








# Multidecadal underwater surveys reveal declines in marine turtles

Julia Saltzman<sup>1,2</sup>  | Alex R. Hearn<sup>3,4</sup>  | Mariana M. P. B. Fuentes<sup>5</sup>  |  
Todd Steiner<sup>4,6</sup>  | Randall Arauz<sup>4,7</sup>  | Catherine Macdonald<sup>2,8,9</sup>  |  
Maike Heidemeyer<sup>10,11,12</sup> | Easton R. White<sup>1</sup> 

<sup>1</sup>Department of Biological Sciences, University of New Hampshire, Durham, New Hampshire, USA

<sup>2</sup>Field School, Coconut Grove, Florida, USA

<sup>3</sup>Galapagos Science Center, Universidad San Francisco de Quito USFQ, Quito, Ecuador

<sup>4</sup>MigraMar, Bodega Bay, California, USA

<sup>5</sup>Department of Earth, Ocean, and Atmospheric Science, Florida State University, Tallahassee, Florida, USA

<sup>6</sup>Turtle Island Restoration Network, Forest Knolls, California, USA

<sup>7</sup>Marine Watch International, San Francisco, California, USA

<sup>8</sup>Shark Research and Conservation Program (SRC), Department of Environmental Science and Policy, Rosenstiel School of Marine, Atmospheric, and Earth Science, Miami, Florida, USA

<sup>9</sup>Johnson Center for Marine Conservation, Rosenstiel School of Marine, Atmospheric, and Earth Science, Miami, Florida, USA

<sup>10</sup>Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica, San José, Costa Rica

<sup>11</sup>Centro de Investigación en Biología Celular y Molecular (CIBCM), Universidad de Costa Rica, San José, Costa Rica

<sup>12</sup>Asociación para la Conservación Integral de Recursos Naturales Equipo Tora Carey, La Cruz, Costa Rica

## Correspondence

Julia Saltzman, Department of Biological Sciences, University of New Hampshire, Durham, NH 03824, USA.  
Email: [julia.saltzman@unh.edu](mailto:julia.saltzman@unh.edu)

## Funding information

University of New Hampshire Graduate School Summer Teaching Assistant Fellowship (STAF); Sandler Foundation; The Goldman Prize; Whitley Fund for Nature

## Abstract

Marine turtles are a group of imperiled marine megafauna particularly vulnerable to anthropogenic stressors. Most long-term studies of marine turtles are based on nesting surveys which focus on numbers of eggs, hatchlings, and nesting females. However, we know less about long-term abundance trends of immature and adult turtles in the marine environment. To address this data gap, we examined records from 35,000 underwater visual census (UVC) dives (1993–2019) and short-term in-water turtle survey data (2009–2014) at Cocos Island, Costa Rica. During UVCs, trained divemasters from UnderSea Hunter recorded observations of two species of marine turtles—green *Chelonia mydas* and hawksbill *Eretmochelys imbricata*. Our short-term in-water surveys revealed that most turtles at Cocos are greens, but both immature and mature greens occur at Cocos. We analyzed long-term UVC data using a hierarchical modeling approach and we modeled a 26% decrease in the relative abundance of turtles observed on dives each year. Our model also revealed potential interactions between tiger sharks and turtles, finding that for each additional tiger

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Conservation Science and Practice* published by Wiley Periodicals LLC on behalf of Society for Conservation Biology.

shark present during a dive, the predicted relative abundance of turtles decreased by 43%. Lastly, our model suggested the influence of environmental variation on marine turtle relative abundance; a 1°C increase in sea surface temperature (SST) decreased the predicted relative abundance of turtles by 7%. Our results suggest that marine turtles are sensitive to long-term environmental and oceanographic changes, and potentially avoid certain areas to reduce exposure to tiger sharks. Given our study area is already protected, there needs to be more focus on protecting adult turtles during their movements across the Eastern Tropical Pacific. Our work also highlights the importance of long-term underwater surveys to monitor adult turtles.

#### KEYWORDS

citizen science, community science, eastern tropical Pacific, endangered species, marine protected area, marine turtles, predator–prey interactions, time series

## 1 | INTRODUCTION

Marine megafauna species are ecologically (Estes et al., 2016; Moran & Bjorndal, 2005), economically (Campbell & Smith, 2006; Macdonald & Wester, 2021), and culturally important (Barney et al., 2005; Grose et al., 2020), and can serve as sentinels or indicators of ecosystem health (Pimiento et al., 2020). Despite their importance, one-third of marine megafauna species are threatened with extinction (Pimiento et al., 2020). One of the most well-known groups of marine megafauna is marine turtles. Although there are only seven species within this group, marine turtles inhabit nearly all oceans (Wallace et al., 2011) and fill distinct and important ecological niches (Bjorndal & Jackson, 2002). Most populations of marine turtles are threatened with extinction (Wallace et al., 2011), although some are showing recovery (Balazs & Chaloupka, 2004; Ceriani et al., 2019; Mazaris et al., 2017). The imperiled status of marine turtle populations can be attributed to a variety of factors, including habitat degradation (Cullen-Unsworth & Unsworth, 2018; Nelson Sella et al., 2019), climate change (Patricio et al., 2021), direct take (Senko et al., 2022), and bycatch (Finkbeiner et al., 2011; Lewison et al., 2014).

The status of marine turtle populations is in part determined by population abundance and trends, with the latter requiring long-term information on the number of individuals across different life stages (Bahlai et al., 2021; Derville et al., 2015; Stokes et al., 2014; White, 2019). Long-term monitoring of marine turtles has typically focused on determining the abundance of nesting females, hatchlings, and eggs (Santos et al., 2021). Long-term monitoring of the oceanic life stages of sea turtles, particularly subadult life stages, is less common

(Wildermann et al., 2018). Indeed, a recent study which identified research priorities for immature sea turtles highlighted the need to improve our knowledge of “population ecology,” including population size, age, and survivorship (Wildermann et al., 2018). Status assessments and risk assessments, such as the IUCN Red List, also benefit from data that are collected across life stages; for marine turtles, this includes a need for comprehensive assessment of oceanic and coastal foraging areas as well as nesting aggregations (Hamann et al., 2010). However, in-water monitoring of marine turtles can be logistically difficult and costly (Balazs & Chaloupka, 2004; Wildermann et al., 2018). A potential alternative method, which can supplement cost- and effort-intensive in-water monitoring by scientists, is the use of dive surveys, including data generated via community science (Williams et al., 2015).

One area of the world where information from community science has complemented data collected by scientists is the Eastern Tropical Pacific (ETP), where marine turtles nest and forage. In this region, *Chelonia mydas* green turtles nest in the Galapagos Islands (Carrión-Cortez et al., 2010) and make extensive post-nesting migrations throughout the ETP (Seminoff et al., 2008). The ETP is also important for *Eretmochelys imbricata* hawksbills with juveniles foraging on the North Pacific coast of Costa Rica (Carrión-Cortez et al., 2013) and adults nesting and foraging throughout the ETP, making it an important region for hawksbills across life stages (Carrión-Cortez et al., 2013; Gaos et al., 2016; Liles et al., 2015). This information contributed to the establishment of a marine protected area along the corridor between Cocos Island and Galapagos (Hermandad Marine Reserve) partly due to its importance for marine turtles and other migratory marine species (e.g., *Sphyrna lewini* scalloped hammerhead) (Bravo-

Ormaza et al., 2023; Hearn, 2022; Nalesso et al., 2019; Peñaherrera-Palma et al., 2018; Pincetich et al., 2012). Despite the potential contributions of this type of data to management, there have not been assessments of the long-term trends, and potential drivers, of population dynamics of oceanic life stages of marine turtles.

Past work has identified the effects of temperature on turtle foraging behavior (Chambault et al., 2016), movement (Crear et al., 2016), and energy expenditure (Enstipp et al., 2011). In addition to environmental variables, sea turtle behavior, reproduction, and population dynamics are also affected by the presence of predators (Heithaus et al., 2002, 2007; Veríssimo et al., 2012). Tiger sharks (*Galeocerdo cuvier*) are one of few natural predators of adult and subadult marine turtles (Heithaus et al., 2002). As such, several studies to date have examined potential interactions between tiger sharks and marine turtles (e.g., Fitzpatrick et al., 2012; Heithaus et al., 2007). These have found a range of lethal and non-lethal impacts on turtles (Heithaus et al., 2007). Recent work, however, has demonstrated that while tiger sharks may alter their behavior to enhance the probability of successful predation on turtles, other biotic and abiotic factors like temperature and food availability may be more important than predation risk in predicting movement and habitat use (Hammerschlag et al., 2015). Despite these studies, limited work has assessed the effects of environmental variables and predation scale to the population level, especially for turtles during oceanic life stages, since most long-term monitoring of marine turtles is related to nesting beaches. To disentangle the effects and interactions of these factors, long-term underwater surveys are needed. These surveys are of need in the Costa Rican Tropical Pacific, where despite the presence of at least seven important turtle foraging areas, there has been little work

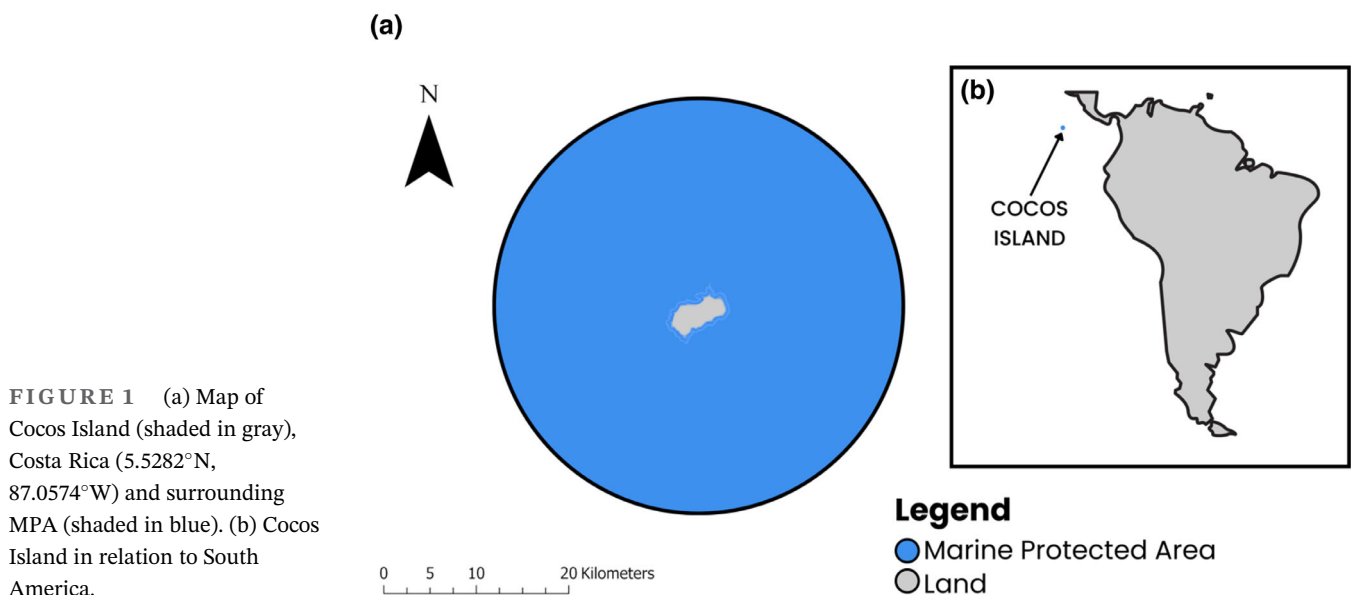
completed to-date on the ecology and population dynamic of the turtles in these areas.

