



Population dynamics of oceanic manta rays (*Mobula birostris*) in the Raja Ampat Archipelago, West Papua, Indonesia, and the impacts of the El Niño–Southern Oscillation on their movement ecology

Calvin S. Beale^{1,2}  | Joshua D. Stewart^{2,3} | Edy Setyawan^{2,4}  | Abraham B. Sianipar⁵ | Mark V. Erdmann⁶ 

¹Misool Manta Project, Sorong, Indonesia

²The Manta Trust, Dorchester, UK

³Scripps Institution of Oceanography, UC San Diego, La Jolla, California

⁴Sea Sanctuaries Trust, London, UK

⁵Conservation International Indonesia, Jakarta, Indonesia

⁶Conservation International Indonesia Marine Program, Bali, Indonesia

Correspondence

Calvin S. Beale, Misool Manta Project, Jalan Basuki Rahmat, Sorong, West Papua 98412, Indonesia.

Email: calvin.beale@live.co.uk

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Abstract

Aim: Our aim was to collect sightings data on oceanic manta rays (*Mobula birostris*) within the Raja Ampat Archipelago to better understand their population dynamics within the region. These data were compared with environmental variables to seek correlates that may explain any variations in observed sightings frequency. Combined, it is hoped this knowledge will be used to aid effective management of this species in the region.

Location: Raja Ampat Archipelago, West Papua, Indonesia.

Methods: We collected and catalogued photo-identification of individuals to create a sightings database. To generate estimates of abundance, survival, sighting probability and recruitment to the population, we used a POPAN mark-recapture model. We considered time-varying and fixed values for each parameter and possible covariate relationships of the El Niño–Southern Oscillation (ENSO) and sex.

Results: A total of 588 individuals were identified over six years, of which 72.4% were female, and 28.2% of individuals were resighted. There was an exponential increase in sightings during the 2015–2016 ENSO event despite constant effort; significant correlation was found between sightings and the multivariate ENSO index and with sea surface temperatures but not with chlorophyll-a. Mark-recapture analysis shows a clear relationship between ENSO and entry probability, and the most parsimonious model estimated a superpopulation size *N* of 1875 individuals.

Main conclusion: Oceanic manta ray distributions appear to be impacted by ENSO-related climate phenomena. Our findings on the relationship of ENSO to manta sightings and distribution indicate that oceanic manta rays are likely sensitive to large-scale climatic variability. This illustrates the potential impacts of climate change on oceanic manta populations and the need to consider climate impacts in developing management strategies. Continued photo-ID, tagging and population genetics would greatly

enhance knowledge and help develop management strategies that bolster conservation of the species.

KEYWORDS

citizen science, climate change, conservation, demographics, marine megafauna, mobulid rays

1 | INTRODUCTION

Human impacts on marine species have increased rapidly in the last 100 years, with many species driven to the verge of extinction by direct exploitation in fisheries (Dulvy et al., 2014; Dulvy, Metcalfe, Glanville, Pawson, & Reynolds, 2000; Jackson et al., 2001; De Mitcheson et al., 2013). Marine megafauna species have been especially vulnerable to severe population declines due to their generally low reproductive rates and susceptibility to harvest in fisheries (Dulvy et al., 2014, 2000; Lewison, Crowder, Read, & Freeman, 2004; McCauley et al., 2015). In addition to fishing pressure, human activities further impact marine species through pollution (Derraik, 2002; Islam & Tanaka, 2004), global climate change (Doney et al., 2012; Harley et al., 2006) and increasing atmospheric carbon dioxide levels (Fabry, Seibel, Feely, & Orr, 2008; Hall-Spencer et al., 2008). These anthropogenic impacts act together to degrade the structure and function of marine ecosystems (Dulvy et al., 2008; Harley et al., 2006; Hawkes, Broderick, Godfrey, & Godley, 2007). Predicted poleward shifts in zooplankton and reductions in tropical zooplankton densities (Chust et al., 2014; Stock, Dunne, & John, 2014; Woodworth-Jefcoats, Polovina, & Drazen, 2017) may have particularly severe consequences for tropical food chains and marine megafauna. Marine megafauna are often philopatric to important aggregation sites such as mating and pupping grounds (Engelhaupt et al., 2009; Mourier & Planes, 2013; Sandoval Laurabaquio-A et al., 2019), and shifts in prey distribution may force them to travel longer distances between foraging grounds and other locations important to life history, impacting individual fitness or population viability (Péron, Weimerskirch, & Bost, 2012; Thorne et al., 2016).

Manta rays (previously genus *Manta* but recently subsumed into *Mobula*) (Marshall, Compagno, & Bennett, 2009; White et al., 2018) are large planktivores found circumglobally in tropical and subtropical waters. In addition to targeted fisheries, manta rays are incidentally captured in a wide variety of fisheries and gear types (Croll et al., 2016). Their low reproductive rates and conservative life history characteristics make them highly susceptible to population declines, and fisheries are likely to be unsustainable even at low catch rates (Dulvy et al., 2014). Although data on population trends are limited, several studies have reported declines in manta and devil ray sightings and fisheries landings, suggesting that fisheries are negatively impacting populations in many regions (Croll et al., 2016; Lewis et al., 2015; Ward-Paige, Davis, & Worm, 2013). Population declines have led to the implementation of several international, national and local management strategies for mobulid rays in the last decade (Croll et al., 2016; Lawson et al., 2017).

Oceanic manta ray (*Mobula birostris*) populations appear to be regionally distinct, and there is evidence for fisheries-induced declines in several isolated subpopulations (Lewis et al., 2015; Moazzam, 2018; Stewart, Beale, et al., 2016). In the closely related reef manta ray (*Mobula alfredi*), local declines have also been recorded in response to fisheries (Croll et al., 2016; Lawson et al., 2017; Marshall et al., 2011). In Indonesia, high-effort gill net fisheries in the Lembeh Strait captured 1,424 manta rays (*Mobula* spp.) in a 10-month period (Cochrane, 1997), leading to an apparent local extirpation (D. Djalal & A. Doali, *personal communication*). Indonesia was reported to be the third largest exporter worldwide (Heinrichs, O'Malley, Medd, & Hilton, 2011) for *Mobula* gill rakers up until the nationwide ban of fishing manta rays in January 2014 (KEPMEN-KP 4/2014), with some communities continuing to illegally harvest manta gills to date (E. Setyawan, *personal communication*). The majority of these reports are based on fisheries-dependent data, sightings per unit effort trends and anecdotal reports; there is a need for more quantitative data on abundance and trends in manta populations.

El Niño–Southern Oscillation (ENSO) events are known to drive range and demographic changes in many species (Holmgren, Scheffer, Ezcurra, Gutiérrez, & Mohren, 2001; Meserve et al., 1995; Ribic, Ainley, & Spear, 1992; Thorne et al., 2016; Ticktin, 2003). Foraging grounds are often affected by ENSO-driven weather changes including precipitation (Brown, Field, & Letnic, 2006; Marshal, Krausman, Bleich, Ballard, & McKeever, 2002) and wind patterns (Schreiber, 2002; Thorne et al., 2016). Temperature extremes and changes of prevailing winds during ENSO events have led to longer and more extreme fire seasons, increased flooding, significant loss of habitat (Alencar, Nepstad, & Diaz, 2006; Andrews, Antweiler, Neiman, & Ralph, 2004; McKenzie, Gedalof, Peterson, & Mote, 2004) and increased infectious disease risks in both terrestrial and marine ecosystems (Harvell et al., 2002).

