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Scalloped hammerhead shark *Sphyrna lewini* relative abundance comparison in three offshore marine protected areas of the Eastern Tropical Pacific

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Abstract The Eastern Tropical Pacific (ETP) is one of the last regions where large aggregations of the critically endangered scalloped hammerhead shark (*Sphyrna lewini*) can still be observed. In this regard, we comparatively assessed the seasonality in *S. lewini*'s relative abundance within three marine protected areas (MPAs) of the ETP and explored its relationship with environmental factors such as temperature. Abundance standardization via generalized linear mixed models revealed that Galapagos Islands (Ecuador) held an overall higher relative abundance of *S. lewini* when compared to Cocos Island (Costa Rica) and Malpelo (Colombia). The greatest relative abundance was observed from June to October for Cocos, followed by Galapagos (January, September, and November) and Malpelo (December, February, and March). Our results suggest that *S. lewini* observed relative abundances are significantly affected by water temperature and years (all three sites), and by the seasons, dive schedule, visibility and moon phase (to a lesser extend). This research contributes to the understanding of the temporal and spatial fluctuations of *S. lewini* at oceanic aggregation sites to improve the decision-making tools for the integral regional climate-smart management of the species. We recommended future studies to model the effect of climate change in the abundance at aggregation sites and potential distribution shifts across the ETP.

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Introduction

The critically endangered scalloped hammerhead shark (*Sphyrna lewini*) is a circumglobal species found in warm temperate and tropical coastal and semi-oceanic waters (Compagno et al. 2005). A characteristic feature of this species is its gregarious behavior and complex social structure, displayed particularly when aggregating around oceanic seamounts and islands (Klimley 1983; Jacoby et al. 2012). At these sites, hammerhead sharks are known to form schools up to 250 individuals, to measure from 1 to 3.5 m in total length (mean 1.8 m) (Klimley and Nelson 1984; Hearn et al. 2014), and to spend their time swimming in windward areas during daytime (Hearn et al. 2010; Jacoby et al. 2022). Individuals of *S. lewini* tend to make solitary movements away at night to feed on pelagic fish and squid, returning to the same or nearby aggregation sites the following days (Klimley 1993; Ketchum et al. 2014b). The species is also characterized by a differential habitat use by juveniles, which are born and grow in shallow coastal bays, and adults, which comprise most of the schools found at oceanic aggregation sites (Klimley 1983; Hall et al. 2000; Hinke et al. 2004).

The Eastern Tropical Pacific (ETP) hosts some of the most renown aggregation sites for this species, particularly those found in the marine protected areas (MPAs) of the Galapagos Islands in Ecuador (Hearn et al. 2014), Cocos Island in Costa Rica (Nalesso et al. 2019), and Malpelo Island in Colombia (Bessudo et al. 2011). At these sites, hammerhead sharks are often seen aggregating in hundreds and in an apparent response to the prevailing seasonal oceanographic setting. For example, in Galapagos, the relative abundance is higher (up to 128 individuals per dive) in the northern islands of Darwin and Wolf from June to October (Hearn et al. 2014; Peñaherrera-Palma et al. 2017); in Cocos, high relative abundance (up to 215 ind/dive) occurs in July with a sharp decline in December (Sibaja-Cordero 2008; White et al. 2015); and in Malpelo, the relative abundance (up to 120 ind/dive) is higher from January to April with a decline from May to December (Soler et al. 2013). This seasonality has also been suggested for newly identified aggregation sites recently found in Australia (López et al. 2022) and Japan (Jacoby et al. 2022), although more data is needed to define seasonal trends as those observed in the ETP.

Few studies have assessed the response in the abundance of *S. lewini* at aggregation sites as a function of environmental variables. Globally, it has been reported this species prefers temperature ranges from 15 to 32 °C (Rodriguez-Burgos 2022), and depths from 0 to 1000 m (Jorgensen et al. 2009), although it is mostly found from 24 to 26 °C (Zhang 2022) and between 0 to 50 m deep (Ketchum et al. 2014a). Using a long-term dataset recorded by divers in Cocos, White et al. (2015) inferred the aggregations of *S. lewini* are negatively influenced by El Niño conditions, water temperature and the overall seasonality of the island, and positively influenced by the current and water visibility. Differently, Soler et al. (2013) suggested no effect of El Niño but the seasons to significantly influence the observed numbers by divers at Malpelo Island. Soler et al. (2013) study did not assess other variables, which in conjunction with the differences in methodology and assessed time frame with White et al. (2015) make it impossible to compare and draw conclusions on the habitat preferences of *S. lewini* at these three MPAs. Understanding the environmental effect over the abundance of a species is critical to provide precise predictions of the population dynamics and the extinction risk of a species (Lawton 1994; Burgess and Marshall 2011). Given the population decline reported at the regional (Peñaherrera-Palma et al. 2018b) and global scale (Rigby et al. 2019), the importance of quantifying the environmental drivers that define *S. lewini* aggregations becomes critical for the development of climate-smart management frameworks and conservation strategies. Furthermore, the prominent connectivity *S. lewini* displays across the ETP (e.g., Ketchum et al. 2014b) compels such evaluations to be carried out simultaneously in all MPAs to provide decision support tools tailored to each site but that address issues from a regional perspective.

The present study is thus aimed to comparatively assess the variations in the relative abundance of the *S. lewini* in the aggregation hotspots of these three MPAs. Using a generalized linear mixed model with visual surveys and environmental data, we modelled the relative abundance of *S. lewini* to assess which environmental variable may be driving the relative abundance at Cocos, Galapagos, and Malpelo. Finally, we hypothesized that temperature influences the abundance of *S. lewini*, and that a temperature range of 24 to 25° C defines the existence of larger numbers at any given site.