Most work which has examined the effects of environmental variation on marine turtles is short-term, and no studies examine the potential synergistic effects of predation pressure and environmental variation on marine turtles. To assess long-term underwater abundance trends and examine the potential role of predation pressure on sea turtles, we used 22 years of diver visual census data from Cocos Island, Costa Rica in the ETP. To date, these visual census data have been used to examine long-term population trends of elasmobranchs (Osgood et al., 2021; Saltzman & White, 2022; Ward-Paige et al., 2011; Ward-Paige & Lotze, 2011; White et al., 2015). To better understand the species composition of marine turtles at Cocos, these data were supplemented with short-term data from in-water surveys undertaken in the same area. In addition, despite being identified as an important foraging area for marine turtles, little is known about the population dynamics of turtles at Cocos Island (Piedra-Chacón et al., 2021). We used these datasets to (1) provide insights into long-term trends in the relative abundances of marine turtles at Cocos Island; (2) examine potential interactions between tiger sharks and marine turtles; and (3) predict how environmental and ecological factors may impact the relative abundance of marine turtles.

## 2 | MATERIALS AND METHODS

### 2.1 | Study location

This study was conducted at Cocos Island (Isla del Coco) (hereafter “Cocos”), Costa Rica (Figure 1). Cocos is a



**FIGURE 1** (a) Map of Cocos Island (shaded in gray), Costa Rica (5.5282°N, 87.0574°W) and surrounding MPA (shaded in blue). (b) Cocos Island in relation to South America.

small (23.85 km<sup>2</sup>) island, with no permanent residents other than Costa Rican Park rangers. In 1978, Cocos was designated as a Costa Rican National Park and in 1984 its Marine Protected Area (MPA) was established, making it one of the world's oldest MPAs (White et al., 2015). As of 2001, the MPA was expanded to encompass a 12 NM radius around Cocos (Alvarado et al., 2012). Funding for monitoring and enforcement of the MPA has been limited (White et al., 2015), and illegal fishing occurs in the park's waters (Arias et al., 2016). Cocos is of ecological importance in the Eastern Tropical Pacific and pelagic environment, as it allows for reef-associated communities to interact with pelagic species at many different trophic levels (Friedlander et al., 2012). Additionally, for highly migratory species such as sharks and marine turtles, oceanic islands serve as navigation reference points and provide refuge (Hamilton & Watt, 1970). Cocos has been identified as an understudied, but potentially important foraging area for green turtles *Chelonia mydas* (Piedra-Chacón et al., 2021).

## 2.2 | Biological data collected during in-water marine turtle surveys

From August 2009 to June 2014 ( $n = 5$  years), trained scientists conducted marine turtle in-water surveys under permits issued by the authorities of the Cocos Island Marine Conservation Area of the Ministry of Environment of Costa Rica (Resolución Nos. ACMIC-002-2009, 2010-I-ACMIC-006, 2011-I-ACMIC-001, 2012-I-ACMIC006, ACMIC-I-2013-0012, and ACMIC-I-2014-007). Juvenile and adult green turtles and juvenile hawksbill turtles were caught directly by hand during scuba diving operations at the most commonly visited dive sites. During capture, divers worked in teams of two, with one diver securing the turtle while the other safely controlled the ascent (catches occurred at depths of up to 35 m). Data recorded included Curved Carapace Width and Curved Carapace Length (Eckert et al., 1986). Mature male turtles were identified based on the presence of their developed long tails (Eckert et al., 1986).

## 2.3 | Dive surveys

From January 1997 to December 2019 ( $n = 22$  years), experienced divemasters ( $n = 36$ ) at UnderSea Hunter conducted dives at 17 sites around Cocos Island (Figure 1). Depth of dives was a maximum of 40 m, but within each of the 17 sites depth was consistent. Dive effort was not standardized in terms of length of dives or which sites were selected. However, dive profiles were relatively standard within each site, so we account for

some of the potential impact of lack of standardization using random effects (described further below). Furthermore, the proportion and relative effort in which dive sites were visited remained relatively constant over the duration of the study. Following each dive, divemasters recorded the count, presence, and absence of several species of elasmobranchs (see Osgood et al., 2021; Saltzman & White, 2022; White et al., 2015) as well as marine turtles. While there are two species of turtles at Cocos Island (green and hawksbill), observations often took place at relatively far distances, so individual turtles were not identified to species level. We transcribed and compiled all data from Undersea Hunter's divemasters into a single database, filtered out and removed dives which occurred at night, and corrected for transcription errors (Osgood et al., 2021; White et al., 2015). After this process, 35,706 individual dives (each approximately 45–60 min) remained for analysis.

## 2.4 | Environmental data and predation risk

For each dive, divemasters recorded several environmental parameters including estimated visibility (meters), rated current on a scale of 0 (none) to 4 (strong), and temperature at depth where counts were recorded using their dive computers. These data were supplemented with open source, remotely sensed environmental data which included mean daily sea surface temperature (SST), lunar phase, lunar distance, mean monthly salinity, mean monthly chlorophyll-a, and Ocean Niño Index (ONI) (Table 1). To account for seasonality, we included the sine and cosine of Julian Date (Baum & Blanchard, 2010).

Our high-resolution daily (0.25° latitude by 0.25° longitude) SST covariate was obtained from NOAA (see <https://psl.noaa.gov/>). We obtained lunar data (e.g., lunar distance and lunar phase) using the package “lunar” (Lazaridis, 2022) in R (R Core Development Team, 2021). Salinity data were obtained from the Met Office Hadley Centre observations datasets (see <https://www.metoffice.gov.uk/hadobs/en4/>). Chlorophyll-a data were available beginning in 2002 from the NASA combined-satellite (NASACombo) time series, a multiple-satellite cross-calibrated chlorophyll product (see <https://oceancolor.gsfc.nasa.gov/>). Finally, ONI data were obtained from NOAA at their website (see <https://www.cpc.ncep.noaa.gov/data/indices/oni.ascii.txt>) (Osgood et al., 2021). We adapted the methods from Osgood et al. (2021) and included temperature at depth of dive, SST, and ONI index. ONI represents the running 3-month mean of SST anomalies in the Niño3.4 region of the east-central Pacific and

**TABLE 1** Environmental covariates, their respective ranges, sources, spatial scale, and temporal scale.

Parameter	Source	Description	Range (5th–95th percentile)	Spatial scale	Temporal scale
Tiger sharks	UnderSea Hunter	Count of tiger sharks observed on dives	0–11 (full range)	Location of dive	Dive-specific
Ocean Niño Index	NOAA: <a href="https://psl.noaa.gov/">psl.noaa.gov/</a>	Multivariate El Niño–Southern Oscillation index	–1.38 to 1.31	East-central tropical Pacific between 120° and 170°W	3 months
Temperature at depth	UnderSea Hunter	Water temperature recorded by divers on their personal dive computers at depth	24–29 (°C)	Location of dive	Dive-specific
Sea surface temperature	NOAA: <a href="https://psl.noaa.gov/">psl.noaa.gov/</a>	NOAA High Resolution SST data (0.25-degree latitude × 0.25 degree-longitude grid) (Reynolds et al., 2007)	26.17–29.62 (°C)	0.25° latitude × 0.25° longitude	Daily
Salinity	Met Office Hadley Centre observations datasets: <a href="https://metoffice.gov.uk/hadobs/en4/">metoffice.gov.uk/hadobs/en4/</a>	Hadley EN4 subsurface salinity objective analysis (Good et al., 2013)	31.47–33.42 (ppt)	1° latitude × 1° longitude	Monthly
Chlorophyll-a	NASACombo time series: <a href="https://oceancolor.gsfc.nasa.gov/">oceancolor.gsfc.nasa</a>	A multiple-satellite cross-calibrated chlorophyll product	0.108–0.257 (mg/m <sup>3</sup> )	0.25° latitude × 0.25° longitude	Monthly
Current code	UnderSea Hunter	Estimation of current strength by diver	0 (none)–4 (strong)	Location of dive	Dive-specific
Visibility	UnderSea Hunter	Water visibility (meters), estimated by diver	10–30 (m)	Location of dive	Dive-specific

correlates with more general oceanographic features, and sea surface temperature captures the immediate local conditions at the surface (Osgood et al., 2021; White et al., 2015). None of the three temperature variables were correlated via Spearman's rho; all correlations were weak ( $<|0.36|$ ) (Table A1). Tiger shark count data from the visual census were used as a proxy for risk of predation since tiger sharks are known to prey upon turtles. Like with turtle observations, the number of tiger sharks observed by divers was recorded after each dive and used as an indicator of tiger shark relative abundance and turtle predation risk.

## 2.5 | Generalized linear mixed models

We modeled the counts of marine turtles per dive using a hierarchical generalized linear mixed model (GLMM) framework with random effects to account for variation in observations made by the same diver or within the same dive site. Specifically, we used Zero-Inflated Negative Binomial Models (ZINB) to account for the high number of dives without any turtles and overdispersion

(Zuur et al., 2009). We used a threshold of  $p \leq 0.001$  to determine the significance of each covariate. This  $p$ -value was selected over the convention  $p < 0.05$  to reduce the likelihood of false positives and because a “stricter”  $p$ -value ensures robust findings which have limited likelihood of being due to random chance. In these models, we are modeling turtle counts on a per dive basis, rather than a sum per month or year, so adjustments for effort are not necessary. Furthermore, because the models were run per dive, there was no standardizing or aggregating to a larger scale (e.g., all data points within a single month, as listed in under temporal scale in Table 1, would have the same salinity value). We used Akaike information criterion (AIC) for model selection (Zuur et al., 2009). Rather than a drop one approach for AIC, we compared AIC values to select our top model from seven different models (Table A2), which each included or omitted parameters with specific biological significance. We performed AIC with the “AICcmodavg” (Mazerolle, 2023) package in R (R Core Development Team, 2021). After running our models in “lme4” (Bates et al., 2023), and determining the top model with “AICcmodavg,” we examined the outputs of our model

using “sjPlot” (Lüdecke et al., 2023) and “ggplot2” (Wickham et al., 2023). Effects of statistically significant covariates were visualized holding all other respective covariates at their respective means of the observed data.

### 3 | RESULTS

#### 3.1 | Biological data collected during in-water marine turtle surveys

From 2009 to 2014, 129 turtles were captured and tagged (Figure 2). Of these 93% were greens ( $n = 120$ ), and 7% were hawksbills ( $n = 9$ ) (Figure 2). All of tagged hawksbills had a curved carapace length of  $\geq 74$  cm. Fifty percent ( $n = 60$ ) of greens were identified as sexually mature males based on the presence of their developed long tails (Eckert et al., 1986).

