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



Joshua D. Stewart^{a,b,*}, Calvin S. Beale^c, Daniel Fernando^{d,b,e}, Abraham B. Sianipar^f,
Ronald S. Burton^a, Brice X. Semmens^a, Octavio Aburto-Oropeza^a

^a Scripps Institution of Oceanography, University of California, San Diego, 9500 Gilman Dr., La Jolla, CA 92093, USA

^b The Manta Trust, Catemwood House, Corscombe, Dorchester, Dorset DT2 0NT, UK

^c Misool Manta Project, Jalan Gunung Umsini No. 51, RT 03/RW 03 Kampung Baru, Sorong, Papua Barat 98413, Indonesia

^d Department of Biology and Environmental Science, Linnaeus University, 39182 Kalmar, Sweden

^e Blue Resources, 86 Barnes Place, Colombo 00700, Sri Lanka

^f Conservation International, Jalan Pejaten Barat No. 16A, Kemang, Jakarta 12550, Indonesia

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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.

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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

* Corresponding author at: Scripps Institution of Oceanography, University of California, San Diego, 9500 Gilman Dr., La Jolla, CA 92093, USA.

E-mail addresses: j8stewart@ucsd.edu (J.D. Stewart), calvin@misoolecoresort.com (C.S. Beale), daniel@mantatrust.org (D. Fernando), abraham.sianipar@gmail.com (A.B. Sianipar), rburton@ucsd.edu (R.S. Burton), bsemmens@ucsd.edu (B.X. Semmens), maburto@ucsd.edu (O. Aburto-Oropeza).

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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 km² (Indonesia), 70,926 km² (Mexico Offshore), and 66,680 km² (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 $\delta^{15}\text{N}$ values between eastern Pacific populations and western Pacific/Indian Ocean populations that are consistent with patterns observed in different regional denitrification regimes, with enriched $\delta^{15}\text{N}$ values in more productive eastern Pacific waters and depleted $\delta^{15}\text{N}$ values in oligotrophic waters of the western Pacific and Indian ocean (Seminoff et al., 2012) (Fig. 2). We also observed differences in $\delta^{13}\text{C}$ values between the two populations in Mexico that are typically observed between coastal and offshore environments (Hobson, 1999), with more enriched $\delta^{13}\text{C}$ values in coastal manta samples and depleted $\delta^{13}\text{C}$ 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

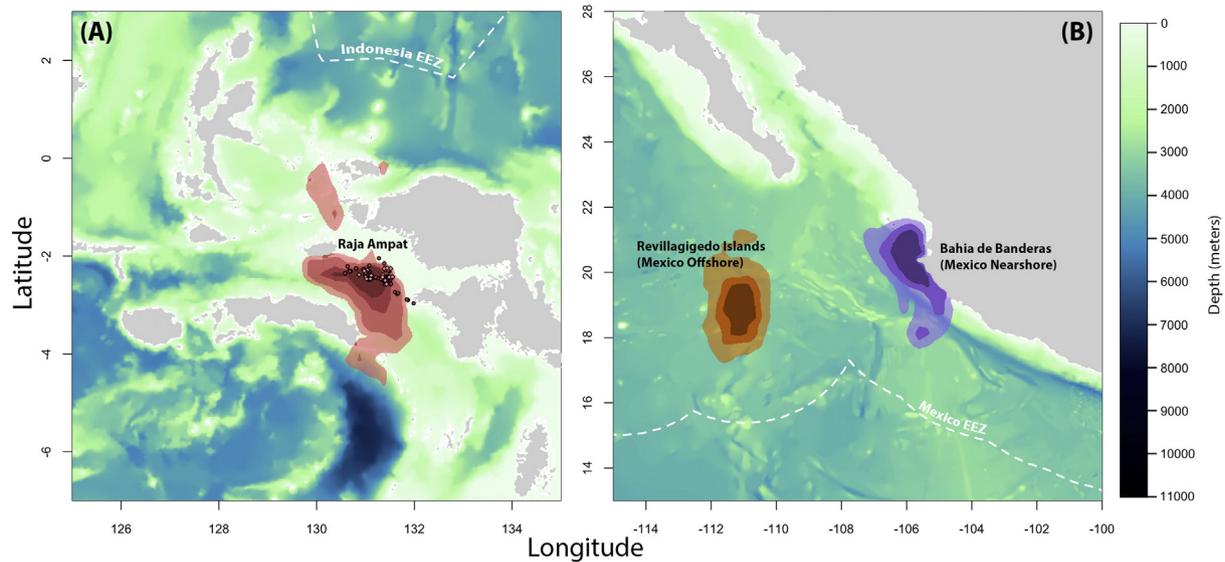


Fig. 1. Tag locations from mantas tagged in (A) Raja Ampat, Indonesia and (B) Pacific Mexico. Polygons represent probability density surfaces for all tags from a given deployment location. Light to dark shades represent 95%, 75%, and 50% probability contours. The 95% contour represents the smallest area where tagged animals were expected to spend 95% of their time. Filled circles (dark red) and diamonds (light red) in (A) represent GPS and Argos satellite locations, respectively, recorded by the single deployed SPLASH tag. Maps and probability density surfaces were created using R. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