Marine species are heavily impacted by ENSO-related climatic variables including sea surface temperature (SST) and associated phytoplankton and zooplankton densities (Campbell, Liu, Nolla, & Vault, 1997; Diaz, Hoerling, & Eischeid, 2001; Iriarte & González, 2004; Yoder & Kennelly, 2003) often causing distributional shifts within species (Forcada & Trathan, 2009; Kumar, Pillai, & Manjusha, 2014; Lo-Yat et al., 2011; Péron et al., 2012; Quiñones, Carman, Zeballos, Purca, & Mianzan, 2010). These ENSO-induced distributional changes also have the potential to influence fisheries catch rates and population viability as species migrate through or into fishing zones (Kumar et al., 2014; Wallace, Kilham, Paladino, & Spotila, 2006). Changes in prevailing ocean currents during ENSO years diverting productive waters and zooplankton have also been shown

to affect population dynamics (Lo-Yat et al., 2011; Pearce & Phillips, 1988). Mass mortalities of coral reefs have occurred due to long periods of high-temperature exposure with far-reaching impacts on reef-reliant species viability (Glynn, 1999; Graham et al., 2007; Lo-Yat et al., 2011; Quiñones et al., 2010; Wallace et al., 2006). As ENSO events appear to be increasing in frequency and strength (National Oceanic & Atmospheric Administration, 2017), understanding their impacts on manta ray species will be important for developing effective management strategies.

Within the Raja Ampat Archipelago and along the coastline of West Papua, there are a number of cleaning stations that are visited seasonally by both reef and oceanic manta rays (Setyawan et al., 2018). This area is renowned for both its high marine biodiversity and its strong ocean currents (Mangubhai et al., 2012). Known as the Indonesian Throughflow, warm western Pacific Ocean water pushes down into the Ceram and Halmahera Seas and through Indonesia to the Indian Ocean (Gordon, 2005; Gordon, Susanto, & Vranes, 2003). This generally oligotrophic water is regularly mixed vertically by south-east monsoon ocean upwelling throughout the region, leading to local productivity hotspots during Autumn months (Tang, Kester, Ni, Kawamura, & Hong, 2002; Wyrski, 1962). The region is a heavily trafficked tourism destination, with

a number of live-aboard vessels and resorts providing access to cleaning stations and other coral reef habitats where manta rays are frequently encountered.

In this study, we describe the demographic characteristics of the oceanic manta ray population, sighting trends across time, the relationship of environmental covariates to sightings, and perform a mark-recapture analysis. In particular, we emphasize the apparent importance of the El Niño–Southern Oscillation in driving sightings trends and possible distributional changes in the regional oceanic manta ray population.

2 | METHODS

2.1 | Study area

Raja Ampat covers approximately 50,000 km² of land and sea off the north-western tip of New Guinea, in the Indonesian province of West Papua. We catalogued manta ray sightings from three regions: Dampier including all sightings recorded in central and northern Raja Ampat; Misool including all sightings in southern Raja Ampat; and Fakfak including all those recorded south-east of Raja Ampat along the Fakfak coastline of West Papua (Figure 1).

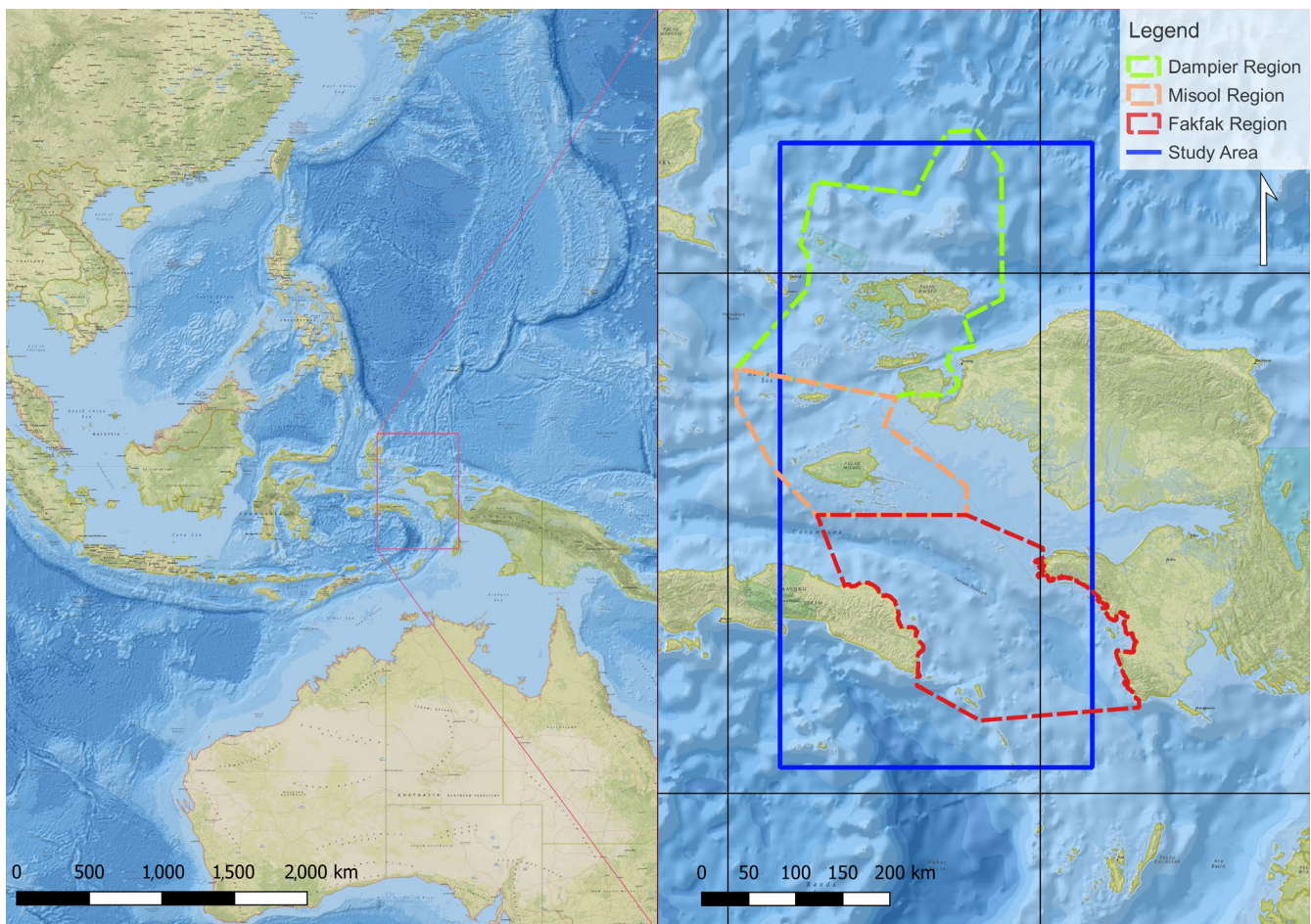


FIGURE 1 Raja Ampat and West Papua. Study area denoted by blue square. Dashed green & orange lines (Dampier and Misool regions) outline Raja Ampat Archipelago. Red outline indicates the Fakfak region

2.2 | Data collection/photo-identification

2.2.1 | Sighting records

The majority (75.4 %) of photo-IDs were collected by tourists and submitted to the project's photo-ID database. All data were collected from cleaning stations. We used the unique ventral spot patterns found on manta rays to identify and catalogue individual oceanic manta rays, a technique applied to both species of manta rays (Marshall & Pierce, 2012). Starting in 2011, data were collected annually by the authors during the tourism season, running from September to June. The strong monsoon winds during the months of July and August prevented trips from running and therefore precluded the collection of data (no data were submitted from other sources during this period either). Photo-ID images collected prior to August 2011 were added to the catalogue only when date and location were verifiable by the observer. These images were mostly from April 2011 but include sightings back to May 2004.