#### 3.2 | Dive surveys

From 1997 to 2019, a total of 12,479 marine turtles and 3194 tiger sharks were observed across 35,706 dives (Figure 3). Turtles were present on 21.8% ( $n = 7775$ ) of dives. A mean of 0.35 turtles (SD = 1.27) were observed on each dive throughout the duration of the study. The top model was the global model without lunar factors (Tables A2–A4, Figures A1–A3). Accounting for all environmental variability, we modeled a 26% decrease in the relative abundance of turtles observed on a dive each year ( $p < 0.001$ , SE = 0.01) (Figure 4b). We found that increases in temperature at depth and increases in SST were associated with decreases in the relative abundance of turtles (Figure 4d,e); specifically, we found a 1°C

increase in SST produces a 7% decrease in the predicted relative abundance of turtles ( $p < 0.001$ , SE = 0.02), and a 1°C increase in temperature at depth yields an 8% decrease in the predicted relative abundance of turtles observed ( $p < 0.001$ , SE = 0.01). In addition to responses to daily temperature changes, long-term trends in climate also appeared to influence the number of turtles observed on dives. We found that for a 1-unit increase in ONI, the predicted relative abundance of turtles on a dive increased by 8% ( $p = 0.001$ , SE = 0.02) (Figure 4c). For each additional tiger shark present, we predicted a 43% decrease in the relative abundance of turtles on a dive ( $p < 0.001$ , SE = 0.04) (Figure 4a). Salinity did not have a statistically significant effect on turtle relative abundance; however, an increase in primary productivity appeared to be related to large decreases in the predicted number of turtles observed. We observed that for a 0.10 mg/m<sup>3</sup> increase in chlorophyll-a, the predicted relative abundance of turtles decreases by 21% ( $p < 0.001$ , SE = 0.03) (Figure 4f). While visibility did not affect the relative abundance of turtles, a 1-unit increase in current strength yielded an 8% decrease in the predicted relative abundance of turtles ( $p < 0.001$ , SE = 0.01).

### 4 | DISCUSSION

After accounting for environmental variability, we modeled a 26% decrease in the predicted relative abundance of turtles each year ( $p < 0.001$ ). This decrease in relative abundance occurred despite the establishment of a 5 km radius Marine Protected Area at Cocos since 1984, and its expansion to 15 km radius in 1991 and to 22.22 km in 2001. One potential explanation for this decrease in relative abundance of marine turtles over time is fishing-

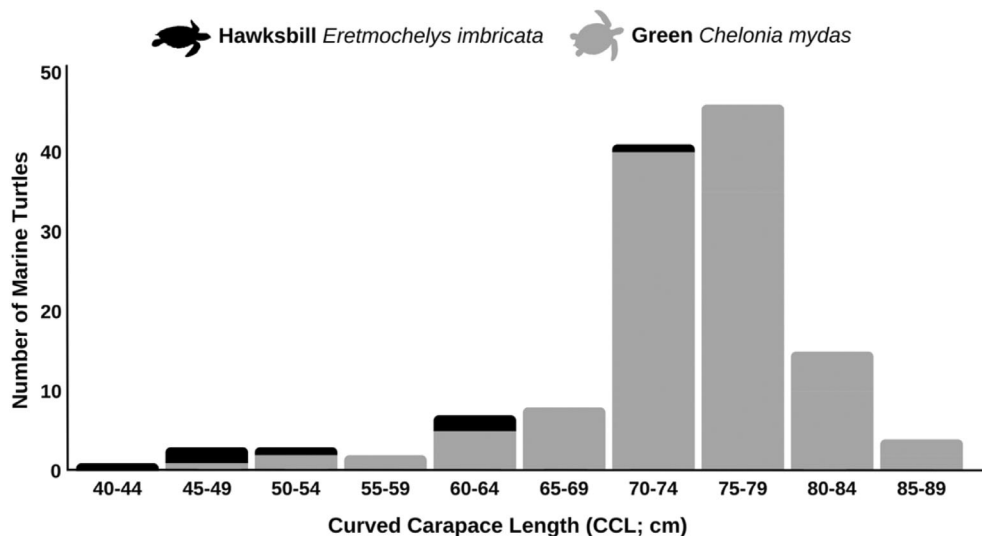
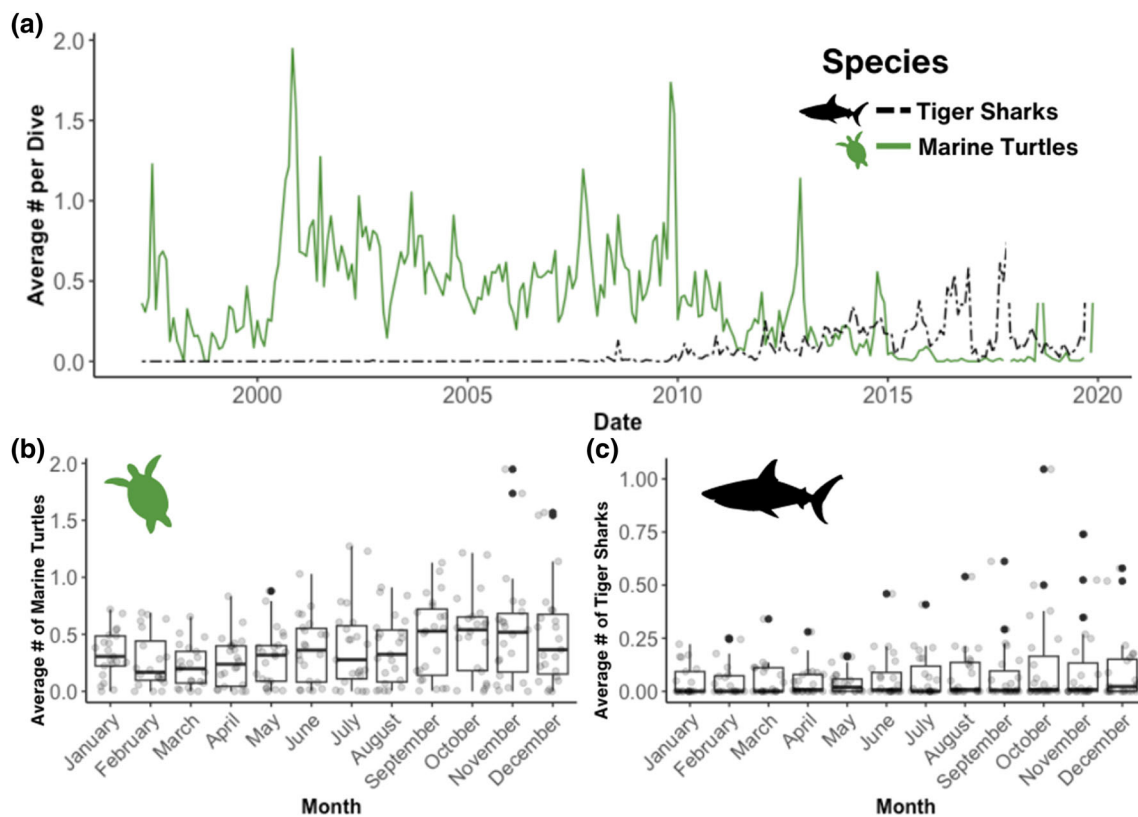


FIGURE 2 Number of *Eretmochelys imbricata* and *Chelonia mydas* recorded at a range of Curved Carapace Length (CCL; cm) tagged at Cocos Island from 2009 to 2014.

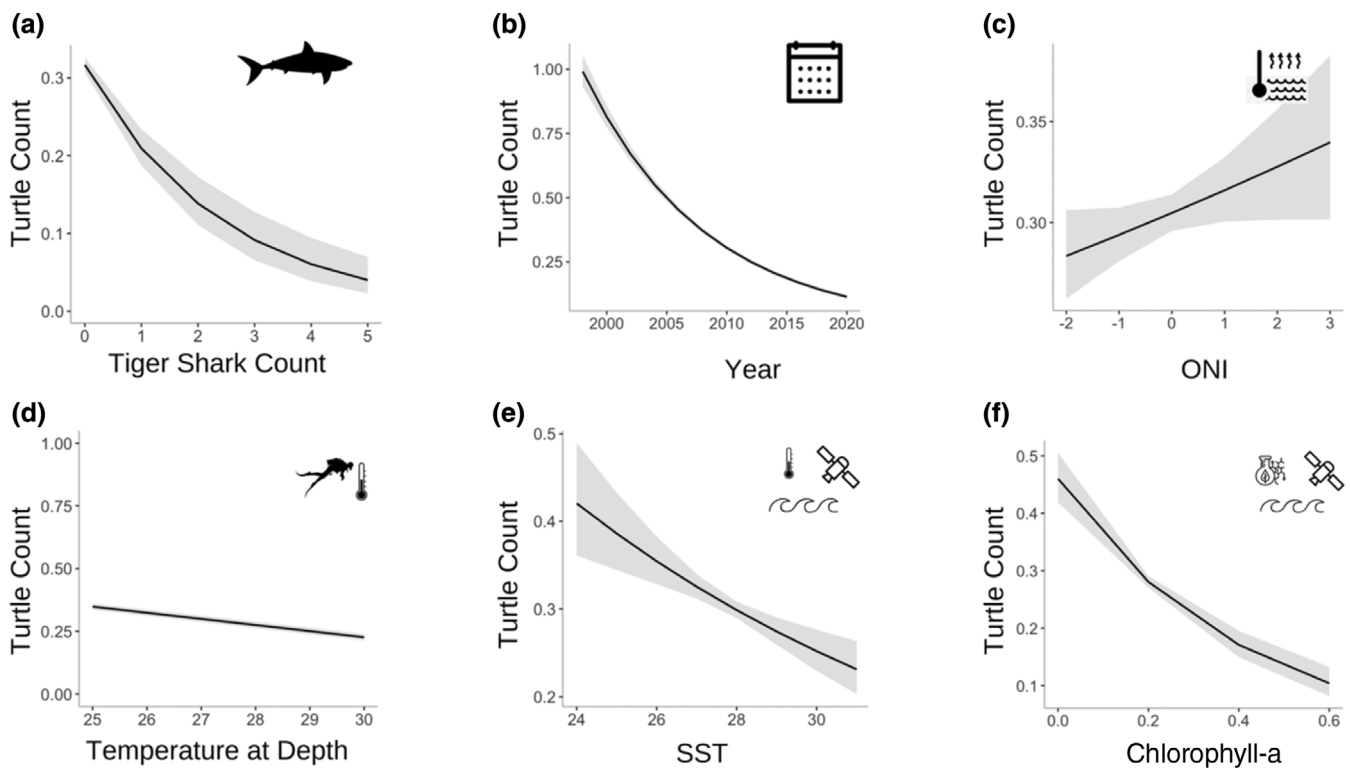


**FIGURE 3** (a) Monthly mean numbers of tiger shark and marine turtle counts (per-dive) throughout the duration of the study. (b) Mean number of marine turtles observed each month throughout the duration of the study. (c) Mean number of tiger sharks observed each month throughout the duration of the study. In (b, c) opaque black dots indicate outliers, while the transparent black dots show the raw data.

related mortality. Indeed, in Costa Rica, the longline fishery took 699,600 olive ridley turtles as bycatch from 1999 to 2010 (Dapp et al., 2013) and even with modified gear, rates of sea turtle bycatch are high (Swimmer et al., 2011). Inside the Cocos Island MPA, turtles are protected; however, turtles are highly migratory, and area protection may not be adequate to protect populations across regions (Nel et al., 2013). The highly migratory nature of marine turtles likely means bycatch impacts occur prior to reaching the Cocos MPA. Furthermore, despite being a protected area since the 1980s, funding for monitoring and enforcement of the Cocos MPA has been limited (White et al., 2015), and illegal fishing occurs in park waters (Arias et al., 2016). In general, the Eastern Tropical Pacific faces ongoing industrial fishing operations which are depleting populations of marine megafauna, including those present in marine reserves, at vast scales (Bonaccorso et al., 2021). As such, one potential explanation for our modeled decrease in turtles over time is population depletion due to bycatch. The declines in marine turtle abundance over the duration of this study, however, could be due to other threats faced by marine turtles. For

example, egg poaching and meat consumption is of particular concern in Costa Rica (Pheasey et al., 2021).

