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Evaluation of MPA designs that protect highly mobile megafauna now and under climate change scenarios

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ABSTRACT

Marine protected area (MPA) designs, including large-scale MPAs (LSMPAs; >150,000 km^2), mobile MPAs (fluid spatiotemporal boundaries), and MPA networks, may offer different benefits to species and could enhance protection by encompassing spatiotemporal scales of animal movement. We sought to understand how well LSMPAs could benefit nine highly-mobile marine species in the tropics now and into the future by: 1) evaluating current range overlap within a LSMPA; 2) evaluating range overlap under climate change projections; and 3) evaluating how well theoretical MPA designs benefit these nine species. We focused on Palmyra Atoll and Kingman Reef, a 2000 km^2 area within the 1.2 million km^2 U.S. Pacific Remote Islands Marine National Monument (PRIMNM) that contains marine megafauna (reef and pelagic fishes; sea turtles; seabirds; cetaceans) reflecting different behaviors and habitat use. Our approach is useful for evaluating the effectiveness of the Palmyra-Kingman MPA and PRIMNM in protecting these species, and tropical LSMPAs in general, and for informing future MPA design. Stationary MPAs provided protection at varying scales. Reef manta rays (*Mobula alfredi*), grey reef sharks (*Carcharhinus amblyrhynchos*), green sea turtles (*Chelonia mydas*), and bottlenose dolphins (*Tursiops truncatus*) had overall small ranges (<100 km from Palmyra-Kingman) and could benefit from stationary MPAs that contained heterogenous reef habitats. Yellowfin tuna (*Thunnus albacares*), sooty terns (*Onychoprion fuscatus*), red-footed boobies (*Sula sula*), great frigatebirds

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(*Fregata minor*), and melon-headed whales (*Peponocephala electra*) navigated complex oceanographic processes and may benefit most from mobile MPAs that shift with features including thermal fronts, cyclic regions of elevated productivity, and eddies, if relationships with these features are established and predictable. All species had capacity to travel to nearby reef systems, illustrating potential benefits of MPA networks and protected corridors. Suitable habitats will likely contract for all species as warm water expands under climate change scenarios (species habitats were predicted to decrease by 4–49% at Palmyra-Kingman) and MPAs may not protect suitable habitats into the future. Species habitat requirements and movement ecologies are critical aspects of marine spatial planning, especially with respect to dynamic ocean processes and a changing climate.

1. Introduction

From 2010–2018, marine protected areas (MPAs) increased in combined areas from 10 million km^2 to > 23 million km^2, covering 7.9% of the world's oceans (UNEP-WCMC and IUCN, 2022). These new and expanded MPAs are expected to amplify ecosystem benefits by protecting more species, a greater diversity of habitats, and in some cases, entire foodwebs (e.g. Hays et al., 2020a). Furthermore, MPAs may help species, populations and communities respond and adapt to climate change (e.g. Hindell et al., 2020; Rassweiler et al., 2020). Among protected areas, large-scale MPAs (LSMPAs; also called blue water MPAs) protect areas > 150,000 km^2 (Lewis et al., 2017); there are currently 67 LSMPAs globally (Marine Conservation Institute, 2021). LSMPAs provide more coverage to

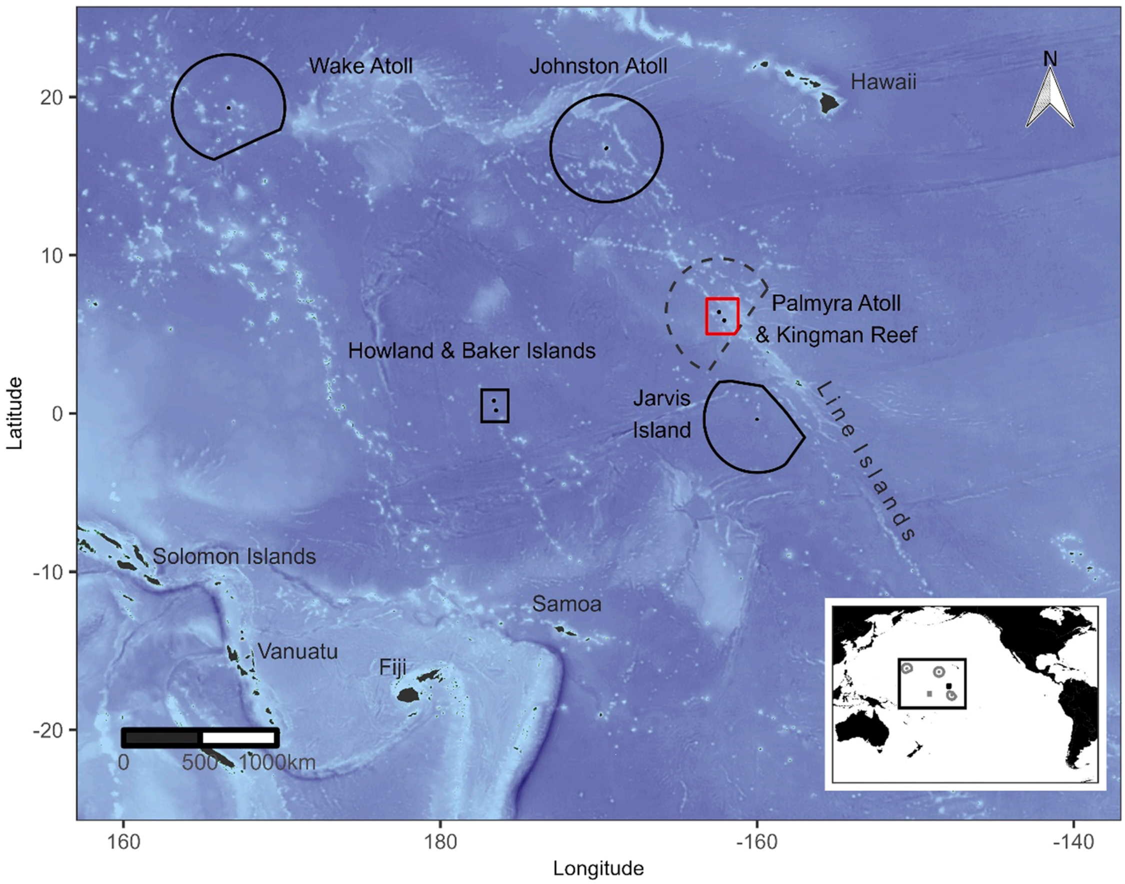

Fig. 1. Map of Pacific Remote Islands Marine National Monument (PRIMNM, USA). The Palmyra Atoll and Kingman Reef MPA is highlighted in red. The exclusive economic zone (EEZ) around Palmyra and Kingman is indicated by the dashed grey line. Inset: Location of PRIMNM within the context of the Pacific Ocean. Although PRIMNM was expanded in 2014 to include the exclusive economic zone (EEZ) around most of the atolls within PRIMNM, the expansion did not include the Palmyra-Kingman MPA. (U.S. Presidential Proclamation, 9173, 2014). Shaded blue background represents bathymetry, with light and dark colors representing relatively shallow and relatively deep depths, respectively, and was sourced from NOAA National Centers for Environmental Information ETOPO1 database (Amante and Eakins, 2009). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Summary of focal species assessed in this study and how they are expected to benefit from LSMPAs. Proximate mechanisms like protected habitat and regulated human activities within the MPA could result in positive outcomes for species like protected nursery habitats and reduced by-catch. The specific ways in which species could benefit from these protections are marked with X.

Primary mechanism		Protected habitat		Regulations					
Secondary mechanism		Reduced habitat destruction/ alteration		Restricted fisheries				Restricted entry	
Tertiary mechanism		Protected life history stage	Protected resources	Reduced harvest				Decreased boat disturbance	
Outcome for species		Nursery/ juvenile habitat	Foraging	Larger individuals; increased abundance	Increased prey abundance	Reduced by-catch/ entanglements	Increased access to sub-surface predators	Decreased local noise pollution	Decreased local chemical pollution
Primary habitat	Species								
Reef	Manta ray (*Mobula alfredi*)	X	X			X			X
	Grey reef shark (*Carcharhinus amblyrhynchos*)	X	X		X	X			X
	Green sea turtle (*Chelonia mydas*)	X	X		X	X			X
Pelagic	Yellowfin tuna (*Thunnus albacares*)	X	X	X	X	X			X
	Sooty tern (*Onychoprion fuscatus*)	X[a]	X		X		X		X
	Red-footed booby (*Sula sula*)	X[a]	X		X		X		X
	Great frigatebird (*Fregata minor*)	X[a]	X		X		X		X
Nearshore & Pelagic	Bottlenose dolphin (*Tursiops truncatus*)	X	X		X			X	X
	Melon-headed whale (*Peponocephala electra*)	X	X		X			X	X

Notes: [a] Seabirds' land-based nesting habitat may be protected within an MPA if emergent land is included in the extent of the protected area, which occurs within the Pacific Remote Islands Marine National Monument, for example (U.S. Presidential Proclamation 8336, 2009).

help attain international sustainable development goals (SDG 17, United Nations, 2015) and conservation targets (e.g., “30 by 30”; IUCN, 2016), though existing MPA targets have not been met (e.g., 2020 target that called for 10% of oceans to be protected was not reached; Convention on Biological Diversity (CBD), 2011; UNEP-WCMC and IUCN, 2022). Although these initiatives are expected to benefit biodiversity, wide-ranging species (i.e., species that may regularly move hundreds to thousands of kilometers, like albatrosses and tuna) may move beyond stationary LSMPA boundaries. To evaluate current LSMPAs and inform current and future marine spatial planning, we might consider how to better protect the many highly-mobile species that may spend part or most of their lives outside MPAs, yet are an important part of MPA-aided biodiversity conservation (Grüss et al., 2011).

