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Spatial ecology and conservation of *Manta birostris* in the Indo-Pacific

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ABSTRACT

Information on the movements and population connectivity of the oceanic manta ray (*Manta birostris*) is scarce. The species has been anecdotally classified as a highly migratory species based on the pelagic habitats it often occupies, and migratory behavior exhibited by similar species. As a result, in the absence of ecological data, population declines in oceanic manta have been addressed primarily with international-scale management and conservation efforts. Using a combination of satellite telemetry, stable isotope and genetic analyses we demonstrate that, contrary to previous assumptions, the species appears to exhibit restricted movements and fine-scale population structure. *M. birostris* tagged at four sites in the Indo-Pacific exhibited no long-range migratory movements and had non-overlapping geographic ranges. Using genetic and isotopic analysis, we demonstrate that the observed movements and population structure persist on multi-year and generational time scales. These data provide the first insights into the long-term movements and population structure of oceanic manta rays, and suggest that bottom-up, local or regional approaches to managing oceanic mantas could prove more effective than existing, international-scale management strategies. This case study highlights the importance of matching the scales at which management and relevant ecological processes occur to facilitate the effective conservation of threatened species.

1. Introduction

Oceanic manta rays (*Manta birostris*) are an iconic and poorly studied species of marine megafauna. Despite decades of interest from the public and a high value in the recreational dive industry (O'Malley et al., 2013), manta rays have only recently received scientific attention (Couturier et al., 2012). Most ecological studies focus on the smaller, coastally associated reef manta ray (*Manta alfredi*), and demonstrate patterns of residency with few long-distance movements (Dewar et al., 2008; Deakos et al., 2011; Jaine et al., 2014; Braun et al., 2015). Oceanic manta rays tend to occupy more pelagic, offshore habitats than their coastal sister species (Kashiwagi et al., 2011), and they are presumed to be highly migratory based primarily on the behaviors exhibited by species similar in habitat preference, foraging strategies and size (Skomal et al., 2009; Hueter et al., 2013; Thorrold et al., 2014).

Oceanic mantas, along with closely related mobula rays (*Mobula* spp.), are caught frequently as bycatch in pelagic fisheries, and have been increasingly targeted over the last decade as demand for their gill plates grows in Asian markets (Couturier et al., 2012). Low fecundity and small population sizes make mantas highly susceptible to fisheries impacts (Dulvy et al., 2014). Targeted fisheries and bycatch are driving family-wide declines of mobulids (Ward-Paige et al., 2013; Croll et al., 2015) and long-term monitoring efforts have recorded local declines in manta and mobula sighting frequency (White et al., 2015).

As with other migratory species, conservation efforts for oceanic manta rays primarily focus on international agreements such as the Convention on International Trade in Endangered Species (CITES) and the Convention on the Conservation of Migratory Species (CMS) in an attempt to restrict the main economic drivers of manta fisheries and prevent targeted capture. However, the effectiveness of international approaches to managing migratory marine species is questionable. For example, a recent meta-analysis of global elasmobranch catches concluded that populations continue to be overexploited by countries that

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have signed international agreements to curb elasmobranch fisheries (Davidson et al., 2015). In recent years, local and national level management strategies have also been implemented to protect both reef and oceanic manta rays, including national fisheries bans in several countries and local spatial protections such as marine protected areas or sanctuaries focused on mantas. Local management approaches such as these can have substantial benefits to large, threatened elasmobranchs (Graham et al., 2016).

Given the lack of data on the ecology and stock structure of oceanic manta rays, it is unclear at which spatial scale management efforts for the species should be focused (e.g. international, national, or local). The few published tagging studies on the species have so far identified few long-distance movements (Graham et al., 2012; Hearn et al., 2014), and stock structure and population connectivity remain entirely unexplored. Additional information on the spatial ecology and population structure of the species is necessary to evaluate current management plans and develop new strategies to improve their efficacy in halting or reversing ongoing population declines.

Here we examine the movements and connectivity of *M. birostris* populations at four sites in the Indo-Pacific separated by 600 to 13,000 km in an attempt to identify the most relevant ecological and management unit to inform conservation decisions. We use a combination of satellite telemetry, stable isotope and genetic analysis to examine the movements and connectivity of populations on a range of spatial and temporal scales from daily movements to generational connectivity. We selected sites that had varying productivity regimes, oceanographic patterns, and sighting frequencies of oceanic mantas to make this work as broadly applicable to the species as possible, given the paucity of published data.

2. Methods

Our study sites included: (1) A productive coastal upwelling region in Bahia de Banderas (Mexico Nearshore) where mantas are found in large numbers from February through May each year. (2) The pelagic Revillagigedo Islands (Mexico Offshore), 400 km southwest of Baja California and 600 km west of the Mexico Nearshore site, where mantas can be found reliably from October through June. (3) The Raja Ampat region of eastern Indonesia, a complex archipelago habitat where shifting monsoon winds lead to substantial variability in productivity between summer and winter months (Schalk, 1987), and peak oceanic manta sightings occur in November and April each year. (4) Sri Lanka, where monsoon winds drive shifting productivity regimes in both coastal and pelagic systems (Charles et al., 2012), and artisanal fishermen frequently catch oceanic manta rays in pelagic habitats between May and September. While not exhaustive, these four sites are representative of the majority of habitats where the species is found (Kashiwagi et al., 2011).