All submitted photographs and videos were dated, and all usable images were subsequently compared against the existing ID catalogue to determine whether the individual was a new capture or recapture. A new sighting record was then added to the database to reflect this. A *sighting* was defined as a capture record on a specific site on a specific day; a *recapture* was defined as a sighting of a previously identified individual on a different day, or on a different site at least one-hour post-initial sighting. Similar to Stevick, Palsbøll, Smith, Bravington, and Hammond (2001), very low-quality images were discarded to reduce identification errors. Secondary verification of IDs was performed manually by an outside expert and a third time using the Manta Trust's "IDTheManta" matching software by trained research staff (The Manta Trust, 2018).

2.2.2 | Physical characteristics

Additional information recorded for each individual included colour morph, sex, estimated size, sexual maturity (identified via pregnancy or presence of mating scars for females and calcified claspers for males), and external injuries as per Marshall and Bennett (2010) and Stevens (2016).

2.2.3 | Sighting seasonality and survey effort

We pooled sightings data by month and split them into equal periods of six months. We classified August through January as the Autumn season and February through July as the Spring season. This split maintains equal sightings opportunities for both seasons while separating the two major influencing weather patterns in the area: the very windy south-east monsoon in Autumn and the rainier north-west monsoon in Spring. We recorded survey effort from Autumn 2011 through Spring 2016. The effort value is reported as the number of divers who dived on the primary oceanic manta ray cleaning site Magic Mountain per month in the Misool region, southern Raja Ampat. Effort data prior to Autumn 2011, or from other regions, were not available

and so not included in the analysis. While this is an imperfect metric of effort, 77% of sightings were collected at Magic Mountain, and precise records of diver visitation to the site were recorded by Misool Eco Resort, making it the best available proxy for survey effort.

2.2.4 | Climate conditions

During 2015, an El Niño–Southern Oscillation (ENSO) event occurred which altered normal weather patterns around the globe (National Oceanic & Atmospheric Administration, 2017). This event was the third strongest ever recorded (L'Heureux et al., 2017) and caused local anomalies in Raja Ampat including a drop in sea temperature and level, increased precipitation and an extended south-east monsoon. We examined the relationship between ENSO climatic factors and manta sightings to determine whether the regional population is sensitive to large-scale climatic events. The multivariate El Niño–Southern Oscillation index (MEI) recorded by the US National Oceanic and Atmospheric Administration (National Oceanic & Atmospheric Administration, 2017) was chosen as the index value best representing the climate conditions throughout the year in the study area. This index takes into account weighted averages of six meteorological variables across the tropical Pacific (Bamston, Chelliah, & Goldenberg, 1997). We averaged the MEI across the seasonal sighting periods, from February to July for the Spring season and August to January for the Autumn season for use in our analysis. To examine a possible mechanism for increased sightings in the region, we also explored the relationship between sightings and sea surface temperature (SST) and chlorophyll-a (Chl-a). We used the Xtractomatic R package (Mendelssohn, Bessey, & Foley, 2018) to download satellite-derived seasonal averages of SST and Chl-a for the study region. We used Bayesian linear models to explore relationships between the number of manta sightings per season, and MEI, SST and Chl-a covariates. We considered all seasons together, only Autumn seasons, and only Spring seasons independently to determine if covariate effects were most relevant in a certain season. We custom coded the linear models in R using the software Just Another Gibbs Sampler (JAGS) (Plummer, 2004).

2.3 | Abundance and survivorship

2.3.1 | Mark-recapture modelling

To generate estimates of abundance, survival, sighting probability and recruitment to the population, we used a POPAN mark-recapture model in the R package RMark (Cooch & White, 2011; Laake, 2013). The model estimates four main parameters: survival probability (Φ), entry probability ($pent$), sighting probability (p) and superpopulation size (N). We considered time-varying and fixed values for each parameter and possible covariate relationships of ENSO and sex. We tested models with every possible combination of time-varying/fixed and covariate relationships for every parameter, which resulted in a suite of 125 candidate models (Appendix S1: Table S1.1). We used Akaike's information criterion for small

sample sizes (AIC_c) to compare candidate model fits and select the best-fit model (Burnham and Anderson, 2004), and we report the top 19 models in the results (where AIC_c weight ≥ 0.002). Given the paucity of photo-ID contributions prior to 2010, we only included sightings from the Spring 2010 season onwards in the mark-recapture analysis. Analysis code is provided in Data S1. Survival estimates are best interpreted as apparent survival, which is equivalent to $(1 - [\text{mortality} + \text{emigration}])$ (White & Burnham, 1999).

3 | RESULTS

3.1 | Data collection/Photo-identification

3.1.1 | Sighting records

We identified a total of 588 individual oceanic manta rays within the 856 total photo-ID sightings dated between 17/05/2004 and 13/06/2016 (Table 1). Only 12 sightings were submitted from prior to Spring 2010. Records were submitted from 18 dive sites within Raja Ampat and West Papua.

Due to the nature of collecting data from volunteer sources, time stamps were often inaccurate or missing from submitted data. Only 36% ($n = 306$) of sightings were recorded with accompanying time of day, 213 of which were from Misool Eco Resort operations. Sighting times were heavily influenced by the trip schedule of the resort. Sightings were most frequent between 12:00 and 13:00, accounting for 26% of records, while the two-hour period between 11:30 and 13:30 accounted for 43.4% of all sighting records.

3.1.2 | Sighting regions

The Misool region accounted for 84.8% of all oceanic manta ray sightings ($n = 726$), forming the major part of the database. The Dampier region accounted for a further 14.8% ($n = 127$) of all sighting records, and just three sightings were contributed from the Fakfak region. Six individuals were recaptured at two different cleaning stations at least 200 km apart (between the Dampier and Misool regions of Raja Ampat); the shortest time between these sightings was 229 days (mean 856 days \pm 249 SE). 80.6% of recaptures were on the same dive site at least one day later. A mean of 32 km (range 0.72 km–212.25 km) shortest distance (without crossing land) was found between recaptures on different sites.

One site in Misool region (Magic Mountain) made up 77.3% ($n = 662$) of the total sightings, while another in the Dampier region in central Raja Ampat (Blue Magic) contributed a further 10.9% ($n = 94$). These two easily accessible cleaning stations provide dive operators with the most frequent sightings of oceanic manta rays in Raja Ampat. The remaining 11.7% of sightings ($n = 100$) were spread over 16 other dive sites.

A total of 165 individuals were recaptured at least once (28.1% of database). The maximum number of sightings for one individual was seven, with 13 individuals captured five or more times. Of these

TABLE 1 Population demographic data

Sex	Number of individuals	Chevron	Melanistic	Recaptured	Sexually Mature	Observed Pregnant	Immature	Unknown Maturity
Female	409 (69.6%)	403 (98.5%)	6 (1.5%)	120 (29.3%)	122 (29.8%)	29 (7.1%)	13 (3.2%)	274 (67.0%)
Male	156 (26.5%)	151 (96.8%)	5 (3.2%)	46 (29.5%)	122 (78.2%)	-	18 (11.5%)	16 (10.3%)
Unknown	23 (3.9%)	22 (95.7%)	1 (4.3%)	0	-	-	0	23 (100%)
Total	588	576 (98.0%)	12 (2.0%)	166 (28.2%)	244 (41.5%)	29 (7.1%)	31 (5.3%)	313 (53.2%)

13 individuals, a total of 60 out of 70 recaptures were at Magic Mountain and all recaptures were in the Misool region. The longest period between sighting events of the same individual was 4,156 days from 2004/05/19 to 2015/10/05 (mean time between recaptures was 285 days \pm 32 SE). April showed the highest site recapture rate at Magic Mountain, with 23 individuals returning in at least two different years. Of these, seven were male and 16 were female, with 10 being seen in consecutive years.

