginally significantly different between sites (within species); however, these differences were less pronounced and slightly different from home ranges estimated using MCP (Tables 1 and 2, SI Fig. 1). At Palmyra, BRBOs had the largest core gridded UD areas, followed by RFBOs, then MABOs. A similar pattern was seen at Tern with RFBOs having slightly larger core gridded UD areas than MABOs (Table 1). Core gridded UD areas at Palmyra were 29% and 19% smaller than those at Tern for MABOs and RFBOs respec-

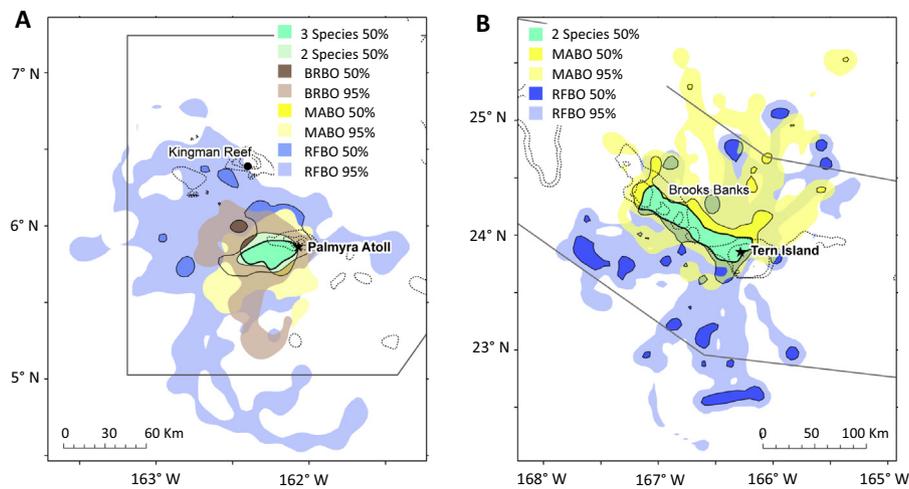
tively. For no species did we observe a significant effect of sex, year, or nesting status on any foraging parameters within a site.

### 3.2. Bathymetry

Bathymetry underlying the habitats used by birds varied considerably between sites (Fig. 4), particularly because Tern Island is adjacent to Brooks Banks, a high use area for both RFBO and MABO (Fig. 5). Bathymetry was significantly different between foraging and transiting segments, (Welch's *t*-tests, all  $p < 0.001$ ; BRBO Palmyra,  $t_{3555} = 25.7$ ; MABO Palmyra  $t_{10900} = -31.9$ ; RFBO Palmyra,  $t_{20309} = 27.3$ ; MABO Tern,  $t_{3660} = 3.45$ ; RFBO Tern,  $t_{20252} = -2.50$ ),



**Fig. 4.** Bathymetric depth of locations where foraging and transiting occurred for all species across all sites. After sample size adjustments differences between foraging and transiting were significant for all species at all sites.



**Fig. 5.** Kernel density utilization distribution maps for Tern Island (A) and Palmyra Atoll (B). Colony location, and the location of major subsurface features (Kingman Reef and Brooks Banks) are both noted. Percentages indicate the percent of kernel UD, either full (95%) or core (50%) kernel UD.

**Table 3**  
Proportion of foraging parameters outside of monument for all species combined (site population level).

Site	Species	Trips outside/total trips	% Time outside	% Landings outside	% Distance outside	% MCP outside	% Core kernel UD outside
Palmyra	BRBO	0/30	0	0	0	0	0
Palmyra	MABO	0/55	0	0	0	0	0
Tern	MABO	7/39	48 ± 17	33 ± 17	74 ± 31	35.7	19.9
Palmyra	RFBO	5/39	33 ± 19	22 ± 15	51 ± 33	20.9	10
Tern	RFBO	11/33	43 ± 25	31 ± 19	61 ± 33	28.2	20.8

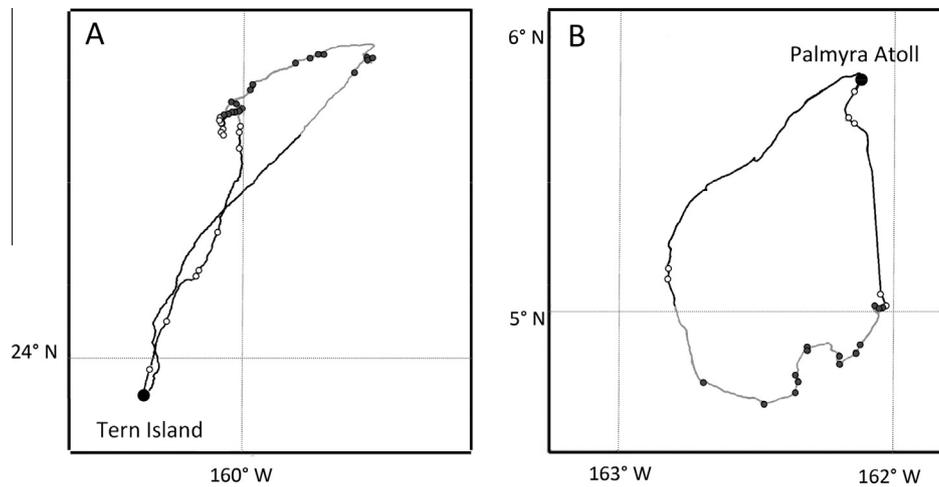
with foraging being conducted in deeper waters for all species except for RFBOs at Palmyra and MABOs at Tern, where foraging tended to occur in shallower waters, although in most cases the absolute differences in foraging and transiting were subtle (Fig. 4).