MPAs designed to protect reef species can partly protect pelagic species that use both nearshore and pelagic habitats differently for foraging, breeding, nurseries, commuting, and resting (Bucaram et al., 2018; Hays et al., 2020a). Some far-ranging species use nearshore or onshore habitats for breeding or juvenile life stages but then use pelagic habitats for feeding or adult life history stages (McCauley et al., 2012b; Tobeña et al., 2014). Some nearshore species regularly travel offshore and provide important ecosystem links through nutrient subsidies (e.g., seabirds bring pelagic nutrients to islands; McCauley et al., 2012a; reef sharks transfer nutrients within coral reef systems; Williams et al., 2018). Connectivity between reef systems also facilitates animal movement between nearshore and pelagic habitats (Espinoza et al., 2015b; Schill et al., 2015). Less well understood, especially for offshore pelagic habitats, are animals’ fine scale movements and which environmental features provide resources or facilitate movement. Knowledge of the climatological persistence of these features, combined with knowledge of species ecology (e.g., habitats, behaviors, scales of movements) could contribute to research and conservation priorities (e.g., McClanahan et al., 2012) and inform whether the scale and siting of an MPA matches the movement patterns of the species that the MPA is expected to protect. Identification and inclusion of these attributes within LSMPAs at the implementation phase (Hogg et al., 2018) could greatly increase MPA efficacy via species attraction and retention, and could help inform MPA design that can potentially better accommodate climate-driven environmental changes (Sequeira et al., 2019a).

Because incorporating pelagic species movements into LSMPA design is challenging and adjusting misplaced MPAs can be costly (Critchley et al., 2018), we reviewed factors that may affect movement patterns for species that interact with atolls within LSMPAs. This information was evaluated within the context of MPA design in a relatively undisturbed ecosystem in the tropical Pacific surrounding Palmyra Atoll and Kingman Reef, which are a part of the United States Pacific Remote Islands Marine National Monument (PRIMNM). PRIMNM is one of the largest MPAs in the world, with a total protected area of 1,258,511 km^2 (Fig. 1). Within the PRIMNM network, a stationary protected area extends 92.6 km (covering a total of 2038 km^2) around Palmyra Atoll and Kingman Reef (U.S. Presidential Proclamation 8836, 2009; Fig. 1), referred to here as the “Palmyra-Kingman MPA.” This MPA protects coral reef, lagoon, and pelagic habitats. PRIMNM was established in 2009 to preserve the marine environment for the care and management of historic and scientific objects within it, which include flora and fauna in the water and on submerged and emergent land. To facilitate the preservation, care, and management of PRIMNM resources, activities including all forms of entry, commercial fishing, and habitat destruction, appropriation and removal are prohibited (U.S. Presidential Proclamation 8336, 2009). Within the context of these objectives, we sought to understand whether: 1) the boundaries of the Palmyra-Kingman MPA matched the scales of movements of nine focal species; 2) the Palmyra-Kingman MPA could provide protected habitat to nine focal species under climate change scenarios; and 3) how nine focal species were best protected by theoretical MPA designs.

We chose nine vertebrate focal species that represented diverse habitat use within and outside atolls and thus may have differential benefits from MPA protection (Table 1). These species encompassed reef habitats (reef manta ray, *Mobula alfredi*; grey reef shark, *Carcharhinus amblyrhynchos*; green sea turtle, *Chelonia mydas*), pelagic habitats (yellowfin tuna, *Thunnus albacares*; sooty tern, *Onychoprion fuscatus*; red-footed booby, *Sula sula*; great frigatebird, *Fregata minor*) and both nearshore and pelagic habitats (bottlenose dolphin, *Tursiops truncatus*; melon-headed whale, *Peponocephala electra*). For example, yellowfin tuna and grey reef sharks could benefit from restricted fishing activities, which should increase fish populations, fish abundance, and fish diversity (e.g. Caselle et al., 2015), though species are at-risk to fisheries outside Palmyra’s MPA boundaries (White et al., 2017). In protected areas, fish population structures should shift toward older, larger individuals, allow more development time for young, and include greater size class diversity (Lester et al., 2009) and these changes should also provide more food for predators like seabirds and cetaceans, though these trophic relationships are complex at Palmyra (Bradley et al., 2017). Seabirds depend on subsurface predators for foraging (Au and Pitman, 1986), and can benefit from increased access to prey via facilitated foraging in concert with subsurface predators (Maxwell and Morgan, 2013). Decreased fisheries interactions, reduced entanglements, and reduced by-catch are also expected (Handley et al., 2020), which could benefit reef manta rays and green sea turtles. Restricted human entry should greatly reduce disturbance by boats and people and decrease the risks for point-source chemical and anthropogenic noise pollution and accidental introduction of invasive species (Merchant et al., 2014; New et al., 2020; Shahidul Islam and Tanaka, 2004). Restrictions on development and mineral extraction should also limit habitat alteration, destruction, and species displacement (Kaiser et al., 2002; Pirotta et al., 2013; Woods and Verones, 2019).

Despite the protections afforded by MPA legislation, climate-related changes in oceanographic processes could reduce suitable habitats for many species throughout the tropical Pacific, including within the Palmyra-Kingman MPA. In this area, increased sea surface temperature (SST; van Weelden et al., 2021) is expected to manifest fastest at the equator while decreased winds will reduce mixing, promote stratification, and shoal the thermocline (Collins et al., 2010). Regional warming is also expected to decrease horizontal SST gradients (Martínez-Moreno et al., 2021). Local climate velocities (the rate and direction that isotherms move) could cause concurrent shifts in species habitats and ranges (Pinsky et al., 2013). Marine heatwave events can increase both SST and sand temperature, causing decreased hatch rates in sea turtles (Hays et al., 2021) and negatively affect prey availability, reducing nesting attempts and lifetime reproductive success (Stubbs et al., 2020). The inter-tropical convergence zone (ITCZ), which is the convergence of hemispheric trade winds that influence thermocline depth, is predicted to shift equatorward (Broccoli et al., 2006) and become narrower (Byrne and Schneider, 2016) and stronger (Byrne et al., 2018). Thus, productivity in the Pacific equatorial divergence (PEQD) biogeographical province (at which Palmyra and Kingman sit at the western edge; Reygondeau et al., 2013) is complex: mixed layer depth will decrease but persistent equatorial upwelling may continue to provide adequate nitrate concentrations to enable sufficient primary production (Le Borgne et al., 2011). The PEQD is predicted to shrink in size and move eastward, away from Palmyra as the western warm pool expands (Polovina et al., 2011). Atolls like Palmyra and Kingman are also particularly vulnerable to projected increases in storm intensity; wave and wind energy will drive flooding, erosion and sedimentation patterns (Shope et al., 2017; Storlazzi et al., 2018; Walsh et al., 2012). Indeed, large storm events turnover deep lagoon water, which, at Palmyra, is anoxic and sulfidic (Gardner et al., 2014a). Sea level rise could decrease terrestrial nesting habitat among seabirds on these low-lying atolls, especially if habitats reach carrying capacity and restrict reproduction (e.g., Hatfield et al., 2012). Although generalist foragers are already adapted to prey-switching and are expected to be more buffered against climate change than specialist foragers (Davey et al.,