3.2 | Population data

It was possible to determine the sex of 565 (96.1%) of the identified oceanic manta rays (Table 1). The majority of sexed individuals (72.4%) were female. Of the mature females, 29 were observed pregnant (19 during Spring seasons). Males only made up 27.6% of sexed individuals, producing a statistically significant female-biased

sex ratio of 2.62:1 ($\chi^2 = 113.29$, $df = 1$, $p < 0.001$). Recapture percentages of females (29.3%) and males (29.5%) were almost identical (Table 1), as were mean number of recaptures per individual: 1.47 for females and 1.48 for males. Of total sexed sightings, males were most common in 2013 (45% of the 53 sighting records) and 2014 (36% of the 59 sighting records) versus the overall annual mean of 29% (± 4.1 SE). The lowest monthly mean ratio of females to males was in June (1.94:1 \pm 0.43 SE) and highest in February (4.01:1 \pm 2.64 SE); overall, the monthly mean was 2.43:1 (± 0.36 SE).

Of the 833 sexed sighting records, there was a difference in sex ratios between regions of Raja Ampat. In the Dampier region, 14% of sightings were of males ($n = 16$) while in the Misool region male sightings contributed 30% of the total ($n = 213$). A total of 244 individuals were recorded showing mating scars, swollen & calcified claspers or in a state of pregnancy. Mating scars were only observed on the left pectoral fin similar to reef manta rays (Marshall & Bennett, 2010).

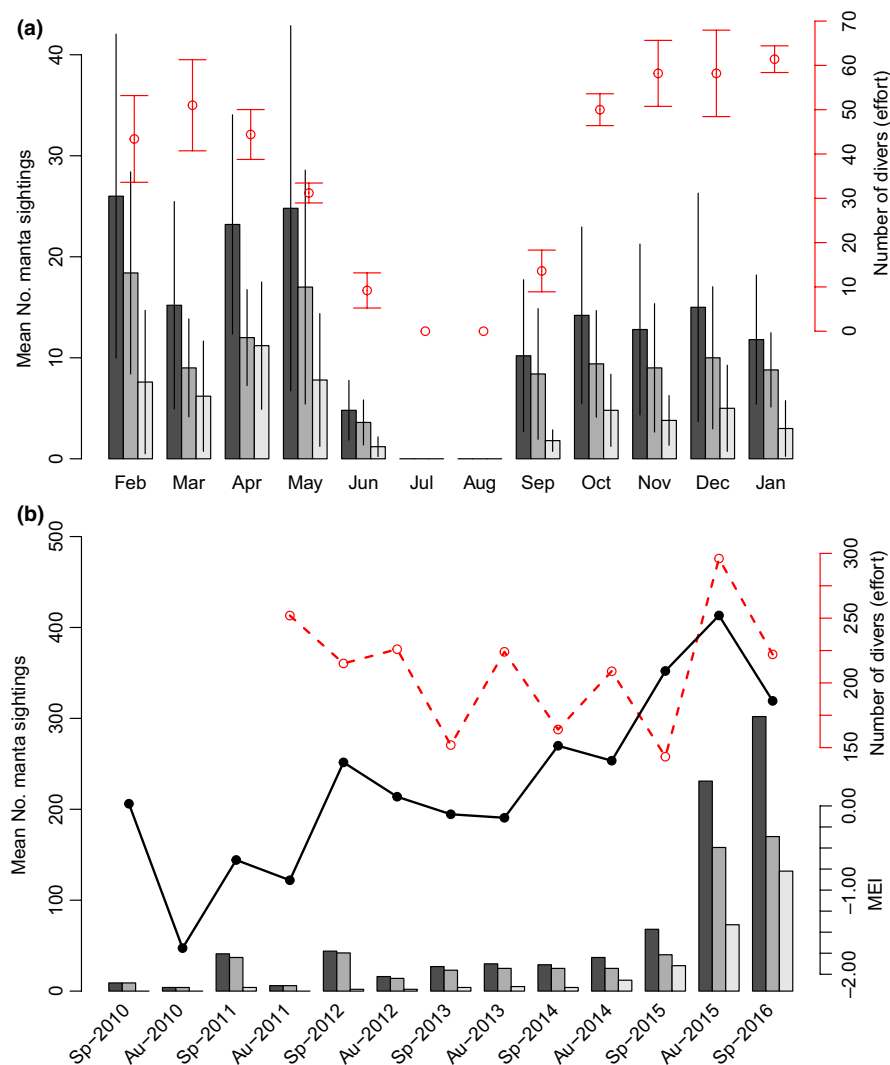


FIGURE 2 Sighting frequencies of oceanic manta rays (*Mobula birostris*) (Marshall et al., 2009; White et al., 2018) during the study period. Black bars represent total sightings, dark grey bars represent new captures, and light grey bars represent recaptures. Red represents survey effort. Panel (a): monthly variance of mean sightings (\pm SE) against mean survey effort (\pm SE) between Autumn 2011 and Spring 2016. Panel (b): seasonal sighting counts against both total effort and mean multivariate El Niño–Southern Oscillation index (MEI—black dots & line) for Spring (Sp) and Autumn (Au) seasons between Spring 2010 and Spring 2016

A total of 110 females had mating scars, and almost all mating scars were ventral (only two were recorded solely from the dorsal side).

3.3 | Sighting seasonality and survey effort

3.3.1 | Monthly sightings variation

Mean monthly total sightings were $13.2 (\pm 2.5 \text{ SE})$, with a distinct peak during February (mean $26.0 \pm 16.0 \text{ SE}$) and again during April–May (mean $24.0 \pm 9.9 \text{ SE}$). Overall, February had the highest mean total sightings recorded, while April had the highest mean recapture rates of $11.4\% (\pm 6.53 \text{ SE})$. Peak Autumn months' recapture rates occurred during December with mean $5.0\% (\pm 4.27 \text{ SE})$, less than half of peak Spring months' recapture rates (Figure 2a). Monthly survey effort was consistently highest from November through January (mean number of divers at Magic Mountain $59.3 \pm 3.9 \text{ SE}$) and again in March (mean $51.0 \pm 10.3 \text{ SE}$) (Figure 2).

3.3.2 | Seasonal variation

Sightings data collected between August 2011 and July 2016 (the period during which survey effort was also recorded) included 790 sightings, 528 of which were new captures and 262 recaptures (Figure 2a). Mean total sightings, new captures and recaptures were all higher during Spring (Sp) than Autumn (Au). Significant differences were found on total sightings ($\chi^2 = 28.48$), recaptures ($\chi^2 = 22.73$) and new captures ($\chi^2 = 9.82$) between Spring and Autumn ($df = 1$, $p < 0.01$ for all tests). Effort was significantly higher in Autumns ($\chi^2 = 45.99$, $df = 1$, $p < 0.001$) than Springs (Figure 2b). We found weak correlations between effort and sightings both on monthly and seasonal time scales (correlation coefficients < 0.5 in all cases). The effort per season slowly decreased over time with seasonal Autumn peaks, but increased greatly in Autumn 2015 during the period when sightings of manta rays were the highest ever recorded (Figure 2).

