



# Determining the role of environmental covariates on planktivorous elasmobranch population trends within an isolated marine protected area

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**ABSTRACT:** Studies have found predictable relationships between the behavior of planktivores and environmental conditions, suggesting that they may be especially sensitive to environmental change. Most studies to date, however, are based on limited observations, include few of the environmental covariates that influence planktivore behavior, and often do not occur over long enough durations to determine the effects of environmental change. As such, exploration of long-term data sets on planktivores is necessary to disentangle the potential impacts of oceanographic and environmental variability. To elucidate the relationship between 3 groups of planktivorous elasmobranchs (whale sharks *Rhincodon typus*, mobula rays *Mobula* spp., and manta rays *Manta birostris*) and environmental variability, we employ hierarchical modeling to examine trends in elasmobranch counts from underwater visual censuses (UVCs), conducted over the last 27 yr (1993–2019) by divemasters from Cocos Island, Costa Rica. Data from UVCs were integrated with primarily remotely sensed environmental and oceanographic data. Models revealed that for planktivorous elasmobranchs, environmental variables (chlorophyll *a*, lunar cycle, and salinity) are correlated with occurrence and predicted relative abundances. In lunar phases of lower illuminations, there were significant predicted increases in relative abundances of mobula rays, increased chlorophyll *a* decreased whale shark relative abundance, and increases in salinity correlated with increases in mobula relative abundance but did not correlate with increased observations of mantas or whale sharks. Our findings highlight the need to consider environmental conditions when evaluating the efficacy of marine protection and demonstrate the potential ranging effects of environmental variability on planktivores at Cocos.

**KEY WORDS:** Elasmobranchs · Time series · Marine protected areas · Global change

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## 1. INTRODUCTION

Planktivorous elasmobranchs are highly influenced by environmental variability and food availability. Unlike species and groups of elasmobranchs that are generalists (Wilga et al. 2007), planktivorous elasmobranchs feed primarily on zooplankton (Sims et al. 2003b, Stevens 2007, Nakaya et al. 2008, Couturier et al. 2013), the abundance and distribution of which are driven primarily by predictable environmental

changes (Richardson 2008). Past studies have found that the aggregations, abundance, behavior, and movements of planktivorous elasmobranchs can be predicted by known zooplankton food pulses (Clark & Nelson 1997, Heyman et al. 2001, Armstrong et al. 2016, Guzman et al. 2022). In the Eastern Tropical Pacific, electronic tagging of whale sharks revealed that foraging behavior is associated with areas of high primary productivity (Guzman et al. 2022). Similar phenomena have been documented near La Paz, Mexico,

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where juvenile whale sharks aggregate to feed on copepod blooms (Clark & Nelson 1997), and at the Belize Barrier Reef, where whale sharks form aggregations that correspond with the spawning aggregations of various species of snapper (Heyman et al. 2001, Graham et al. 2006). Some studies have revealed similar patterns for planktivorous rays: on the Great Barrier Reef, manta rays feed in locations and at times of higher zooplankton biomass (Armstrong et al. 2016), and the presence of giant devil rays in the eastern Pacific is influenced by seasonal upwelling events (Lezama-Ochoa et al. 2019).

In addition to food availability, environmental conditions are key factors that influence planktivorous elasmobranch aggregations and behavior. In the western Indian Ocean and off Ningaloo Reef, Australia, the number of whale sharks in pelagic surface waters is strongly correlated with sea surface temperature (SST) (Sequeira et al. 2012). In addition, the Southern Oscillation Index and wind shear are linked to the abundance and distribution of planktivorous elasmobranchs (Wilson et al. 2001, Sleeman et al. 2010a). Environmental variation related to the lunar cycle also has documented impacts on planktivorous elasmobranchs; for example, tidal density, new, and full moons increase the aggregations of mantas at Komodo Marine Park (Dewar et al. 2008) and at the Great Barrier Reef, there are more manta rays during new and full moons (Jaine et al. 2012). Notably, however, other studies have reported minimal influence of the lunar cycle on the behavior of large planktivores; for example, foraging observations were not statistically different across lunar phases for whale sharks at Baja California Norte, México (Nelson & Eckert 2007). Nevertheless, the lunar cycle has a documented influence on behavior across marine taxa: surveys of fishers in Ghana revealed that the best catches of fishes are reported when there is partial or no lunar illumination (Seidu et al. 2022). The largetooth sawfish, a large shark-like ray, displays diel behaviors that are influenced by lunar illumination levels (Whitty et al. 2017). There is also evidence that foraging behavior is influenced by lunar phase; for example, cape fur seal predation by white sharks is reduced during full moons (Hammerschlag et al. 2006) and white shark sightings occur with the lowest frequency at full moon and peak at new moon (Weltz et al. 2013). Finally, in some bony fishes, moonlight-related periodicities are used as reliable information for synchronizing the timing of reproductive events (Ikegami et al. 2014).

Environmental variability has an apparent impact on the abundance and behavior of planktivorous elasmobranchs and other marine species. However, stud-

ies on the efficacy of marine protected areas (MPAs), assessments of elasmobranch population dynamics, and studies of elasmobranch movement ecology do not always account for environmental factors or include only one environmental covariate (e.g. temperature or depth) (Goetze & Fullwood 2013, Juhel et al. 2018, Albano et al. 2021, Hammerschlag et al. 2022). Conversely, incorporating a broad array of environmental factors, especially those associated with climate change, is essential to make well-supported ecological inferences and generate critical data for management. While some studies to date have examined the potential effects of different environmental covariates on planktivorous elasmobranchs, most of these studies are short-term, anecdotal, observational, based on small sizes, or account for limited covariates (e.g. Nelson & Eckert 2007, Dewar et al. 2008, Armstrong et al. 2021, Montero-Quintana et al. 2021). Long-term data sets that incorporate a range of environmental covariates are critical to developing an understanding of the ecology and biology of planktivorous elasmobranchs (Stewart et al. 2018, White 2019).

In the present study, we leverage the recent advent of open-access remotely sensed environmental data (e.g. chlorophyll *a* [chl *a*], SST, ocean Niño index [ONI], surface salinity, and lunar cycle data) to assess trends in the populations of planktivorous elasmobranchs in a 28 yr underwater visual census (UVC) data set. This UVC represents one of the longest underwater censuses of sharks and rays. By using this data set, we can untangle the many previously suggested relationships between environmental covariates and planktivorous elasmobranchs. The specific aims of this study are threefold. First, we expand on past studies on the same system (White et al. 2015, Osgood et al. 2021) to examine the role of food availability (e.g. primary productivity), acute climate changes (e.g. SST, temperature at depth), long-term climate trends (e.g. ONI), oceanographic conditions (e.g. current, salinity), and lunar cycle (e.g. lunar phase, lunar distance) on the population trends of planktivorous elasmobranchs. We hypothesized that high primary productivity would increase the abundance of planktivores because they are known to follow physical and biological oceanographic cues to locate successful foraging grounds (Nelson & Eckert 2007). Second, we examine how accounting for environmental covariates shifts predictions about population trends compared to models that examined population trends over time without accounting for environmental variability. Finally, we examine species/group-specific differences in the influences of environmental covariates.