While anthropogenic threats across the ETP may explain some of the observed variations in turtle relative abundance at Cocos, according to our models, ecological interactions and environment variation also affect relative abundance of turtles. With respect to ecological interactions, the increase in probability of encountering tiger sharks could influence relative abundance of marine turtles. It is possible that we could be observing consumptive or non-consumptive effects of the presence of tiger sharks on turtle relative abundances in specific habitats. Turtles could be avoiding Cocos or specific areas within it due to occupancy by tiger sharks, or turtle relative abundances at Cocos could have decreased due to predation by tiger sharks. It is possible that with the development of the MPA, populations of tiger sharks have increased, exerting both lethal and non-lethal impacts on marine turtles (e.g., direct mortality through predation and risk effects which resulted in behavioral shifts). This is consistent with other studies which have documented the apparent effects of apex predators on ecosystems, including on prey species habitat use (Frank et al., 2005; Gregr



**FIGURE 4** Graphs of selected statistically significant covariates ( $p \leq 0.001$ ) from the top zero-inflated negative binomial model. Graphs display the count of marine turtles (relative abundance) for statistically significant covariates (a) count of tiger sharks, (b) year of survey, (c) Ocean Niño Index, (d) temperature at depth, (e) sea surface temperature, and (f) chlorophyll-a. 95% confidence intervals are displayed in gray. Variable current was also statistically significant.

et al., 2020). Additionally, it is consistent with studies which have documented the semi-rapid emergence and recovery of marine predators upon the establishment of marine protection (Prato et al., 2013). It is notable, however, that the changes observed in marine turtle relative abundance observed in this study could be the result of changes in turtle detectability, due to different locations around the island, turbidity, and observer. Indeed, detection of turtles is likely influenced by a variety of factors, including the presence of tiger sharks. It is also important to note that tiger shark presence may be impacting marine turtle detectability, rather than actual abundance of turtles at Cocos.

We believe our results may show the “landscape of fear” phenomena occurring, in which predator presence elicits fear in prey due to risk of predation; in turn, fear can alter the physiology, movement, behavior, and life history of prey species (Gallagher et al., 2017; Laundré et al., 2001). Studies in the neighboring Galapagos Marine Reserve, approximately 700 km southwest of Cocos, have found tiger sharks occupy waters off green turtle nesting beaches (Acuña-Marrero et al., 2017) and stable isotope studies have shown that not only do green turtles form part of tiger shark diet, but also that tiger

sharks exhibit site fidelity around turtle nesting sites (Salinas-de-León et al., 2019). Nevertheless, to confirm the presence of the “landscape of fear” at Cocos Island, an assessment of the fine-scale behavioral response of turtle to tiger sharks is necessary. This study is limited, because during dive surveys, turtles were not identified to the species-level; as such, we cannot make any conclusions about species-specific behavioral responses to tiger sharks. The deployment of multichannel dataloggers (e.g., CATSCam) has shed light on the fine-scale behaviors of marine turtles (Díaz et al., 2024; Hounslow et al., 2021). Thus, we suggest the deployment of similar bio-logging devices on the turtles at Cocos Island to obtain information on species-specific responses of turtles to predators (Hounslow et al., 2021).

Aside from potential ecological interactions, environmental variation and oceanographic conditions also appear to influence marine turtles at Cocos Island. We found that increased sea surface temperature was correlated with decreases in the predicted relative abundance of marine turtles (highest temperature was 29.6°C). In general, shifts in climate have exerted significant impacts on migratory marine species (e.g., marine mammals, turtles, and sharks) (Hauser et al., 2018; Niella et al., 2022;

Osgood et al., 2021; Saltzman & White, 2022; Tulloch et al., 2019). Increased temperature at sea turtle foraging grounds influences the reproductive phenology of marine turtles, where higher SST at foraging grounds leads to fewer nests (Mazaris et al., 2009). Other work has also related increased SST to earlier nesting in loggerheads and green turtles (Pike et al., 2006; Weishampel et al., 2010). Furthermore, climate models have predicted that increases in seawater temperature will impact primary production, which affects the composition of prey communities and turtle foraging (Polovina et al., 2011).

Our results also support the contention that marine turtles may be sensitive to colder waters. We included Ocean Niño Index in our models to examine the influence of long-term climate variability on marine turtles. In this index, values of 0.5 or higher indicate El Niño, while values of  $-0.5$  or lower indicate La Niña (see [climate.gov/enso](https://climate.gov/enso)). Our results show that increased ONI (i.e., El Niño years) is associated with a greater probability of encountering turtles. One potential reason for the decline in the predicted relative abundance of turtles during years with lower ONIs (i.e., La Niña years) is that, in general, La Niña events lead to cooler waters region-wide in the Eastern Tropical Pacific (Okumura & Deser, 2010). While the temperatures at Cocos were not below the thermal tolerance for turtles of  $10\text{--}15^{\circ}\text{C}$  (Witt et al., 2007), our models support past studies which have found that cold waters can influence the distribution of marine turtles and that distribution of sea turtles is often linked to thermal niches (Polovina et al., 2011). For example, in the Mediterranean, loggerhead stranding events increase during times with colder SST (Báez et al., 2011). In the northeast Pacific, juvenile green turtles tend to avoid colder waters and associate with artificial warm waters near power plants (Crear et al., 2016).

Collectively, this study underscores the importance of long-term monitoring for turtles, and other marine megafauna, to account for temperature and other potential environmental covariates when assessing population dynamics. Our results show that environmental variability impacts the in-water relative abundance of marine turtles. This is especially important, since many studies on marine turtles and climate change, to date, have focused on nesting populations, and more research is needed to understand the effects of climate change outside of turtle nesting (Patricio et al., 2021). With this in mind, we suggest expansion of this survey to include other methods to assess turtle population size; for example, genetic studies could be a useful tool to monitor biodiversity and relatedness (Daly-Engel et al., 2012; Kynoch et al., 2022). Through genetic analysis, estimates of population size and identification of distinct population units can be achieved, and used to inform conservation efforts

and confirm abundance estimates. Stable isotope analysis of tissue samples could help to disentangle the trophic ecology and species interactions at Cocos (Pankow et al., 2021; Silver-Gorges et al., 2023; Weber et al., 2023), for example, stable isotope analysis of turtle, and other shark prey items as well as shark tissue could confirm if tiger sharks are consuming turtles at Cocos Island, and the contribution of turtles to their diet. Animal-borne cameras could be employed to examine the risk-effects of tiger sharks on marine turtles (Gallagher et al., 2021; Heaslip et al., 2012; Papastamatiou et al., 2018; Watanabe et al., 2019), and baited remote underwater video camera surveys could effectively assess relative abundance of tiger sharks and other species in and outside of the MPA (MacNeil et al., 2020; Osgood et al., 2019). Lastly, repeat surveys, like the ones in this study, with enough observers, can be used for more robust statistical analysis such as occupancy modeling and the determination of probability of recording false absence (Issaris et al., 2012).

This study is also significant in the broader context of marine conservation, highlighting the potential role of community science in long-term monitoring efforts. Long-term monitoring is logistically difficult, and often expensive. Despite the difficulties associated with it, long-term monitoring is critical to determine trends in populations over time (White, 2019), especially as they relate to anthropogenic pressures and environmental change. Recent work has suggested that population monitoring can be achieved on a local and global scale (Neate-Clegg et al., 2020) with community obtained data. In the case of Cocos Island, this is amplified because the island is isolated, and only reachable by boat; however, Cocos is an important area for a variety of marine species (Arias et al., 2016; Nalesso et al., 2019; Piedra-Chacón et al., 2021; White et al., 2015), which makes monitoring particularly important. Similar phenomena are likely to occur in important marine habitats globally, where long-term monitoring is logistically difficult for scientists, but can be achieved by collaborating with dive companies and ecotours. We suggest that when developing long-term monitoring studies, determining species statuses, and evaluating the efficacy of protected areas, scientists could consider how community science can be integrated with studies to answer their research questions. Ecotourism occurs in biodiversity hotspots (e.g., around predictable prey pulses, reproductive events, or social aggregations) of marine and terrestrial species. With this in mind, if tour operators can maintain long-term census of data, trends in biodiversity can be teased out, and relationships between biodiversity and environmental conditions can be assessed. These data are invaluable for conservation efforts and adaptive management; for example, data around predictable aggregations of vulnerable

marine megafauna can be used to inform seasonal regulations around fishing gear and effort. While community science data may not provide answers to questions about fine-scale movement, or individual traits, we suggest they can be an avenue for the examination of broader scale and coarse population data. For example, data from dive surveys could be used to answer questions like those which are answered via baited remote underwater video stations (e.g., exploring presence and absence of different trophic levels or species overtime).

One marine habitat where tourism, more specifically dive-related tourism, could be leveraged by scientists to achieve long-term monitoring is coral reefs. As of 2017, the global value of reef tourism were \$36 Billion USD (Spalding et al., 2017), considering the large spatial extent of coral reef-related tourism, the diversity of species which occur on coral reefs, and the common use of photography and videography by members of the dive community, community-science based long term monitoring on coral reefs is especially feasible. Collaboration with dive companies has proved useful for disentangling cycles and species migrations; for example, logbook data from cage dives in Hawaii was used to indicate migrations and the exclusion of smaller individual sharks from dive sites (Meyer et al., 2009). Collaboration with the tourism industry has proven especially effective for research on cetaceans; recent analysis suggested that sending researchers onboard whale-watch vessels and providing vessels with logbooks and cameras to record species for identification provides researchers with cost-effective and valuable data (Currie et al., 2018). These kinds of surveys can be especially useful when evaluating the efficacy of marine protection, and when proposing new Marine Protected Areas.

The results of this point to the need for larger scale marine protection for those species, such as marine turtles, which are highly migratory, rather than endemic to a marine protected area. In this vane, a newly established marine swimway (the Hermandad Reserve) between the Galapagos and Cocos (Hearn, 2022; White et al., 2023) may help to reduce turtle bycatch. We suggest a migratory corridor could be effective for marine turtles in Cocos and the Eastern Tropical Pacific because they exhibit minimal seasonality; in other words, marine turtles are around throughout the year at varying frequencies. Their occurrence is driven by a variety of factors, which are stochastic in nature (Fernández et al., 2016). Because of this, seasonal fishing regulations or closures would not be as effective as complete protection in the form of a migratory corridor. Our model did reveal that predicted marine turtle numbers were influenced by daily temperature variations and peaked at lowest values for temperature (between 24°C and 26°C), so if managers

implemented temperature-based regulations, cooler waters would be more optimal for protection. Analysis of similar data, however, for other species could reveal seasonal trends around predictable environmental variation, suggesting that seasonal regulations or gear restrictions could be effective for the conservation of these species.

## 5 | CONCLUSION

This study provides, to our knowledge, the longest running underwater visual census of marine turtles. Despite the study occurring within an isolated marine protected area, accounting for all other covariates, our modeled marine turtle abundance decreased by 26% each year. Our observations are largely consistent with the observed decline of nesting green turtles in the Eastern Pacific (Seminoff et al., 2018) and consistent with historic nesting trends for Hawksbill in Costa Rica, where between 1982 and 2009, just 48 individuals were recorded nesting (Piedra-Chacón et al., 2021). While this study does provide valuable insights into the potential drivers of relative abundance of marine turtles at Cocos Island, future work could employ more systematic surveys and occupancy models to account for changes in species detectability to make more robust conclusions about the population dynamics of marine turtles at Cocos. The data in this study are invaluable; by collaborating with a dive company, we were able to obtain data which would be logistically and financially difficult for a lab or group of scientists on their own. Future work could expand on these community science partnerships to monitor population trends, trophic interactions, and efficacy of marine protected areas. Given that Cocos is already a protected area with enforcement, additional actions may be needed outside the protected area, such as changes in fishing management, to reduce turtle bycatch (Putman et al., 2020). We suggest the data in this study be used at Cocos for the expansion of protection around the Island, and in migratory corridors.