3.3.3 | Climate conditions and sightings

Between Spring 2010 and Autumn 2015, mean manta photo-ID sightings per month were $4.6 (\pm 1.3 \text{ SE})$ and mean manta photo-ID sightings per season were $28.3 (\pm 5.8 \text{ SE})$. Sightings across the study region in Autumn 2015 totalled 231 coinciding with the peak multivariate El Niño–Southern Oscillation index (MEI) value of 2.53 during August–September 2015, and the maximum number of sightings in one season followed this in Spring 2016 ($n = 302$). During Autumn 2015 and Spring 2016, 533 sightings were recorded, comprising 62% of the total sightings, with 26 oceanic manta rays recorded during one hour of diving on 30 September 2015. February 2016 had the highest monthly total sightings for Misool (47 new individuals, 37 recaptures). Across the whole study timeframe, May 2016 set the record with 62 new individuals and 34 recaptures recorded.

The recapture rate remained very low from 2011 through Spring 2014, $10.3\% (\pm 3.0 \text{ SE of total sightings})$ increased to 41% and then

44% during the Springs of 2015 and 2016, respectively (Figure 2b). Pregnancies had been observed on only two occasions (June 2011 & October 2014) before the El Niño. During the period June 2015 through June 2016, a further 27 pregnancies were recorded along with multiple cases of courtship behaviour observed at Magic Mountain.

Seasonal sea surface temperature (SST) changes within the study area show a trend of cooler surface waters during the Autumn period, appearing to push into southern Raja Ampat from the Ceram Sea. This cooling was much stronger during the El Niño (Autumn 2014 & Autumn 2015), showing a drop of approximately two degrees Celsius throughout the study area (Figure 3). Changes in chlorophyll-a (Chl-a) concentration across the study period were very minor, with a range of just 0.1 mg m^{-3} in the seasonal mean values for the study region (Appendix S1: Figure S1.1; Figure 4).

We found positive relationships between $\log(\text{sightings})$ and MEI, with the strongest relationships when considering Autumn seasons alone (median slope $\beta = 1.05$), or all seasons together (median $\beta = 1.00$), compared with only Spring seasons (median $\beta = 0.78$) (Figure 4). Bayesian posterior distributions provide a probability that a linear relationship is greater than or less than zero, analogous to a frequentist p value for slope terms. The probability of a positive slope β ($p > 0$) in $\log(\text{sightings}) \sim \text{MEI}$ was 0.99 for Autumn seasons only, 1.0 for all seasons together and 0.88 for Spring seasons only. We found negative relationships between $\log(\text{sightings})$ and SST, with the strongest relationships for Autumn (median $\beta = -3.1$; $p(\beta < 0) = 0.99$) and all seasons together (median $\beta = -1.99$; $p(\beta < 0) = 0.97$), and a weaker and less probable relationship in Spring seasons only (median $\beta = -0.37$; $p(\beta < 0) = 0.56$). We found less clear relationships between $\log(\text{sightings})$ and Chl-a in Autumn (median $\beta = 33.7$; $p(\beta > 0) = 0.85$), Spring (median $\beta = -1.99$; $p(\beta < 0) = 0.45$) or all seasons together (median $\beta = 14.6$; $p(\beta > 0) = 0.86$) (Figure 4).

3.4 | Abundance and survivorship

3.4.1 | Mark-recapture modelling

The top four POPAN mark-recapture models were within two Akaike information criterion (AICc) points of one another and had similar AICc weights (range 0.143 to 0.316) (Table 2) and are therefore all reasonable fits to the sightings data. The parameter estimates of all four top models were similar, and we report the best-fit model results here and include the next three model results in the Supporting Information (Appendix S1: Tables S1.2, S1.3 & S1.4). The model $\text{Phi}(\sim \text{Sex})p(\sim t)\text{pent}(\sim \text{ENSO})N(\sim \text{Sex})$ was the most parsimonious and accounted for the highest AICc weight of the potential models investigated (0.316). The most relevant consistency in all four top models was the relationship between El Niño–Southern Oscillation (ENSO) and pent, or the probability of an individual recruiting to the population, which is reflected in the sightings and covariate data reported earlier in this section. In addition, N (total population size or superpopulation) varies by sex in all four top models. Phi (survival probability) appears to vary by sex and may also be influenced by ENSO. Sighting probability (p) unsurprisingly varied across seasons

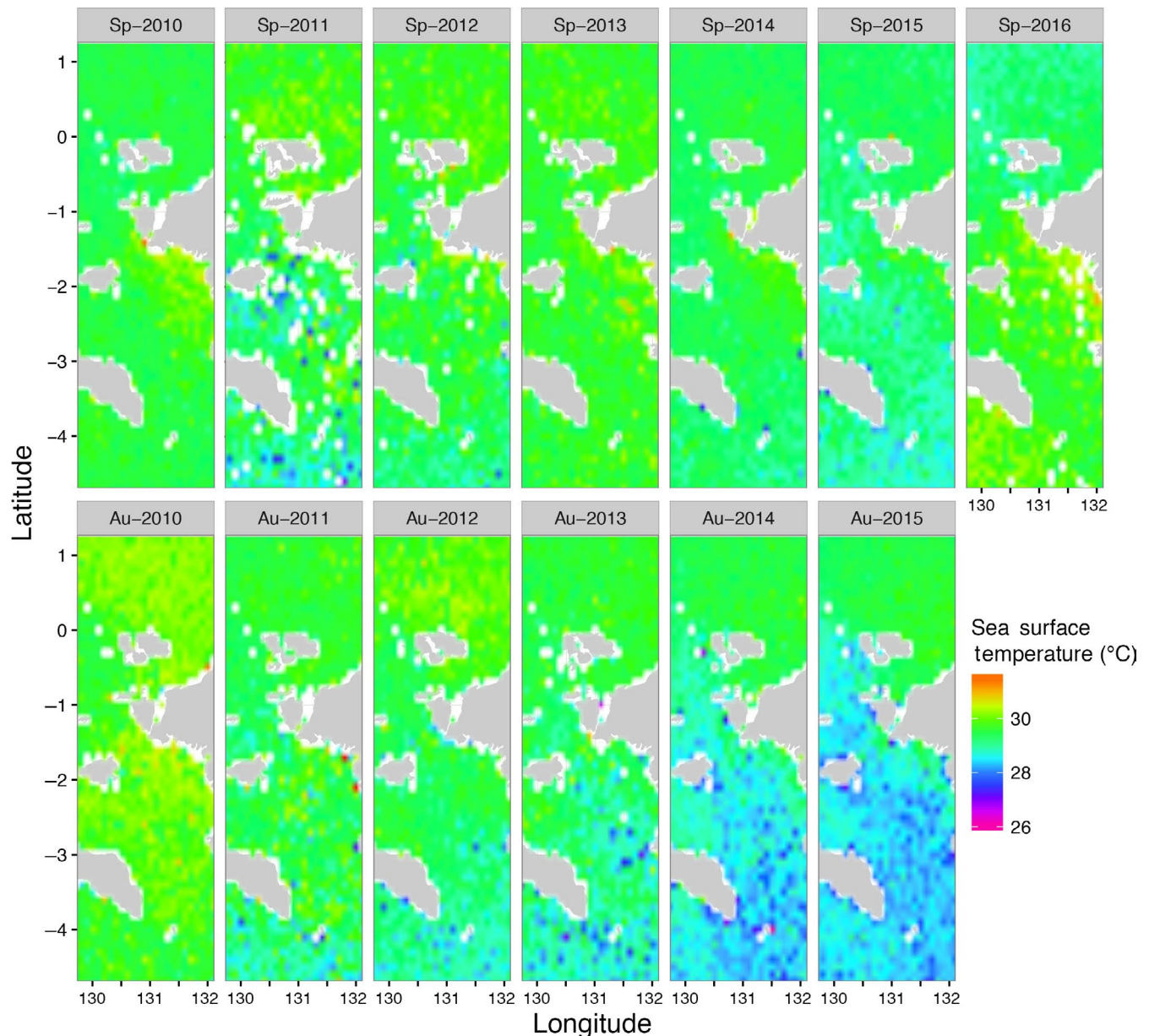


FIGURE 3 Mean sea surface temperature (°C) throughout the study area for Spring (Sp) and Autumn (Au) seasons from Spring 2010 through Spring 2016

and may be influenced by sex, although this was only included in the fourth most parsimonious model by AICc selection.