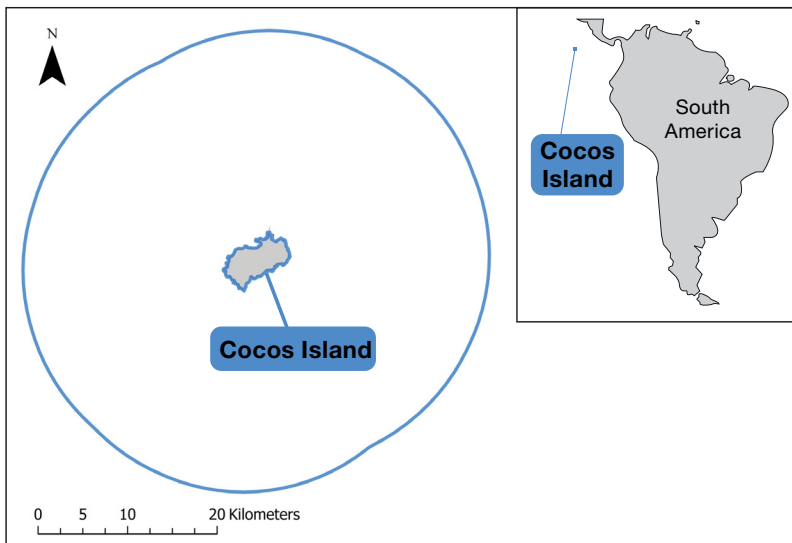


Fig. 1. Map of Cocos Island (grey) and surrounding marine protected area (outlined in blue) in relation to South America (inset)

## 2. MATERIALS AND METHODS

### 2.1. Study site

Cocos Island National Park (Isla del Coco; 5° 31' N, 87° 4' W) is a small (23.85 km<sup>2</sup>), uninhabited island 550 km from mainland Costa Rica, surrounded by an MPA that was established in 1984, making it the world's oldest MPA (White et al. 2015) (Fig. 1). Cocos Island provides exceptional habitat for marine organisms—located at the nexus of reef and seamount complexes and at the confluence of major ocean currents, Cocos is a biodiversity hotspot, home to the unique intersection of pelagic and coastal species. Oceanic islands like Cocos provide important habitats in the pelagic environment because they allow reef-associated communities to interact with pelagic species across many different trophic levels (Friedlander et al. 2012). In this study, the dive sites encompassed the range of shallow-water environments and seamount complexes at Cocos Island.

### 2.2. UVC protocol

From January 1993 to December 2019 (n = 28 yr), experienced diver guides (n = 36) from Undersea Hunter, a Costa Rica-based dive company specializing in liveaboard expeditions, conducted a total of 35 706 dives at 17 sites around Cocos Island (Fig. 1). This data set represents one of the largest UVCs for sharks and rays (White et al. 2015, Osgood et al. 2021). These

dives cannot be considered a scientific UVC because there was no defined field of view. However, protocol was consistent throughout the study. Dives averaged ~60 min and were led by experienced and trained divemasters, with one divemaster per dive. At each site, the depth range was consistently between 10 and 40 m.

Upon completion of each dive, divers used a standardized datasheet to record the observed number of 3 planktivorous elasmobranchs: mobula rays *Mobula* spp., manta rays *Manta birostris*, and whale sharks *Rhincodon typus* (Table 1). We transcribed and compiled all data from the 53 Undersea Hunter divemasters into a single database. We also applied filters (e.g. removing night dives and sites not common to all divers) and corrected

transcription errors (e.g. site name entry errors). We document this process completely in our corresponding code. After this process, 35 706 individual dives conducted by 36 divemasters remained for analysis.

### 2.3. Environmental data

In addition to the primary UVC data (counts), divemasters recorded environmental parameters (current, visibility, temperature at depth); currents and visibility were estimated by divemasters. Temperature at depth was obtained at the depth where the individuals of each species were counted from the dive computers of the divemasters. We supplemented this survey data with several open-source environmental data sets that included mean monthly SST, lunar phase, lunar distance, lunar illumination means, mean monthly salinity, mean monthly chl *a*,

Table 1. Species of focus in this study and their IUCN status, including all potential species in the 'mobula species' category based on known ranges

Common name	Scientific name	IUCN status
Whale shark	<i>Rhincodon typus</i>	Endangered
Manta ray	<i>Manta birostris</i>	Endangered
Mobula species	<i>Mobula</i> spp.	
Munk's pygmy devil ray	<i>M. munkiana</i>	Vulnerable
Bentfin devil ray	<i>M. thurstoni</i>	Endangered
Spinetail devil ray	<i>M. mobular</i>	Endangered
Sicklefin devil ray	<i>M. tarapacana</i>	Endangered

Table 2. All covariates (environmental data) used in models with a description of their respective sources. To account for seasonality, we included the sine and cosine functions of day-of-year as explanatory variables (Baum & Blanchard 2010). N/A: not applicable

Variable	Range (5 <sup>th</sup> to 95 <sup>th</sup> percentile)	Source	Description	Fixed or random effect	Spatial scale	Temporal scale
Sea surface temperature (SST)	26.2–29.6°C	NOAA <a href="https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html">https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html</a>	Daily SST (Reynolds et al. 2007)	Fixed	0.25° latitude × 0.25° longitude	Daily
Ocean Niño Index (ONI)	–1.38 to 1.31	NOAA <a href="https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html">https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html</a>	NOAA's primary indicator for monitoring El Niño–Southern Oscillation. A multivariate El Niño–Southern Oscillation index. ONI is based on the running 3 month average SST in the east-central tropical Pacific and if they are warmer or cooler than average temperatures.	Fixed	East-central Tropical Pacific between 120° and 170° W	3 mo
Chl <i>a</i>	0.11–0.25 mg m <sup>–3</sup>	NASACombo time series <a href="https://oceancolor.gsfc.nasa.gov/">https://oceancolor.gsfc.nasa.gov/</a>	A multiple-satellite cross-calibrated chlorophyll product	Fixed	0.25° latitude × 0.25° longitude	Monthly
Salinity	31.5–33.4 ppt	Met Office Hadley Centre observations data sets <a href="https://www.metoffice.gov.uk/hadobs/en4/">https://www.metoffice.gov.uk/hadobs/en4/</a>	Hadley EN4 subsurface salinity objective analysis (Good et al. 2013)	Fixed	1° latitude 1° longitude	Monthly
Lunar phase	N/A	'lunar' package in R <a href="https://CRAN.R-project.org/package=lunar">https://CRAN.R-project.org/package=lunar</a>	Category names that correspond to phases of the moon on a given day at Cocos Island.	Fixed	N/A (adjusted for location of Cocos)	Daily
Lunar distance	56.62–63.67	'lunar' package in R <a href="https://CRAN.R-project.org/package=lunar">https://CRAN.R-project.org/package=lunar</a>	Distance to the moon returned in units of earth radii, or as a 5 level factor variable referring to the moon's perigee (at about 56 earth radii) and apogee (at about 63.8 earth radii).	Fixed	N/A (adjusted for location of Cocos)	Daily
Dive temperature	24.0–29.0°C	Original data set	Water temperature recorded by dive masters on their personal dive computers at depth	Fixed	Location of dive	Dive-specific
Current	0 (none) to 5 (strong)	Original data set	Estimation of current strength by divemaster	Fixed	Location of dive	Dive-specific
Visibility	10.0–30.0 m	Original data set	Water visibility, estimated by dive masters	Fixed	Location of dive	Dive-specific
Year	1998–2019 (full range)	Original data set	Year of study	Fixed	N/A	N/A
Site	17 unique sites	Original data set	Identification number of each dive site	Random	N/A	N/A
Divemaster	36 unique divemasters	Original data set	Identification number of each divemaster	Random	N/A	N/A