Methods

Study sites and diving locations

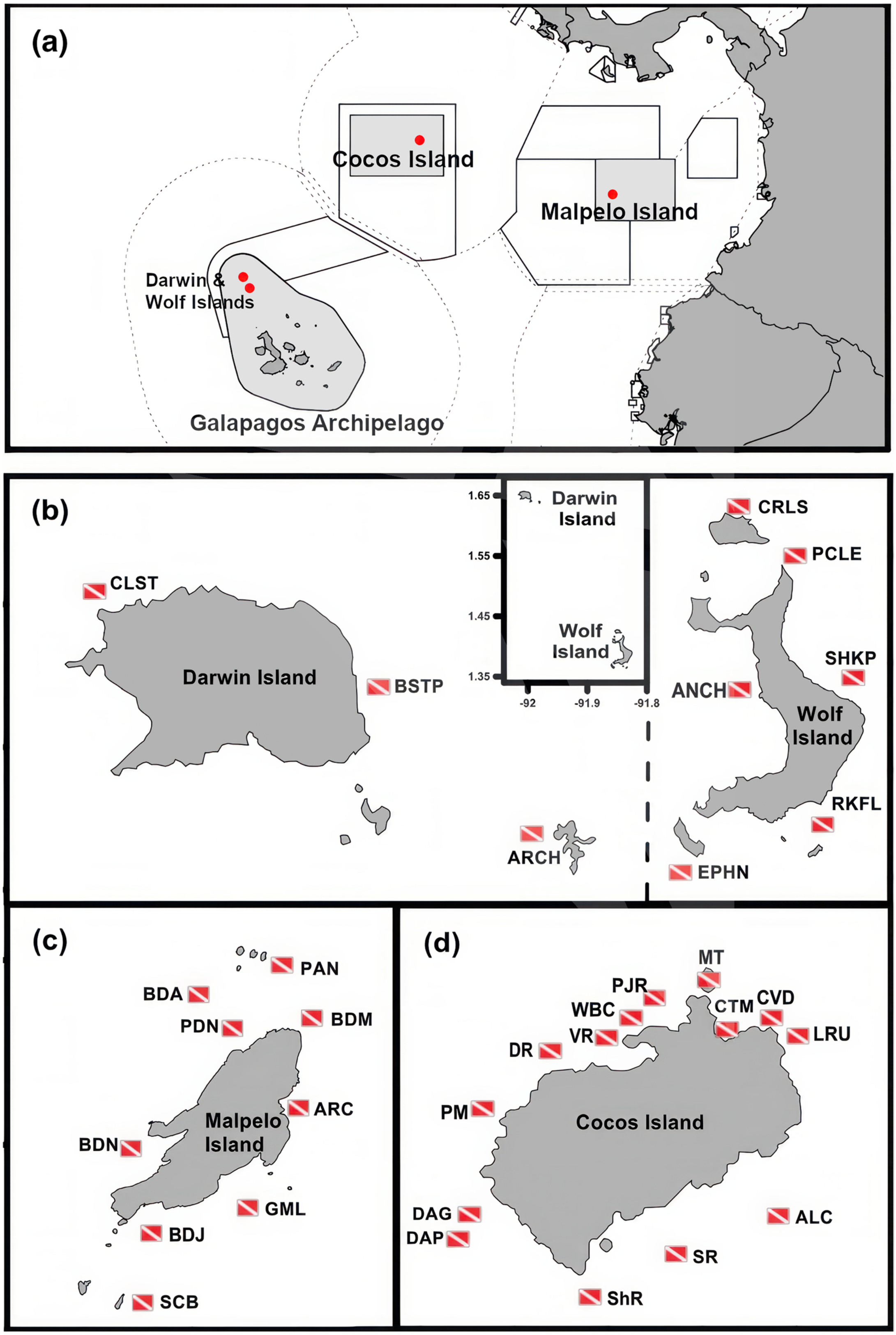
The Galapagos Marine Reserve (hereafter Galapagos) is located 1000 km west off the coast of Ecuador (Walsh and Mena 2016), while the Cocos Island National Park (hereafter Cocos) is 500 km southwest off the coast of Costa Rica (Alvarado et al. 2016), and the Malpelo Fauna and Flora Sanctuary (hereafter Malpelo) is 500 km west off the Pacific coast of Colombia (Bessudo-Lion and Álvarez-León 2014) (Fig. 1a). These three MPAs are in the southern region of the ETP and at the heart of the Eastern Tropical Pacific Marine Corridor (CMAR), a regional cooperation mechanism created by Colombia, Costa Rica, Ecuador, and Panama to promote the sustainable use and conservation of their marine resources from a regional perspective (Enright et al. 2021).

The three MPAs share a common volcanic origin, strong oceanographic, and ecological similarities and are physically and biologically connected (Peñaherrera-Palma et al. 2018a). The mean sea surface temperature (SST) of the region ranges between 27 and 28 °C, except for areas where temporal upwelling occurs (Feldman 1986; Palacios 2004). SST in north of Galapagos (Darwin and Wolf Islands) varies from 28 °C during the warm season (January to May) to 22 °C during the cold season (July to November), for Cocos the annual SST varies from 29 °C during the warm season (December to April) to 27 °C during the cold season (May to November). For Malpelo, the warm season occurs from May to December with a mean temperature of 28 °C, while the cool season occurs from January to April with a mean temperature of 26.5 °C. Chlorophyll *a* concentration fluctuates from 0.15 to 0.35 mg m^{-3} where Malpelo exhibits its highest values from February to May and lowest from June to December. In Cocos, the highest productivity occurs from June to August and lowest from March to May, while in Galapagos, productivity is highest from March to August and lowest from September to February (Zevallos-Rosado et al. Accepted). Darwin and Wolf Islands are partially influenced by the Cromwell Current with cold, nutrient-rich waters and the Panama Current with warm waters (Banks 2002). Both islands are surrounded by a small number of islets and exposed rocks, the intensity of currents at dive sites range from medium to strong (Hearn et al. 2010; Davis 2019). Cocos and Malpelo are influenced by the Equatorial Countercurrent (Fiedler 2002; Rodríguez-Rubio et al. 2007). In Malpelo, the dive sites are characterized by caves and strong currents (Soler et al. 2013), while the sites in Cocos have mild to strong currents and are characterized by one to three cleaning stations (Gordon 2000; Chasqui-Velasco 2008).

Data collection

We used *in situ* observations of *S. lewini* collected from 2007 to 2013 in Galapagos (Hearn et al. 2014), Cocos (White et al. 2015), and Malpelo (Soler et al. 2013). Visual surveys were conducted by 31 divers at Galapagos, 29 divers at Cocos and 11 divers at Malpelo. A total of 18 dive sites were evaluated at Cocos and nine sites for both Galapagos and Malpelo. Surveys of *S. lewini* and other pelagic fishes were carried out two to five times per year at Wolf and Darwin Islands (Galapagos) by MigraMar, in Cocos by the Undersea Hunter (www.underseahunter.com), and by the Malpelo Foundation at Malpelo. Visual surveys at each site were carried out using the Roving Diver Technique (RDT) (Schmitt and Sullivan 1996), which involves counting all individual sharks sighted by the diver during an immersion (30 min). The divers were either stationary or moving, depending on the location and current velocity. In order to reduce the bias related to the divers' experience, we eliminated the records provided by divers with less than 100 dives, and the dive sites where too few (<10) observations were recorded (White et al. 2015). Finally, the relative abundance of *S. lewini* was standardized as the number of individuals sighted per dive (Ind/dive).

Environmental data were recorded by divers at each study site and downloaded from remote sensors (satellites). The recorded parameters in each dive were as follows: (1) current strength, ranging from 0 representing no perceptible current to 3 with strong current; (2) visibility in meters (m); and (3)


(a)
Cocos Island
Malpelo Island
Darwin &
Wolf Islands
Galapagos Archipelago
(b)
CLST
Darwin Island
BSTP
1.65
1.55
1.45
1.35
-92
-91.9
-91.8
Darwin
Island
Wolf
Island
ARCH
CRLS
PCLE
SHKP
ANCH
Wolf
Island
RKFL
EPHN
(c)
PAN
BDA
PDN
BDM
ARC
Malpelo
Island
BDN
GML
BDJ
SCB
(d)
MT
PJR
WBC
CTM
CVD
VR
LRU
DR
PM
Cocos Island
DAG
DAP
ALC
SR
ShR