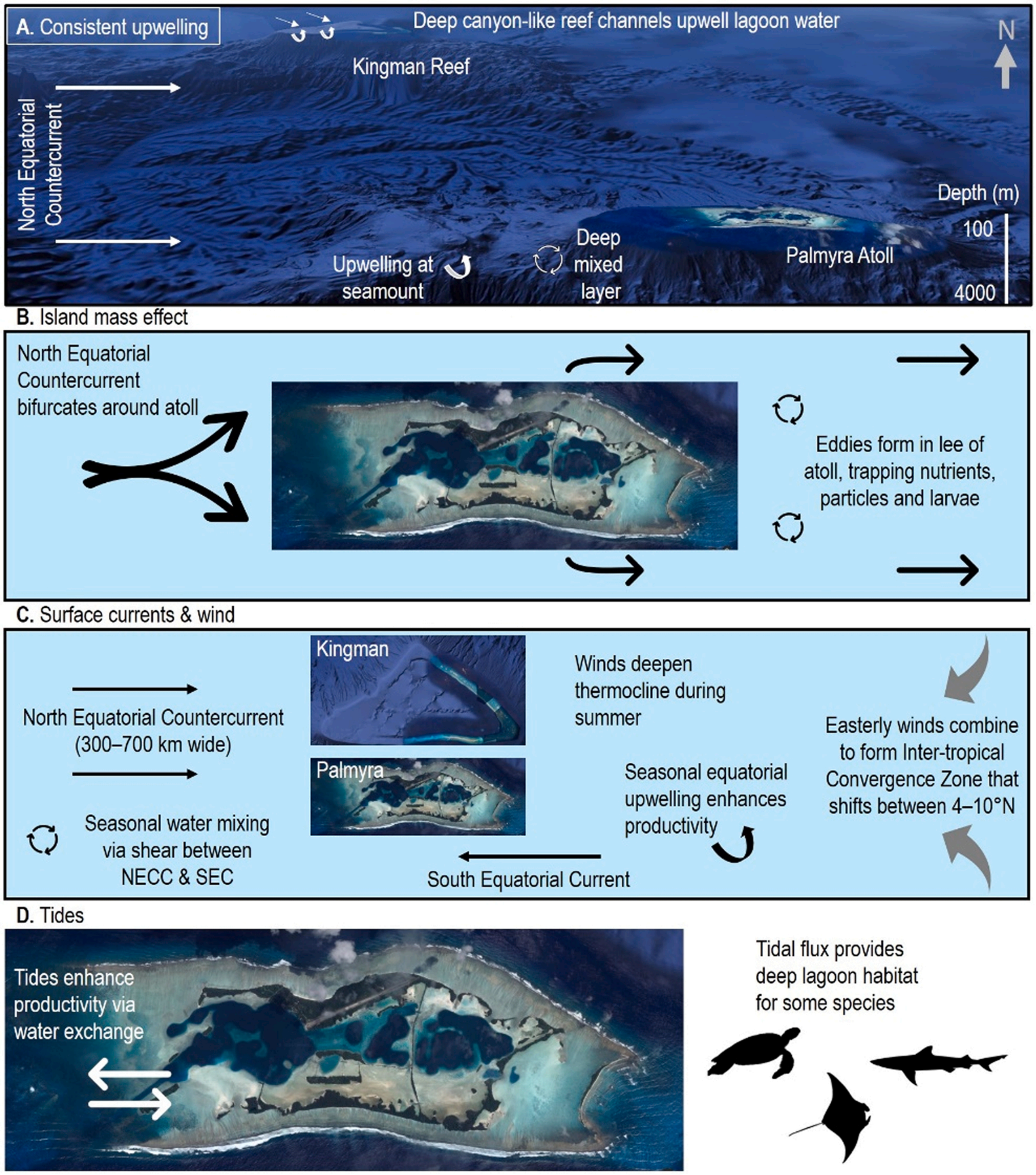

Fig. 2. Schematic representations of oceanographic processes that enhance productivity and contribute to species' habitats at Palmyra Atoll and Kingman Reef. These features include **A)** consistent upwelling via currents and a local seamount, illustrated by underwater topography; **B)** the island mass effect; **C)** surface currents and wind; and **D)** tides. Satellite images obtained from Google Earth (www.earth.google.com).

2011; Magurran et al., 2015), a reduction in suitable habitat may still cause species to shift behaviors and movements in order to track suitable habitats, which could lead focal species outside of MPA protections. Species and MPAs could thus benefit from evaluation of MPA protections that could inform management plans and future planning in current and candidate MPAs.

2. Methods

2.1. Focal species

We assessed nine species that inhabit the Palmyra-Kingman MPA and regularly use reef, pelagic, and nearshore and pelagic habitats (Table 1). These nine species have diverse physiological and habitat requirements that enabled a comprehensive examination of marine habitat use. In reef habitats, all age classes of reef manta ray use atolls like Palmyra and Kingman as foraging grounds (Germanov et al., 2019; McCauley et al., 2014). Reef mantas demonstrate diverse within-atoll habitat use: they use distinctly different habitats for foraging and to attend cleaning stations (Jaine et al., 2012). Grey reef sharks are top predators within coral reef ecosystems (Frisch et al., 2016) and connect pelagic, reef, and lagoon ecosystems at Palmyra (McCauley et al., 2012b; Williams et al., 2018). In addition to horizontal movements among habitats, grey reef sharks are known to dive to depths of 120 m at Palmyra (Papastamatiou et al., 2018). Palmyra is a foraging area for green sea turtles and provides year-round protection to adults that breed every three years and to juvenile green sea turtles that originate from broadly distributed hatching areas (Luke et al., 2004; Naro-Maciel et al., 2018).

In pelagic habitats, the yellowfin tuna is a large, economically important pelagic fish that is wide-ranging and can be found at depths of up to several hundred meters, making extensive use of the epipelagic zone (Fonteneau and Hallier, 2015; Lam et al., 2020). Yellowfin tuna also shoal prey species, facilitating foraging for other predators and providing an important ecosystem service (Au and Pitman, 1986; Maxwell and Morgan, 2013). Seabirds (sooty tern, red-footed booby, great frigatebird) are central-place foragers when caring for offspring and are constrained by how far they can travel from the nest to search for food. Seabirds also represent an important ecological link between terrestrial features of atolls and pelagic ecosystems via nutrient capture and deposition (McCauley et al., 2012a).

Some species use both nearshore and pelagic habitats regularly. Bottlenose dolphins and melon-headed whales use both nearshore and pelagic regions for resting and foraging (Baumann-Pickering et al., 2015; Tobeña et al., 2014). Bottlenose dolphins are represented by two ecotypes, coastal and oceanic, that may occur in adjacent areas, but fulfill specific niches in distinct habitats (Díaz-Gamboa et al., 2018; Zaeschmar et al., 2020). At Palmyra, melon-headed whales rest nearshore during the day and forage offshore at night (Baumann-Pickering et al., 2015). At night, they can dive up to 400 m (Joyce et al., 2017), thus demonstrating daily use of multiple horizontal and vertical habitats around atolls. Collectively, these nine species regularly use diverse habitats available within the Palmyra-Kingman MPA and often move across multiple habitat types per day.

2.2. Study site

Palmyra-Kingman's stationary MPA design protects habitat and resources in nearshore atoll and pelagic ecosystems used by focal species. Important features that define this unique habitat are highlighted below and in Fig. 2. For example, topographic complexity and seamounts provide consistent upwelling (Miller et al., 2008; Fig. 2**A**). Palmyra Atoll and Kingman Reef are 60 km apart and sit on distinct plateaus with steep slopes. Seasonal changes in the North Equatorial Countercurrent (NECC) result in mixed layers that vary in depth (Hamann et al., 2004). Topographic upwelling does not occur at Kingman Reef because of its shallow western slopes and because the Equatorial Undercurrent does not extend north to this latitude (Brainard et al., 2019a; Maragos et al., 2008b). The easterly NECC is approximately 300–700 km wide (Wyrtki and Kendall, 1967) and eddies form in the lee of Palmyra-Kingman, trapping nutrients, particles, and larvae (Boehlert and Mundy, 1993; Hamann et al., 2004; Signorini et al., 1999) via the island mass effect (Doty and Oguri, 1956; Fig. 2**B**). Thus, atoll-generated productivity can extend up to 25 km offshore; at Palmyra, nutrients from seabird guano and forests enhance nutrient concentrations (Gove et al., 2016). Seasonal currents and winds also contribute to upwelling (Fig. 2**C**). Horizontal shear between the Southern Equatorial Current and the NECC enhances seasonal water mixing and creates greater oceanographic variability south of Palmyra Atoll (Maragos et al., 2008b). Primary productivity also fluctuates seasonally due to easterly trade winds (boreal winter) that enable equatorial upwelling south of Palmyra, and convergence of northern and southern trade winds between 4° and 10°N (boreal summer) that form the ITCZ (Ramage et al., 1981), pushing warm (SST: 25–30 °C, Brainard et al., 2019b) surface water down and deepening the thermocline during summer. Tides enhance productivity via water exchange in shallow areas and increase habitat availability (e.g., more water is present during high tide, providing deeper water for shelter and foraging; Rogers et al., 2017; Fig. 2**D**). At Kingman Reef, 1.2 ha of emergent land at low tide provide roosting space for seabirds and sea turtles (Maragos et al., 2008b). Coral reefs encircle deep lagoons (up to 55 m deep at Palmyra; >100 m deep at Kingman) that receive continuous input of oceanic water from currents and tides. At Kingman, deep canyon-like reef channels upwell lagoon water that generates locally high nutrient concentrations that contribute to locally high productivity (Brainard et al., 2019a). Conversely, Palmyra has several enclosed basins that receive varying amounts of outside water, resulting in a well-mixed surface layer (0–10 m) and stratified, anoxic, sulfidic, and temporally stable deep water (Gardner et al., 2011). Water exchange can also contribute to localized differences in turbidity, substrates, and larval recruitment of coral species across the atoll (Elmer et al., 2016).