and ONI data (Table 2). The Hadley EN4 subsurface salinity objective analysis (<https://www.metoffice.gov.uk/hadobs/en4/>) was used to create a time series of surface salinity (at 5 m depth) for the duration of the study (Table 2). This time series was then integrated with our original data set and used as the salinity covariate. Chl *a* data were available beginning in 2002, using NASA's combined-satellite (<https://oceancolor.gsfc.nasa.gov/>) time series, a multiple-satellite, cross-calibrated chlorophyll product, to create a time series of primary productivity (Table 2). We selected the chl *a* covariate to serve as a proxy for zooplankton. Chl *a* is an indicator of phytoplankton, and phytoplankton and zooplankton abundance are often correlated (Ware & Thomson 2005, Richardson 2008). Furthermore, chl *a* has been used as a proxy for zooplankton levels in several other studies on planktivorous marine megafauna (Burtenshaw et al. 2004, Hlista et al. 2009, Sleeman et al. 2010b, Rohner et al. 2018, Harris et al. 2021, Shaw et al. 2021); however, it is not a perfect indicator of zooplankton abundance. We also integrated SST using a high-resolution blended product based on satellite and *in situ* data (HadISST) (Table 2). We obtained lunar data (e.g. lunar distance, lunar phase, and lunar illumination mean) using the package 'lunar' (Lazaridis 2014) in R version 4.1 (R Core Team 2021) (Table 2). Using the same methods as a previous study on the same system, ONI data were obtained from NOAA (Osgood et al. 2021) (Table 2). We adapted the methods of Osgood et al. (2021) and included temperature of dive, mean monthly SST, and ONI index. We selected these factors because they each represent a different type of temperature change. ONI represents the running 3 month mean of SST anomalies in the Niño-3.4 region of the east-central Pacific and correlates with more general oceanographic features of the Eastern Tropical Pacific. Temperature of dive captures the immediate responses of each species at depth. SST captures the immediate responses of each species at the surface. SST and temperature at depth were not correlated ( $\rho = 0.336$ ), temperature at depth and ONI were not correlated ( $\rho = 0.291$ ), and SST and ONI were not correlated ( $\rho = 0.336$ ).

#### 2.4. Modeling environmental influences on elasmobranchs

We modeled the counts of each focal species using a hierarchical generalized linear mixed model framework. We selected these mixed-effect models to im-

plement random effects to account for observations made by the same divemaster or at the same dive site. To account for seasonality, we included the sine and cosine functions of day-of-year as explanatory variables (Baum & Blanchard 2010). We adapted each model to the data type and distribution of the species. For all 3 species included in our models, count data were recorded; however, these species were rarely observed. Because of the low frequency of observation, we employed zero-inflated mixed models with a negative binomial distribution. All models were implemented in the 'glmmTMB' package (Brooks et al. 2023) in R (R Core Team 2021).

For model selection, rather than using a 'drop-one' approach for Akaike's information criterion (AIC), we choose to select a series of models that each have a biologically sensible and plausible interpretation (Arnold 2010). We selected these models to include or omit a combination of environmental covariates that had a range of influences on planktivorous elasmobranchs or elasmobranchs in general, as described in the literature. We used the 'AICcmod avg' (Mazerolle 2023) package in R (R Core Team 2021) to select the top models from our series of biologically sensible models (Tables S4–S6). If several models fell within 2 AIC points of the best model, we used a model-averaging approach (Zuur et al. 2009) to generate parameter estimates. We employed this model-averaging approach with the 'model.avg' function in the 'MuMIn' package (Bartoń 2023) in R (R Core Team 2021).

### 3. RESULTS

#### 3.1. Model comparison

For whale sharks, the model that did not account for environmental variability and the model that included environmental covariates estimated similar trends (i.e. abundance increases each year). However, when environmental variability is not accounted for in models, the predicted increases in relative abundance each year are smaller than when environmental variation is accounted for. Our top model estimated a 6% increase in whale shark relative abundances each year ( $p < 0.001$ ), whereas our model that did not account for environmental variability estimated a 5% increase in whale shark relative abundances each year ( $p < 0.001$ ) (Fig. 2A). For mobula rays, failure to account for environmental covariates leads to underestimates of abundance decreases. Our model average of our top 2 models esti-

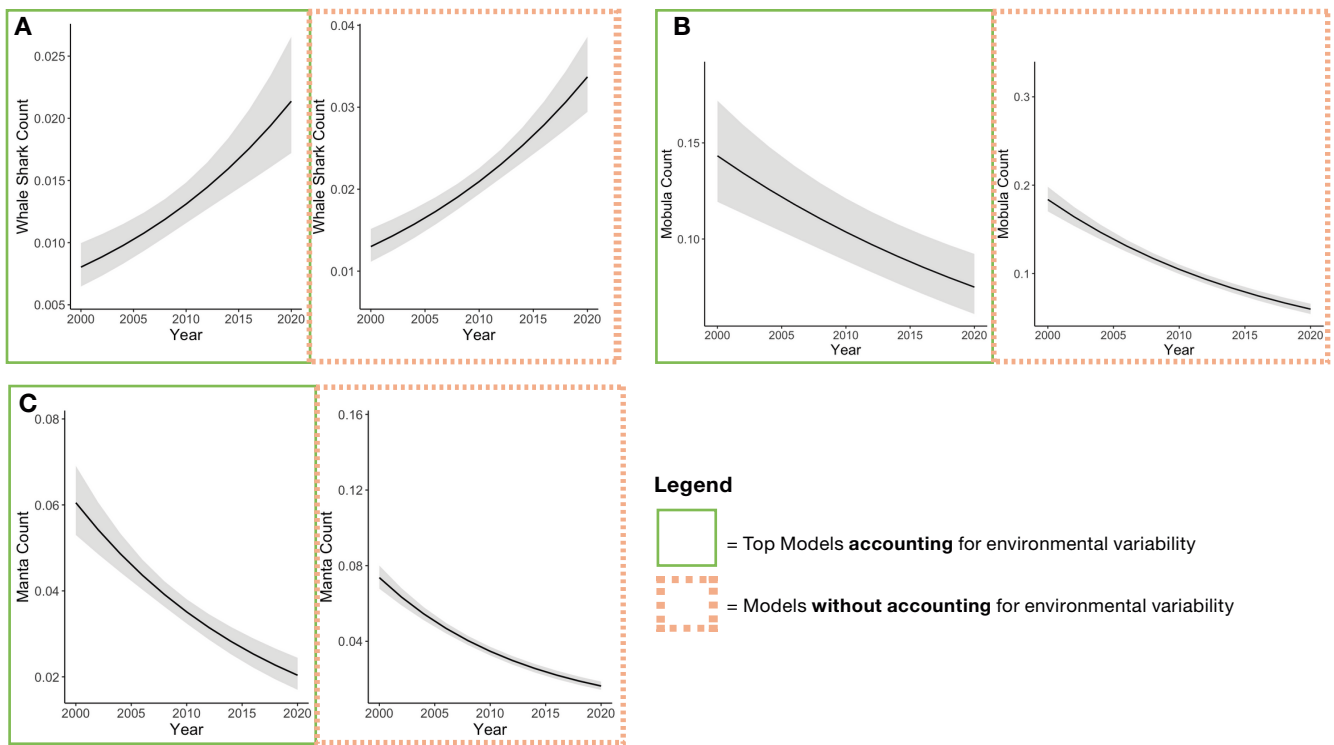


Fig. 2. Model comparison for abundances over time when accounting for Ocean Niño Index, temperature at depth, sea surface temperature, salinity, chlorophyll *a*, estimated current and visibility, year, seasonality, lunar phase (only mobulas), and lunar distance (only mobulas) (outlined in green) and accounting only for year (outlined in orange). Comparisons are shown for (A) whale sharks, (B) mobulas, and (C) mantas. Gray shading: 95% CI

mated a 5% decrease in mobula ray relative abundance each year ( $p < 0.001$ ); however, the model that did not account for environmental variability estimated a 3% decrease in relative abundance of mobulas each year ( $p < 0.001$ ) (Fig. 2B). Finally, accounting for environmental variability, our top model estimated a 5% decrease ( $p < 0.001$ ) in the relative abundance of manta rays each year, while our model that did not account for environmental variability estimated a larger 6% decrease in relative abundance of manta rays each year ( $p < 0.001$ ) (Fig. 2C).