◂**Fig. 1** Study area and specific study sites. **a** Eastern Tropical Pacific (ETP), with the Galapagos, Cocos, and Malpelo (highlighted with red dots), including surrounding exclusive economic zones (EEZs). **b** Darwin and Wolf Islands in Galapagos, **c** Malpelo, and **d** Cocos. Specific dive sites where the observations were made are identified by acronyms and a full list can be found in Supplemental Table 3

in situ temperature in Celsius (°C). Dive schedule was categorized in three periods: (1) morning from 6:00 to 10:30 h, (2) midday from 10:30 to 14:00 h, and (3) afternoon from 14:00 to 18:00 h. Moon phase was determined by dark phase or new moon, ranging from 0% to its brightest phase or full moon at 100% (Llerena-Martillo et al. 2018). Monthly means of SST were downloaded from the Multi-Scale Ultra High-Resolution (MUR) fv04.1 database with a spatial resolution of 0.65 km (JPL MUR MEaSUREs Project 2015). Monthly means of chlorophyll *a* (mg m^{-3}) were downloaded from the MODIS-Aqua Moderate Resolution Imaging Spectroradiometer satellite database, with a spatial resolution of 4 km (NASA GFSC 2018). Chlorophyll *a* was only used for descriptive analysis so it was not included in the statistical analysis. Data from these sources were extracted using the package "rerddapXtracto" v.1.1.0 available in R statistical software (R Core Team 2021).

Data analysis

The relative abundance of each MPA was related to the environmental variables using a generalized linear mixed model (GLMM) (McLean et al. 1991). This approach is useful to reduce the bias associated with the collection of catch and effort data over time, particularly from factors such as observer experience, study area, time of the day and environmental variables (Maunder and Punt 2004). GLMM is a more flexible extension of generalized linear model (GLM) and used mainly for non-metric data. These models use a transformation of expected values to produce linearity (Nelder and Wedderburn 1972) and allow for the representation of a series of random effects that may indirectly affect the response variable (Blanco 2013). In this type of model, the random component does not always follow a normal distribution and for that reason is adjusted to an exponential distribution (López-González and Ruiz-Soler 2011). Models were built using the number of individuals counted per 30 min/dive as the response variable. Abundances were fitted to a negative binomial distribution to address over-dispersion of the dataset (see Supplemental Fig. 1) (Zuur et al. 2009). GLMMs were used to model the unique and additive effect that allows to predict the behavior of the response variable in relation to the explanatory variables of subsurface temperature, SST, current strength, visibility, dive schedule, and moon phase. Dive site and diver were used as random effects within the GLMMs for each MPA (White et al. 2015).

To assess multi-collinearity and to avoid variance inflation and bias, all explanatory variables were analyzed using a Pearson correlation test and the variance inflation factor (VIF) under a GLM model fitted to a negative binomial distribution. VIF identifies the level at which the variance is affected by lack of independence among several variables within the model (Zuur et al. 2009; Murillo-Posada et al. 2019). For Galapagos, the analysis identified island and month as collinear variables, while month was identified for Cocos and Malpelo (see Supplemental Figs. 2–4 and Table 1). All variables identified as collinear were eliminated from subsequent analyses for each area.

The GLMM selection process began with a saturated model assessing the interaction of all explanatory variables. Then, each variable was eliminated one by one according to their contribution (see Supplemental Table 2) (Maunder and Punt 2004; Zuur et al. 2009). Significant differences between models were estimated using an analysis of variance (ANOVA) ($\alpha = 0.05$) (Zar 2010). For each model, Parsimony expressed as the goodness-of-fit index (PGFI) was evaluated using the Akaike information criterion (AIC) and the Bayesian information criterion (BIC) (Hastie and Tibshirani 1986; Guisan et al. 2002). We used both criteria to choose the best model because they complement each other minimizing the quadratic error of prediction between the data set. BIC is more efficient against the limitations of AIC for finite data, while AIC minimizes the risk of choosing the wrong model (Vrieze 2012). To further validate model selection, the deviation residuals versus the adjusted residuals were examined for each explanatory variable following Zuur et al. (2009) (see Supplemental Figs. 2–4). All statistical analyses were computed using the R statistical software (R Core Team 2021).

Table 1 Final models statistics for the studied MPAs

MPAs	Model	AIC	BIC	Adjusted R^2	Deviance
Cocos	Fixed effects (year + season + temperature + moon phase + current strength + dive schedule + visibility) + random effects (diver + site)	78,536.93	78,671.36	0.091	81881.8
Galapagos	Fixed effects (year + temperature + dive schedule) + random effects (diver + site)	5100.34	5171.63	0.234	5074.3
Malpelo	Fixed effects (year + season + temperature + moon phase + visibility) + random effects (diver + site)	3690.09	3746.29	0.053	3662.1

Results

A total of 78,932 individuals of *S. lewini* were counted during the study period including 27,069 for Darwin and Wolf Islands in Galapagos, 36,816 for Cocos, and 15,047 for Malpelo. The mean relative abundance of sharks was 63 ind/dive (individuals per dive) for Galapagos, 26 ind/dive for Cocos, and 37 ind/dive for Malpelo. Maximum number of sharks observed per dive reached 300 for both Galapagos and Malpelo, and 500 at Cocos (Fig. 2a–c). The number of sharks at Cocos showed a steady decline