### 3.3. Seabird usage of PMPA

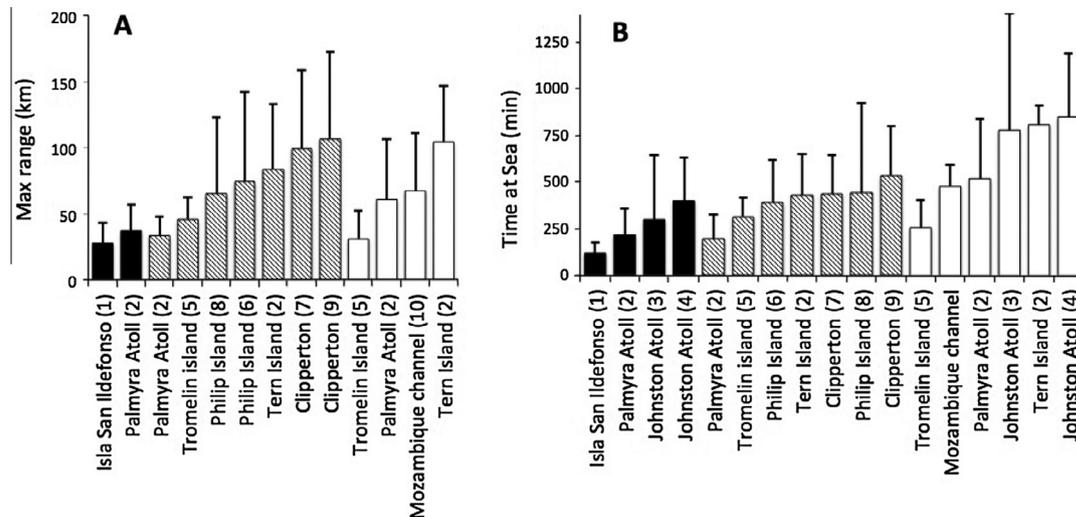
Foraging parameters, MCP, and kernel UD, all showed that all individuals of each species at each site spent the majority of their foraging effort and time inside monument waters. Only RFBOs at both sites and MABOs at Tern spent time outside the PMPAs, and the area outside of the monuments was less than 30% across both MCP and core kernel UD for each species group at the population level (Table 3). Only 13% of all trips included time spent outside the monument (Table 3). There were significant site differences ( $\chi^2 = 19.0, P \gg 0.001$ ) and overall species differences ( $\chi^2 = 14.1,$

$P < 0.001$ ) of time outside the monuments. Across sites, birds were more likely to forage outside the monument at Tern than at Palmyra, and across species, RFBOs were more likely to forage outside the monument than either MABOs or BRBOs. BRBOs and MABOs at Palmyra never travelled outside the monument (Figs. 2, 4 and 5; Table 3). Within sites, differences in time spent foraging outside the monument between species were significant ( $\chi^2 = 12.6, P < 0.01$ ) for Palmyra only. At Tern, the difference in time spent foraging outside the monument was not significant between MABO and RFBO ( $\chi^2 = 2.6, P = 0.1$ ).

However, for birds that did forage outside of the monument (26 of 140 individuals), 42% of their total duration at sea, and 64% of their total landing activity (indicative of foraging behavior) took place outside the monument (Fig. 6). Considering only those individuals that travelled outside of monument waters, there were no significant effects of species or site on the proportion of time,



**Fig. 6.** Figure 6: As seen in these two representative tracks from Tern Island (A) and Palmyra Atoll (B), while foraging outside the reserve was limited, those individuals that did forage outside the reserve used it extensively. GPS locations outside monument waters are indicated by light grey lines while those inside monument waters are in black. Foraging locations outside monument waters are in dark grey while those inside monument waters are in white.