Additional details on modelling comparison and modelling averaging can be found in the Supplement at [www.int-res.com/articles/suppl/m722p107\\_supp.pdf](http://www.int-res.com/articles/suppl/m722p107_supp.pdf).

### 3.2. Whale sharks

Whale sharks were observed on 2.11% of dives. The top model for whale sharks was the global model (for the purpose of this study, we define 'global model' as the model that includes all environmental covariates listed in Table 2) without the lunar covari-

ates. We estimated that over the last 2 decades, there was a significant increase in the abundance of whale sharks; specifically, we modeled that each year there is a 6% increase in the abundance of whale sharks ( $p < 0.001$ ). Increases in temperature at depth and visibility yielded significant increases in the predicted relative abundance of whale sharks; more specifically, a 1°C increase in temperature at depth yielded a 6% increase in the abundance of whale sharks ( $p = 0.031$ ) and for a 1 m increase in visibility there is a 3% increase in the abundance of whale sharks ( $p = 0.001$ ; Fig. 3). Despite the relationship between temperature at depth and whale shark relative abundance, we found no significant effect of SST on whale shark relative abundance. Increases in ONI and chl *a* yielded decreases in the predicted relative abundance of whale sharks: a 1 unit increase in ONI yields a 30% decrease in the abundance of whale sharks ( $p < 0.001$ ) and a 0.10 mg m<sup>-3</sup> increase in surface chl *a* yields a 26% decrease in the abundance of whale sharks ( $p < 0.001$ ; Fig. 3). Finally, the sine and cosine of day-of-year revealed that there is a significant effect of seasonality on whale shark abundance ( $p < 0.001$ ).

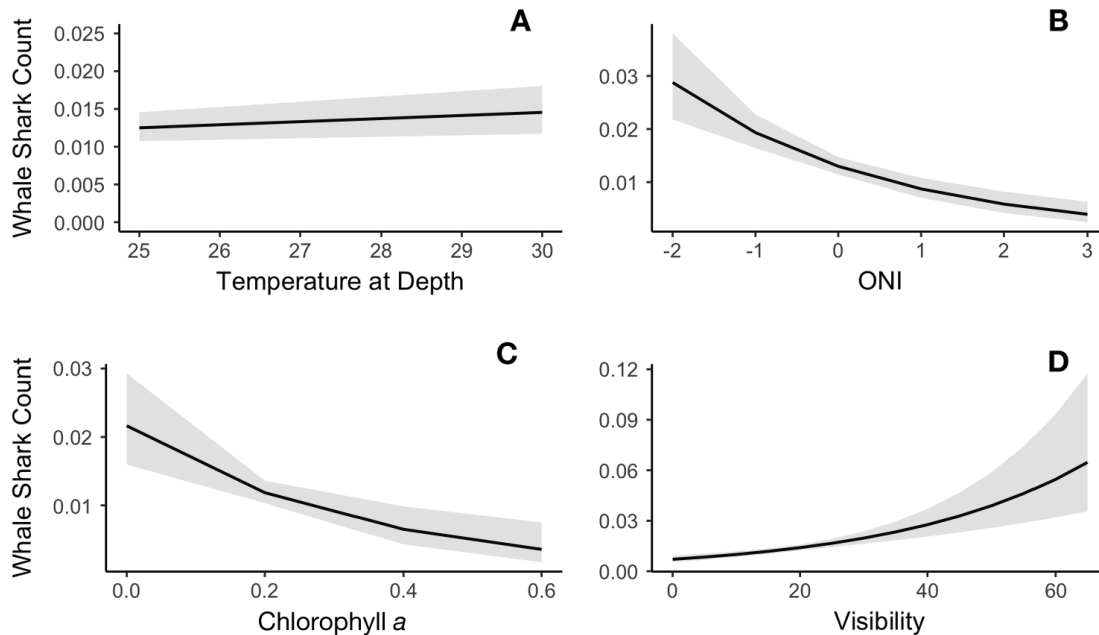


Fig. 3. Predicted whale shark count per dive for statistically significant (continuous) covariates (A) temperature at depth ( $^{\circ}\text{C}$ ), (B) Ocean Niño Index (ONI), (C) chlorophyll *a* ( $\text{mg m}^{-3}$ ), and (D) estimated water visibility (m). Gray shading: 95% CI

### 3.3. Mobula rays

Mobula rays were observed on 11.9% of dives. Two models fell within 2 AIC points of each other (Table 3). The following results are based on a model-averaging approach of our global model without lunar factors and salinity. We found that over the last 2 decades, there has been a statistically significant decrease in mobula ray abundance. Specifically, we modeled a 5% decrease in the abundance of mobulas each year ( $p < 0.001$ ). Increased SST and temperature at depth yielded significant decreases in the abundance of mobula rays. A  $1^{\circ}\text{C}$  increase in SST and temperature at depth yielded a 22% decrease ( $p < 0.001$ ) and a 4% decrease ( $p = 0.049$ ), respectively (Fig. 4). On the other hand, increased ONI, salinity, visibility, and current all yielded significant increases in the abundance of mobulas (Fig. 4). The effect size of these varied widely: a 1 unit increase in ONI yielded a 17% increase in the abundance of mobulas ( $p = 0.002$ ), a 1 unit increase in surface PSU yielded a 16% increase in the abundance of mobula rays ( $p = 0.048$ ), a 1 m increase in visibility yielded a 4% increase in the abundance of mobulas ( $p < 0.001$ ), and a 1 unit increase in current strength yielded a 12% increase in the abundance of mobulas ( $p < 0.001$ ). Our models revealed information about the potential increase in mobula abundance during lunar phases. We found that during the last quarter, there is a 34% increase in

mobulas relative to the first quarter ( $p = 0.016$ ), and during the new moon there is a 42% increase relative to the first quarter ( $p = 0.004$ ; Fig. 5). The sine and cosine of day-of-year revealed that there is a significant effect of seasonality on mobula rays (sin,  $p < 0.001$ ; cos,  $p = 0.01$ ). Finally, we found no significant effect of chl *a* on mobula ray relative abundances.