outlined above. Based on an estimated weight of 1500 kg for an individual of 5 m disc width (Notarbartolo-Di-Sciara, 1988) we calculated a 100% tissue turnover time of 665 days using published body mass-tissue incorporation rates for teleosts and elasmobranchs (Weidel et al., 2011; Kim et al., 2012). This suggests that isotope values reported here represent multi-year averages, and that the separation between populations observed in satellite telemetry results remains true on multi-year time scales.

We included a subset of tissue samples in genetic analyses (Mexico Nearshore, $n = 12$; Mexico Offshore, $n = 10$; Indonesia, $n = 8$; Sri Lanka, $n = 12$). Genetic results were consistent with satellite telemetry and stable isotope analysis. We recovered 25,040 Single Nucleotide Polymorphisms (SNPs) from double digest Restriction-site Associated DNA (ddRAD) sequencing and included 3108 SNPs in the final

population structure analysis (See Supplementary Information). While our sample size per location was relatively low, high-throughput sequencing methods such as ddRAD provide many thousands of SNPs across which to estimate population structure. As a result, the large number of loci reduces the probability of miss-assigning an individual to a population based on allele frequencies, despite small sample sizes that may confound population structure analyses using traditional sequencing methods (Nikolic et al., 2009). Analysis with Structure 2.3 provided the greatest support for 3 populations, which demonstrate structure between Coastal Mexico, Offshore Mexico and Sri Lanka (Fig. 3). We did not include tissue samples from Indonesia due to low DNA yields (see Supplementary information).

4. Discussion

Using three separate methodologies that provide data at multiple spatial and temporal scales, we provide the first long-term information on the population structure and spatial ecology of the world's largest ray. The consistent agreement between satellite tagging, stable isotope and genetic results strongly suggest that oceanic manta rays in these regions form well-structured subpopulations and exhibit a high degree of residency.

These findings do not preclude occasional long-distance movements by the species. The large body size of oceanic manta rays makes the species physiologically capable of swimming long distances. For example, one individual was recorded traveling from mainland Ecuador to the Galapagos Islands, over 1400 km straight-line distance (Hearn et al., 2014). Additionally, long-distance movements may account for the occasional sightings of oceanic manta rays in regions outside their typical distribution (Duffy and Abbott, 2003; Couturier et al., 2015). However, the stable isotope and genetic data we present in this study demonstrate that such cases of long-distance movements are likely rare and do not generate substantial gene flow or interpopulation exchange of individuals. This is in contrast to other large filter-feeding elasmobranchs that exhibit low genetic differentiation and must therefore maintain higher rates of interpopulation exchange (Hoelzel et al., 2006; Schmidt et al., 2009). In the case of Hearn et al., 2014, eight out of nine tagged oceanic mantas remained within a restricted geographic range, and Graham et al., 2012 recorded no long-distance movements by oceanic mantas tagged in the Gulf of Mexico. Many of the locations

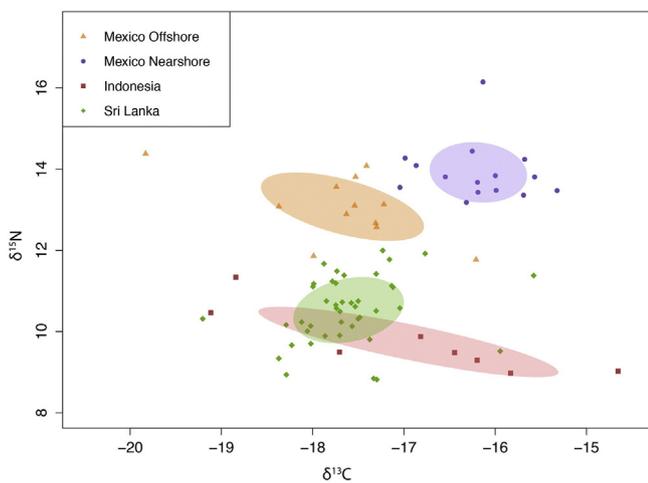


Fig. 2. Isotope signatures of manta populations across the Indo-Pacific. Shaded polygons represent sample-size corrected standard ellipses for each population, calculated using the package 'SIBER' in R. Differences in $\delta^{15}\text{N}$ values between populations from Mexico and those from Indonesia and Sri Lanka correspond to higher baseline $\delta^{15}\text{N}$ values in the highly productive Tropical Eastern Pacific as compared with the more oligotrophic waters of the Western Pacific and Indian Oceans. The shift in $\delta^{13}\text{C}$ values between the two populations in Mexico corresponds to differences in baseline $\delta^{13}\text{C}$ values between the coastal and offshore habitats occupied by the two populations.