**Fig. 7.** Comparison of foraging patterns (A – maximum range, B – time at sea) of our three focal species (black bars BRBO, hatched bars MABO, white bars RFBO) across sites, highlights the strong spatial variation in foraging ecology often observed within a species. We include all studies known to us with >5 birds per species, and use species averages per site. When multiple studies used subsets of the same data as other studies, we use data from the study with the larger sample size. Data from (1) Weimerskirch et al. (2009b), (2) Young et al., this study, (3) Lewis et al. (2005), (4) Lewis et al. (2004), (5) Kappes et al. (2011), (6) Sommerfeld et al. (2013b), (7) Weimerskirch et al. (2009b), (8) Sommerfeld et al. (2013a), (9) Weimerskirch et al. (2008), (10) Weimerskirch et al. (2006).

distance, or landings conducted outside as compared to inside the monument.

#### 4. Discussion

Despite the fact that the pelagic realm is the largest habitat on the planet, and contributes more than half of the Earth's net productivity, explicit protection of this ecosystem is minimal (Field et al., 1998; Pauly et al., 2002; Game et al., 2009). Best estimates indicate that 2% of the pelagic environment is included within any type of protected area (McCauley et al., in press), and some argue that protecting adequate discrete pelagic environments is likely to be both biologically inappropriate and politically infeasible (Angel, 1993; Boersma and Parrish, 1999). Biologically, the argument is that many pelagic species, particularly predators and including many seabirds, are extremely vagile (Block et al., 2005, 2011); furthermore the physical features of pelagic environments are often variable and unpredictable (Martell et al., 2005). The sug-

gestion is that PMPAs will thus be unlikely to be able to contain relevant habitat as effectively as do their coastal MPA counterparts without being exorbitantly large (Hyrenbach et al., 2000). However, a counter argument has been that many marine species are most vulnerable during certain life history stages, notably during breeding periods (Maxwell et al., 2011), when movements are constrained by the need to attend to eggs or young. Thus even if PMPAs provide habitat conservation for that period only, they still may serve a vital role in species conservation, reinforcing the need for studies measuring population level impacts of PMPAs on mobile species. Politically, a primary argument against PMPAs has been the fact that to protect entire habitats or critical areas, many PMPAs would extend beyond the EEZ of a country (Game et al., 2009). However, as 35% of all pelagic systems are within national boundaries (Norse, 2005) there seems to be strong possibilities for PMPAs to provide substantial conservation within those systems.

Working within two of the world's largest PMPAs, we were able to evaluate the extent to which these reserves contain relevant

foraging habitat for three seabird species in the tropical Pacific during the vulnerable breeding period. Based on 216 individual trips, we quantified extensive variation in the foraging ecology of three seabird species at two sites. Yet, despite this variability, we found strong evidence that both PMPAs effectively contained the vast majority of foraging habitat utilized by three sympatric species during their incubation and early chick rearing periods.

#### 4.1. Differences among species and sites in foraging behavior and monument efficacy

The differences in foraging behavior among species, and the ultimate implications for the efficacy of PMPAs in protecting habitat, were largely consistent with *a priori* expectations based on results from other studies. Previous research using both isotopic signatures and tracking methods documented significant niche partitioning among tropical sulid species (Kai et al., 2009; Weimerskirch et al., 2009; Young et al., 2010a,b; Kappes et al., 2011). Consistent with previous studies, smaller sulid species foraged significantly farther from their nesting areas, travelled at slower rates, and spent more total time at sea (likely due to differences in energetic costs of flight, although direct competitive exclusion by larger species may also factor in) (Young et al., 2010b). Within species, we observed profound differences in foraging behavior across sites. For example, RFBO and MABO foraged farther, faster, and for longer durations around Tern Island than at Palmyra Atoll. Comparisons of foraging behavior of these same species across other studies demonstrate that there is extensive range in foraging behavior among sites and species (Fig. 7). Many explanations for the source of this variation have been proposed including variation in oceanic productivity, density of conspecifics, presence of oceanographic features, and number of species in an area (Grémillet et al., 2004; Davies et al., 2013; Harding et al., 2013). Understanding drivers of such variation will be critical in allowing for effective design of PMPAs in the future. In this case, we suggest that variation in bathymetry may be part of the explanation; boobies foraging around Tern Island may seek out distinct bathymetric features because they increase productivity or entrain prey through oceanographic features created from bathymetric variability (e.g., Bograd et al., 1997; Maxwell et al., 2012). For example, MABO travelled to and foraged in much shallower waters at Tern compared to Palmyra, focusing most of their foraging effort in the Brooks Banks area (Fig. 5). RFBO showed similar affinity for this foraging area (Fig. 5), but also foraged farther from Tern. Regardless of bathymetry, however, at both sites only 13% of trips by the birds tracked extended beyond the PMPAs, though some differences between the sites occurred. The core kernel UD area among all three species at Palmyra was within PRIMNM, and less than 20% was outside PNMN for the two species at Tern (Table 3). Given that bird foraging varied by site, with birds travelling much farther, faster, and longer at Tern than at Palmyra, it is not surprising that PMPAs contained greater bird habitat at Palmyra than Tern. Nearly twice as large an area is needed at Tern, compared to Palmyra, in order to protect the full extent of foraging habitat identified. Whereas both monuments covered the majority of the birds' core habitat, the PRIMNM monument at Palmyra was actually larger than needed for all three species, whereas PNMN, despite its similar distance to the edge of monument, was operating at the edge of needed scale for these species.