### 3.4. Manta rays

Manta rays were observed on 4.21% of dives. As with whale sharks, the top model for manta rays was the global model without lunar-related parameters (Table 3). Our top model estimated that over the last 2 decades, manta ray abundance decreased each year by 5% ( $p < 0.001$ ). Our models found no statistically significant effect of primary productivity, salinity, ONI, seasonality (sine and cosine of day-of-year), or current on manta ray presence. However, mantas did appear to be sensitive to acute temperature changes; specifically, our models estimated that a  $1^{\circ}\text{C}$  increase in temperature at depth leads to a 6% decrease in the abundance of mantas ( $p = 0.026$ ; Fig. 6). More impactful than temperature at depth was SST, where a  $1^{\circ}\text{C}$  increase yields a 16% decrease in the abundance of mantas ( $p = 0.014$ ). Finally, we modeled that a 1 m increase in visibility yields a 2% increase in the abundance of mantas ( $p < 0.001$ ; Fig. 6).

Table 3. Top model, model without environmental covariates, and model type for each species included in this study. All models also include sine and cosine of day-of-year to account for seasonality, and each model includes the random effects of site and diver/master. Comparison with the top model is a description of how the predicted relative abundance in the model that does not account for environmental variation compares with the predicted relative abundance from the top model. GLMM: generalized linear mixed model; ZINB: zero-inflated negative binomial. Asterisk indicates significance ( $*p \leq 0.05$ )

Species	Top model(s)	Model without environmental covariates	Model type
Whale sharks	Ocean Nino Index* + Temperature at Depth* + Sea Surface Temperature + Salinity + Chlorophyll a* + Current + Visibility* + Year*	Whale Sharks ~ Year* Comparison with top model: underestimate abundance increases	GLMM, ZINB
Mobula rays	A. Ocean Nino Index* + Temperature at Depth* + Sea Surface Temperature* + Salinity* + Chlorophyll a + Current* + Visibility* + Year* B. Ocean Nino Index* + Temperature at Depth* + Sea Surface Temperature* + Chlorophyll a + Lunar Distance + Lunar Phase* + Current* + Visibility* + Year*	Mobula Rays ~ Year* Comparison with top model: underestimate abundances decreases	GLMM, ZINB
Manta rays	Ocean Nino Index + Temperature at Depth* + Sea Surface Temperature* + Salinity + Chlorophyll a + Current + Visibility* + Year*	Manta Rays ~ Year* Comparison with top model: overestimate abundance decreases	GLMM, ZINB

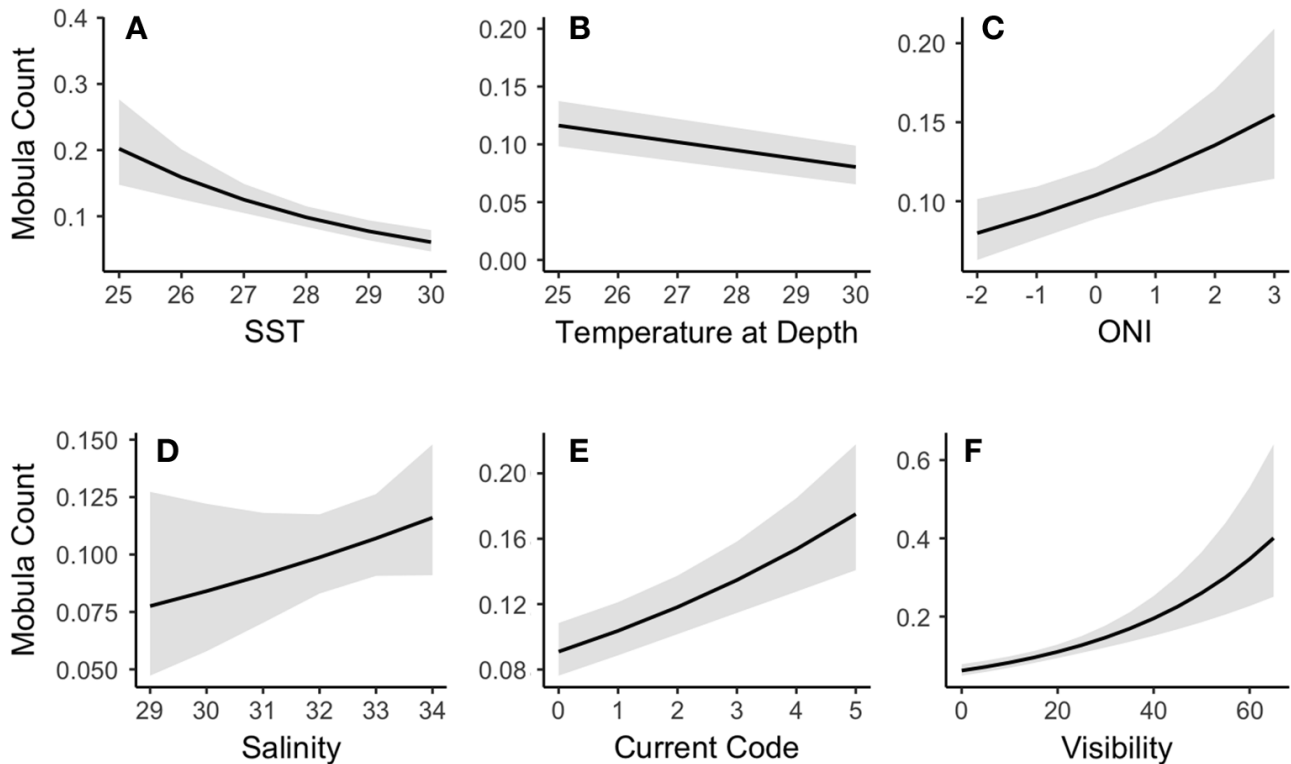


Fig. 4. Predicted mobula count for statistically significant (continuous) covariates (A) sea surface temperature (SST) ( $^{\circ}\text{C}$ ), (B) temperature at depth ( $^{\circ}\text{C}$ ), (C) Ocean Niño Index (ONI), (D) salinity (ppt), (E) estimated current, and (F) estimated water visibility (m). Gray shading: 95% CI