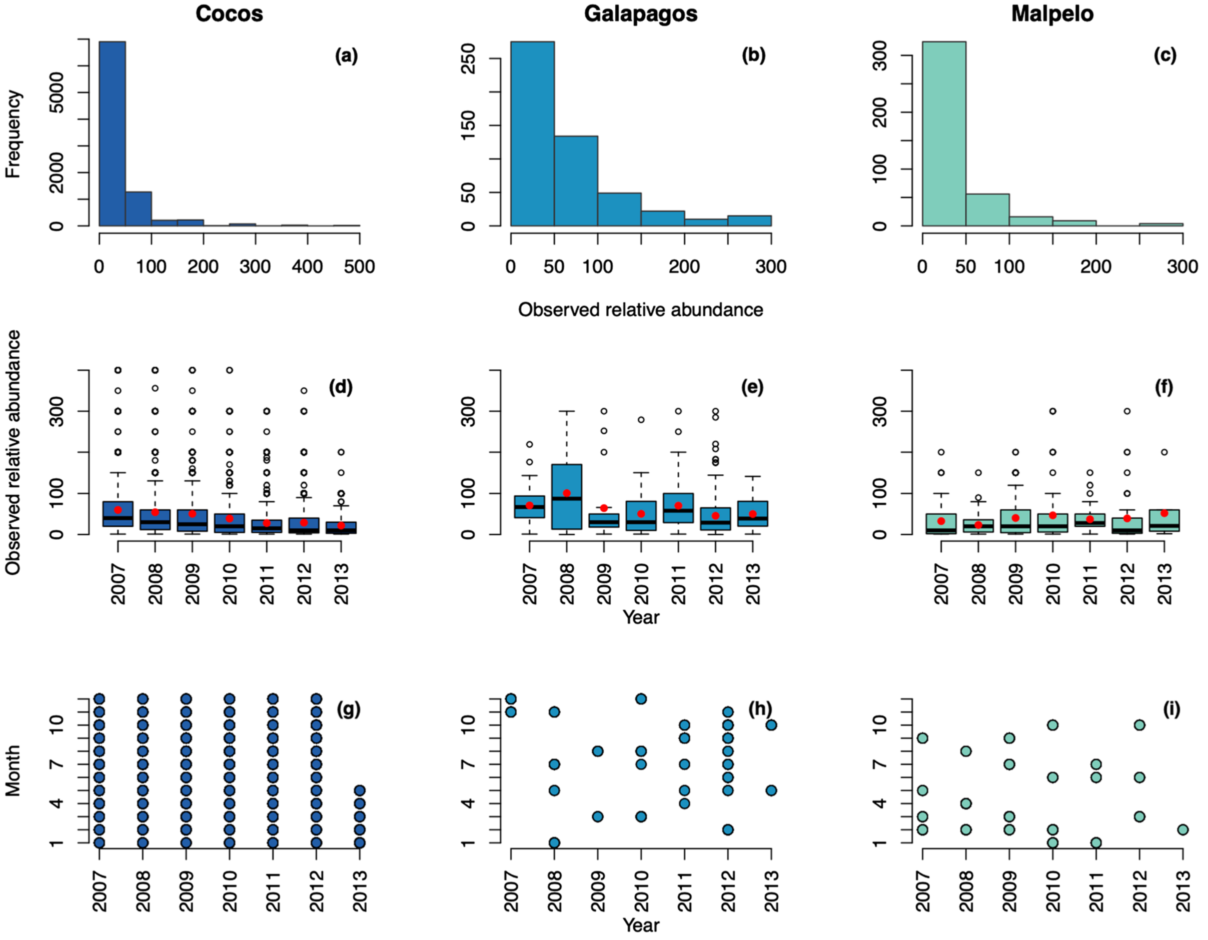


Fig. 2 Frequency of *S. lewini* relative abundance observed in Cocos, Galapagos, and Malpelo (**a**–**c**), including annual relative abundances (**d**–**f**) and the distribution of observations per month and year (**g**–**i**). Red dots represent the mean relative abundance value per year

over the assessed years, with the highest in 2007 (mean of 56 ind/dive) and consequently the lowest in 2013 (21 ind/dive; Fig. 2d). The highest mean relative abundance was observed in cold season (June to December; mean of 46 ind/dive), while the lowest was observed in warm season (from January to April, mean of 31 ind/dive). In Galapagos, annual mean relative abundance was higher during 2008 (101 ind/dive), but the lowest in 2012 (46 ind/dive; Fig. 2e). A larger number of individuals was observed in warm season (from January to May, mean of 88 ind/dive), and the lowest in cold season (from July to November, mean of 56 ind/dive). At Malpelo, the highest mean relative abundance occurred in 2013 (52 ind/dive), and the lowest in 2008 (23 ind/dive; Fig. 2f). Individuals of *S. lewini* were more abundant during the cold season (particularly in February and March, mean of 39 ind/dive), but less abundant in warm season (May and June, mean of 34 ind/dive). Shark Point (SHKP) at Wolf and Bus Stop (BSTP) at Darwin (Galapagos) were the sites in which most individuals were observed, while in Cocos was Alcyone (ALC) and Dirty Rock (DR), and in Malpelo, Bajo de Junior (BDJ) and El Arrecife (ARC). Cocos was the only place with data coverage in all months and years, while Galapagos had data from 2 to 8 months per year, and Malpelo, from 2 to 4 months (Fig. 2g–i).

Differences in environmental conditions were recorded between years. For Galapagos (Darwin and Wolf), the mean water temperature recorded by the divers was ~ 25.17 °C, with a maximum of 27 °C in 2016, and a minimum of 23 °C in 2008. Warmer SST (26.4 to 27 °C) occurred from January to May, while cooler SST (23 to 24.7 °C) from June to December (Fig. 3a). The year with the highest chlorophyll *a* was 2012, while the year with the lowest values was 2013 (Fig. 3c). The highest value of chlorophyll *a* (0.27 mg m^{-3}) was recorded from March to August and the lowest (0.15 mg m^{-3}) from September to February (Fig. 3d). For Malpelo, the highest water temperature recorded by divers was 27.53 °C in 2016, and the lowest was 26.04 °C in 2008. The warmest SST ranged from 26.9 to 27.53 °C from May to September, while the coldest SST ranged from 26.04 to 26.7 °C from October to April (Fig. 3b). The highest chlorophyll *a* (0.45 mg m^{-3}) was observed in 2016 from February to May (Fig. 3c), and the lowest chlorophyll *a* (0.25 mg m^{-3}) was recorded in 2012 from June to December (Fig. 3d). For Cocos, the mean water temperature recorded by divers was 26.1 °C, with a maximum of 31.2 °C, and a minimum of 20 °C. The warmest SST recorded was 29.7 °C in 2016, while the coolest was 25.7 °C in 2007. Monthly SST variation was similar at Galapagos, except in November and December when lower SST were recorded at Cocos (Fig. 3b). The highest chlorophyll *a* was 0.25 mg m^{-3} in 2005, and the lowest was 0.1 mg m^{-3} in 2015 (Fig. 3c). The chlorophyll *a* monthly pattern reached its highest from July to December and reached its lowest from March to June (Fig. 3d). Visibility values varied between 3–30 m for Galapagos, 0–40 m for Malpelo, and 1.52–60.98 m for Cocos. All survey dives were carried out during all moon phases.

Each site differed in the type and number of variables that significantly contribute to the final models. For Cocos, the best model included year, season, visibility, dive schedule, temperature, moon phase, and current strength as significant fixed variables ($p < 0.05$) (Table 1, see Supplemental Table 5). For Galapagos, the GLMM indicated that year, water temperature, and dive schedule significantly influenced the relative abundance of *S. lewini* (Table 1, see Supplemental Table 7). For Malpelo, the best model was significantly influenced by year, season, water temperature, moon phase, and visibility (Table 1, see Supplemental Table 9). Adjusted-R^2 values were rather low for all three models (0.05–0.26), yet residual spread was relatively homogeneous indicating an appropriate model fit for each case (Supplemental Figs. 5–7).

Each explanatory variable from the chosen final models had an individual effect on the response variable. For Cocos, year, season, and water temperature had a negative effect on the relative abundance, while current strength, dive schedule, and visibility had a positive effect (Fig. 4a). According to the predicted response estimates, a higher abundance was observed during years 2007 and 2009, current of medium (2) and strong (3) strength, midday diving hours (Fig. 5a–g). For Galapagos, the relative abundance of *S. lewini* was negatively influenced by year and temperature, while diving schedule positively influenced it (Fig. 4b). Model results predict higher abundances to occur during morning diving hours, water temperatures below 24 °C and during the year 2009 (Fig. 5d–f). For Malpelo, relative abundance was positively influenced by the years 2009 to 2013, visibility, and moon phase, while season and water