#### 4.2. Conclusions, applications, and future research directions

Our results suggest strong potential of PMPAs for protecting relevant habitat for at least some tropical pelagic species. In this study, we find the critical breeding habitat of all three focal sulid species appears to be well contained within the studied PMPAs. However, as previously noted, these PMPAs are some of the largest

in the world, and these species are, among tropical pelagic foraging seabirds, likely to have some of the smallest foraging home range requirements when breeding. Thus, these are likely best case scenarios for tropical PMPAs. Although the vast majority of birds tracked were in a single breeding stage, incubation, it represents the breeding stage where sulid species make the longest and farthest foraging trips (Lormee et al., 2005; Weimerskirch et al., 2005), so our work is a conservative estimate of the efficacy of the PMPA for these species across the breeding season. The chick-brood is the most energetically-demanding stage for most breeding seabirds and adults foraging during this stage are likely to be even more protected than the incubating birds of our study. Though it is unclear how far sulid species range during the non-breeding season, most birds roost on the colony overnight throughout the year, suggesting their range may not be greater than during the breeding season.

Still, the efficacy of these PMPAs in covering relevant habitat for more vagile central place foragers is still an outstanding question. The sulid species studied here are unlikely to serve as effective "umbrella" species that can be expected to reasonably approximate the efficacy of the monument for other seabirds (Louzao et al., 2006; Pichegru et al., 2012). Not only do these species likely represent some of the shortest distance foragers, they all have very similar foraging strategies (flock foraging, plunge divers, likely heavily reliant on subsurface foragers) (Spear et al., 2007). A multi-species, multi-guild approach, ideally incorporating temporal variability, will be critical to gather a more robust sense of the full efficacy of these PMPAs (Montevecchi et al., 2012; Thaxter et al., 2012; Maxwell et al., 2013). PMPAs for more vagile species may still require alternative approaches, such as dynamic MPAs, or dynamic management approaches that allow for specific threats to be mitigated over larger space and time scales that better match species movements (Howell et al., 2008; Game et al., 2009; Hobday et al., 2014).

Notably, we evaluated only the efficacy of the PMPAs in covering the foraging area of these birds, not the efficacy of the PMPAs in protecting the species or interactions needed to sustain these birds. If PMPAs are poorly enforced, or are inadequate for sustaining robust populations of prey or subsurface predators, this habitat protection may still be insufficient. Our work was also temporarily constrained to a relatively short period of time during which no major El Niño Oscillations occurred. As ocean ecosystems change, due to both changing global temperatures and predicted net declines in large epipelagic predator populations, the habitat needs of these seabirds may well also change (Hazen et al., 2012; Dueri et al., 2014). Ongoing monitoring to examine inter-annual variation in extent of foraging outside of monuments, and work tying foraging ecology to reproductive success under different climatic conditions will allow us to understand how effective these monuments will be as oceans change.

Our results also document strong within species variation in seabird foraging behavior. Unfortunately synthetic analyses across sites, examining drivers of variation in foraging ecology across sites remains limited. Such comparative work would allow us to better identify the biotic and abiotic features that lead to foraging hot-spots, and to variation in foraging ecology within a species. This in turn could lead to more effective methods to identify pelagic areas for protection. Such integrative work across multiple species has proven highly fruitful (Block et al., 2011; Maxwell et al., 2013), and we suggest that within species analyses may be equally productive. Without such data, managers and policy makers will remain dependent on time consuming, site-by-site and species-by-species analysis of seabird foraging behavior, to make effective reserve design decisions.

Despite these limitations, this work does demonstrate the potential of fixed PMPAs to protect relevant habitat for tropical

pelagic species, during critical life history periods, even in the unpredictable and patchy nature of tropical foraging environment. Such demonstrations of the efficacy of PMPAs for seabirds and other large pelagic animals will be critical to arguing for the value of such protected areas more broadly.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.10.027>.