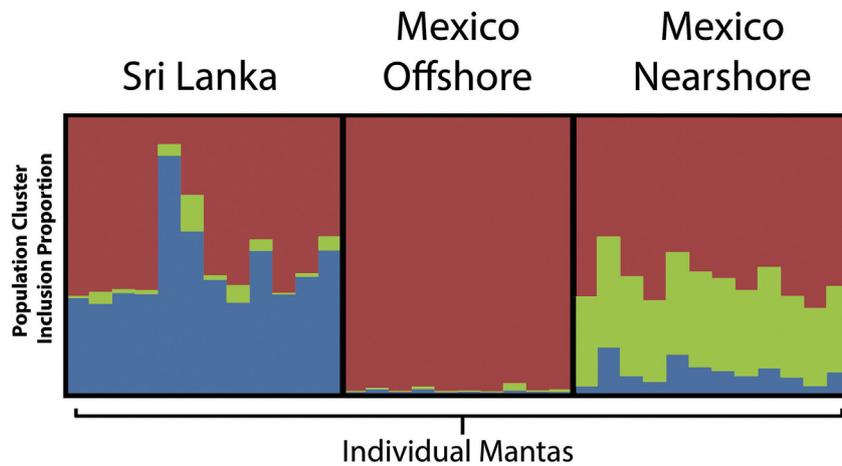


Fig. 3. Estimated genetic structure of oceanic manta populations in Pacific Mexico and Sri Lanka. Each individual included in the genetic analysis is represented by a vertical line, which is partitioned into colored segments representing the estimated membership of an individual in three model-defined population clusters (not necessarily related to geographic populations). Three population clusters ($K = 3$) received the highest likelihood score in three replicates of Structure analyses for a range of $K = 1$ to $K = 5$. We did not include Indonesian samples in the final population structure interpretation due to low DNA yield. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

where *M. birostris* is found regularly, including all of the field sites in this study, are seasonal aggregation sites with peaks in manta occurrence that last for several weeks or months, and long periods with few or no sightings (Luiz et al., 2009; Giron dot et al., 2014). Despite our satellite tag deployments covering both peak sighting periods and subsequent low seasons, all tagged mantas remained close to their respective tag deployment location. Our findings suggest that these seasonal cycles do not include long-distance movements, but instead may simply represent transitions from coastal aggregation sites to nearby offshore habitats where there is far less survey effort and therefore fewer sightings. Consequently, the available data on *M. birostris* suggest that the most relevant management unit for the species exists at the local or regional scale.

Since the genus was split into two species (Marshall et al., 2009), *M. alfredi* has been considered a predominantly coastal, resident species while *M. birostris* has been considered a pelagic migrant (Couturier et al., 2012). However, recent studies have blurred the proposed ecological characteristics that define the movements and habitat selection of the two species (Kashiwagi et al., 2011). For example, while reef manta rays are predominantly resident, they also undertake occasional long-distance movements of several hundred kilometers (Germanov and Marshall, 2014; Jaïne et al., 2014; Braun et al., 2015). Further, reef manta rays access both coastal habitats and offshore, pelagic habitats where they are presumably foraging (Braun et al., 2014; Jaïne et al., 2014). Similarly, oceanic manta rays are predominantly resident based on our findings, but also make occasional long-distance movements (Hearn et al., 2014), and feed both in coastal (JDS unpubl.) and deeper, offshore habitats (Stewart et al., in press). Given these similarities in the two species' spatial ecology and habitat use, it remains unclear what factors originally drove speciation and continue to maintain a species boundary. Past introgression (Kashiwagi et al., 2012) and recent evidence of hybridization (Walter et al., 2014) suggest that this boundary may only be weakly maintained, perhaps in part due to the overlap in the two species' ecology.

Our tagging data were collected over several years, while the life span of these animals may exceed 40 years (Couturier et al., 2012). While the stable isotope and genetic results suggest that occasional long-distance movements do not contribute substantially to mixing between populations, further studies are necessary to quantify rates of interpopulation exchange, a useful parameter in identifying the extinction risk of local populations (Hanski, 1999). It is also important to note that we did not deploy tags in Sri Lanka, and we were not able to obtain genetic results from Indonesia. Consequently, our two sites in Mexico were the only populations in this study where we obtained results

from all three methods. However, these two sites are also the most geographically proximate, and all three methods indicate population structure and spatial segregation between the two populations. Future genetic studies incorporating samples from a broader range of sites would contribute greatly to our understanding of the species' global population structure and gene flow.