## ACKNOWLEDGMENTS

This study would not have been possible without the support and assistance of our collaborators at UnderSea Hunter and the Baum Lab, and every divemaster who obtained and recorded data. This study was improved greatly with the generous feedback and support of N. Furey, E. Harvey, S. Wulfing, A. Silverio, W. Burns, E. Yeager, and R. Moll. This work was funded by the Sandler Foundation (US), The Goldman Prize (US), the Whitley Fund for Nature (UK), and University of New Hampshire Graduate School Summer Teaching Assistant Fellowship (STAF).

## ORCID

Julia Saltzman  <https://orcid.org/0000-0002-4666-6268>

Alex R. Hearn  <https://orcid.org/0000-0002-4986-098X>

Mariana M. P. B. Fuentes  <https://orcid.org/0000-0002-2789-824X>

Todd Steiner  <https://orcid.org/0000-0002-4094-7501>

Randall Arauz  <https://orcid.org/0000-0003-4907-0424>

Catherine Macdonald  <https://orcid.org/0000-0003-2146-4966>

Easton R. White  <https://orcid.org/0000-0002-0768-9555>

## REFERENCES

- Acuña-Marrero, D., Smith, A. N. H., Hammerschlag, N., Hearn, A., Anderson, M. J., Calich, H., Pawley, M. D. M., Fischer, C., & Salinas-de-León, P. (2017). Residency and movement patterns of an apex predatory shark (*Galeocerdo cuvier*) at the Galapagos Marine Reserve. *PLoS One*, *12*(8), e0183669. <https://doi.org/10.1371/journal.pone.0183669>
- Alvarado, J. J., Cortés, J., Esquivel, M. F., & Salas, E. (2012). Costa Rica's marine protected areas: Status and perspectives. *Revista de Biología Tropical*, *60*(1), 129–142. <https://doi.org/10.15517/rbt.v60i1.2657>
- Arias, A., Pressey, R. L., Jones, R. E., Álvarez-Romero, J. G., & Cinner, J. E. (2016). Optimizing enforcement and compliance in offshore marine protected areas: A case study from Cocos Island, Costa Rica. *Oryx*, *50*(1), 18–26. <https://doi.org/10.1017/S0030605314000337>
- Báez, J. C., Bellido, J. J., Ferri-Yáñez, F., Castillo, J. J., Martín, J. J., Mons, J. L., Romero, D., & Real, R. (2011). The North Atlantic Oscillation and sea surface temperature affect loggerhead abundance around the Strait of Gibraltar. *Scientia Marina*, *75*(3), 3. <https://doi.org/10.3989/scimar.2011.75n3571>
- Bahlai, C. A., White, E. R., Perrone, J. D., Cusser, S., & Stack Whitney, K. (2021). The broken window: An algorithm for quantifying and characterizing misleading trajectories in ecological processes. *Ecological Informatics*, *64*, 101336. <https://doi.org/10.1016/j.ecoinf.2021.101336>
- Balazs, G. H., & Chaloupka, M. (2004). Thirty-year recovery trend in the once depleted Hawaiian green sea turtle stock. *Biological Conservation*, *117*(5), 491–498. <https://doi.org/10.1016/j.biocon.2003.08.008>
- Barney, E. C., Mintzes, J. J., & Yen, C.-F. (2005). Assessing knowledge, attitudes, and behavior toward charismatic megafauna: The case of dolphins. *Journal of Environmental Education*, *36*(2), 41–55. <https://doi.org/10.3200/JOEE.36.2.41-55>
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Bauer, A., Krivitsky, P. N., Tanaka, E., & Jagan, M. (2023). *lme4: Linear mixed-effects models using "Eigen" and S4 (version 1.1-34)* [Computer software]. Retrieved from <https://cran.r-project.org/web/packages/lme4/index.html>
- Baum, J. K., & Blanchard, W. (2010). Inferring shark population trends from generalized linear mixed models of pelagic longline catch and effort data. *Fisheries Research*, *102*(3), 229–239. <https://doi.org/10.1016/j.fishres.2009.11.006>
- Bjorndal, K., & Jackson, J. (2002). Roles of sea turtles in marine ecosystems: Reconstructing the past. In P. Lutz, J. Musick, & J. Wyneken (Eds.), *The biology of sea turtles* (pp. 259–273). CRC Press. <https://doi.org/10.1201/9781420040807.ch10>
- Bonaccorso, E., Ordóñez-Garza, N., Pazmiño, D. A., Hearn, A., Páez-Rosas, D., Cruz, S., Muñoz-Pérez, J. P., Espinoza, E., Suárez, J., Muñoz-Rosado, L. D., Vizuete, A., Chaves, J. A., Torres, M., Bustos, W., Rueda, D., Hirschfeld, M., & Guayasamin, J. M. (2021). International fisheries threaten globally endangered sharks in the eastern tropical Pacific Ocean: The case of the Fu Yuan Yu Leng 999 reefer vessel seized within the Galápagos Marine Reserve. *Scientific Reports*, *11*(1), 1. <https://doi.org/10.1038/s41598-021-94126-3>
- Bravo-Ormaza, E., Arauz, R., Bessudo, S., Hearn, A., Klimley, A. P., Ladino-Archila, F., López-Macias, J., Steiner, T., & Peñaherrera-Palma, C. (2023). Scalloped hammerhead shark *Sphyrna lewini* relative abundance comparison in three offshore marine protected areas of the eastern tropical Pacific. *Environmental Biology of Fishes*, *106*(8), 1767–1784. <https://doi.org/10.1007/s10641-023-01454-6>
- Campbell, L. M., & Smith, C. (2006). What makes them pay? Values of volunteer tourists working for sea turtle conservation. *Environmental Management*, *38*(1), 84–98. <https://doi.org/10.1007/s00267-005-0188-0>
- Carrión-Cortez, J., Canales-Cerro, C., Arauz, R., & Riosmena-Rodríguez, R. (2013). Habitat use and diet of juvenile eastern Pacific hawksbill turtles (*Eretmochelys imbricata*) in the North Pacific coast of Costa Rica. *Chelonian Conservation and Biology*, *12*(2), 235–245. <https://doi.org/10.2744/CCB-1024.1>
- Carrión-Cortez, J. A., Zárate, P., & Seminoff, J. A. (2010). Feeding ecology of the green sea turtle (*Chelonia mydas*) in the Galapagos Islands. *Journal of the Marine Biological Association of the United Kingdom*, *90*(5), 1005–1013. <https://doi.org/10.1017/s0025315410000226>
- Ceriani, S. A., Casale, P., Brost, M., Leone, E. H., & Witherington, B. E. (2019). Conservation implications of sea turtle nesting trends: Elusive recovery of a globally important loggerhead population. *Ecosphere*, *10*(11), e02936. <https://doi.org/10.1002/ecs2.2936>
- Chambault, P., de Thoisy, B., Heerah, K., Conchon, A., Barrioz, S., Dos Reis, V., Berzins, R., Kelle, L., Picard, B., Roquet, F., Le Maho, Y., & Chevallier, D. (2016). The influence of oceanographic features on the foraging behavior of the olive ridley sea turtle *Lepidochelys olivacea* along the Guiana coast. *Progress in Oceanography*, *142*, 58–71. <https://doi.org/10.1016/j.pocean.2016.01.006>
- Crear, D., Lawson, D., Seminoff, J., Eguchi, T., LeRoux, R., & Lowe, C. (2016). Seasonal shifts in the movement and distribution of green sea turtles *Chelonia mydas* in response to anthropogenically altered water temperatures. *Marine Ecology Progress Series*, *548*, 219–232. <https://doi.org/10.3354/meps11696>
- Cullen-Unsworth, L. C., & Unsworth, R. (2018). A call for seagrass protection. *Science*, *361*(6401), 446–448. <https://doi.org/10.1126/science.aat7318>
- Currie, J. J., Stack, S. H., & Kaufman, G. D. (2018). Conservation and education through ecotourism: Using citizen science to monitor cetaceans in the Four-Island region of Maui, Hawaii. *Tourism in Marine Environments*, *13*(2–3), 65–71. <https://doi.org/10.3727/154427318X15270394903273>
- Daly-Engel, T. S., Seraphin, K. D., Holland, K. N., Coffey, J. P., Nance, H. A., Toonen, R. J., & Bowen, B. W. (2012). Global phylogeography with mixed-marker analysis reveals male-