2.3. Assessment of MPA efficacy

To assess species ranges in relation to the Palmyra-Kingman MPA, we synthesized habitat and movement ecology information reported in the literature for each species (Appendix A). We quantified species non-migratory movements and calculated a mean range relative to Palmyra-Kingman MPA boundaries from values reported in biotelemetry studies (Table B1). Satellite telemetry and geolocation data were the most direct ways to report ranges because tracking tags reported all movements of tagged individuals whereas other types of data (e.g., acoustic tagging and ship-based monitoring) only reported when an animal was in range of a sensor or observer and could not report the maximum range that an animal traveled. Distance measurements reported by tracking studies varied, and we calculated species ranges based on the most frequent metrics reported among species: 1) mean distances traveled from the tagging site; 2) mean maximum distance from tagging site or offshore; 3) distance between the tagging site and the tag's pop-up location; 4) linear displacement; 5) total track length; 6) greatest distance across home range. Distances were considered non-migratory if animals regularly returned to a central location (e.g., tagging site). We combined data from all age classes (adult and juveniles) and breeding stages (e.g., seabirds during incubation, brooding of young chicks, and provisioning of older chicks) to maximize available data and to best represent overall habitat use.

2.4. Assessment of climate change

Stationary MPAs protect defined geographic regions but dynamic oceanographic conditions and ecosystem variability may alter the types of available habitats and resources within these static spaces. We assessed broad-scale habitat changes expected given climate change projections with AquaMaps (www.aquamaps.org; (Kaschner et al., 2019)), which generated predictions of suitable, available habitat that are based on species distributions and environmental envelope models (Kaschner et al., 2019). For each species, we obtained current and future probabilities of occurrence in the central Pacific Ocean; future habitat was modeled by the IPCC RCP8.5 scenario for 2050 ("business as usual"; 2019). A probability threshold of ≥ 0.5 was used as a conservative estimate that encompassed species presence and likely habitat (Davies et al., 2017). To illustrate potential habitat shifts, we plotted the percent change in suitable habitat in the program R (R Core Team, 2020).

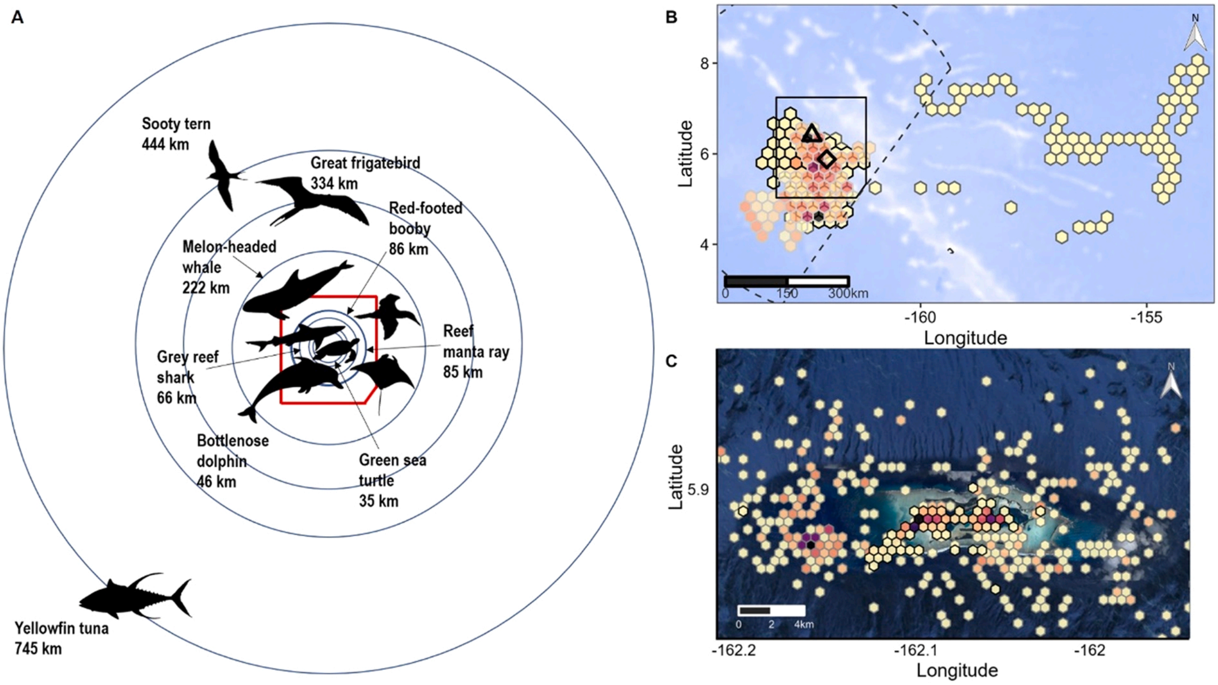

Fig. 3. Focal species movements in relation to the Palmyra-Kingman Marine Protected Area. A) Diagram depicting the mean non-migratory movement distances of megafauna (blue circles) around the Palmyra Atoll MPA boundaries (red polygon). Mean non-migratory distances were summarized from published tracking studies (**Table B1**). **B)** Pelagic habitat use exceeds the Palmyra-Kingman MPA (black polygon). Telemetry data are plotted as points summarized by count within equal-area hexagons for grey reef sharks (hexagons outlined in dark grey; telemetry data from White et al., 2017), red-footed boobies (hexagons outlined in black; telemetry data from Young et al., 2015), and great frigatebirds (hexagons outlined in white; telemetry data from Gilmour et al., 2019). Hexagons are colored by a scale indicative of point density, such that darker colors (pink, purple, black) indicate areas of high density and light colors (yellow, orange) indicate areas of low density. Black diamond indicates Palmyra Atoll, black triangle indicates Kingman Reef, and grey dashed line indicates the Palmyra-Kingman exclusive economic zone (EEZ). Shaded blue background represents bathymetry, with light and dark colors representing relatively shallow and relatively deep depths, respectively, and was sourced from NOAA National Centers for Environmental Information ETOPO1 database (Amante and Eakins, 2009). **C)** Near-atoll habitat use by reef manta rays (hexagons outlined in black; telemetry data from McCauley et al., 2014) and grey reef sharks (hexagons outlined in dark grey) at Palmyra Atoll. Satellite image obtained from Google Earth (www.earth.google.com). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