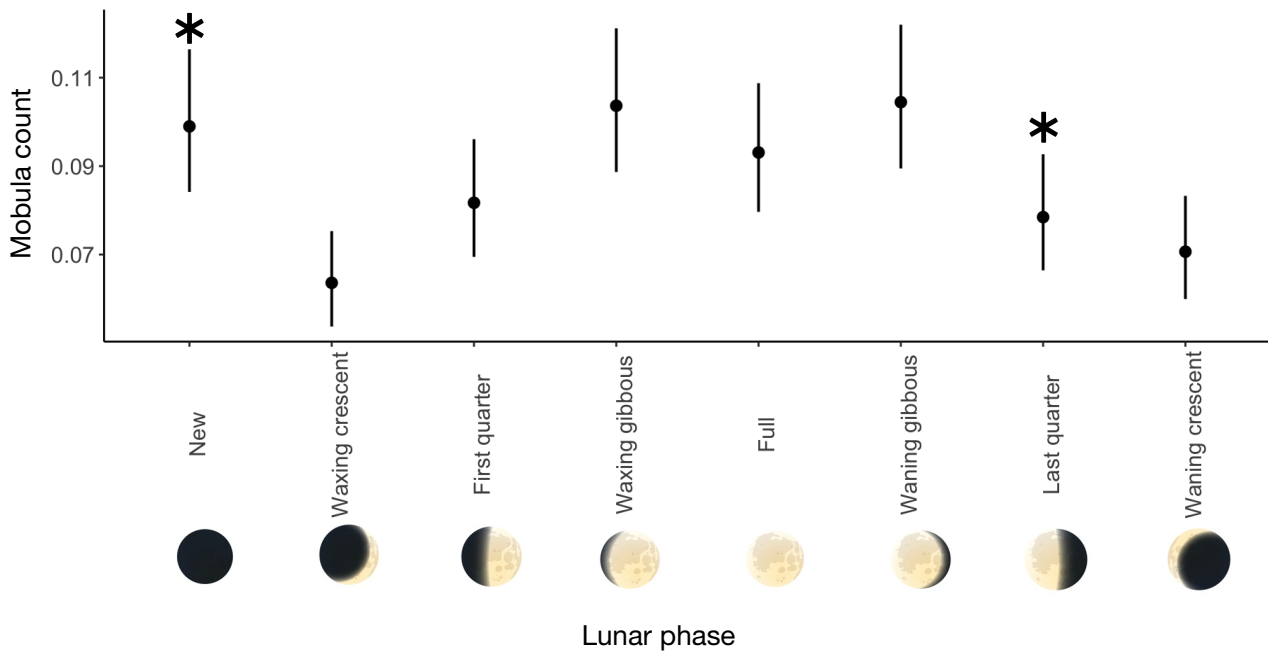


Fig. 5. Effects of lunar phase on mobula counts ( $\pm 95\%$  CI), with graphic representation of lunar phase. Statistical significance ( $*p < 0.05$ ) is indicated relative to the first quarter

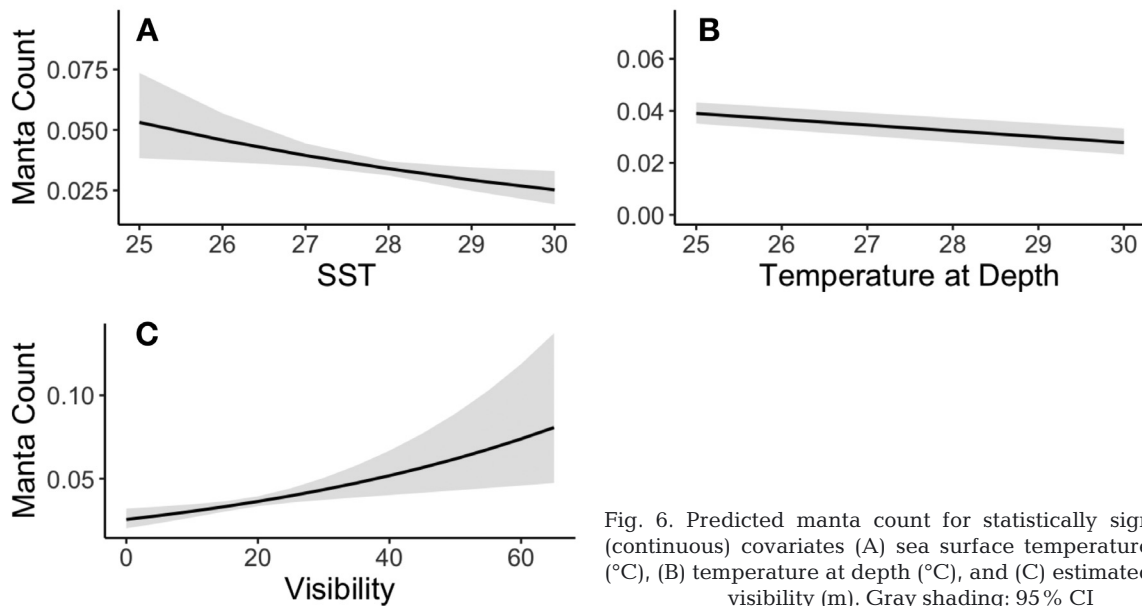


Fig. 6. Predicted manta count for statistically significant (continuous) covariates (A) sea surface temperature (SST) ( $^{\circ}\text{C}$ ), (B) temperature at depth ( $^{\circ}\text{C}$ ), and (C) estimated water visibility (m). Gray shading: 95% CI

## 4. DISCUSSION

### 4.1. Population trends and model comparisons

We observed significant decreases in the abundance of both mantas and mobulas over time. The aggregations of devil rays make them particularly susceptible to bycatch in purse seine and longline

fisheries (Duffy & Griffiths 2017). Devil rays are considered easy to target because of their 'large size, slow swimming speed, tendency to aggregate, predictable habitat use, and lack of human avoidance' (Marshall et al. 2020, p. 7). Retainment during incidental catches of manta rays is common because of their high trade value (Croll et al. 2016, Lawson et al. 2017, Marshall et al. 2020), and even when re-

leased alive, they are often injured as a result of being captured and suffer high post-release mortality (Tremblay-Boyer et al. 2016).

We observed an increase in the abundance of whale sharks over time. We believe a possible explanation for this finding involves range shifts or niche partitioning associated with the decrease in abundance of manta and mobula rays, as whale sharks and devil rays occupy a similar ecological niche as pelagic filter-feeders in tropical seas where plankton is scarce (Couturier et al. 2013). For example, in Hawaii, data from dietary analysis revealed that interspecific competition highly influences the distribution of carcharhinid sharks (Papastamatiou et al. 2006). Our results may be an example of one of the most basic ecological principles: competition. With fewer manta rays and mobula rays observed on dives each year (Fig. 7), there may be greater resources for whale sharks and an associated increase in their foraging behavior and relative abundance around Cocos Island.

One of the goals of this study was to examine what happens when models do not account for environmental variability and how this affects the interpretations of model outputs. In our models for all 3 species, there were differences in the predicted relative abundance each year when we accounted for and did not account for environmental variability. For manta rays and whale sharks, when we did not account for environmental vari-

ability in our models we overestimated population changes each year. For whale sharks, we estimated a larger increase in populations, and for mantas, we estimated a larger decrease in populations. For mobula rays, we underestimated population decreases when we failed to account for environmental variability, likely because mobulas were highly influenced by a variety of environmental covariates (see Fig. 4). As studies like these are often used to inform management strategies and IUCN Red List assessment statuses, discrepancies in estimations can be problematic. We show the necessity of accounting for environmental variation when examining population trends.

#### 4.2. Temperature and climatic conditions

The results of our study support the findings of several past studies that found that El Niño and La Niña influence the abundance of whale sharks (Wilson et al. 2001, Sleeman et al. 2010a). It is thought that whale shark movements are related to ocean currents, which are fundamentally shifted during La Niña and El Niño years. One potential explanation for this involves the physiology of whale sharks, which, like many other species of large fish, are known to have a wide thermal tolerance. A 2020 study suggested that the large body size of whale sharks minimizes heat loss during