## References

- Agardy, T., Di Sciara, G.N., Christie, P., 2011. Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Mar. Policy* 35, 226–232.
- Alpine, J., Hobday, A., 2007. Area requirements and pelagic protected areas: is size an impediment to implementation? *Mar. Freshwater Res.* 58, 558–569.
- Anderson, D.J., Ricklefs, R.E., 1987. Radio-tracking masked and blue-footed boobies (*Sula* spp.) in the Galapagos Islands. *Nat. Geog. Res.* 3, 152–163.
- Angel, M.V., 1993. Biodiversity of the pelagic ocean. *Conserv. Biol.* 7, 760–772.
- Ashmole, N., Ashmole, M., 1967. Comparative feeding ecology of sea bird of a tropical oceanic island. *Peabody Museum Nat. Hist. Bull.* 24, 1–131.
- Au, D.W., Pitman, R.L., 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. *Condor* 88, 304–317.
- Ballard, G., Jongsomjit, D., Veloz, S.D., Ainley, D.G., 2012. Coexistence of mesopredators in an intact polar ocean ecosystem: the basis for defining a Ross Sea marine protected area. *Biol. Conserv.* 156, 72–82.
- Block, B.A., Teo, S.L., Walli, A., Boustany, A., Stokesbury, M.J., Farwell, C.J., Weng, K.C., Dewar, H., Williams, T.D., 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* 434, 1121–1127.
- Block, B.A., Jonsen, I., Jorgensen, S., Winship, A., Shaffer, S.A., Bograd, S., Hazen, E., Foley, D., Breed, G., Harrison, A.-L., 2011. Tracking apex marine predator movements in a dynamic ocean. *Nature* 475, 86–90.
- Boersma, P.D., Parrish, J.K., 1999. Limiting abuse: marine protected areas, a limited solution. *Ecol. Econ.* 31, 287–304.
- Bograd, S.J., Rabinovich, A.B., LeBlond, P.H., Shore, J.A., 1997. Observations of seamount-attached eddies in the north Pacific. *J. Geophys. Res.–Oceans* 102, 12441–12456.
- Calenge, C., 2007. Exploring habitat selection by wildlife with adehabitat. *J. Stat. Softw.* 22, 1–19.
- Cox, S.P., Martell, S.J., Walters, C.J., Essington, T.E., Kitchell, J.F., Boggs, C., Kaplan, I., 2002. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. I. Estimating population biomass and recruitment of tunas and billfishes. *Can. J. Fish. Aquat. Sci.* 59, 1724–1735.
- Croxall, J.P., Butchart, S.H., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A., Taylor, P., 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv. Int.* 22, 1–34.
- Davies, R.D., Wanless, S., Lewis, S., Hamer, K.C., 2013. Density-dependent foraging and colony growth in a pelagic seabird species under varying environmental conditions. *Mar. Ecol. Prog. Ser.* 485, 287–294.
- Dawdy, D.R., Matalas, N.C., 1964. Statistical and probability analysis of hydrologic data, part III: analysis of variance, covariance and time series. In: Chow, V.T. (Ed.), *Handbook of Applied Hydrology, A Compendium of Water-resources Technology*. McGraw-Hill Book Company, New York, pp. 868–890.
- Depkin, C.D., 2002. Trip report to Palmyra Atoll, 06 August 2001–07. October 2002. U.S. Fish and Wildlife Service, Honolulu, Hawai'i.
- Dueri, S., Bopp, L., Maury, O., 2014. Projecting the impacts of climate change on skipjack tuna abundance and spatial distribution. *Global Change Biol.* 20, 742–753.
- Federal Register, 2006. Presidential Proclamation 8031 of June 15, 2006: Establishment of the Northwestern Hawaiian Islands Marine National Monument. pp. 36443–36475. US Federal Register.
- Federal Register, 2009. Establishment of the Pacific Remote Islands Marine National Monument, Presidential Proclamation 8336. pp. 1565–1575. US Federal Register.
- Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R., Lotze, H.K., 2010. Patterns and ecosystem consequences of shark declines in the ocean. *Ecol. Lett.* 13, 1055–1071.
- Fieberg, J., 2007. Utilization distribution estimation using weighted kernel density estimators. *J. Wildlife Manage.* 71, 1669–1675.
- Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281, 237–240.
- Gaines, S.D., Lester, S.E., Grorud-Colver, K., Costello, C., Pollnac, R., 2010. Evolving science of marine reserves: new developments and emerging research frontiers. *Proc. Natl. Acad. Sci.* 107, 18251–18255.
- Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H.P., Richardson, A.J., 2009. Pelagic protected areas: the missing dimension in ocean conservation. *Trends Ecol. Evol.* 24, 360–369.
- Garthe, S., Markones, N., Mendel, B., Sonntag, N., Krause, J.C., 2012. Protected areas for seabirds in German offshore waters: designation, retrospective consideration and current perspectives. *Biol. Conserv.* 156, 126–135.
- Grémillet, D., Dell'Omo, G., Ryan, P.G., Peters, G., Ropert-Coudert, Y., Weeks, S.J., 2004. Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Mar. Ecol. Prog. Ser.* 268, 265–279.
- Harding, A., Paredes, R., Suryan, R., Roby, D., Irons, D., Orben, R., Renner, H., Young, R., Barger, C., Dorresteijn, I., 2013. Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. *Deep Sea Res. Part II: Topical Stud. Oceanogr.* 94, 178–191.
- Harrison, C.S., Hida, T.S., Seki, M.P., 1983. Hawaiian seabird feeding ecology. *Wildlife Monogr.* 85, 3–71.
- Hartzell, P.L., Youngren, S.M., Rapp, D.C., 2012. Biological status and trends, terrestrial component at French Frigate Shoals, Northwestern Hawaiian Islands (1986–2011). Technical Report, Honolulu, Hawaii.
- Hazen, E.L., Jorgensen, S.J., Rykaczewski, R., Bograd, S.J., Foley, D.G., Jonsen, I.D., Shaffer, S.A., Dunne, J., Costa, D.P., Crowder, L.B., Block, B.A., 2012. Predicted habitat shifts of Pacific top predators in a changing climate. *Nat. Climate Change* 3, 234–238.
- Hobday, A.J., Maxwell, S.M., Forgie, J., McDonald, J., Darby, M., Seto, K., Bailey, H., Bograd, S.J., Briscoe, D.K., Costa, D.P., Crowder, L.B., Dunn, D.C., Fossette, S., Halpin, P.N., Hartog, J.R., Hazen, E.L., Lascelles, B.G., Lewison, R.L., Poulos, G., Powers, A., 2014. Dynamic ocean management: integrating scientific and technological capacity with law, policy and management. *Stanford Environ. Law J.* 33, 125–165.
- Hooker, S.K., Cañadas, A., Hyrenbach, K.D., Corrigan, C., Polovina, J.J., Reeves, R.R., 2011. Making protected area networks effective for marine top predators. *Endangered Species Res.* 13, 203–218.
- Howell, E., Kobayashi, D., Parker, D., Balazs, G., 2008. TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endangered Species Res.* 5, 267–278.
- Hyrenbach, K.D., Forney, K.A., Dayton, P., 2000. Marine protected areas and ocean basin management. *Aquat. Conserv.: Mar. Freshwater Ecosyst.* 10, 437–458.
- Hyrenbach, K.D., Keiper, C., Allen, S.G., Ainley, D.G., Anderson, D.J., 2006. Use of marine sanctuaries by far-ranging predators: commuting flights to the California current system by breeding Hawaiian albatrosses. *Fish. Oceanogr.* 15, 95–103.
- Itano, D.G., Holland, K.N., 2000. Movement and vulnerability of bigeye (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) in relation to FADs and natural aggregation points. *Aquat. Living Resour.* 13, 213–223.
- Kai, E.T., Rossi, V., Sudre, J., Weimerskirch, H., Lopez, C., Hernandez-Garcia, E., Marsac, F., Garçon, V., 2009. Top marine predators track Lagrangian coherent structures. *Proc. Natl. Acad. Sci.* 106, 8245–8250.
- Kappes, M.A., Weimerskirch, H., Pinaud, D., Le Corre, M., 2011. Variability of resource partitioning in sympatric tropical boobies. *Mar. Ecol. Prog. Series* 441, 281–294.
- Keating, K.A., Cherry, S., 2009. Modeling utilization distributions in space and time. *Ecology* 90, 1971–1980.
- Kenyon, J., Maragos, J., Vroom, P., 2012. Monitoring supports establishment of Pacific Remote Islands Marine National Monument. In: *Proceedings of the 12th International Coral Reef Symposium*. pp. 9–13.
- Kernohan, B., Gitzen, R.A., Millsbaugh, J., 2001. Analysis of animal space use and movements. In: Millsbaugh, J., Marzluff, J. (Eds.), *Radio Tracking and Animal Populations*. Academic Press, San Diego, pp. 126–168.
- Langley, A., Harley, S., Hoyle, S., Davies, N., Hampton, J., Kleiber, P., 2009. Stock assessment of yellowfin tuna in the western and central Pacific Ocean. Western Central Pacific Fisheries Commission, Scientific Committee, 5th Regular Session.
- Lascelles, B.G., Langham, G.M., Ronconi, R.A., Reid, J.B., 2012. From hotspots to site protection: identifying marine protected areas for seabirds around the globe. *Biol. Conserv.* 156, 5–14.