Tag-recorded diving behavior and submersible observations at the same offshore Mexican islands in this study (Stewart et al., in press) indicate that mantas exhibit a high degree of behavioral plasticity and change their vertical habitat use seasonally in order to exploit zooplankton aggregations that remain relatively constant in abundance, but not vertical location, throughout the year (Blackburn et al., 1970). Along with a year-round food source, suitable juvenile habitat overlapping with or adjacent to adult habitat would eliminate the main incentives for long-range migratory behavior. Researchers rarely observe juvenile oceanic manta rays in the wild at seamounts or islands, where the majority of in-water encounters occur. However, gill-net fisheries land high numbers of juveniles at our study site in Sri Lanka, primarily in offshore pelagic habitats, and juvenile oceanic manta rays are sometimes encountered in oceanic habitats far from shore in Mexico (R. Rubin, Pers. Comm.). This suggests that oceanic manta rays may exhibit age- or size-based habitat segregation, remaining within the same geographic region but exploiting different habitats. Alternatively, adult and juvenile oceanic mantas may use similar offshore pelagic habitats but juveniles may avoid cleaning stations and other near-shore habitats in an effort to reduce predation until they reach a sufficient size, paralleling the use of nursery habitats common in other elasmobranchs (Heupel et al., 2007).

While the movements of highly mobile marine species across international boundaries often necessitates management by international agencies, agreements or conventions, these large-scale efforts at management often fall short of preventing the overharvest of vulnerable marine species (Fonteneau, 2007; Ferretti et al., 2010; Rocha et al., 2014). On the other hand, species with poorly connected subpopulations and smaller geographic ranges have a higher local extinction risk than species that form well-connected metapopulations (Hanski, 1999), presenting a different set of management challenges. However, managing non-mobile species can be more straightforward for socioeconomic reasons (e.g. fewer stakeholder groups, proximity of consumers to resource) (Ostrom, 1999) and practical management considerations (e.g. jurisdictional considerations, smaller enforcement area). Nonetheless, in cases where adequate management action is not taken, non-mobile species often suffer more dramatic local population impacts than mobile species (McCauley et al., 2015).

Although our observations are based on samples from only four populations, their ecological and oceanographic characteristics span much of the range that oceanic mantas are known to inhabit. Therefore, the apparent insularity of the study populations has substantial implications for the species' conservation and management. Our results indicate that fisheries for manta rays are drawing on vulnerable, local populations, increasing the rate of population decline and the risk of local extinctions. In light of these findings, at least one major population decline of oceanic manta rays can be interpreted as a virtual extirpation of the species. A fishery for mantas in southern Baja California, Mexico in the 1980s and '90s led to the near disappearance of the species in what was perhaps the best-known location for diver interactions with mantas (R. Rubin, G. Notarbartolo di Sciarra, Pers. Comm.). Even after twelve years of continuous protection by the Mexican government, there are no signs of recovery in the Gulf of California's manta population, which is consistent with the insularity of the two populations in Pacific Mexico studied here.

The restricted geographic ranges revealed by tagging data suggest that oceanic manta rays can benefit from local management initiatives, and that reducing or eliminating local fisheries will play a critical role in preventing population declines. The effectiveness of local-scale management is exemplified by the community-driven Raja Ampat Shark and Ray Sanctuary in Indonesia. The sanctuary covers a substantial portion of the geographic range of mantas we tagged in Indonesia, and has a strong track record of self-enforcement and community engagement. In Mexico, local-scale management action could include expanding the Revillagigedo Islands Biosphere Reserve to cover the pelagic habitat between the islands and increasing the existing 12-mile buffer zone around each island to further protect the manta population throughout its geographic range. Furthermore, the spatial ecology of oceanic manta ray populations should be incorporated into marine protected area planning, especially in the case of so-called 'mega-MPAs' that could cover the entire geographic range of a population, to increase the value of these large designations to the species. Local management actions such as these are far less challenging to implement than the international management efforts that have thus far dominated manta ray conservation (Ostrom, 1999).

In some cases even populations of oceanic manta rays with relatively restricted ranges can straddle international borders, for example in Peruvian and Ecuadorian waters (Hearn et al., 2014). Under such circumstances international efforts to coordinate management action remain a valuable conservation tool and should not be abandoned. However, our study suggests that local and national management efforts may operate at scales most relevant to oceanic manta ray populations, and such efforts have been underutilized in addressing population declines of this vulnerable species. This study highlights the importance of identifying ecological units and understanding the relevant scales at which ecological processes occur in threatened species in order to design and implement effective conservation strategies.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.05.016>.

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