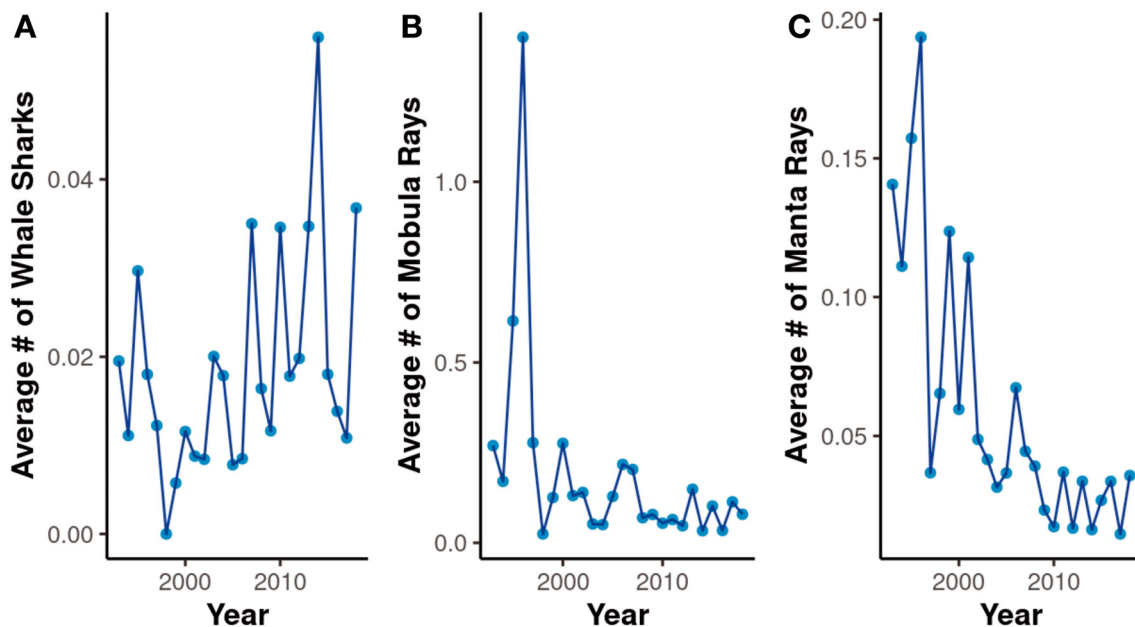


Fig. 7. Average number of (A) whale sharks, (B) mobula rays, and (C) manta rays observed on dives each year over the duration of the study (1993–2019)

deep excursions without incurring high metabolic costs to maintain body temperature (Nakamura et al. 2020).

For mobula and manta rays, we found that increases in temperature correlate with significant decreases in abundance. Mobulas were influenced by SST, with a 1°C increase in SST leading to a 12% decrease in abundance. Temperature at depth also played a small but significant role in the abundance of mobula rays, with a 1°C increase in temperature at depth yielding a 4% decrease in abundance. Manta rays were influenced by both temperature at depth and SST, with a 1°C increase in SST yielding a 13% decrease in abundance and a 1°C increase in temperature at depth yielding a 6% decrease in abundance. One of the key takeaways of Osgood et al. (2021) was that mobula rays (mantas and mobulas combined) showed little response to ONI. Unlike Osgood et al. (2021), we chose to keep the categorization of manta and mobula rays separate, with 'mantas' referring to *Manta birostris* and mobulas including all other members of the *Mobula* genus. Our results for mantas were similar to those of Osgood et al. (2021), finding no significant relationship between mantas and ONI. However, ONI did play an important role in mobula abundances, with a 1 unit increase in ONI yielding a 17% increase in mobula abundance. While in this study we show that acute temperature changes, specifically warming, lead to decreases in abundance of rays, other studies have shown that ocean warming can exert a variety of effects on elasmobranchs. For example, there is evidence for habitat shifts in elasmobranchs because of climate change; Bangle et al. (2018) found that climate-change-driven temperature increases allowed bull sharks *Carcharhinus leucas* to expand their nursery habitats. Similarly, a 2022 study forecasted range expansion of tiger sharks *Galeocerdo cuvier* under climate change (Niella et al. 2022), and another study reported potential northward range expansion of white sharks due to climate change (Bastien et al. 2020). In the future, a more comprehensive analysis of differences in thermal niches could reveal the potential reasons why ONI impacts mobula rays but does not appear to have the same effect on whale sharks and manta rays.

### 4.3. Primary productivity

To better understand how elasmobranch abundance is related to physical transport mechanisms and primary productivity, we included chl *a* concen-

tration. We hypothesized that high primary productivity would increase the abundance of planktivores because they are known to follow physical and biological oceanographic cues to locate successful foraging grounds (Nelson & Eckert 2007). Our results, however, were in contrast to this hypothesis. We found that manta and mobula ray abundance was not significantly affected by primary productivity. For whale sharks, increased primary productivity decreased abundance.

Upon examination of this finding, there are some plausible explanations for this seemingly odd phenomenon of planktivores avoiding areas of high primary productivity. Throughout this study, divemasters noted that, unlike other known whale shark aggregation sites, the whale sharks at Cocos Island did not appear to be feeding. It is possible that the whale sharks surveyed in this study were not practicing surface feeding, but rather exhibiting deep-dive foraging behavior, which the species is known to exhibit in other locations (Graham et al. 2006). Tracked whale sharks in the Sea of Cortez spend long periods at depth and short sporadic periods near the surface (Eckert & Stewart 2001). Another study that found a lack of strong correlation between whale shark movement patterns and measured chl *a* suggested that chl *a* is a poor proxy for zooplankton biomass (Sleeman et al. 2010b). Species of filter feeders are known to exhibit broad-scale habitat use across surface and pelagic zones. Basking sharks *Cetorhinus maximus* dive to forage on zooplankton communities in the mesopelagic and epipelagic zones (Sims et al. 2003a). A study that investigated whale shark diving patterns on the Mesoamerican barrier reef suggested that whale shark diving patterns (including deep dives) may be influenced by a seasonally available food source (Graham et al. 2006). Another possibility is that whale sharks are responding to changes in zooplankton community composition (i.e. specific species present) rather than the concentrations of species. Keeping in mind the foraging behavior of planktivores, the most notable limitation of the chl *a* data used in this study is that it was obtained through satellite measurements, data which only indicates levels of primary productivity at the sea surface. Indeed, a true understanding of the role of primary productivity and chl *a* concentration in shaping the behavior of planktivores that exhibit broad-scale foraging behavior requires measurements of chl *a* and plankton abundance beyond surface measurements. Nevertheless, we chose to include chl *a* in our models because for this location it was the best available proxy for zooplankton abundance.

#### 4.4. Salinity

Another commonly assessed oceanographic parameter is salinity. Salinity had a large effect on the abundance of mobula rays; we found that for a one-unit increase in surface PSU there is a 22% increase in mobula rays. Salinity did not have a statistically significant effect on the abundance of whale sharks or manta rays. A past study on whale shark behavior found that dives were not associated with hydrographic features (salinity and temperature) and cited food availability as the primary reason for variation in behaviors (Gunn et al. 1999). One of the few studies on the spinetail devil ray *Mobula mobular* found that their presence is influenced by a variety of environmental variables, including salinity (Lezama-Ochoa et al. 2019).

Nevertheless, other studies on elasmobranchs have found that salinity can play an important role in physiology, metabolism, and behavior. Physiologically, at least some elasmobranch species can adapt to low salinities; a study on captive sharks found coordinated molecular responses to low salinity in the rectal glands and gills (Dowd et al. 2010). Similarly, a study on the habitat partitioning of bull sharks *Carcharhinus leucas* found that juvenile bull sharks may have specific salinity preferences that affect their habitat use (Simpfendorfer et al. 2005). The results of our study may point to similar preferences among mobula rays; they may prefer waters with higher salinities. However, for manta rays and whale sharks, factors other than salinity appear to have a greater effect on their abundance and behavior. In other locations, manta rays have been found to seasonally use estuarine complexes (Medeiros et al. 2015); this may mean that giant mantas have a greater or wider salinity tolerance. This potentially broad tolerance may explain why salinity did not have a large impact on mantas in this study. Nevertheless, there is limited literature on the impacts of salinity on whale sharks, mantas, and mobulas since many studies are the results of field observations or the deployment of electronic tags. With this in mind, we suggest that future studies, especially those that employ electronic tagging, integrate salinity data as a covariate to further examine the role of salinity in the habitat use and behavior of planktivorous elasmobranchs.