- Le Corre, M., Cherel, Y., Lagarde, F., Lormée, H., Jouventin, P., 2003. Seasonal and inter-annual variation in the feeding ecology of a tropical oceanic seabird, the red-tailed tropicbird *Phaethon rubricauda*. *Mar. Ecol. Prog. Series* 255, 289–301.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Series* 384, 33–46.
- Lewis, S., Schreiber, E.A., Daunt, F., Schenk, G.A., Wanless, S., Hamer, K.C., 2004. Flexible foraging patterns under different time constraints in tropical boobies. *Animal Behav.* 68, 1331–1337.
- Lewis, S., Schreiber, E.A., Daunt, F., Schenk, G.A., Orr, K., Adams, A., Wanless, S., Hamer, K.C., 2005. Sex-specific foraging behaviour in tropical boobies: does size matter? *Ibis* 147, 408–414.
- Lormée, H., Barbraud, C., Chastel, O., 2005. Reversed sexual size dimorphism and parental care in the Red-footed Booby *Sula sula*. *IBIS* 147, 307–315.
- Lotze, H.K., Coll, M., Magera, A.M., Ward-Paige, C., Airolidi, L., 2011. Recovery of marine animal populations and ecosystems. *Trends Ecol. Evol.* 26, 595–605.
- Louzao, M., Hyrenbach, K.D., Arcos, J.M., Abelló, P., Sola, L.G.D., Oro, D., 2006. Oceanographic habitat of an endangered Mediterranean procellariiform: implications for marine protected areas. *Ecol. Appl.* 16, 1683–1695.
- Louzao, M., Pinaud, D., Peron, C., Delord, K., Wiegand, T., Weimerskirch, H., 2011. Conserving pelagic habitats: seascape modelling of an oceanic top predator. *J. Appl. Ecol.* 48, 121–132.
- Ludynia, K., Kemper, J., Roux, J.-P., 2012. The Namibian Islands' marine protected area: using seabird tracking data to define boundaries and assess their adequacy. *Biol. Conserv.* 156, 136–145.
- Martell, S.J., Essington, T.E., Lessard, B., Kitchell, J.F., Walters, C.J., Boggs, C.H., 2005. Interactions of productivity, predation risk, and fishing effort in the efficacy of marine protected areas for the central Pacific. *Can. J. Fish. Aquat. Sci.* 62, 1320–1336.
- Maxwell, S.M., Frank, J.J., Breed, G.A., Robinson, P.W., Simmons, S.E., Crocker, D.E., Gallo-Reynoso, J.P., Costa, D.P., 2012. Benthic foraging on seamounts: A specialized foraging behavior in a deep-diving pinniped. *Mar. Mamm. Sci.* 28, E333–E344.
- Maxwell, S.M., Morgan, L.E., 2013. Facilitated foraging of seabirds on pelagic fishes: implications for management of pelagic marine protected areas. *Mar. Ecol. Prog. Series* 481, 289–303.
- Maxwell, S.M., Breed, G.A., Nickel, B.A., Makanga-Bahouna, J., Pemo-Makaya, E., Parnell, R.J., Formia, A., Ngouesso, S., Godley, B.J., Costa, D.P., Witt, M.J., Coyne, M.S., 2011. Using satellite tracking to optimize protection of long-lived marine species: Olive Ridley sea turtle conservation in Central Africa. *PLoS ONE* 6, e19905.
- Maxwell, S.M., Hazen, E.L., Bograd, S.J., Halpern, B.S., Breed, G.A., Nickel, B., Teutscher, N.M., Crowder, L.B., Benson, S., Dutton, P.H., Bailey, H., Kappes, M.A., Kuhn, C., Weise, M.J., Mate, B., Shaffer, S.A., Hassrick, J.L., Henry, R.W., Irvine, L., McDonald, B.I., Robinson, P.W., Block, B.A., Costa, D.P., 2013. Cumulative human impacts on marine predators. *Nat. Commun.* 4, 1–9.
- Maxwell, S.M., Ban, N., Morgan, L.E., 2014. Pragmatic approaches for effective pelagic marine protected area management. *Endangered Species Res.* 26, 59–74.
- McCauley, D., Pinsky, M., Estes, J., Palumbi, S., Joyce, F., Warner, R., in press. Marine defaunation: the past, present, and future of animal loss in the global ocean. *Science*.
- Montevecchi, W., Hedd, A., McFarlane Tranquilla, L., Fifield, D., Burke, C., Regular, P., Davoren, G., Garthe, S., Robertson, G., Phillips, R., 2012. Tracking seabirds to identify ecologically important and high risk marine areas in the western North Atlantic. *Biol. Conserv.* 156, 62–71.
- Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Norse, E., 2005. Pelagic protected areas: the greatest parks challenge of the 21st century. *Parks* 15, 32–39.
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. *Nature* 418, 689–695.
- Péron, C., Grémillet, D., Prudor, A., Pettex, E., Saraux, C., Soriano-Redondo, A., Authier, M., Fort, J., 2013. Importance of coastal Marine protected areas for the conservation of pelagic seabirds: the case of Vulnerable yelkouan shearwaters in the Mediterranean Sea. *Biol. Conserv.* 168, 210–221.
- Pichegru, L., Ryan, P., van Eeden, R., Reid, T., Grémillet, D., Wanless, R., 2012. Industrial fishing, no-take zones and endangered penguins. *Biol. Conserv.* 156, 117–125.