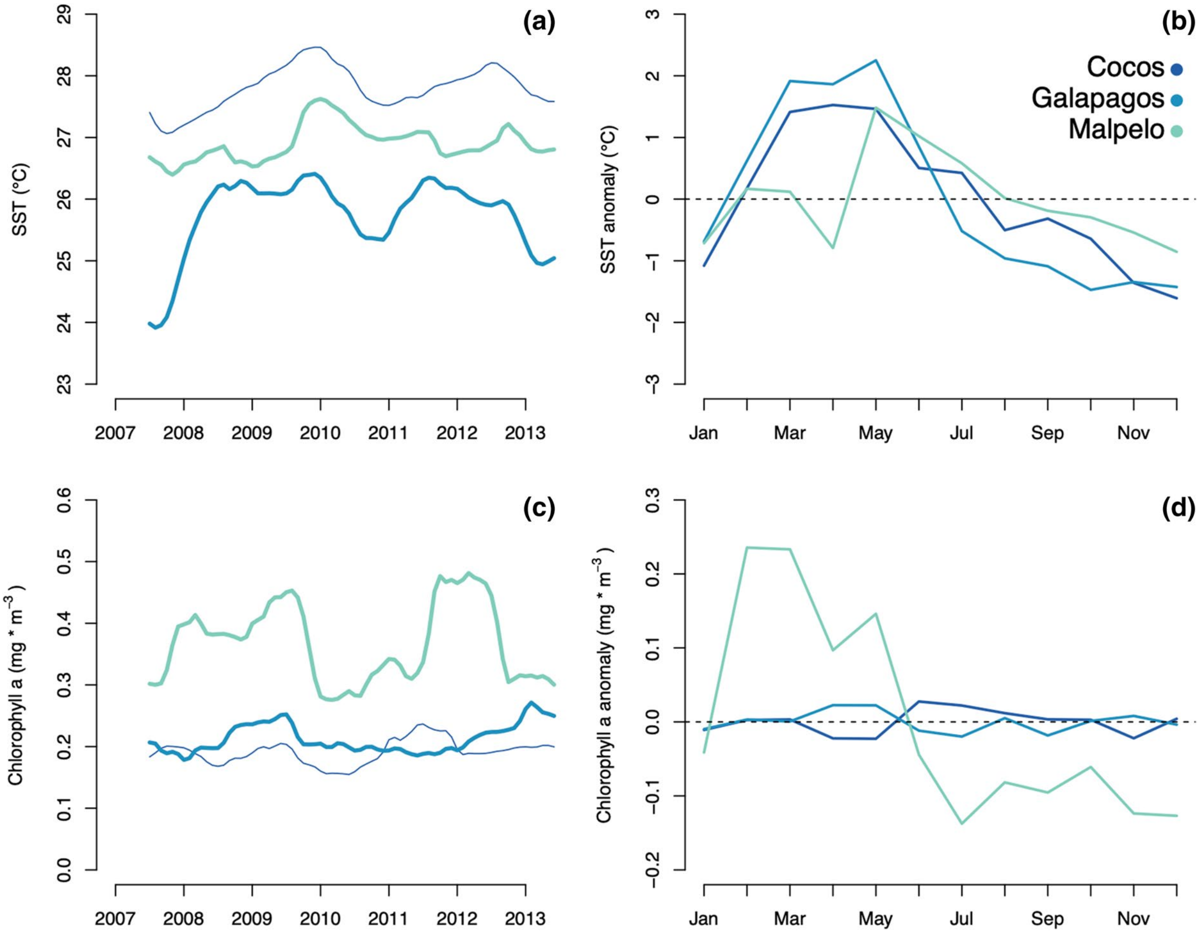


Fig. 3 Mean annual (**a**, **c**) and monthly (**b**, **d**) variation of SST and chlorophyll *a* for Cocos (*dark blue*), Galapagos (*light blue*), and the Malpelo (*turquoise*). SST and chlorophyll *a* variations are represented as the decomposed trend (annual) and seasonal (monthly) component from 2007 to 2013 time series used in this analysis

temperature negatively influenced it (Fig. 4c). Particularly, a greater abundance was predicted to occur towards full moon (> 75% of moon brightness), water visibility greater than 20 m, and during the cold season (Fig. 5g–k).

For all MPAs, predicted response estimates of abundance generally peaked when temperatures were below 24 °C, which are common during the cold seasons at all the studied MPAs (Fig. 5e, i, m). This response was not apparent when plotting the standardized relative abundance by season (Fig. 6), although model predicted response estimates for Cocos and Malpelo showed higher abundances during their cold seasons (Fig. 5d, l). Mean standardized abundance values were 46.1 for Cocos and 39.1 for Malpelo during the cold season, and 34.1 for Cocos and 33 for Malpelo, during the warm one. The distribution of the standardized relative abundance by season shows an inverse scenario at Galapagos, with a higher mean standardized relative abundance during the warm season (Fig. 6b). Mean standardized abundance values were 55.3 for the cold and 70.1 for the warm seasons. The larger abundance recorded in the warm season at Galapagos resulted from a particular large aggregation observed during January 2008. Nevertheless, the highest abundances (350 individuals) were observed at Cocos from June to November, when the lowest SST anomalies were also observed (corresponding to the cold season), while in Galapagos, high abundance values were observed in September and November, which are normally related to low SST anomalies. Distribution of standardized abundance for Malpelo

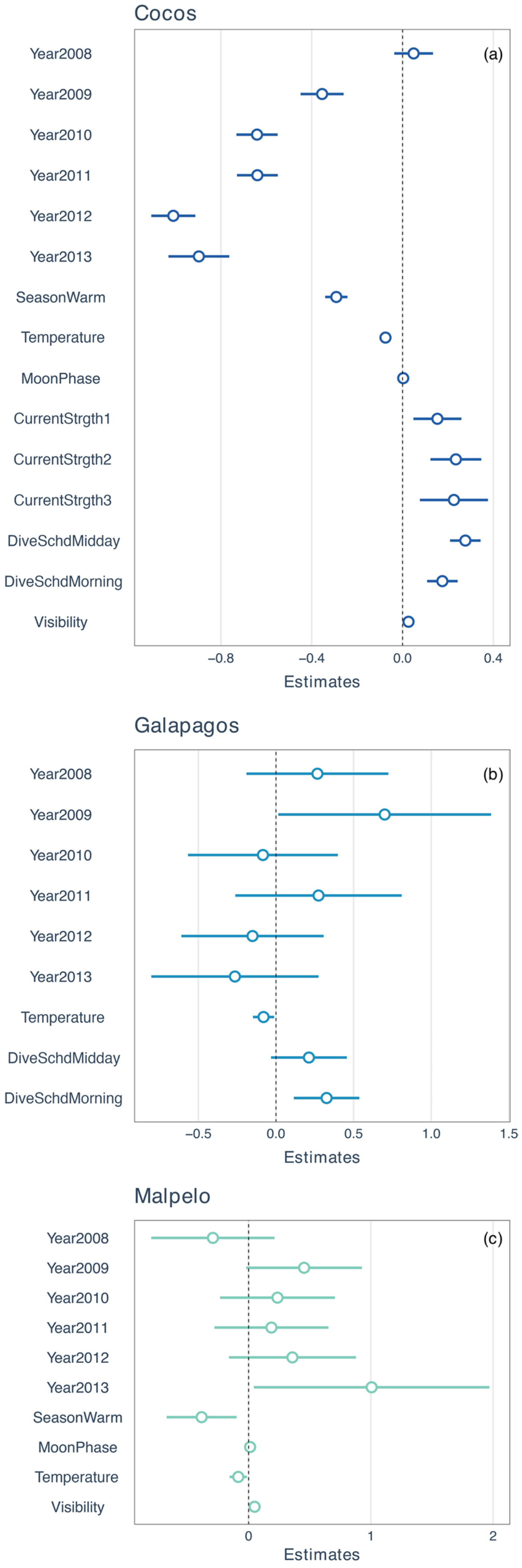


Fig. 4 Effects of the explanatory variables over the response ▸ variable for Cocos, Galapagos, and Malpelo

were rather similar for both seasons, yet high abundance values were observed in December, February, and March when low SST anomalies occurred (cold season).