#### 4.5. Lunar factors

Lunar factors are known to impact reproduction (Szmant-Froelich et al. 1986, Perea et al. 2022), mi-

gration (Somers & Stechey 1986, Sleeman et al. 2010a, Norevik et al. 2019), behavior (Naylor 2001, Mestre et al. 2019), and physiology (Portugal et al. 2019) across different species and ecosystems. For planktivorous elasmobranchs at Cocos Island, lunar factors ranged from having no influence to having a significant or large influence on the presence of species. On the larger-bodied manta rays and whale sharks, lunar factors were not included in the top models. This is in contrast to some past work that was done at the Belize Barrier Reef, where whale sharks aggregate seasonally around predictable spawning aggregations of various species of snapper (Heyman et al. 2001, Graham et al. 2006), and at Ningaloo Reef, where whale sharks form aggregations around the timing of known coral spawning events (Gunn et al. 1999).

We found that there is a significant increase in the abundance of mobula rays during new moons and last quarters relative to the first quarter. The literature on other species of elasmobranchs suggests that circadian rhythm may regulate diving and metabolic patterns for some species (Nelson & Johnson 1970, Nixon & Gruber 1988). The significant role of lunar factors on mobula abundance may be due to the known role of the lunar cycle in fish and coral spawning and the influence of these events on the foraging behavior of planktivorous elasmobranchs. However, the fish and coral communities at Cocos Island are relatively under-studied, making it difficult to confirm this hypothesis. Still, we reason that if lunar factors have ramifications on spawning and, in turn, impact the foraging behavior of the species that consume the spawn, it will impact whale sharks, mobula rays, and manta rays. One potential reason for this could be differences in preferred prey, or depths of foraging behavior.

We hypothesize that a potential reason for the increase in the number of encountered rays when lunar illumination decreases is anti-predatory behavior. In areas where lunar illumination is high, it is possible that they move away from foraging locations where increased light at the surface would leave them vulnerable to predation by larger sharks (e.g. scalloped hammerheads, tiger sharks, and other carcharhinid species). Other studies have supported that the lunar phase impacts movement and foraging behavior; for example, a study on the movements of gray reef sharks found that the mean depth inhabited increased throughout the lunar cycle (Vianna et al. 2013). If our hypothesis that the lunar cycle influences behavior by eliciting an anti-predatory response in smaller-bodied mobula rays under in-

creased light conditions is correct, it is plausible that whale sharks and larger-bodied mantas would not exhibit the same antipredator response since they are both (at this study location) too large to be preyed upon by the medium- to large-bodied carcharhinids present at Cocos Island.

#### 4.6. Limitations and future work

One of the major limitations of this study was that chl *a* is not the best indicator of zooplankton abundance, as primary productivity levels and zooplankton abundance are not the same. In the future, especially for studies on planktivorous elasmobranchs, we suggest additional methods to comprehensively assess levels of zooplankton communities. For example, a 2019 study developed a satellite-derived proxy of mesozooplankton (Druon et al. 2019). In the future, we could include a covariate like this one in models to indicate food availability for planktivores. Additionally, to better understand how zooplankton abundances affect planktivores, surveys of zooplankton at the species level in conjunction with observation of planktivores (e.g. zooplankton samples in conjunction with all dive surveys) are necessary. In the future, water samples at known foraging sites could be DNA sequenced to examine zooplankton assemblages, providing accurate information on the abundance and diversity of invertebrates within the water column (Hajibabaei et al. 2011). Likewise, plankton tows or continuous plankton recorders are employed at other locations to monitor plankton assemblages and have the potential for use in studies on planktivorous elasmobranchs (Head et al. 2022).

Other studies on planktivores have incorporated additional available environmental covariates; for instance, a study that examined the environmental characteristics associated with the presence of the spinetail devil ray *Mobula mobular* identified chlorophyll and sea surface height as the main predictors of devil ray presence or absence (Lezama-Ochoa et al. 2019). Those authors included sea surface height (SSH) because of its relationship to upwelling systems; thus, in systems where this data is obtainable or monitorable, SSH should be included as a predictor. In our systems, however, SSH may not be a suitable covariate because of the relatively small footprint of Cocos Island.

Although we had high statistical power in our study (White 2019), there could still be potential is-

ues while using community science data. Diver surveys do not have a consistent field of view or length of dive. Throughout the study, visibility varied, which has an inherent impact on the detectability of an individual. Indeed, we cannot say whether increased visibility reflected increased relative abundance or simply an increased field of view. Furthermore, while we found no correlation, it is plausible that visibility could also be related to primary productivity. However, the protocols were the same over 28 yr and a relatively small group of experienced divemasters were responsible for all data collection. Nevertheless, there could be sampling bias in terms of which sites are visited most frequently over time (Fournier et al. 2019, White & Bahlai 2021). Additionally, observation accuracy was likely impacted by diving conditions (e.g. visibility and conditions where diving is not feasible). Thus, future work could couple scientifically standardized survey methods with divemaster-collected data for a more complete picture of population trends in the area. We suggest that future studies should include other methods such as standardized underwater video surveys (Osgood et al. 2019, Smith et al. 2020), photo ID (Araujo et al. 2019), drone surveys (Setyawan et al. 2022), isotope analysis (Pankow et al. 2021, Silver-Gorges et al. 2023, Weber et al. 2023), and examining the movement of animals via telemetry (Guzman et al. 2022).

## 5. CONCLUSIONS

Our findings highlight that it is critical when evaluating the efficacy of marine protections to also consider the potential effects of environmental variability. Many studies evaluate the success of MPAs based on population data, and many report success based on various metrics, but studies often do not account for environmental variability. For example, a study done in South Africa suggested that the relative abundance of sharks is higher inside a marine reserve compared with abundances outside the marine reserve; however, this study only included depth as a proxy for temperature in models but did not incorporate any other environmental covariates (e.g. primary productivity, salinity, tides) (Albano et al. 2021). Similarly, a recent study on white sharks in the Mediterranean Sea analyzed encounter data using generalized additive models and information on human population abundance as a proxy for observation effort; however, they did not account for environmental variation within their models, although

they suggest temperature and productivity as potential explanations for observed fluctuations in abundances (Moro et al. 2020). In contrast, other studies have successfully integrated environmental variation to make inferences about abundance trends; for example, a 2020 study used a set of environmental predictors, similar to those included in our study, to estimate the distribution of several species of sharks and propose expansion of protected areas, and suggested that because of decreases in suitable habitat, climate change scenarios should be included as part of shark management strategies (Birkmanis et al. 2020).

In this study, we show that environmental parameters can have significant effects on the abundance and habitat selection of planktivores. If we fail to include environmental data in models, we could infer increases or decreases in species abundances are the result of policy successes or failures, when the true cause of the shift may be environmental change and variability shaping habitat use. The long-term time series data employed in this study provided us with a unique opportunity to explore environmental variability and species trends within an isolated protected area over many years. Additionally, findings support the conclusions of past studies, which suggest that in the future, researchers should seek to understand how environmental change affects species' interactions in order to predict emergent ecological changes (Kindinger et al. 2022).

**Data availability.** All code for models and data integration is available at <https://github.com/juliasaltzman1/Planktivores>. The data set used for this study is the property of Undersea Hunter, and is used with their permission; therefore, the data are not available online.

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