- mediated dispersal in the endangered scalloped hammerhead shark (*Sphyrna lewini*). *PLoS One*, 7(1), e29986.
- Dapp, D., Arauz, R., Spotila, J. R., & O'Connor, M. P. (2013). Impact of Costa Rican longline fishery on its bycatch of sharks, stingrays, bony fish and olive ridley turtles (*Lepidochelys olivacea*). *Journal of Experimental Marine Biology and Ecology*, 448, 228–239. <https://doi.org/10.1016/j.jembe.2013.07.014>
- Derville, S., Jean, C., Dalleau, M., Le Gall, J.-Y., Ciccione, S., & Bourjea, J. (2015). Long-term monitoring of Green turtle nesting on Tromelin Island demonstrates stable reproduction and population parameters. *Chelonian Conservation and Biology*, 14(1), 11–20. <https://doi.org/10.2744/ccab-14-01-11-20.1>
- Díaz, M. P., Kunc, H. P., & Houghton, J. D. R. (2024). Anthropogenic noise predicts sea turtle behavioural responses. *Marine Pollution Bulletin*, 198, 115907. <https://doi.org/10.1016/j.marpolbul.2023.115907>
- Eckert, K. L., Bjørndal, K. A., Abreu-Grobois, F. A., & Donnelly, M. (1986). Techniques for measuring sea turtles. In *Research and management techniques for the conservation of sea turtles*. IUCN/SSC Marine Turtle Specialist Group Publication.
- Enstipp, M. R., Ciccione, S., Gineste, B., Milbergue, M., Ballorain, K., Ropert-Coudert, Y., Kato, A., Plot, V., & Georges, J.-Y. (2011). Energy expenditure of freely swimming adult green turtles (*Chelonia mydas*) and its link with body acceleration. *Journal of Experimental Biology*, 214(23), 4010–4020. <https://doi.org/10.1242/jeb.062943>
- Estes, J. A., Heithaus, M., McCauley, D. J., Rasher, D. B., & Worm, B. (2016). Megafaunal impacts on structure and function of ocean ecosystems. *Annual Review of Environment and Resources*, 41(1), 83–116. <https://doi.org/10.1146/annurev-environ-110615-085622>
- Fernández, N., Román, J., & Delibes, M. (2016). Variability in primary productivity determines metapopulation dynamics. *Proceedings of the Royal Society B: Biological Sciences*, 283(1828), 20152998. <https://doi.org/10.1098/rspb.2015.2998>
- Finkbeiner, E. M., Wallace, B. P., Moore, J. E., Lewison, R. L., Crowder, L. B., & Read, A. J. (2011). Cumulative estimates of sea turtle bycatch and mortality in USA fisheries between 1990 and 2007. *Biological Conservation*, 144(11), 2719–2727.
- Fitzpatrick, R., Thums, M., Bell, I., Meekan, M. G., Stevens, J. D., & Barnett, A. (2012). A comparison of the seasonal movements of tiger sharks and green turtles provides insight into their predator-prey relationship. *PLoS One*, 7(12), e51927.
- Frank, K. T., Petrie, B., Choi, J. S., & Leggett, W. C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308(5728), 1621–1623. <https://doi.org/10.1126/science.1113075>
- Friedlander, A. M., Zgliczynski, B. J., Ballesteros, E., Aburto-Oropeza, O., Bolaños, A., & Sala, E. (2012). The shallow-water fish assemblage of Isla del Coco National Park, Costa Rica: Structure and patterns in an isolated, predator-dominated ecosystem. *Revista de Biología Tropical*, 60, 321–338.
- Gallagher, A. J., Alsudairy, N. A., Shea, B. D., Payne, N. L., & Duarte, C. M. (2021). First application of 360-degree camera technology to marine predator bio-logging. *Frontiers in Marine Science*, 8, 707376. <https://doi.org/10.3389/fmars.2021.707376>
- Gallagher, A. J., Creel, S., Wilson, R. P., & Cooke, S. J. (2017). Energy landscapes and the landscape of fear. *Trends in Ecology & Evolution*, 32(2), 88–96. <https://doi.org/10.1016/j.tree.2016.10.010>
- Gaos, A. R., Lewison, R. L., Liles, M. J., Gadea, V., Altamirano, E., Henríquez, A. V., Torres, P., Urteaga, J., Vallejo, F., & Baquero, A. (2016). Hawksbill turtle terra incognita: Conservation genetics of eastern Pacific rookeries. *Ecology and Evolution*, 6(4), 1251–1264.
- Good, S. A., Martin, M. J., & Rayner, N. A. (2013). EN4: Quality controlled ocean temperature and salinity profiles and monthly objective analyses with uncertainty estimates. *Journal of Geophysical Research: Oceans*, 118(12), 6704–6716.
- Gregg, E. J., Christensen, V., Nichol, L., Martone, R. G., Markel, R. W., Watson, J. C., Harley, C. D. G., Pakhomov, E. A., Shurin, J. B., & Chan, K. M. A. (2020). Cascading social-ecological costs and benefits triggered by a recovering keystone predator. *Science*, 368(6496), 1243–1247. <https://doi.org/10.1126/science.aay5342>
- Grose, S. O., Pendleton, L., Leathers, A., Cornish, A., & Waitai, S. (2020). Climate change will re-draw the map for marine megafauna and the people who depend on them. *Frontiers in Marine Science*, 7, 547. <https://doi.org/10.3389/fmars.2020.00547>
- Hamann, M., Godfrey, M. H., Seminoff, J. A., Arthur, K., Barata, P. C. R., Bjørndal, K. A., Bolten, A. B., Broderick, A. C., Campbell, L. M., Carreras, C., Casale, P., Chaloupka, M., Chan, S. K. F., Coyne, M. S., Crowder, L. B., Diez, C. E., Dutton, P. H., Epperly, S. P., FitzSimmons, N. N., ... Godley, B. J. (2010). Global research priorities for sea turtles: Informing management and conservation in the 21st century. *Endangered Species Research*, 11(3), 245–269. <https://doi.org/10.3354/esr00279>
- Hamilton, W. J., & Watt, K. E. F. (1970). Refuging. *Annual Review of Ecology and Systematics*, 1(1), 263–286. <https://doi.org/10.1146/annurev.es.01.110170.001403>
- Hammerschlag, N., Broderick, A. C., Coker, J. W., Coyne, M. S., Dodd, M., Frick, M. G., Godfrey, M. H., Godley, B. J., Griffin, D. B., Hartog, K., Murphy, S. R., Murphy, T. M., Nelson, E. R., Williams, K. L., Witt, M. J., & Hawkes, L. A. (2015). Evaluating the landscape of fear between apex predatory sharks and mobile sea turtles across a large dynamic seascape. *Ecology*, 96(8), 2117–2126. <https://doi.org/10.1890/14-2113.1>
- Hauser, D. D. W., Laidre, K. L., Stern, H. L., Suydam, R. S., & Richard, P. R. (2018). Indirect effects of sea ice loss on summer-fall habitat and behaviour for sympatric populations of an Arctic marine predator. *Diversity and Distributions*, 24(6), 791–799. <https://doi.org/10.1111/ddi.12722>
- Hearn, A. (2022). *A blueprint for marine spatial planning of Ecuador's Exclusive Economic Zone around the Galápagos Marine Reserve*. Universidad San Francisco de Quito Quito, Ecuador.
- Heaslip, S. G., Iverson, S. J., Bowen, W. D., & James, M. C. (2012). Jellyfish support high energy intake of leatherback sea turtles (*Dermodochelys coriacea*): Video evidence from animal-borne cameras. *PLoS One*, 7(3), e33259.
- Heithaus, M., Dill, L., Marshall, G., & Buhleier, B. (2002). Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Marine Biology*, 140(2), 237–248. <https://doi.org/10.1007/s00227-001-0711-7>
- Heithaus, M., Frid, A., Wirsing, A. J., Dill, L. M., Fourqurean, J. W., Burkholder, D., Thomson, J., & Bejder, L. (2007). State-dependent risk-taking by green sea turtles mediates top-down

- effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal Ecology*, 76(5), 837–844. <https://doi.org/10.1111/j.1365-2656.2007.01260.x>
- Hounslow, J. L., Jewell, O. J. D., Fossette, S., Whiting, S., Tucker, A. D., Richardson, A., Edwards, D., & Gleiss, A. C. (2021). Animal-borne video from a sea turtle reveals novel anti-predator behaviors. *Ecology*, 102(4), 1–4.
- Issaris, Y., Katsanevakis, S., Salomidi, M., Tsiamis, K., Katsiaras, N., & Verriopoulos, G. (2012). Occupancy estimation of marine species: Dealing with imperfect detectability. *Marine Ecology Progress Series*, 453, 95–106. <https://doi.org/10.3354/meps09668>
- Kynoch, C., Fuentes, M. M. P. B., Dutton, P. H., LaCasella, E. L., & Silver-Gorges, I. (2022). Origins of juvenile green sea turtles (*Chelonia mydas*) in The Bahamas: A comparison of recent and historical rookery contributions. *Ecology and Evolution*, 12(11), e9548. <https://doi.org/10.1002/ece3.9548>
- Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, 79(8), 1401–1409. <https://doi.org/10.1139/z01-094>
- Lazaridis, E. (2022). *lunar: calculate lunar phase & distance, seasons and related environmental factors (version 0.2-1)* [Computer software]. Retrieved from <https://cran.r-project.org/web/packages/lunar/index.html>
- Lewison, R. L., Crowder, L. B., Wallace, B. P., Moore, J. E., Cox, T., Zydalis, R., McDonald, S., DiMatteo, A., Dunn, D. C., Kot, C. Y., Bjorkland, R., Kelez, S., Soykan, C., Stewart, K. R., Sims, M., Boustany, A., Read, A. J., Halpin, P., Nichols, W. J., & Safina, C. (2014). Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. *Proceedings of the National Academy of Sciences of the United States of America*, 111(14), 5271–5276. <https://doi.org/10.1073/pnas.1318960111>
- Liles, M. J., Peterson, M. J., Lincoln, Y. S., Seminoff, J. A., Gaos, A. R., & Peterson, T. R. (2015). Connecting international priorities with human wellbeing in low-income regions: Lessons from hawksbill turtle conservation in El Salvador. *Local Environment*, 20(11), 1383–1404. <https://doi.org/10.1080/13549839.2014.905516>
- Lüdecke, D., Bartel, A., Schwemmer, C., Powell, C., Djalovski, A., & Titz, J. (2023). *sjPlot: Data visualization for statistics in social science (version 2.8.15)* [Computer software]. Retrieved from <https://cran.r-project.org/web/packages/sjPlot/index.html>
- Macdonald, C., & Wester, J. (2021). Public understanding of wildlife tourism: Defining terms, harms, and benefits. *Journal of Ecotourism*, 20(2), 198–209. <https://doi.org/10.1080/14724049.2020.1817930>
- MacNeil, M. A., Chapman, D. D., Heupel, M., Simpfendorfer, C. A., Heithaus, M., Meekan, M., Harvey, E., Goetze, J., Kiszka, J., & Bond, M. E. (2020). Global status and conservation potential of reef sharks. *Nature*, 583(7818), 801–806.
- Mazaris, A. D., Matsinos, G., & Pantis, J. D. (2009). Evaluating the impacts of coastal squeeze on sea turtle nesting. *Ocean & Coastal Management*, 52(2), 139–145.
- Mazaris, A. D., Schofield, G., Gkazinou, C., Almpnidou, V., & Hays, G. C. (2017). Global sea turtle conservation successes. *Science Advances*, 3(9), e1600730.
- Mazerolle, M. J. (2023). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c) (version 2.3-2)* [Computer software]. Retrieved from <https://cran.r-project.org/web/packages/AICcmodavg/index.html>
- Meyer, C. G., Dale, J. J., Papastamatiou, Y. P., Whitney, N. M., & Holland, K. N. (2009). Seasonal cycles and long-term trends in abundance and species composition of sharks associated with cage diving ecotourism activities in Hawaii. *Environmental Conservation*, 36(2), 104–111. <https://doi.org/10.1017/S0376892909990038>
- Moran, K. L., & Bjorndal, K. A. (2005). Simulated green turtle grazing affects structure and productivity of seagrass pastures. *Marine Ecology Progress Series*, 305, 235–247. <https://doi.org/10.3354/meps305235>
- Nalesso, E., Hearn, A., Sosa-Nishizaki, O., Steiner, T., Antoniou, A., Reid, A., Bessudo, S., Soler, G., Klimley, A. P., Lara, F., Ketchum, J. T., & Arauz, R. (2019). Movements of scalloped hammerhead sharks (*Sphyrna lewini*) at Cocos Island, Costa Rica and between oceanic islands in the eastern tropical Pacific. *PLoS One*, 14(3), e0213741. <https://doi.org/10.1371/journal.pone.0213741>
- Neate-Clegg, M. H. C., Horns, J. J., Adler, F. R., Kemahlı Aytekin, M. Ç., & Şekercioglu, Ç. H. (2020). Monitoring the world's bird populations with community science data. *Biological Conservation*, 248, 108653. <https://doi.org/10.1016/j.biocon.2020.108653>
- Nel, R., Punt, A. E., & Hughes, G. R. (2013). Are coastal protected areas always effective in achieving population recovery for nesting sea turtles? *PLoS One*, 8(5), e63525. <https://doi.org/10.1371/journal.pone.0063525>
- Nelson Sella, K. A., Sicius, L., & Fuentes, M. M. P. B. (2019). Using expert elicitation to determine the relative impact of coastal modifications on marine turtle nesting grounds. *Coastal Management*, 47(5), 492–506. <https://doi.org/10.1080/08920753.2019.1642176>
- Niella, Y., Butcher, P., Holmes, B., Barnett, A., & Harcourt, R. (2022). Forecasting intraspecific changes in distribution of a wide-ranging marine predator under climate change. *Oecologia*, 198(1), 111–124. <https://doi.org/10.1007/s00442-021-05075-7>
- Okumura, Y. M., & Deser, C. (2010). Asymmetry in the duration of El Niño and La Niña. *Journal of Climate*, 23(21), 5826–5843. <https://doi.org/10.1175/2010JCLI3592.1>
- Osgood, G. J., McCord, M. E., & Baum, J. K. (2019). Using baited remote underwater videos (BRUVs) to characterize chondrichthyan communities in a global biodiversity hotspot. *PLoS One*, 14(12), e0225859.
- Osgood, G. J., White, E. R., & Baum, J. K. (2021). Effects of climate-change-driven gradual and acute temperature changes on shark and ray species. *Journal of Animal Ecology*, 90(11), 2547–2559.
- Pankow, C. J., Macdonald, C. C., Shiffman, D. S., Wester, J., & Abel, D. (2021). Stable isotopic dynamics of juvenile elasmobranchs in a South Carolina Nursery Area. *Southeastern Naturalist*, 20(1), 92–104. <https://doi.org/10.1656/058.020.0107>
- Papastamatiou, Y. P., Meyer, C. G., Watanabe, Y. Y., & Heithaus, M. R. (2018). Animal-borne video cameras and their use to study shark ecology and conservation. In *Shark Research: Emerging technologies and applications for the field and laboratory* (Vol. 3, pp. 83–91). CRC Press.
- Patrício, A. R., Hawkes, L. A., Monsinjon, J. R., Godley, B. J., & Fuentes, M. M. P. B. (2021). Climate change and marine turtles:

- Recent advances and future directions. *Endangered Species Research*, 44, 363–395. <https://doi.org/10.3354/esr01110>
- Peñaherrera-Palma, C., van Putten, I., Karpievitch, Y. V., Frusher, S., Llerena-Martillo, Y., Hearn, A. R., & Semmens, J. M. (2018). Evaluating abundance trends of iconic species using local ecological knowledge. *Biological Conservation*, 225, 197–207.
- Pheasey, H., Glen, G., Allison, N. L., Fonseca, L. G., Chacón, D., Restrepo, J., & Valverde, R. A. (2021). Quantifying illegal extraction of sea turtles in Costa Rica. *Frontiers in Conservation Science*, 2. <https://doi.org/10.3389/fcsc.2021.705556>
- Piedra-Chacón R., Vélez-Carballo E., Chacón-Chaverri, D., Santidrián-Tomillo, P., Fonseca-López, L., Fallas-Bonilla, G., Brenes-Arias, O., Rojas-Cañizares, D., Arauz-Naranjo, D., Selles-Ríos, B., Cruz-Díaz, J.C., Heidemeyer, M., Guthrie, V., Alvarez-Ramírez, F., Orrego, C.M., Ward, M., Paladino, F., Cedeño-Solís, Y., & Diaz-Chuquisengo, C. (2021). *Sea turtles in the Eastern Pacific region*. IUCN SSC Marine Turtle Specialist Group.
- Pike, D. A., Antworth, R. L., & Stiner, J. C. (2006). Earlier nesting contributes to shorter nesting seasons for the loggerhead sea-turtle, *Caretta caretta*. *Journal of Herpetology*, 40(1), 91–94. <https://doi.org/10.1670/100-05N.1>
- Pimiento, C., Leprieur, F., Silvestro, D., Lefcheck, J. S., Albouy, C., Rasher, D. B., Davis, M., Svenning, J.-C., & Griffin, J. N. (2020). Functional diversity of marine megafauna in the Anthropocene. *Science Advances*, 6(16), eaay7650. <https://doi.org/10.1126/sciadv.aay7650>
- Pincetich, C., Ong, M., & Steiner, T. (2012). Conservation advocacy increases protections for critically endangered Pacific leatherback sea turtles. *Asian Journal of Conservation Biology*, 1, 16–19.
- Polovina, J. J., Dunne, J. P., Woodworth, P. A., & Howell, E. A. (2011). Projected expansion of the subtropical biome and contraction of the temperate and equatorial upwelling biomes in the North Pacific under global warming. *ICES Journal of Marine Science*, 68(6), 986–995. <https://doi.org/10.1093/icesjms/fsq198>
- Prato, G., Guidetti, P., Bartolini, F., Mangialajo, L., & Francour, P. (2013). The importance of high-level predators in marine protected area management: Consequences of their decline and their potential recovery in the Mediterranean context. *Advances in Oceanography and Limnology*, 4(2), 176–193. <https://doi.org/10.1080/19475721.2013.841754>
- Putman, N. F., Hawkins, J., & Gallaway, B. J. (2020). Managing fisheries in a world with more sea turtles. *Proceedings of the Royal Society B: Biological Sciences*, 287(1930), 20200220. <https://doi.org/10.1098/rspb.2020.0220>
- R Core Development Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Reynolds, R. W., Smith, T. M., Liu, C., Chelton, D. B., Casey, K. S., & Schlax, M. G. (2007). Daily high-resolution-blended analyses for sea surface temperature. *Journal of climate*, 20(22), 5473–5496.
- Salinas-de-León, P., Fierro-Arcos, D., Suarez-Moncada, J., Proaño, A., Guachisaca-Salinas, J., & Páez-Rosas, D. (2019). A matter of taste: Spatial and ontogenetic variations on the trophic ecology of the tiger shark at the Galapagos Marine Reserve. *PLoS One*, 14(9), e0222754. <https://doi.org/10.1371/journal.pone.0222754>
- Saltzman, J., & White, E. R. (2022). Determining the role of environmental covariates on *Planktivorous elasmobranch* population trends within an isolated marine protected area. <https://doi.org/10.1101/2022.09.28.509935>
- Santos, A. J., Vieira, D. H., Bellini, C., Corso, G., A Ceriani, S., & Fuentes, M. M. (2021). Using data from nesting beach monitoring and satellite telemetry to improve estimates of marine turtle clutch frequency and population abundance. *Marine Biology*, 168, 1–16.
- Seminoff, J., Bustos, L., Quiñones, J., & Espinoza, E. (2018). Inter-American convention for the protection and conservation of sea turtles green turtle (*Chelonia mydas*) nesting trends in the eastern Pacific Ocean: Status update and conservation priorities. Technical Document CIT-CC15-2018-Tec, 15. Retrieved from [http://www.iacseaturtle.org/eng-docs/publicaciones/CIT-CC15-2018-Tec.15%20-Green%20Turtle%20EP\\_22.May.2020\\_FINAL-v2.pdf](http://www.iacseaturtle.org/eng-docs/publicaciones/CIT-CC15-2018-Tec.15%20-Green%20Turtle%20EP_22.May.2020_FINAL-v2.pdf)
- Seminoff, J. A., Zárata, P., Coyne, M., Foley, D. G., Parker, D., Lyon, B. N., & Dutton, P. H. (2008). Post-nesting migrations of Galápagos green turtles *Chelonia mydas* in relation to oceanographic conditions: Integrating satellite telemetry with remotely sensed ocean data. *Endangered Species Research*, 4(1–2), 57–72. <https://doi.org/10.3354/esr00066>
- Senko, J. F., Burgher, K. M., del Mar Mancha-Cisneros, M., Godley, B. J., Kinan-Kelly, I., Fox, T., Humber, F., Koch, V., Smith, A. T., & Wallace, B. P. (2022). Global patterns of illegal marine turtle exploitation. *Global Change Biology*, 28(22), 6509–6523. <https://doi.org/10.1111/gcb.16378>
- Silver-Gorges, I., Ceriani, S. A., & Fuentes, M. M. P. B. (2023). Fine-scale intraspecific niche partitioning in a highly mobile, marine megafauna species: Implications for ecology and conservation. *Royal Society Open Science*, 10(6), 221529. <https://doi.org/10.1098/rsos.221529>
- Spalding, M., Burke, L., Wood, S. A., Ashpole, J., Hutchison, J., & Zu Ermgassen, P. (2017). Mapping the global value and distribution of coral reef tourism. *Marine Policy*, 82, 104–113. <https://doi.org/10.1016/j.marpol.2017.05.014>
- Stokes, K. L., Fuller, W. J., Glen, F., Godley, B. J., Hodgson, D. J., Rhodes, K. A., Snape, R. T., & Broderick, A. C. (2014). Detecting green shoots of recovery: The importance of long-term individual-based monitoring of marine turtles. *Animal Conservation*, 17(6), 593–602.
- Swimmer, Y., Suter, J., Arauz, R., Bigelow, K., López, A., Zanela, I., Bolaños, A., Ballester, J., Suárez, R., Wang, J., & Boggs, C. (2011). Sustainable fishing gear: The case of modified circle hooks in a Costa Rican longline fishery. *Marine Biology*, 158(4), 757–767. <https://doi.org/10.1007/s00227-010-1604-4>
- Tomaszewicz, C. N. T., Seminoff, J. A., Avens, L., Goshe, L. R., Rguez-Baron, J. M., Peckham, S. H., & Kurle, C. M. (2018). Expanding the coastal forager paradigm: Long-term pelagic habitat use by green turtles *Chelonia mydas* in the eastern Pacific Ocean. *Marine Ecology Progress Series*, 587, 217–234. <https://doi.org/10.3354/meps12372>
- Tulloch, V. J. D., Plagányi, É. E., Brown, C., Richardson, A. J., & Matear, R. (2019). Future recovery of baleen whales is imperiled by climate change. *Global Change Biology*, 25(4), 1263–1281. <https://doi.org/10.1111/gcb.14573>