Discussion

Here, we recorded the relative abundance of *S. lewini* and related them to environmental factors in three distant but ecologically connected MPAs. Our results show similar relative abundance for Malpelo and Cocos, and slightly higher for Galapagos. Seasonal abundance trends were similar in Malpelo and Cocos, but slightly different for Galapagos. Our results suggest that *S. lewini*'s relative abundance is driven by its habitat preferences, mainly to changes in temperature. We provide comparative information that supports independent observations carried out at each MPA (Soler et al. 2013; Hearn et al. 2014; White et al. 2015), suggesting that individuals of *S. lewini* do not aggregate simultaneously at the three MPAs. Here we discussed the ecological implications for the management of this critically endangered species.

Modelling approach and associated bias

The RDT allows highly mobile populations to be counted more efficiently when compared to other visual census techniques, particularly when it is performed in a greater number (Samoilys and Carlos 2000). This method, as any other underwater visual survey technique, is fast, easy to use and non-invasive to nature (Watson and Quinn 1997), and its results have proven useful and comparable to transect methodology when observing rare species associated with fishing (Schmitt et al. 2002). However, this technique may be susceptible to bias due to the cryptic behavior of fish (Thresher and Gunn 1986), fish behavior towards the divers (Dickens et al. 2011), oceanographic conditions (Harvey et al. 2002), and observer's experience (Williams et al. 2006). *S. lewini* is a species with a unique gregarious behavior and morphologic characteristics among sharks that makes them easily identifiable during dives (Compagno et al. 2005). Since this species does not display any

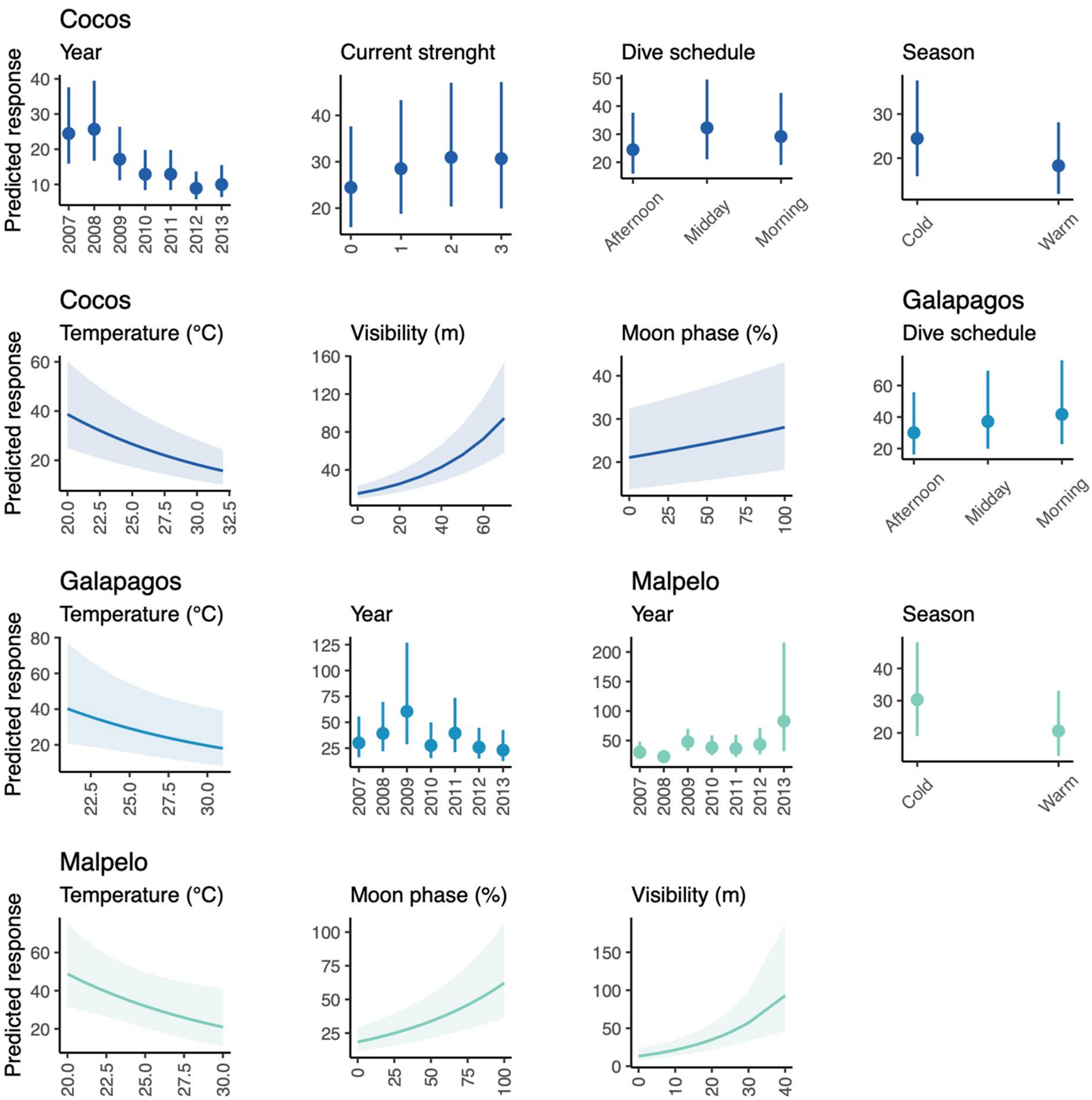
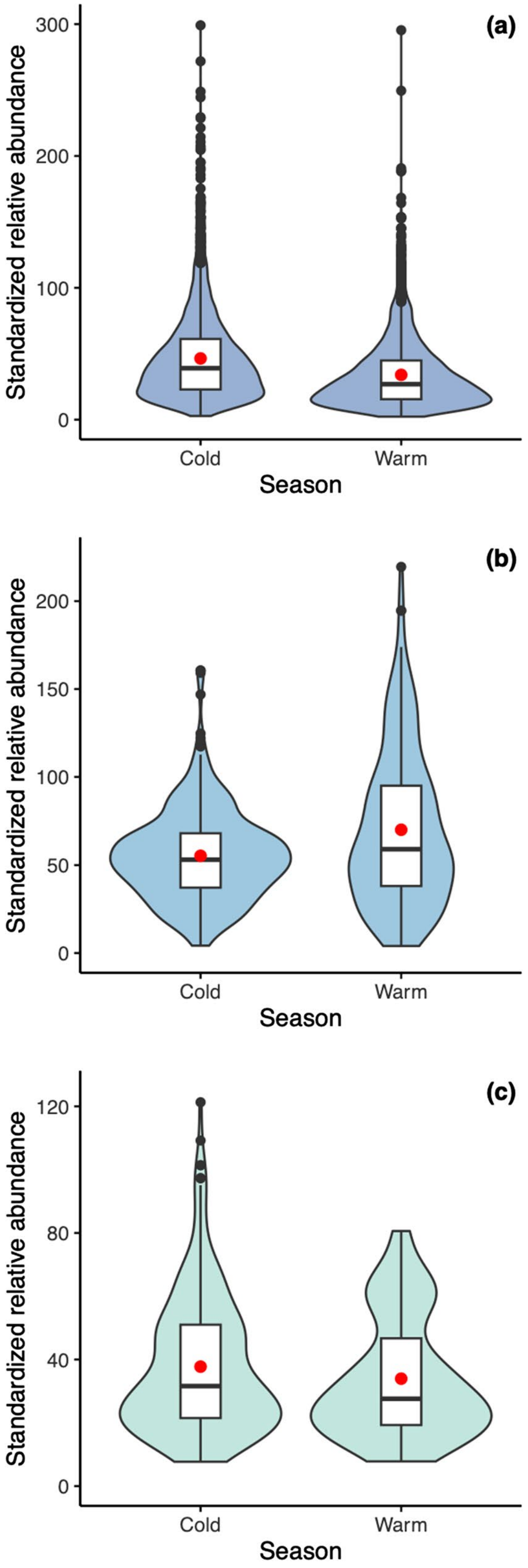