The most parsimonious model (Table 3) superpopulation size estimate (N) for both males and females totals 1,875 individuals (females mean $N = 1,415 \pm 178$ SE and males mean $N = 460 \pm 76$ SE). Mean female N reported by the four top models was 1,336 (± 177 mean SE) and males 458 (± 76 mean SE). Capture probability across seasons varied from 0.006% (Sp-2010) to 27.3% (Sp-2016). Entry probability into the population (pent) was reported as approximately zero for all seasons except for between Spring and Autumn 2015 when the pent rose abruptly to 0.356 (± 0.063 SE) for both males and females, coinciding with the dramatic increase in overall sightings. Apparent survival for females 0.88 (± 0.02 SE) was slightly lower than for males 0.91 (± 0.03 SE).

4 | DISCUSSION

Active photo-identification within the Raja Ampat Archipelago since August 2011 has catalogued 588 individuals from 856 sighting records, of which 72.4% are female. There was an exponential increase in sightings during the 2015–2016 El Niño–Southern Oscillation (ENSO) event despite constant effort; significant correlation was found between sightings and the multivariate ENSO index (MEI) and with sea surface temperatures (SST) but not with chlorophyll-*a* (Chl-*a*). Mark-recapture analysis shows a clear relationship between ENSO and entry probability in the top four modelled results, and the most parsimonious model estimated a superpopulation size N of 1,875 individuals.

Similar to well-documented reef manta ray populations, there is a heavy female bias within the study population (Couturier et al.,

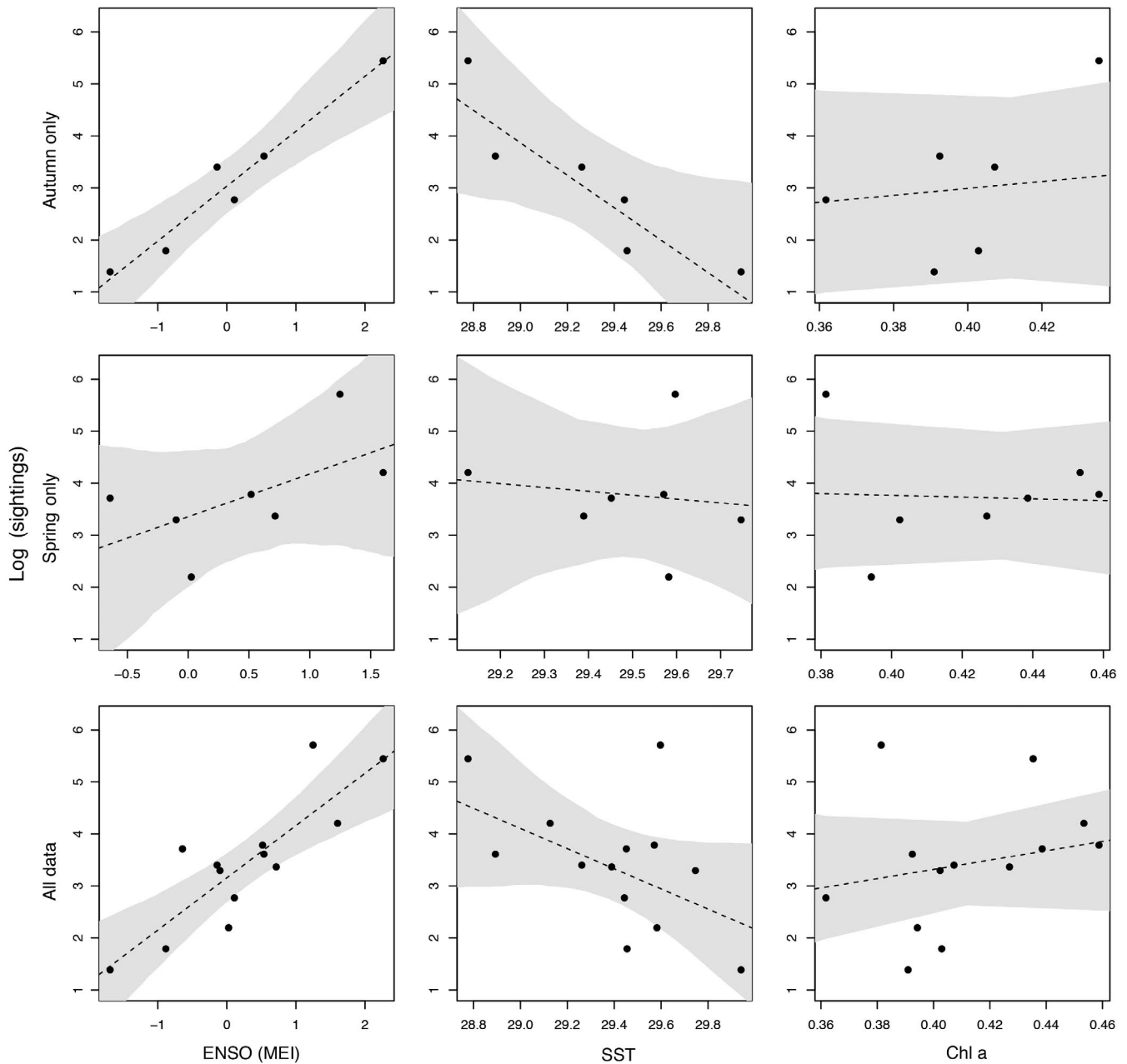


FIGURE 4 Scatter plots of log (total sightings) for Autumn only, Spring only and pooled all data against the covariates: El Niño–Southern Oscillation, Sea Surface Temperature and Chlorophyll-a. Dashed lines are median parameter estimates. Grey shaded regions are 95% credible intervals

2014; Marshall & Bennett, 2010). Studies of reef manta rays have shown that females are significantly more likely to be observed at cleaning stations than males (Couturier et al., 2014; Stevens, 2016). Sex-specific site selection factors, including proximity to food sources, birthing grounds or reproduction opportunities (Marshall & Bennett, 2010), may explain the female bias observed as our sampling coverage is entirely from cleaning stations. The cause of the sudden increase in male sex ratios in 2013 could be linked to an increase in reproductive activity drawing males to cleaning stations, which may act as a lek (Stevens, 2016), but could also be explained by relatively low sample sizes. This period follows a La Niña event and likely an increase in local zooplankton densities correlated with

SST drops (Beaugrand & Reid, 2003), both of which have been linked with increased reproductive activity of reef manta rays (Stevens, 2016). Sexual maturity rates may be higher than reported, as we often lacked photographs of claspers or female wingtips to confirm maturity status, and eight of 29 visibly pregnant manta rays did not have mating scars, suggesting that our measures of sexual maturity underestimate actual levels.