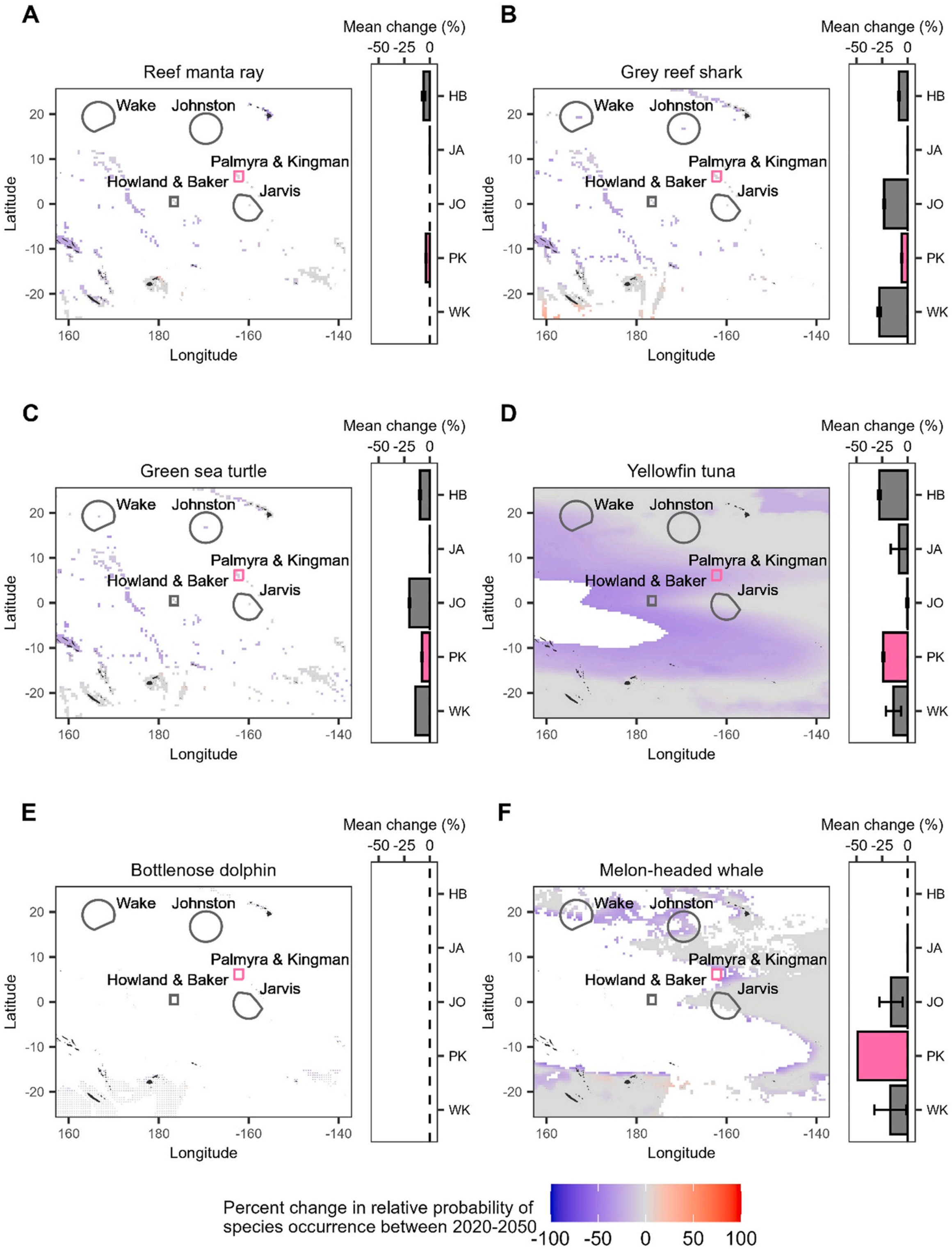

Fig. 4. Probabilities of change in aquatic species habitats under climate change. A) Reef manta ray; **B)** grey reef shark; **C)** green sea turtle; **D)** yellowfin tuna; **E)** bottlenose dolphin; **F)** melon-headed whale. Within each panel, changes in suitable habitat are mapped (left), and a bar plot represents the mean (± SD error bars) change within each MPA of the Pacific Remote Island Marine National Monument (PRIMNM; right). Divergent color scale indicates future habitat reduction (blue colors) or future habitat expansion (red colors), with grey indicating no change; white corresponds to no available suitable habitat. Changes in habitat suitability were modeled based on environmental envelope models for each species for the year 2020 and under scenario IPCC RCP8.5 for the year 2050, conducted with tools from AquaMaps (Kaschner et al., 2019). Grey polygons

denote PRIMNM. Dashed lines in bar plots indicate that suitable habitat was not available. The Palmyra-Kingman MPA is highlighted with pink. MPA abbreviations: HB= Howland and Baker; JA= Jarvis; JO= Johnston; PK= Palmyra and Kingman; WK= Wake. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.5. *Assessment of theoretical MPA designs*

Multiple MPA designs are used throughout the world ocean. MPAs often have stationary boundaries whereas mobile MPAs have boundaries that shift at spatial and temporal scales that coincide with dynamic biological and oceanic processes like spawning and thermal fronts (Maxwell et al., 2015). MPA networks are a collection of MPAs that function cooperatively to meet objectives that would not be obtainable by single MPAs; individual MPAs within the network may operate at various spatial scales and protection levels (IUCN World Commission, 2008). We assessed how species might interact with different theoretical MPA designs by applying species movement ranges (Table B1) and synthesized habitat information (Appendix A) to network and mobile MPA design concepts. To evaluate stationary MPAs, we considered MPA boundaries in relation to varying size classes. Two size categories, "small" and "large," were calculated from the mean sizes of MPAs listed by the Marine Protection Atlas (www.mptalas.org; Marine Conservation Institute, 2021) from "Very Small" (<10 km^2) and "Small" (10–100 km^2) MPAs ($n = 133$) and from "Large" (100–100,000 km^2) and "Very Large" ($\geq$100,000 km^2) MPAs ($n = 75$) that met the following criteria: protection status was "fully" or "highly" protected from fishing, establishment stages were "designated" or "implemented," and were located in a pelagic location (not located on a continental shelf). This resulted in a mean ($\pm$ SD) "small" theoretical MPA with size 13.7 ± 20.6 km^2 and a mean "large" MPA with size $101,967 \pm 237,625$ km^2.

3. Results

3.1. *Does the Palmyra-Kingman MPA protect species' scales of movement?*

The nine species have widely varying scales of non-migratory movements (Fig. 3**A**; Table B1). For species that use primarily reef habitats, grey reef sharks and green sea turtles received the most protection. Although a short average range indicated full protection of grey reef sharks (Fig. 3**A**), previous tracking at Palmyra indicates occasional travel outside the MPA (White et al., 2017; Fig. 3**B**). Green sea turtles generally have extremely small home ranges at foraging grounds (Table B1), including at Palmyra, where they remain within 10 km of the atoll (Naro-Maciel et al., 2018). Manta rays remain almost exclusively within the atoll (McCauley et al., 2014; Fig. 3**C**).

Species that primarily use pelagic habitats were related to preference for offshore prey (Appendix A). Red-footed booby flight efficiency constrains at-sea habitats to within an average of 80 km of nests (Table B1). At Palmyra, red-footed boobies mostly remain within the MPA, with occasional travel outside of it (Young et al., 2015; Fig. 3**B**). The other pelagic species had mean non-migratory movements that go beyond the current Palmyra-Kingman MPA (Fig. 3**A**). Yellowfin tuna had the largest mean ranges (Fig. 3**A**), but movement patterns within PRIMNM are unknown. Sooty terns and great frigatebirds rely on sub-surface predators to shoal prey to the surface (Au and Pitman, 1986; Maxwell and Morgan, 2013) and at Palmyra, great frigatebirds foraged both inside and outside MPA boundaries (Gilmour et al., 2019; Fig. 3**B**).

For the species that use both nearshore and pelagic habitats daily, mixed protection was provided by the MPA. The mean bottlenose dolphin movement range fit within the Palmyra-Kingman MPA (Fig. 3**A**). However, although melon-headed whales rest near reefs during the day, they also depend on offshore prey (Baumann-Pickering et al., 2015; Young et al., 2017) and the mean non-migratory movement placed them outside the current Palmyra-Kingman MPA (Fig. 3**A**).

3.2. *Does the Palmyra-Kingman MPA protect species under climate change?*

Reduced suitable habitat was predicted for all aquatic focal species at Palmyra-Kingman and the other MPAs within PRIMNM between 2020 and 2050 (Fig. 4). In primarily reef habitats, grey reef sharks experienced little change at Palmyra-Kingman, but predicted suitable habitat decreased by 23–28% in the northern PRIMNM (Johnston and Wake atolls; Fig. 4**B**). Green sea turtle suitable habitat was predicted to decrease 7.5–20% throughout PRIMNM, especially in the northern region (Fig. 4**C**). Reef manta rays experienced the smallest predicted change in PRIMNM habitat (a decrease of 4–6%) among the focal species, though a large habitat reduction was predicted throughout the central Pacific (Fig. 4**A**).

In primarily pelagic habitats, yellowfin tuna were predicted to have reduced suitable habitat throughout the central Pacific, with a 24% reduction at Palmyra-Kingman but very little predicted change (<1%) in northern PRIMNM (Fig. 4**D**).

For species that use both nearshore and pelagic habitats, melon-headed whales were predicted to lose the most habitat within PRIMNM (up to 49%; Fig. 4**F**). No suitable habitat was available for bottlenose dolphins throughout PRIMNM according to AquaMaps (Fig. 4**E**) though the species is regularly reported there (Baumann-Pickering et al., 2010; Young et al., 2017). In fact, only the sub-tropical south Pacific provided suitable habitat, though that was also predicted to decrease (Fig. 4**E**).

3.3. *How do focal species align with MPA design?*

Species differed in their response to different theoretical MPA designs (Table 2). MPAs with stationary boundaries could provide

Table 2
Summary of focal species ecologies in relation to the current Palmyra MPA and theoretical MPA designs. Species life history stages either occurred (√) or did not occur (X) at or near Palmyra-Kingman or were unknown (UNK). Colored boxes indicate whether species would likely benefit (blue boxes), would likely not benefit (red boxes), or would likely partially benefit (e.g., certain life stages or parts of diurnal habitats would be protected by MPA; yellow boxes) from different theoretical MPA designs.