Fig. 5 Predicted response estimates and confidence intervals of *Sphyrna lewini*'s abundance to all the significant variables modelled per island

drastic evasive behavior in front of divers (Cubero-Pardo et al. 2011), the likelihood of any misidentification or other count bias were likely kept to a minimum, even under poor visibility conditions (Edgar et al. 2004). Moreover, Ward-Paige and Lotze (2011) suggested that inexperienced recreational divers can identify and count elasmobranchs as good as experienced recreational divers, which in long-term studies, can provide important insights into the population dynamics and trends. Regardless of this, we ensured a higher quality of our data by eliminating the records provided by divers with little experience, as suggested by Bernard et al. (2013) and Edgar et al. (2004). In addition to this, each site was analyzed separately to avoid increasing the complexity of the models and to fulfill independence and homogeneity assumptions

Fig. 6 Comparison of the standardized relative abundance per ▶ season for Cocos (**a**), Galapagos (**b**), and Malpelo (**c**). Violin plots depict the overall distribution of the standardized abundance; boxplots depict the quartiles and data range; and red dots, the mean standardized abundance per season



(Zuur et al. 2009). Modelling was carried out in an iterative process that firstly avoided any confounding effects due to variable collinearity (Zuur et al. 2010). Then the abundance was modeled incorporating oceanographic and effort variables (fixed and random) that may have an impact on the behavior, mobility and occurrence of the species (Forney 2000; Dail and Madsen 2011). This careful data processing, coupled with *S. lewini*'s behavioral and morphological characteristics, provide support to our analysis and thus suggest our data did not suffer from a greater bias during collection and data analysis.

GLMM models are robust tools to standardize abundance records with other models that are based on units of effort, arithmetic means or even spatial interpolations (Venables and Dichmont 2004; Yu et al. 2013). GLMMs allow the correction based on the nature of effort, the spatial structure and the environmental effect on data trends (Zuur et al. 2009), reducing the under or over-estimation of fishery catches (Punt et al. 2000; Murillo-Posada et al. 2019) or abundance of marine species (Forney 2000; White et al. 2015). In our study, the explained variation values (adjusted R^2) were relatively low (9% for Cocos, 23% Galapagos, and 5% for Malpelo), yet they provide useful approximations for representing the necessary detail of the obtained models (Dunn and Smyth 2018). First, our results lied within expected values due to the nature of the data (Ye et al. 2009). For instance, studies by Anderson (2003) and Yamada et al. (2006) reported deviances ranging from 7.5 to 14.5% and from 17.2 to 23.8% respectively during the standardization models of fishery records. Second, the analysis of residuals provided statistical support to consider our models were adequately adjusted to the observed data (see Supplemental Table 4–9). According to Zuur et al. (2009), residual plots are more useful to understand the goodness of fit of a model as they can expose bias far more effectively than the numeric output of other statistical parameters, such as the adjusted R^2.

Environmental drivers of abundance

Our results show that temperature and year were the only common variables significant to the final models of all MPAs, while dive schedule, season, visibility, and moon phase were for at least two. The magnitude of the effect of these variables differed between sites, perhaps in relation to the heterogeneity in the oceanographic setting of the region, and the species use of each site (Kessler 2006; Amador et al. 2016; Fiedler and Lavín 2017). Previous studies have shown that this species preferences change depending on the site and time of the year. For example, in Galapagos and Malpelo, *S. lewini* shows affinity with areas of prevailing currents (Hearn et al. 2010; Bessudo et al. 2011), which has been linked to prey abundance (Ketchum 2011; Ketchum et al. 2014b). Sharks tagged with acoustic transmitters at Espiritu Santo seamount in the Gulf of California were almost equally detected by autonomous receivers at any time of the day (Klimley et al. 1988), yet in Revillagigedo (Mexico) and Cocos, they are more frequent during daytime hours (Nalesso et al. 2019; Aldana-Moreno et al. 2020). These differences were also observed in our study, particularly in terms of the years and dive schedule. In Galapagos, aggregations of *S. lewini* were larger during morning dives, a condition that has been related to the early arrival of individuals after night foraging excursions in offshore waters (Klimley and Butler 1988; Ketchum et al. 2014a). Yet, this scenario was slightly different for Cocos, in which the larger aggregations were observed during midday hours. Regardless of these, there are also important similitudes in terms of the other environmental variables and how *S. lewini* responded to them. For example, aggregations were larger at Cocos and Malpelo during or closer to full moon (brightness of 100%) and when the water visibility was clearer and allowed to see further than 20 m. While there is a lot of common sense related to the impossibility of counting sharks when the water is particularly murky (Edgar et al. 2004), the effect of the moon phase has not being previously described for this species at an aggregation site. A positive correlation between full moon and abundance has been already reported for aggregations of other fish (e.g. Pet et al. 2005) and corals species (e.g., Glynn et al. 2008), while a negative effect have been observed in the catches of pelagic sharks, such as the blue shark *Prionace glauca* (Petersen et al. 2010). According to our results, moon phase could be acting as a conditional of the abundances of *S. lewini*, yet its effect was the smallest in both models of Cocos and Malpelo. Since it is still unknown if moon phase could be influencing the quality of the aggregation site or behavioral traits on this species, we recommend its further exploration by coupling longer datasets or carrying out focused experiments using other research techniques.

Temperature is regarded as the most important factor shaping the abundance and movement of *S. lewini* (Anislado-Tolentino et al. 2008), with a peak suitable habitat ranging from 26 to 30 °C globally, and from 22 to 28 °C just in the ETP (Zhang 2022). A similar study carried out only in the ETP region suggested the peak suitable habitat lied between 24 and 26 °C (Rodriguez-Burgos et al. 2022). Both studies used information from several sources and not only from aggregation sites, which could explain the subtle differences observed with our study (20–24 °C). Based on the site characteristics where data was collected, all individuals were likely observed between 10–50 m deep and within, near or above the thermocline. At aggregation sites, it is common to find this species cruising in the mixed layer right over the temperatures higher than 20 °C (Ketchum 2011; Ketchum et al. 2014a). This behavior has been previously regarded as a strategy to conserve energy by keeping the body warm in surface waters above the thermocline (Klimley et al. 2002). For instance, *S. lewini* can be observed at depths up to 5 m from the surface in intermediate temperate waters (~20 °C), where the thermocline is near the surface, yet it can go deeper (during the warmer months) when the thermocline is deeper (Bessudo et al. 2011). Darwin and Wolf Islands have a temperature that is two degrees lower compared to Cocos and Malpelo, which could explain the higher number (in average) of individuals observed at these islands.