Significant linear relationships were found between increased oceanic manta ray sighting frequency and an increase in the MEI and a reduction in SST. While ENSO is perhaps best known for its impacts in the Eastern Pacific, the El Niño–La Niña cycle also has a major influence on prevailing winds and precipitation in Indonesia

TABLE 2 Model selection weighting (Akaike information criterion—AICc) for the POPAN mark-recapture models (n = 19)

No.	Model	AICc	ΔAICc	AICc Weight	No. of parameters
1	Phi(~Sex)p(~t)pent(~ENSO)N(~Sex)	1003.723	0.000	0.316	19
2	Phi(~ENSO)p(~t)pent(~ENSO)N(~Sex)	1004.249	0.526	0.243	19
3	Phi(~Sex + ENSO)p(~t)pent(~ENSO)N(~Sex)	1004.831	1.108	0.181	20
4	Phi(~Sex)p(~Sex + t)pent(~ENSO)N(~Sex)	1005.311	1.588	0.143	20
5	Phi(~Sex)p(~t)pent(~Sex + t)N(~Sex)	1008.774	5.050	0.025	30
6	Phi(~ENSO)p(~t)pent(~Sex + t)N(~Sex)	1009.474	5.751	0.018	30
7	Phi(~Sex + ENSO)p(~t)pent(~Sex + t)N(~Sex)	1010.762	7.039	0.009	31
8	Phi(~Sex)p(~Sex + t)pent(~Sex + t)N(~Sex)	1010.855	7.132	0.009	31
9	Phi(~Sex)p(~t)pent(~t)N(~Sex)	1011.293	7.570	0.007	29
10	Phi(~ENSO)p(~Sex + t)pent(~Sex + t)N(~Sex)	1011.655	7.932	0.006	31
11	Phi(~Sex)p(~t)pent(~Sex)N(~Sex)	1011.659	7.936	0.006	19
12	Phi(~ENSO)p(~t)pent(~Sex)N(~Sex)	1011.905	8.181	0.005	19
13	Phi(~ENSO)p(~t)pent(~t)N(~Sex)	1012.545	8.822	0.004	29
14	Phi(~Sex + ENSO)p(~Sex + t)pent(~Sex + t)N(~Sex)	1012.861	9.138	0.003	32
15	Phi(~Sex)p(~Sex + t)pent(~t)N(~Sex)	1013.139	9.416	0.003	30
16	Phi(~Sex + ENSO)p(~t)pent(~t)N(~Sex)	1013.267	9.544	0.003	30
17	Phi(~Sex)p(~t)pent(~t + ENSO)N(~Sex)	1013.457	9.734	0.002	30
18	Phi(~Sex + ENSO)p(~t)pent(~Sex)N(~Sex)	1013.654	9.931	0.002	20
19	Phi(~Sex)p(~Sex + t)pent(~Sex)N(~Sex)	1013.778	10.055	0.002	20

and elsewhere in the western Pacific (Tang et al., 2002; Zhang, Sumi, & Kimoto, 1996). We found an exponential relationship between the number of sightings of oceanic manta rays and the MEI. The fact that almost all of the newly identified individuals in 2015 and 2016 (the peak ENSO period) were apparently mature adults suggests that this was not a recruitment event in the traditional sense of new-borns first recruiting to the adult population. Instead, it appears to be a pool of individuals that were previously not observed and who entered the study region for the first time in our study during the strong El Niño event.

Previous study by Stewart, Beale, et al. (2016) in the region along with unpublished acoustic and satellite tag data (E. Setyawan & A. Sianipar, *personal communication*) supports the idea that individuals seen in Raja Ampat migrate south into the Ceram Sea where they spend the majority of their time. We posit that a substantial portion of the population in the Ceram Sea does not routinely migrate into Raja Ampat. This pool of individuals may demonstrate similar distributional changes as seen in the Indian and Pacific Oceans in tuna

(Kumar et al., 2014; Lehodey, Bertignac, Hampton, Lewis, & Picaut, 1997), black turtles (Quiñones et al., 2010), pacific leatherbacks (Wallace et al., 2006) and whale sharks (Pajuelo et al., 2018; Wilson, Taylor, & Pearce, 2001) related to SST anomalies during ENSO events, which would explain the influx of mantas to the Raja Ampat region during the 2015–2016 El Niño and associated drop in SST. The 2015–2016 increase in manta sightings highlights an inherent limitation in applying mark-recapture methodologies to migratory species with very large ranges. Mark-recapture models assume that all individuals in the population have an equal probability of capture (Laake, 2013). However, in cases where survey effort covers only a portion of the population's entire range, this assumption is not met.

The possibility of a range expansion of the regional oceanic manta ray population during strong El Niño events is supported by our covariate analyses, which also reveal a potential driver for this expansion. Over the study period, Autumn ocean and atmospheric conditions are most heavily impacted by ENSO variability, whereas Spring conditions remain relatively stable (Figure 3). During El Niño

TABLE 3 Best-fit mark-recapture model $\phi(\sim \text{Sex})p(\sim t)\text{pent}(\sim \text{ENSO})N(\sim \text{Sex})$ parameter outputs. Seasons represented by Spring (Sp) and Autumn (Au)

Parameter	Female estimate	Female SE	Male estimate	Male SE
Phi (all seasons)	0.8784	0.0234	0.9092	0.0312
p Sp-2010	0.0066	0.0027	0.0066	0.0027
p Au-2010	0.0028	0.0017	0.0028	0.0017
p Sp-2011	0.0379	0.0087	0.0379	0.0087
p Au-2011	0.0071	0.0031	0.0071	0.0031
p Sp-2012	0.0589	0.0118	0.0589	0.0118
p Au-2012	0.0196	0.0060	0.0196	0.0060
p Sp-2013	0.0358	0.0090	0.0358	0.0090
p Au-2013	0.0539	0.0123	0.0539	0.0123
p Sp-2014	0.0608	0.0141	0.0608	0.0141
p Au-2014	0.0832	0.0188	0.0832	0.0188
p Sp-2015	0.1684	0.0349	0.1684	0.0349
p Au-2015	0.1769	0.0208	0.1769	0.0208
p Sp-2016	0.2736	0.0340	0.2736	0.0340
N (all seasons)	1415.30	178.17	459.85	75.96
pent prior to Au-2015	<2.42E-06		<2.42E-06	
pent Au-2015	0.3557	0.0625	0.3557	0.0625

years, western Pacific sea surface temperatures and sea levels drop, causing a strengthening of SE monsoon winds and a slowing of the Indonesian Throughflow (Chowdhury, Chu, & Schroeder, 2007; Gordon, 2005; Rejeki, Munasik, & Kunarso, 2017). It is likely that this enables south monsoon winds to push cooler waters from the Ceram Sea into the study area (Figure 3) and increases vertical mixing of the water column, which together cause a shallowing of the thermocline (Tang et al., 2002; Wyrski, 1962). SST change has been shown to be associated with changes in the composition and distribution of plankton (Edwards & Richardson, 2004; Rutherford, D'Hondt, & Prell, 1999), with knock-on impacts on the distributions of various large marine planktivores (Cotton, Sims, Fanshawe, & Chadwick, 2005; Simmonds & Isaac, 2007; Wilson, Polovina, Stewart, & Meekan, 2006). While sightings counts were higher in Spring, it is likely the Autumn conditions drive these peaks by increasing vertical mixing and perhaps leading to increased food availability that promotes extended periods of improved foraging and consequently reproduction opportunities (Clark, 2010; Stevens, 2016).