Primary marine habitat	Species	Life history stage occurs at Palmyra-Kingman				Theoretical MPA design			
						Stationary boundaries			Mobile boundaries
		Breeding	Juvenile	Foraging	Migration	Single Small ($13.7\ km^2$)[a]	Single Large ($101{,}967\ km^2$)[a]	Network	
Reef	Manta ray	✓	✓	✓	UNK	Diel behavioral patterns indicate that important habitats (e.g., cleaning stations; movement with tides in coral reef systems [1,2]) could be protected within small area for part of the day.	Small home range[d] fits within single large MPA.	Movement between reefs reported [3–6], so protected networks and corridors could be beneficial.	High site fidelity (to reefs [1,6,7], cleaning habitats [5,8,9], and especially by females [3]) may indicate stationary protection is more beneficial. Mantas track cyclic elevated productivity [10] so mobile MPAs that track this feature could be beneficial in some regions.
	Grey reef shark	✓	✓	✓	X	Diel behavioral patterns in coral reef habitat use [11,12] indicate that important habitats could be protected within small area for part of the day.	Small home range[d] fits within single large MPA.	Habitat continuity important [13] and some movement between reefs reported [14] so protected networks and corridors could be beneficial.	High site fidelity (to reefs [11,14,15] and separate diurnal, nocturnal reef habitats [16]) may indicate stationary protection is more beneficial.
	Green sea turtle	X	✓	✓	X	High retention rate of turtles in foraging areas with consistent, high quality resources indicate that some small areas may provide protection [17].	Small foraging home range[d] fits within single large MPA.	Juveniles move between foraging habitats [18]. Adults migrate between nesting & foraging areas 100's km to 1,000's km apart[d].	High site fidelity (to foraging areas [17,19–22]) may indicate stationary protection is more beneficial. Juveniles track cyclic elevated productivity [18] so mobile MPAs that track this feature could be beneficial in some regions.
Pelagic	Yellowfin tuna	UNK	✓	✓	UNK	Retention near fish aggregating devices (FADs) indicate some protection for multiple size classes in small stationary area [23].	Regular long-distance movements[d], but some evidence of site fidelity and retention near nurseries suggest that stationary MPAs could be beneficial [24–26].	Long-distance movements[d] could traverse large areas such that critical life stages (e.g., spawning, foraging) could be contained in multiple MPAs [26].	Could benefit if habitat shifted with predictable temporal ocean processes (e.g. fronts) [27].
	Sooty tern	✓[b]	UNK	✓	X	Large pre-breeding and foraging ranges [28–30] exceed small MPA	Large pelagic foraging range[d] may exceed large MPA.	Long-distance movements[d] could traverse large area that contained multiple MPAs; site fidelity to commuting routes [28] could also benefit from a network that protected movement corridors.	Could benefit if there was a predictable connection between this species preferred foraging habitat and ocean processes, but these relationships are hard to quantify [31].
	Red-footed booby	✓[b]	✓	✓	X	Foraging range restricted to pelagic regions [32] that typically exceed small MPA.	Small pelagic foraging range[d] fits within large MPA.	Foraging range restricted to pelagic regions [32] that could be encompassed by MPA network.	Foraging range restricted by location of nest, so stationary MPA could be more beneficial. Reliance on dynamic ocean processes for foraging [33] could benefit from mobile MPA.
	Great frigatebird	✓[b]	✓	✓	X	Large pelagic foraging range[d] exceeds small MPA.	Large pelagic foraging range[d] may exceed large MPA.	Large pelagic foraging range[d] could traverse large area within MPA network.	Could benefit if habitat shifted with ocean processes [27]; foraging site fidelity was low [34], so mobile MPA could be beneficial.
Nearshore & Pelagic[c]	Bottlenose dolphin	UNK	✓	✓	UNK	Coastal ecotype with small home ranges[d] may benefit from small MPA.	The home ranges of both ecotypes would likely benefit from large MPA.	Depends on ecotype: Wide-ranging oceanic ecotype and transient populations [35] could benefit from MPA network.	Depends on ecotype: Wide-ranging oceanic ecotype may benefit from mobile MPA; however, site fidelity was high for both ecotypes [36–40], so stationary protection could be more beneficial.
	Melon-headed whale	UNK	✓	✓	UNK	Small MPA may protect diel resting behavior nearshore [41]. Large pelagic foraging range[d] exceeds single MPA.	Large pelagic foraging range[d] may exceed large MPA.	Daily movements between nearshore and pelagic habitats [41] could traverse large area within MPA network.	Daily use of nearshore & pelagic habitats [41], so mobile MPA would need to encompass both habitat types or track oceanic processes like eddies [42]; site fidelity was high in some regions [43,44], so stationary protection could be more beneficial.

Notes: [a]The single MPAs considered here are of two mean (± SD) sizes: Very Small/Small: 13.7 ± 20.6 km^2 and Large/Very Large: 101,967 ± 237,625 km^2. These means were calculated from 133 (Very Small/Small, 1–99 km^2) and 75 (Large/Very Large, >100 km^2) MPAs from the Marine Protection Atlas (Marine Conservation Institute, 2021) that satisfied the following criteria: protection status= fully or highly protected from fishing, establishment stages= designated or implemented, and in a pelagic location (not located on a continental shelf).

[b] Seabird terrestrial breeding habitats are protected as emergent land within the Palmyra-Kingman MPA (U.S. Presidential Proclamation 8336, 2009).

[c] Coastal and oceanic ecotypes of bottlenose dolphins use different habitats; the ecotype that occurs at Palmyra has not been identified, but the species has been sighted in nearshore habitats.

[d] Refer to Table B1 for distances reported for species movements. References: **1**: (Rohner et al., 2013); **2**: (Jaine et al., 2012); **3**: (Germanov et al., 2019); **4**: (Carpentier et al., 2019); **5**: (Venables et al., 2020); **6**: (Setyawan et al., 2018); **7**: (Braun et al., 2015); **8**: (Couturier et al., 2011); **9**: (Perryman et al., 2019); **10**: (Anderson et al., 2011); **11**: (Speed et al., 2011); **12**: (Papastamatiou et al., 2018); **13**: (Filous et al., 2017); **14**: (White et al., 2017); **15**: (Vianna et al., 2013); **16**: (Espinoza et al., 2015a); **17**: (Naro-Maciel et al., 2018); **18**: (González Carman et al., 2012); **19**: (Senko et al., 2010); **20**: (Blumenthal et al., 2006); **21**: (Broderick et al., 2007); **22**: (Dutton et al., 2019); **23**: (Filous et al., 2020); **24**: (Sibert and Hampton, 2003); **25**: (Wells et al., 2012); **26**: (Hernández et al., 2019); **27**: (Tew Kai and Marsac, 2010); **28**: (Soanes et al., 2015); **29**: (Huang et al., 2017); **30**: (Jaeger et al., 2017); **31**: (Jaquemet et al., 2007); **32**: (Young et al., 2015); **33**: (Gilmour et al., 2018); **34**: (Weimerskirch et al., 2004); **35**: (Dinis et al., 2018); **36**: (Baird et al., 2009); **37**: (Milmann et al., 2017); **38**: (Durden et al., 2019); **39**: (Estrade and Dulau, 2020); **40**: (Zaeschmar et al., 2020); **41**: (Baumann-Pickering et al., 2015); **42**: (Woodworth et al., 2012); **43**: (Silberg et al., 2011); **44**: (Aschettino et al., 2012).

protection to most focal species during at least part of the life history cycle, but MPA size and habitat diversity within stationary MPAs were important factors. For example, small MPAs could encompass the small home ranges of reef and nearshore species including foraging green sea turtles and some resident bottlenose dolphin populations (Fig. 5). Small MPAs could also protect parts of habitats that are used daily, like diurnal nearshore resting areas used by melon-headed whales (Fig. 5). However, protection of critical habitats like spawning and foraging areas could provide greater benefit to species. Large (>100 km^2) MPAs could include multiple habitat types used for different behaviors. Large MPAs could also encompass a greater proportion of the mean non-migratory movements of most focal species (Table B1). MPAs that protect diverse habitat types could also be beneficial. For example, manta rays and grey reef sharks use multiple parts of coral reef ecosystems daily, melon-headed whales make daily nearshore-offshore movements, bottlenose dolphin ecotypes use coastal and oceanic habitats, and yellowfin tuna regularly use large ranges of depths and temperatures (Fig. 5; Appendix A). These features would be more likely to exist in large MPAs that contained diverse habitats (Table 2).