- Polovina, J.J., Abecassis, M., Howell, E.A., Woodworth, P., 2009. Increases in the relative abundance of mid-trophic level fishes concurrent with declines in apex predators in the subtropical North Pacific, 1996–2006. *Fish. Bull.* 107, 523–531.
- R Development Core Team, 2012. R: A language and environment for statistical computing. ISBN 3-900051-07-0. R Foundation for Statistical Computing, Vienna, Austria, 2013. <<http://www.R-project.org>>.
- Ricklefs, R.E., 1990. Seabird life histories and the marine environment: some speculations. *Colonial Waterbirds* 13, 1–6.
- Rosenbaum, H.C., Maxwell, S.M., Kershaw, F., Mate, B., 2014. Long-range movement of humpback whales and their overlap with anthropogenic activity in the South Atlantic Ocean. *Conserv. Biol.* 28, 604–615.
- Sheppard, C., Ateweberhan, M., Bowen, B., Carr, P., Chen, C., Clubbe, C., Craig, M., Ebinghaus, R., Eble, J., Fitzsimmons, N., 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. *Aquat. Conserv. Mar. Freshwater Ecosyst.* 22, 232–261.
- Shillinger, G.L., Palacios, D.M., Bailey, H., Bograd, S.J., Swithenbank, A.M., Gaspar, P., Wallace, B.P., Spotila, J.R., Paladino, F.V., Piedra, R., 2008. Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biol.* 6, e171.
- Silverman, B.W., 1986. Density Estimation for Statistics and Data Analysis. CRC Press, Boca Raton FL.
- Sommerfeld, J., Kato, A., Ropert-Coudert, Y., Garthe, S., Hindell, M.A., 2013a. The individual counts: within sex differences in foraging strategies are as important as sex-specific differences in masked boobies *Sula dactylatra*. *J. Avian Biol.* 44, 531–540.
- Sommerfeld, J., Kato, A., Ropert-Coudert, Y., Garthe, S., Hindell, M.A., 2013b. Foraging parameters influencing the detection and interpretation of area-restricted search behaviour in marine predators: A case study with the masked booby. *PLoS one* 8, e63742.
- Spear, L.B., Ainley, D.G., Walker, W., 2007. Foraging dynamics of seabirds in the eastern tropical Pacific Ocean. *Stud. Avian Biol.* 35, 1–99.
- Thaxter, C.B., Lascelles, B., Sugar, K., Cook, A.S., Roos, S., Bolton, M., Langston, R.H., Burton, N.H., 2012. Seabird foraging ranges as a preliminary tool for identifying candidate marine protected areas. *Biol. Conserv.* 156, 53–61.
- U.S. National Geophysical Data Center, 2006. 2-minute Gridded Global Relief Data (ETOPO2). <<http://www.ngdc.noaa.gov/mgg/fliers/06megg01.html>>.
- Ward, P., Myers, R.A., 2005. Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology* 86, 835–847.
- Weimerskirch, H., 2007. Are seabirds foraging for unpredictable resources? *Deep Sea Res. Part II: Topical Stud. Oceanogr.* 54, 211–223.
- Weimerskirch, H., Le Corre, M., Jaquemet, S., Marsac, F., 2005. Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. *Mar. Ecol. Prog. Series* 288, 251–261.
- Weimerskirch, H., Le Corre, M., Ropert-Coudert, Y., Kato, A., Marsac, F., 2006. Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: the red-footed booby. *Oecologia* 146, 681–691.
- Weimerskirch, H., Le Corre, M., Bost, C.A., 2008. Foraging strategy of masked boobies from the largest colony in the world: relationship to environmental conditions and fisheries. *Mar. Ecol. Prog. Ser.* 362, 291–302.
- Weimerskirch, H., Shaffer, S.A., Tremblay, Y., Costa, D.P., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K., Auriolos, D., 2009. Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Mar. Ecol. Prog. Series* 391, 267–278.
- Witt, M.J., Bonguno, E.A., Broderick, A.C., Coyne, M.S., Formia, A., Gibudi, A., Mounquengui, G.A.M., Moussounda, C., Nsafou, M., Nougessono, S., Parnell, R.J., Sounguet, G.P., Verhage, S., Godley, B.J., 2011. Tracking leatherback turtles from the world's largest rookery: assessing threats across the South Atlantic. *Proc. R. Soc. B-Biol. Sci.* 278, 2338–2347.
- Young, H.S., McCauley, D.J., Dirzo, R., Dunbar, R.B., Shaffer, S.A., 2010a. Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis. *Mar. Ecol. Prog. Series* 416, 285–294.
- Young, H.S., Shaffer, S.A., McCauley, D.J., Foley, D.G., Dirzo, R., Block, B.A., 2010b. Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. *Mar. Ecol. Prog. Series* 403, 291–301.
- Zavalaga, C.B., Halls, J.N., Mori, G.P., Taylor, S.A., Dell'Omo, G., 2010. At-sea movement patterns and diving behavior of Peruvian boobies *Sula variegata* in northern Peru. *Mar. Ecol. Prog. Series* 404, 259–274.