Sightings began to increase in Spring 2015 (Figure 2), but it was not until the cool water mass pushed beyond Magic Mountain (approximately 2.25°S latitude) that sightings increased exponentially. Oceanic manta rays, as filter feeders, are likely tied closely to local primary and secondary productivity (Stevens, 2016; Stewart, Hoyos-Padilla, Kumli, & Rubin, 2016). However, surface primary productivity measured by satellite-derived Chl-a did not vary substantially across the study period despite large swings in SST and MEI (Appendix S1: Figure S1.1), and there was not a clear relationship between sightings and Chl-a values. A number of studies suggest that oceanic manta rays target mesopelagic and vertically migrating prey (Burgess et al., 2016; Rohner et al., 2017; Stewart, Hoyos-Padilla, et al., 2016; Stewart et al., 2017). Consequently, surface Chl-a values may not represent prey

availability and distribution in the region, which may explain the lack of a relationship between Chl-a and sightings. Another possible explanation is that oceanic manta rays may have a thermal envelope with an upper bound of approximately 29°C. Oceanic manta rays are seen less frequently than reef manta rays in Raja Ampat, and the increase in sightings during anomalously cold conditions could be due to typical water temperatures in the region being above oceanic manta rays' thermal optimum. However, manta sightings remained high throughout Spring 2016 even as water temperatures returned to their typical Spring highs. This suggests that the range expansion may have been driven by food availability or a different, unknown factor, rather than temperature preference.

The mark-recapture analysis identified MEI as the most important factor influencing the probability of recruitment to the population. Additionally, years with high MEI values also had the highest sighting probabilities for manta rays in our mark-recapture models. The apparent immigration into the study area during the El Niño would mean there was not equal probability of capture over time, and the total abundance estimate from our mark-recapture analysis should be interpreted as a minimum population size, as a large number of individuals may be inaccessible to sampling within Raja Ampat.

The superpopulation estimate of oceanic manta rays in Raja Ampat appears to be of similar size to populations in the Eastern Pacific: a photo-ID study of oceanic manta rays in Pacific Mexico has identified 715 individuals since 1978 (Rubin, 2017). The fact that Raja Ampat and the Ceram Sea, located in a comparatively oligotrophic region (Longhurst, Sathyendranath, Platt, & Caverhill, 1995), can support a population similar in magnitude to the rich waters of the Eastern tropical Pacific suggests the west Papua area may contain abundant food resources that could be important to other species with tropical distributions (Lehodey et al., 1997).

Modelled estimates of survival are lower than expected for these long-lived species and lower than reported estimates from reef manta ray populations (Couturier et al., 2014; Deakos, Baker, & Bejder, 2011). It is likely that this is a result of our incomplete sampling of the entire population distribution and quite likely reflects emigration as opposed to elevated mortality. This theory is supported by satellite tag tracks (Stewart, Beale, et al., 2016) and unpublished satellite tag data which show the tagged individuals primarily foraging along the Ceram trough, south-east of Raja Ampat (A. Sianipar, *personal communication*) and data from an array of acoustic receivers covering all regions of Raja Ampat showing a decrease in detections during the south monsoon (E. Setyawan, *personal communication*), supporting emigration as the cause despite sample bias of effort during this period. While there is still an active targeted fishery for manta rays in Lamakera, south-eastern Indonesia, this is over 900 km from the nearest satellite tag tracks and operates locally only. Even prior to the nationwide fishing ban in 2014, there were no known targeted manta fisheries within 600 km of recorded satellite tag tracks; however, unreported mortality as bycatch in tuna and other fisheries in the Ceram Sea may contribute to the lower than expected survival estimates (Blaber, 2006; Dharmadi & Sumadhiharg, 2008; Dharmadi & White, 2003).

Survey effort was concentrated in the Misool region; this may explain why little regional crossover was observed during the study. We expect as more photo-IDs are submitted by tourists across Raja Ampat, there will be an increase in recaptures between regions. Survey effort showed little to no relationship with sightings peaks and instead was directly related to Misool Eco Resort's occupancy. The apparent correlation of survey effort and sightings in Autumn 2015 was likely driven by increased sightings of manta rays at the main study site and throughout the area leading to increased requests to dive Magic Mountain. While not a perfect measure of effort, as most tourists in Raja Ampat travel with some form of waterproof camera and the authors were present on a large percentage of surveys, we believe it provides the best available metric of relative survey intensity. Further to this, there was considerable effort within the Misool region at sites other than Magic Mountain. Due to scheduling policies at any excursion time, effort was likely higher at other sites than Magic Mountain.

4.1 | Conclusion and implications

Oceanic manta ray distributions appear to be impacted by ENSO-related climate phenomena. Under current carbon dioxide emissions scenarios, global ocean surface temperatures are expected to rise 1–3°C during the 21st century (Church et al., 2013; Collins et al., 2013; Kirtman et al., 2013; Taylor, Stouffer, & Meehl, 2012). These changes in temperature and their associated effects on ocean circulation and water column stratification are expected to have profound impacts on primary and secondary productivity: Zooplankton distributions are expected to shift poleward, and tropical regions may experience declines in zooplankton biomass of more than 50% (Chust et al., 2014; Stock et al., 2014; Woodworth-Jefcoats et al., 2017). Our findings on the relationship of ENSO to manta sightings and distribution indicate that oceanic manta rays are likely sensitive to large-scale climatic

variability. This illustrates the potential impacts of climate change on oceanic manta populations and the need to consider climate impacts in developing management strategies. As changing ocean conditions force distributional shifts, this may separate foraging grounds from other important habitats such as cleaning stations or even pupping/nursery areas, increasing energetic demands and potentially impacting population viability.

Manta rays are an important resource in Indonesia, where the direct economic impact of manta tourism is estimated at US \$10.6 million annually (O'Malley, Lee-Brooks, & Medd, 2013). Despite national laws currently in place (KEPMEN-KP 4/2014), illegal fishing still occurs in Eastern Flores (E. Setyawan, *personal communication*), an area where large decreases in landings were recorded over the last two decades, indicative of population declines (Dewar, 2002; Lewis et al., 2015). Distributional shifts may bring regionally distinct populations of oceanic manta rays with low abundance into regions with higher rates of bycatch or targeted capture of the species, making climate change an important consideration for their management and conservation.

The current database being made up largely of sightings from the Misool region means our conclusions are most applicable to Misool, and that other patterns may emerge for the Dampier and Fakfak regions in the future. In order to confirm the patterns and inferences we have made here, further study of the population is required. Continued photo-ID and complementary acoustic and satellite tag deployments will greatly enhance existing knowledge of critical habitat use, long-term migratory patterns and anthropogenic threats, while population genetics can provide further insight into population size and structure. Combined, this knowledge can be used for development of management strategies that bolster the conservation of the species, both in Raja Ampat and West Papua, as well as more broadly in Indonesia.

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DATA ACCESSIBILITY

The R code and further data supporting the results are provided in the Data S1.

ORCID

Calvin S. Beale  <https://orcid.org/0000-0002-3505-8929>

Edy Setyawan  <https://orcid.org/0000-0001-6629-5997>

Mark V. Erdmann  <https://orcid.org/0000-0002-3644-8347>

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BIOSKETCH

Calvin Beale's primary research experience and interest are Manta Rays: population structure and dynamics, distributions, ecology and conservation. With recent ENSO events heavily impacting species movement ecology and threatening species viability, global climactic factors and their impact on migratory marine species have become his focus of research for long-term protection of these species, all set at the heart of his more general research interest in elasmobranchs.

Author contributions: C.S.B. designed and directed the project, collected the data, performed the analysis and wrote the paper. J.D.S. contributed to designing and writing the R Mark analysis and manuscript editing. E.S., A.B.S. and M.V.E. contributed to data collection and manuscript editing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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