MPA networks could encompass inter-reef travel where animals like manta rays, grey reef sharks, and green sea turtles aggregate for spawning events or seasonal changes in food resources (Fig. 5). Highly mobile pelagic species may also benefit from MPA networks because they could traverse multiple MPAs during long trips. Mobile MPAs could benefit species that have predictable and established relationships with spatial variability driven by ocean climatic events, especially in pelagic habitats. Mobile MPAs that track features in regions where species use them could be beneficial. These features could include mesoscale eddies that may last for several months, or regions with cyclic elevated productivity.

4. Discussion

4.1. Does the Palmyra-Kingman MPA protect species currently and under climate change?

MPAs have potential to protect many tropical species by protecting important habitats and providing regulatory protections (e.g., restricted fishing and entry). Our assessment of MPA protection examined MPA boundaries in relation to species movements and climate change and examined whether focal species ecologies aligned with MPA design. The multi-taxa synthesis that we conducted could be used to evaluate the efficacy of the Palmyra-Kingman MPA to protect the species within it, inform comprehensive management plans, and be useful for future MPA planning and siting. For example, the nine focal species from reef, nearshore and pelagic habitats are analogous to many other species with similar life history strategies. These data can also be transferred to other current and candidate MPAs within tropical regions, where nearly one-third of MPAs are located (21/67 of LSMPAs are in the tropics; Marine Conservation Institute, 2021).

We identified varying scales at which nine focal species from reef, nearshore and pelagic habitats were protected by the current Palmyra-Kingman MPA boundaries and under a climate change scenario. Effective species conservation could be achieved by protecting diverse habitat types, ensuring that habitats encompass multiple life history stages, and by adopting marine spatial planning that considers climate change. Overall, the goals of the Palmyra-Kingman MPA to protect these nine species were partially achieved and depended on the species of interest. Relative to species-specific ranges, the stationary Palmyra-Kingman MPA with a size of 2038 km^2 may effectively protect three reef species (grey reef shark, green sea turtle, bottlenose dolphin), provide intermediate protection for two species at the edge of their ranges (in primarily reef habitat: manta ray; in primarily pelagic habitat: red-footed booby) and only provide partial protection for the remaining four mobile species that use pelagic habitats (yellowfin tuna, sooty tern, great frigatebird, melon-headed whale). In reef habitats, habitat continuity (contiguous reefs) and zooplankton hotspots may retain focal species (Appendix A; McCauley et al., 2012a). Prey hotspots may indicate how pelagic habitats are used as well: yellowfin tuna remain near stationary and drifting fish aggregating devices (FADs; Filous et al., 2020), and remain near spawning regions (Hernández et al., 2019). All focal species are capable of long-distance movements, and the current MPA size does not allow full protections for occasional and regular long-distance travel, indicating that even species considered mostly protected based on our evaluation could still be vulnerable to threats like fisheries (White et al., 2017) and by-catch (e.g., Hays and Scott, 2013) that exist beyond the current MPA. Protection of diverse habitat types is also important to help meet the MPA's objective to protect species. Focal species rely on multiple habitat types (e.g., heterogenous coral reefs; nearshore and offshore regions; emergent land) and approaches

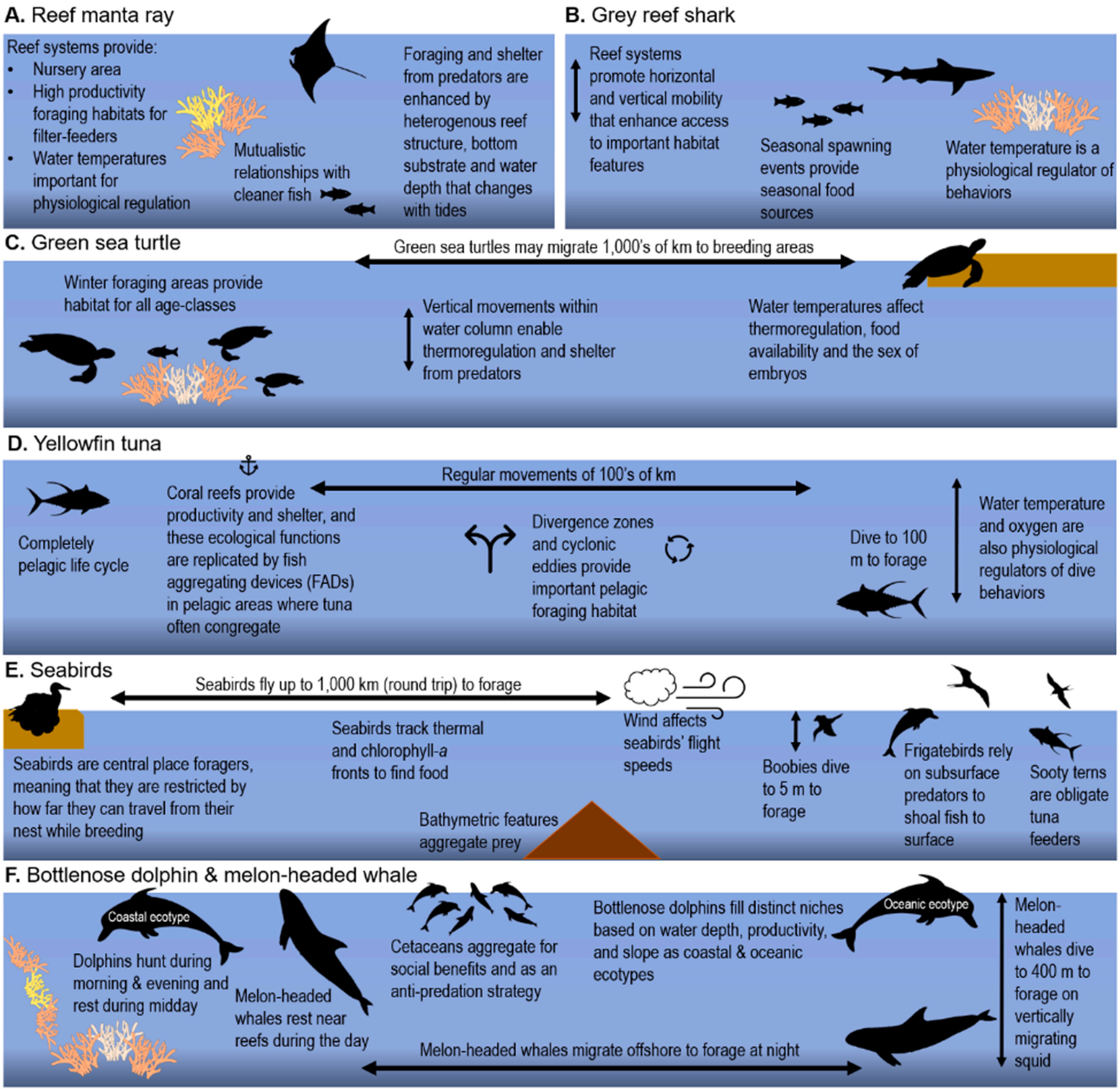

Fig. 5. Diagram highlighting behaviors, environmental features, and inter-specific relationships of **A)** reef manta rays; **B)** grey reef sharks; **C)** green sea turtles; **D)** yellowfin tuna; **E)** seabirds, including sooty terns, red-footed boobies, and great frigatebirds; and **F)** bottlenose dolphins and melon-headed whales. Information is summarized from literature cited in Appendix A.

that improve marine and terrestrial habitats within the MPA could help further achieve the MPA's goal while maximizing protection across taxa and habitats. This is especially important within the context of historic habitat modifications such as dredging, connecting islets, enlarging land area, and building installations at Palmyra that may differentially affect species (Collen et al., 2009; Gardner et al., 2014b; Gilmour et al., 2019; Maragos et al., 2008b, 2008a; McFadden et al., 2014; Williams et al., 2011).

Many tropical species are predicted to increase in abundance under climate change (Poloczanska et al., 2016), but habitats within warm waters may not be suitable for all species (e.g. Fig. 4; Chambers et al., 2011; Stramma et al., 2012). In reef habitats, increased temperatures and salinity could affect grey reef shark physiology (Chin et al., 2010), manta ray habitats could change because the species avoids warm SST and areas of decreased productivity (Dewar et al., 2008), and increased SST may shift green sea turtle diets (Esteban et al., 2020). Green sea turtles primarily forage on coralline algae in this region due to a lack of seagrass beds (Sterling et al., 2013) and could be susceptible to coral bleaching events, which has been observed in other herbivores (Graham et al., 2007). In addition to threats to diet, green sea turtles are also susceptible to climate-related changes in nesting habitat, including reduced nest site availability, decreased nesting success due to tidal inundation, and increased feminization of hatchlings (Laloë et al., 2020; Sönmez et al., 2021). In pelagic habitats, decreases in the oxygen minimum zone could compress vertical tuna habitat, further constraining suitable locations (Stramma et al., 2012). For species that regularly use nearshore and pelagic habitats, habitat shifts by offshore prey could alter habitats used by bottlenose dolphins and melon-headed whales (Moreno and Mathews, 2018; Sydeman et al., 2015). Climate change projections in the current study were based on environmental envelope models for several under-studied species, and species-specific habitat requirements are more complex than the few parameters used by the AquaMaps model (Kaschner et al., 2019). Overall, general trends indicated reduced suitable habitats that were consistent with other projected habitat changes (Hazen et al., 2013; Sydeman et al., 2015) and reinforce the need to consider climate change effects in MPA designs. The scale of these changes is also important; the models only covered the period 2020–2050 and revealed some drastic shifts in just a few decades, underscoring the urgency of considering climate change in MPA design and assessment.