Differences in the magnitude of *S. lewini* aggregations at regional scale may be caused by the species' thermal preferences and the abundance of its prey. The Humboldt squid *Dosidicus gigas* (d 'Orbigny 1835), one of the *S. lewini*'s most important prey items (Estupiñán-Montaño et al. 2009), migrates vertically to the surface at night when SST is under 28 °C (Nigmatullin 2001), a condition that prevails from June to December at Cocos and Galapagos in contrast to Malpelo, where these conditions prevail from

February to March (Fiedler and Lavín 2017). Individuals may aggregate around these MPAs to exploit food resources when conditions are optimal for the presence of its prey, and moving out of them once the oceanographic conditions change (Peñaherrera-Palma 2016). Such behavior has also been observed in several species of dolphins (Reilly 1990) in response to the changes in the horizontal and vertical distribution of *D. gigas* (Stewart et al. 2014). Since the Malpelo seasonal signature is slightly inverted compared to Galapagos and Cocos, these results suggest Malpelo could be acting as a "thermal oasis", providing a preferred habitat to the species during the first half of the year while the rest of the region gets warmer. A similar scenario was observed in the Gulf of California, where the arrival of several species assemblages, including the *S. lewini*, occurred at the tip of the Baja Peninsula when the cold waters from the California Current no longer extended around the peninsula, and warm waters entered the gulf from the ETP (Klimley and Butler 1988). In the same study, individuals of *S. lewini* tagged with acoustic transmitters, migrated from the seamount based on the absence of detections by autonomous receivers, during an upwelling event, returning when warm waters returned to the site. We recommend to develop further studies regarding *S. lewini* aggregations and how they relate to mobility and regional migrations, particularly since regional connectivity has already been reported for this species between the three MPAs (Ketchum et al. 2014b). Such information would not only assess fluctuations of the species aggregations with regards to food availability and changes in the regional SST, but also assess regional mobility caused by the species' reproductive requirements and ontogenetic migrations (Nalesso et al. 2019).

Management implications

Marine reserves are characterized by fostering the growth and reproduction of fishes (Roberts and Hawkins 2000), but these areas provide limited protection for highly migratory species (White et al. 2017). The scalloped hammerhead is known to migrate between the aggregation sites at Darwin and Wolf, Cocos and Malpelo (Bessudo et al. 2011; Ketchum et al. 2014b; Nalesso et al. 2019), and apparently with seamounts located off these islands that have been suggested may also represent potential aggregation sites (Chávez et al. 2020; Cambra et al. 2021; Ladino et al. 2022). The habitat selected by this species depends on the age and sex of specimens (Loor-Andrade et al. 2015), environmental preferences (Adam and Paperno 2007; Jorgensen et al. 2009; Harry et al. 2011) and food availability (Zanella et al. 2010; Loor-Andrade et al. 2015). If the preferential conditions remain stable, it is likely that the aggregation dynamics of this species will remain balanced over time. However, due to the acceleration of climate change (global increase of 0.27 °C per decade since 1979) (Trenberth et al. 2007) and the migratory nature of this species (Ketchum et al. 2014b), there is a high risk for spatial and temporal change in the occurrence of this species within and beyond the protection of the studied MPAs (Dingle 1996). Evidence of increase in SST in the Cocos-Galapagos area, and a drop in the monthly SST for the eastern area of the ETP have been reported (Belkin 2009). This change in oceanographic conditions can directly impact on the localized and large-scale demographic response of marine species (Dingle 1996; Perry et al. 2005). For example, a 1 °C rise in SST reduced counts by over 14%, and dropped the occurrence of their large schools by almost one-fifth (19.4%) of *S. lewini* in Cocos (Osgood et al. 2021). These scenarios increase the concerns on the overall fate of the aggregation sites of *S. lewini* found in the ETP. Further studies should assess other aspects that make them to depart from its aggregation sites and to analyze the characteristics of the MPAs to generate management measures and better protection. Particularly, a comparative analysis of fisheries catches reports, migratory movements and seasonal aggregations should be carried out to assess the spatial and seasonal vulnerability of this species to fisheries and climate change.

Our study contributes to the understanding of the temporal and spatial fluctuations of *S. lewini* at oceanic aggregation sites to better inform the decision-making processes for the integral regional management of the species. We suggest further studies to collect long-term time series datasets and better data resolution. This could complement databases through surveys (Roberts and Hawkins 2000), or accessible tools such as applications that link the participation of citizens visiting these areas (Alarcón 2019). Citizen science is a tool that can reduce the costs of this type of sampling, particularly in these remote areas where tourism activity is constant.

Significance statement

Regardless of its critically endangered status, information about habitat preferences of *S. lewini* within their aggregation sites is scare. This project provides standardized comparative data on the environmental factors that drive this species abundance within three oceanic aggregation sites. Our results show *S. lewini* abundance responds mostly to changes in regional temperature and provides important decision support tools for managing this species.

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Author contribution E.B.—conceived the research, the ideas to explain the results, developed the data analysis, structured the manuscript and led its writing. R.A.—developed the data collection, helped in the writing of the manuscript and was part of the funding. S.B.—developed the data collection, helped in the writing of the manuscript and was part of the funding. A.H.—developed the data collection, helped in the writing of the manuscript and was part of the funding. A.P.K.—developed the data collection, revised and re-drafted the article critically for important intellectual content and the final approval of the version to be submitted for publication. F.L.—developed the data collection, helped in the writing of the manuscript and was part of the funding. J.L.—contributed with new data analysis and manuscript writing. T.S.—developed the data collection, helped in the writing of the manuscript and was part of the funding. C.P.—developed the data collection, conceived the research, the ideas to explain the results, developed the data analysis, structured the manuscript, and led its writing.

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Data availability The data analyzed for this study are available from the corresponding author upon reasonable request.

Code availability The code for this study is available from the corresponding author upon reasonable request.

Declarations

Ethics approval No animals were handled or experimented on during any part of this research. Our underwater visual survey methods complied with animal welfare laws, guidelines, and policies as approved by the University of Tasmania Animal Ethics Committee (permit number A13641), by the Institutional Animal Care and Use Committee of the University of California – Davis (permit number IACUC PROTOCOL #16022), by the Directorate of the Galapagos National Park (permit number PC-60-13), by Cocos Island Marine Conservation Area (ACMIC) from National System of Conservation Area (SINAC) of Costa Rica (permit number ACMIC-008, ACMIC-012, ACMIC-006, ACMIC-001), and by the Ministry of Environment and Sustainable Development of Colombia (permit number DTPA 002-18).

Conflict of interest The authors declare no competing interests.

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