We deployed pop-up satellite archival tags (PSAT) and a single towed satellite tag (SPLASH) (Wildlife Computers (WC), Washington USA; Desert Star (DS), California, USA) approximately evenly on males and females (Supplementary Table S1). We analyzed WC archival tag data using WC GPE3 software, which uses a Hidden Markov Model and incorporates environmental variables, bathymetry and movement speed to create probability surfaces of tag locations. We overlaid raw SPLASH tag GPS and Argos satellite positions in Indonesia, which have an accuracy ranging from finer than 100 m to 1500 m. We decoded raw DS archival tag positions using DS SeaTrack software.

We collected white muscle tissue samples from all study sites for both stable isotope and genetic analyses. We freeze-dried samples for stable isotope analysis and analyzed δ^{13}C and δ^{15}N values to compare isotope signatures between populations. We did not extract lipids from our samples as they had C:N ratios below 3.5 (Post et al., 2007) (mean 3.24 SD 0.25). To identify differences between populations, we used a model selection approach on multiple population grouping scenarios. We then fit the same linear model to each grouping scenario and used Akaike Information Criterion (AIC) values to identify the best-fit model, representing the grouping scenario best supported by the data.

We used double-digest Restriction Associated DNA (ddRAD) sequencing methods to assess population structure using a subset of individuals from each population. We used the program Stacks (Catchen et al., 2013) to clean, process and analyze raw ddRAD data and calculate population metrics. We filtered out low-F_{ST} Single Nucleotide Polymorphisms (SNPs) to better observe population structure, and performed null controls to ensure that filtering methods were not biasing results (Fig. S1). We used the program Structure 2.3 (Pritchard et al., 2000) to identify population clusters among samples. All methods are discussed in further detail in Supplementary information.

3. Results

We deployed PSATs ($n = 21$) on oceanic manta rays in Raja Ampat, Indonesia ($n = 9$) and Pacific Mexico ($n = 12$), and one towed SPLASH tag on an oceanic manta in Raja Ampat. We deployed tags continuously over two years in Indonesia, and in discrete intervals over approximately 20 months when manta aggregations were present and logistical constraints allowed in Mexico. We recovered data from 18 tags (Table S1). Satellite telemetry revealed restricted home ranges, residency, and an absence of large-scale migratory behavior. Tagged mantas in both regions remained within the respective countries' EEZs for the entire tagging periods (Fig. 1). We observed complete separation during the tagging periods between mantas tagged at the Mexico Nearshore site ($n = 5$ tags) and the Mexico Offshore site ($n = 4$ tags), with no recorded movements between sites by mantas tagged at either location. PSAT deployments in Mexico lasted a mean of 175 days (SD 28) for Wildlife Computers tags and 7 and 28 days for the two Desert Star tags that reported. Tags deployed in Mexico popped off a maximum of 92.4 km (offshore; mean 51 SD 36.4) and 81.1 km (nearshore; mean 47.2 SD 24.5) from their deployment sites. PSAT deployments in Indonesia lasted a mean of 165 days (SD 32), and the single SPLASH tag deployment lasted 64 days. Tags deployed in Indonesia popped off a maximum of 259.2 km (mean 158.6 SD 91.9) from their deployment sites. We interpreted the 95% probability polygon for all tags from a given deployment location to be a metric for those animals' combined geographic range (Pedersen et al., 2011). The 95% polygon areas were similar across regions: 79,293 km^2 (Indonesia), 70,926 km^2 (Mexico Offshore), and 66,680 km^2 (Mexico Nearshore), which on average is roughly equivalent to a circle with a radius of 150 km.

We analyzed stable isotope ratios of white muscle tissue samples from 74 mantas across the four study sites (Mexico Nearshore, $n = 15$; Mexico Offshore, $n = 12$; Indonesia, $n = 8$; Sri Lanka, $n = 39$). Results from stable isotope analyses showed differences in δ^{15}N values between eastern Pacific populations and western Pacific/Indian Ocean populations that are consistent with patterns observed in different regional denitrification regimes, with enriched δ^{15}N values in more productive eastern Pacific waters and depleted δ^{15}N values in oligotrophic waters of the western Pacific and Indian ocean (Seminoff et al., 2012) (Fig. 2). We also observed differences in δ^{13}C values between the two populations in Mexico that are typically observed between coastal and offshore environments (Hobson, 1999), with more enriched δ^{13}C values in coastal manta samples and depleted δ^{13}C values in offshore manta samples. This suggests that mantas tagged at the mainland site are foraging in nearshore environments, while those tagged at the offshore site are foraging in more pelagic environments, which is consistent with the movement patterns observed in tagging data. Isotopic differences between mantas sampled in Sri Lanka and Indonesia were less well defined, likely due to the similarity of baseline isotopic signatures in these two regions (Heikoop et al., 2000). Our model selection approach grouped Indonesian and Sri Lankan populations but kept Mexican populations distinct in the best-fit model by an AIC margin of 17.56 (Supplementary information), supporting the observed isotopic differences