- Veríssimo, D., Jones, D. A., Chaverri, R., & Meyer, S. R. (2012). Jaguar *Panthera onca* predation of marine turtles: Conflict between flagship species in Tortuguero, Costa Rica. *Oryx*, *46*(3), 340–347.
- Wallace, B. P., DiMatteo, A. D., Bolten, A. B., Chaloupka, M. Y., Hutchinson, B. J., Abreu-Grobois, F. A., Mortimer, J. A., Seminoff, J. A., Amoroch, D., Bjørndal, K. A., Bourjea, J., Bowen, B. W., Dueñas, R. B., Casale, P., Choudhury, B. C., Costa, A., Dutton, P. H., Fallabrino, A., Finkbeiner, E. M., ... Mast, R. B. (2011). Global conservation priorities for marine turtles. *PLoS One*, *6*(9), e24510. <https://doi.org/10.1371/journal.pone.0024510>
- Ward-Paige, C. A., & Lotze, H. K. (2011). Assessing the value of recreational divers for censusing elasmobranchs. *PLoS One*, *6*(10), e25609.
- Ward-Paige, C. A., Pattengill-Semmens, C., Myers, R. A., & Lotze, H. K. (2011). Spatial and temporal trends in yellow stingray abundance: Evidence from diver surveys. *Environmental Biology of Fishes*, *90*, 263–276.
- Watanabe, Y. Y., Payne, N. L., Semmens, J. M., Fox, A., & Huvener, C. (2019). Hunting behaviour of white sharks recorded by animal-borne accelerometers and cameras. *Marine Ecology Progress Series*, *621*, 221–227.
- Weber, S., Ceriani, S. A., & Fuentes, M. M. P. B. (2023). Foraging ecology of Kemp's ridley (*Lepidochelys kempii*) turtles in the northeastern Gulf of Mexico: Insights from stable isotope analysis. *Marine Biology*, *170*(8), 104. <https://doi.org/10.1007/s00227-023-04251-y>
- Weishampel, J. F., Bagley, D. A., Ehrhart, L. M., & Weishampel, A. C. (2010). Nesting phenologies of two sympatric sea turtle species related to sea surface temperatures. *Endangered Species Research*, *12*(1), 41–47. <https://doi.org/10.3354/esr00290>
- White, E. R. (2019). Minimum time required to detect population trends: The need for long-term monitoring programs. *Bioscience*, *69*(1), 40–46. <https://doi.org/10.1093/biosci/biy144>
- White, E. R., Hearn, A., Moity, N., Ramírez-González, J., Saltzman, J., Viteri-Mejía, C., Enright, S., & Barragán-Paladines, M. J. (2023). *Industrial fishing compliance with a new marine corridor near the Galapagos Islands*. Retrieved from <https://ecoevorxiv.org/repository/view/6178/>
- White, E. R., Myers, M. C., Flemming, J. M., & Baum, J. K. (2015). Shifting elasmobranch community assemblage at Cocos Island—An isolated marine protected area. *Conservation Biology*, *29*(4), 1186–1197.
- Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., & Dunnington, D. (2023). *ggplot2: Create elegant data visualisations using the grammar of graphics (version 3.4.3)* [Computer software]. Retrieved from <https://cran.r-project.org/web/packages/ggplot2/index.html>
- Wildermann, N. E., Gredzens, C., Avens, L., Barrios-Garrido, H. A., Bell, I., Blumenthal, J., Bolten, A. B., McNeill, J. B., Casale, P., Domenico, M. D., Domit, C., Epperly, S. P., Godfrey, M. H., Godley, B. J., González-Carman, V., Hamann, M., Hart, K. M., Ishihara, T., Mansfield, K. L., ... Fuentes, M. M. P. B. (2018). Informing research priorities for immature sea turtles through expert elicitation. *Endangered Species Research*, *37*, 55–76. <https://doi.org/10.3354/esr00916>
- Williams, J. L., Pierce, S. J., Fuentes, M. M., & Hamann, M. (2015). Effectiveness of recreational divers for monitoring sea turtle populations. *Endangered Species Research*, *26*(3), 209–219.
- Witt, M. J., Penrose, R., & Godley, B. J. (2007). Spatio-temporal patterns of juvenile marine turtle occurrence in waters of the European continental shelf. *Marine Biology*, *151*(3), 873–885. <https://doi.org/10.1007/s00227-006-0532-9>
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Zero-truncated and zero-inflated models for count data. In A. F. Zuur, E. N. Ieno, N. Walker, A. A. Saveliev, & G. M. Smith (Eds.), *Mixed effects models and extensions in ecology with R* (pp. 261–293). Springer. [https://doi.org/10.1007/978-0-387-87458-6\\_11](https://doi.org/10.1007/978-0-387-87458-6_11)

**How to cite this article:** Saltzman, J., Hearn, A. R., Fuentes, M. M. P. B., Steiner, T., Arauz, R., Macdonald, C., Heidemeyer, M., & White, E. R. (2024). Multidecadal underwater surveys reveal declines in marine turtles. *Conservation Science and Practice*, e13249. <https://doi.org/10.1111/csp2.13249>

## APPENDIX A

Covariate	SST	ONI	CHLA	SAL	LD	TAD	CUR
SST		0.36	-0.29	-0.62	0.00	0.34	0.01
ONI			-0.37	-0.25	-0.02	0.29	0.14
CHLA				0.29	0.02	-0.18	-0.11
SAL					0.02	-0.21	-0.02
LD						-0.03	-0.02
TAD							0.01

**TABLE A1** Correlations (Spearman's rho) between all environmental covariates (SST = sea surface temperature, ONI = Ocean Niño Index, CHLA = chlorophyll-a, SAL = salinity, LD = lunar distance, TAD = temperature at depth, CUR = current).

**TABLE A2** Models used for AIC. Models were run for the counts of marine turtles, sin() and cos() of Julian date is included in all models to account for seasonality.

Variables	Description
Turtles ~ Predator Abundance + Ocean Nino Index + Temperature at Depth + Sea Surface Temperature + Salinity + Chlorophyll-a + Lunar Distance + Lunar Phase + Current + Visibility + Year + sin() + cos()	Global Model
Turtles ~ Ocean Nino Index + Temperature at Depth + Sea Surface Temperature + Salinity + Chlorophyll-a + Current + Visibility + Year + sin() + cos()	Global Model Without Predators
Turtles ~ Predator Abundance + Ocean Nino Index + Temperature at Depth + Sea Surface Temperature + Salinity + Chlorophyll-a + Current + Visibility + Year + sin() + cos()	Global Model without Lunar Factors
Turtles ~ Predator Abundance + Ocean Nino Index + Temperature at Depth + Sea Surface Temperature + Chlorophyll-a + Lunar Distance + Lunar Phase + Current + Visibility + Year + sin() + cos()	Global Model without Salinity
Turtles ~ Predator Abundance + Ocean Nino Index + Temperature at Depth + Sea Surface Temperature + Salinity + Lunar Distance + Lunar Phase + Current + Visibility + Year + sin() + cos()	Global Model without Chlorophyll-a
Turtles ~ Predator Abundance + Ocean Nino Index + Temperature at Depth + Salinity + Chlorophyll-a + Lunar Distance + Lunar Phase + Current + Visibility + Year + sin() + cos()	Global Model without Sea Surface Temperature
Turtles ~ Predator Abundance + Ocean Nino Index + Sea Surface Temperature + Salinity + Chlorophyll-a + Lunar Distance + Lunar Phase + Current + Visibility + Year + sin() + cos()	Global Model without Temperature at Depth
Turtles ~ Predator Abundance + Ocean Nino Index + Temperature at Depth + Sea Surface Temperature + Salinity + Chlorophyll-a + Lunar Distance + Lunar Phase + Year + sin() + cos()	Global Model without Current and Visibility

**TABLE A3** AIC outputs and the resulted rankings which were used to determine which model best fit the data.

Model {presence/absence models}	AIC	AICc WT	K
Global Model without Lunar	0.00	1	14
Global Model	11.85	0	23
Global Model without Salinity	14.42	0	21
Global Model without SST	33.30	0	21
Global Model without Predator	136.94	0	22
Global Model without Current and Visibility	735.66	0	20
Global Model without Temperature at Depth	1445.96	0	21
Global Model without Chlorophyll-a	2701.74	0	21

**TABLE A4** Outputs for each of the predictors including incidence rate ratios, confidence intervals, *p*-values, intercepts, and random effects of top count model (global model without lunar covariates).

Predictors	Incidence rate ratios	Confidence intervals	<i>p</i> -value
Count model			
Tiger sharks	0.57	0.50–0.65	<0.001
SST	0.93	0.89–0.97	<0.001
Temperature	0.92	0.91–0.94	<0.001
Salinity	1.01	0.95–1.08	0.747
Chlorophyll	0.10	0.05–0.18	<0.001
ONI	1.08	1.03–1.13	0.001
Current code	0.92	0.89–0.94	<0.001
Visibility	1.00	1.00–1.01	0.255
Sin time	0.83	0.78–0.88	<0.001
Cos time	1.19	1.15–1.24	<0.001
Year	0.84	0.83–0.85	<0.001
(Intercept)	2.12	2.02–2.22	
Zero-inflated model			
(Intercept)	0.00	0.00–Inf	0.975
Random effects			
2	0.00		
00 DiverCode	0.73		
00 SiteCode	0.40		
ICC	1.00		
N DiverCode	45		
N SiteCode	17		
Observations	29,801		
Marginal R2/Conditional R2	0.542/1.000		

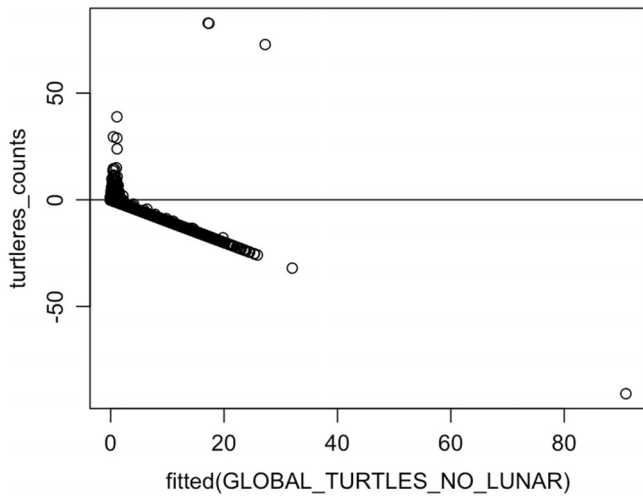


FIGURE A1 Residual versus fitted for top model.

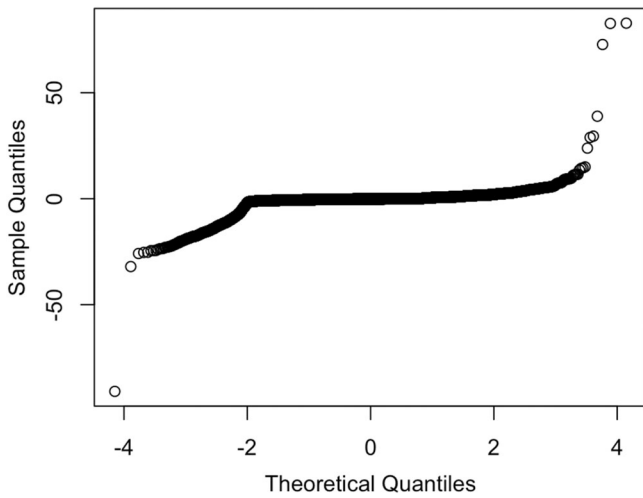


FIGURE A2 Normal Q-Q plot for top model.

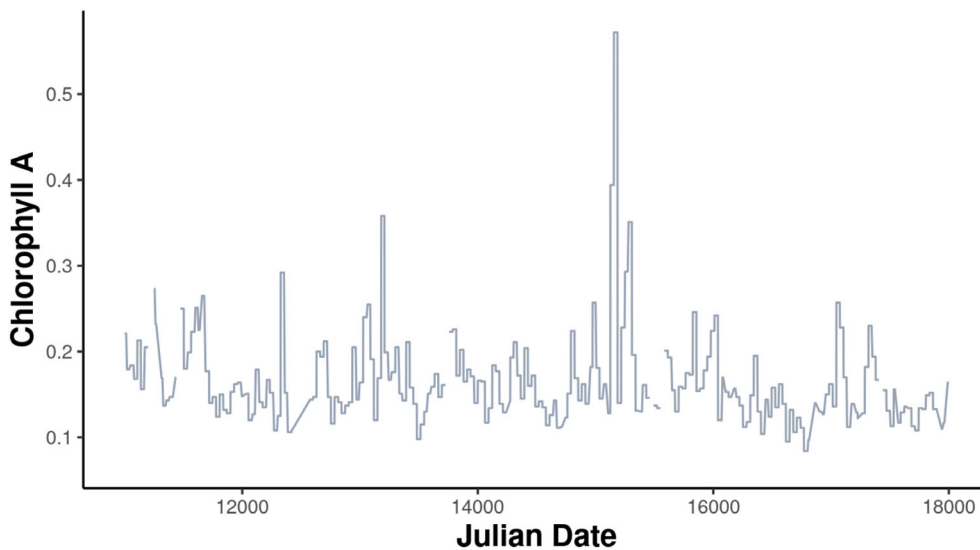


FIGURE A3 Surface chlorophyll-a ( $\text{mg}/\text{m}^3$ ) overtime (Julian date) across dive locations at Cocos Island. Mean monthly chlorophyll-a obtained from NASAcombo time series: <https://oceancolor.gsfc.nasa>. Chlorophyll-a data was not available for the entire time series.