Although the AquaMaps tool did not have data for seabirds, tropical seabirds in the central Pacific Ocean are expected to experience adverse effects from climate change. Predicted decreased wind velocity (Collins et al., 2010) could adversely affect flight efficiency in these soaring species (Ballance, 1995; Weimerskirch and Prudor, 2019). Reliance on sub-surface predators like tuna for foraging opportunities could also negatively impact seabirds if subsurface predators dive deeper to obtain prey or if subsurface predator abundance decreases (Chambers et al., 2011; Maxwell and Morgan, 2013). Variability in SST also cause changes in the growth and phenology of squid prey and can translate to variability in prey species delivered to red-footed booby chicks (Donahue et al., 2021b, 2021a). Terrestrial nesting habitats are at risk to decrease, and in some locations, disappear, due to sea level rise and this is especially an issue for species like great frigatebirds that have reached carrying capacity in some colonies (Hatfield et al., 2012). However, sooty terns have aseasonal breeding cycles in some colonies which could allow flexibility in ocean conditions to choose more optimal conditions during breeding (Reynolds et al., 2015; Schreiber et al., 2020). Therefore, incorporation of species-specific habitat requirements and predicted shifts in distribution or habitat with climate change projections could enhance MPA efficacy.

Our assessment of mean non-migratory movements demonstrated the unevenness of available data among focal species. Telemetry data varied in abundance, spatiotemporal resolution, and availability, with 47 telemetry studies contributing to our assessment of species mobility relative to MPA boundaries (Table B1), and of these, only four studies were conducted within the Palmyra-Kingman MPA. Furthermore, regardless of the number of telemetry studies available for any species, sufficient sample sizes are required to make conclusions about species ranges (Sequeira et al., 2019b) and tagging biases towards particular sexes, life history stages, or limited tag deployment durations may also influence results (Filous et al., 2022; Hays et al., 2020b). However, uneven data availability should not influence our conclusions regarding movement ranges for two reasons. First, we incorporated natural history data from other regions that could be reasonably expected to occur at Palmyra-Kingman. Complementary data can inform animal movements (e.g., Hays et al., 2020b), and in this study included knowledge of diel behavioral patterns, like manta rays' use of distinct foraging and cleaning habitats, and high rates of site fidelity in many bottlenose dolphin populations. These types of observations helped informed our overall assessment (e.g., Table 2). Second, we calculated mean non-migratory movement ranges from available data, and these averages allowed us to encompass varying movements between populations that may be related to local food availability. For example, yellowfin tuna are highly-mobile (Filous et al., 2022), but sufficient food resources may reduce long-distance travel (Filous et al., 2020; Hernández et al., 2019). For tuna and the other focal species, we assumed that movements near Palmyra-Kingman, a productive ecosystem (Gove et al., 2016), are within the average range of movements reported for each species across many ecosystem types. In the absence of locally available data, our results indicate that future studies use regional or ocean-basin-specific data to evaluate species habitat use and relevance to MPA locations and designs in new areas. For species for which no telemetry data are available, behaviors of congener species or ecologically similar taxa may be helpful to elucidate representative movement ranges and behaviors relative to MPA locations and designs.

4.2. How do focal species align with MPA designs?

Evaluation of the ecologies and ranges of the nine focal species demonstrated that reef, nearshore, and pelagic species like those from Palmyra and Kingman could benefit from: 1) protected movement corridors that connect MPA networks and reefs throughout the Line Islands, which could also be temporally dynamic to accommodate migration periods; 2) increased MPA size so that a greater proportion of pelagic habitat is protected, such as expansion of the Palmyra-Kingman MPA to include the U.S. EEZ; and 3) an adaptive management approach that shifts spatial protections with dynamic ocean features to benefit pelagic species that rely on these well-described features for food. Examples of dynamic features include regions with cyclic elevated productivity that provide key foraging areas for manta rays and juvenile green sea turtles (Anderson et al., 2011; González Carman et al., 2012) and mesoscale eddy boundaries that provide important foraging habitats for great frigatebirds and melon-headed whales (Tew Kai and Marsac, 2010; Woodworth et al., 2012). MPA protection could be most beneficial if species movements were predictable (e.g., high rates of intra-seasonal and inter-annual site fidelity to foraging and breeding areas or commuting routes; Hooker et al., 2011; Shimada et al., 2020). Adaptable and dynamic approaches could also better buffer species against predicted habitat shifts due to climate change (Maxwell et al., 2015; Melbourne-Thomas et al., 2021) and could be applied to specific high sea habitats, further extending protection to wide-ranging species (Maxwell et al., 2020).

Assessment of risks outside MPA boundaries (Bradley et al., 2019; White et al., 2017), how MPA management facilitates sustainable harvesting (Filous et al., 2020; Hernández et al., 2019), and increased visitation due to ecotourism are additional considerations of MPA design that affect species. For example, despite the ability of many pelagic species to move great distances, some individuals will spend their entire life inside an MPA, thus increasing the density of marine life inside the boundaries, boosting genetic diversity, and increasing local reproductive output, which will in turn benefit adjacent fisheries (Hernández et al., 2019). Decreased movement rates by far-ranging fishes like tuna evolved following the establishment of marine reserves, and this evolution occurred more rapidly with higher fishing pressure, thus augmenting the efficacy of MPAs (Sibert and Hampton, 2003). Mobile MPAs can also address species-specific threats with real-time satellite data (e.g., WhaleWatch; Hazen et al., 2017; and TurtleWatch; Howell et al., 2008) and user-generated data like by-catch reporting (Little et al., 2015). However, MPA regulations vary widely and expected MPA benefits like decreased human activity and disturbance could be contradicted by increased visitation for ecotourism. Some MPAs allow ecotourism to view and interact with manta rays and reef sharks (Huveneers et al., 2017; Mangubhai et al., 2020; Mustika et al., 2020). Visitors and boats can cause injury and disturbance to target and non-target species (e.g., sea turtles; Denkinger et al., 2013). Local ecological factors like poor prey availability can also compound the adverse effects experienced by animals in regions with tourism; bottlenose dolphin populations that are food-limited are sensitive to disturbance from boats and people (New et al., 2020).

5. Conclusions

Highly mobile and wide-ranging species are inherently challenging to manage and protect (Allan et al., 2021). MPAs are one of several tools that enhance species conservation, but whether MPAs are the best approach to protect highly mobile species is complex (Costello and Ballantine, 2015; Ulate et al., 2018). MPA protections enhance resources and populations within, and adjacent to, boundaries (Caselle et al., 2015; Garces et al., 2013) but may be limited by differential management, enforcement, and support by multiple stakeholders (Fenberg et al., 2012). Additionally, species responses to climate change are varied and may not be predictable in relation to conservation measures (Hobday, 2011). Thus, multi-faceted approaches that include one or several MPA designs can work in concert with other measures, like investments in methods and gear that reduce by-catch, address climate change, reduce pollution, institute improved, dynamic fisheries management, and include traditional management techniques and high rates of community involvement (Allan et al., 2021; McClanahan et al., 2006; Ulate et al., 2018). MPAs, when established and managed for conservation objectives (Allan et al., 2021) and when implemented alongside other conservation actions, could support marine spatial planning that benefits highly mobile species (Game et al., 2009; O'Leary et al., 2018).

Long-term ecological research, natural history data, and establishment of ecological baselines comprise critical information that could help inform MPA design, management, and site selection for candidate MPAs. To better inform how MPAs could maximize protection for multiple species, especially at the intersection of coral reef and pelagic habitats, investment in biotelemetry and long-term studies could be beneficial (Hays et al., 2019). A structure that quantifies spatiotemporal protective measures could result in significant management and conservation successes (e.g., Pendoley et al., 2014). Ultimately, to better contribute to the protection of whole marine communities, megafaunal movement ecologies could be incorporated into the ecological, socioeconomic, and regulatory aspects of MPA design, establishment, and monitoring (e.g. Meehan et al., 2020).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02070

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