RESEARCH ARTICLE

Effects of climate-change-driven gradual and acute temperature changes on shark and ray species

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Abstract

1. Climate change is altering distributions and abundances of marine species through both gradual and acute changes in temperature and productivity. Due to their high mobility and metabolic rates, elasmobranchs (sharks and rays) are likely to redistribute across latitudes and depths as they thermoregulate, but little is known about their responses to these climatic changes, which could vary widely across this diverse group of species.

2. Here, we assessed how species with differing mobility and ecology responded to gradual changes in daily sea surface temperature (SST) and acute temperature anomalies, caused by the El Niño–Southern Oscillation (ENSO), at Cocos Island, Costa Rica, the site of multiple marine heatwaves.

3. We used generalized linear mixed models to analyse 34,342 records of relative abundance or frequency of occurrence for seven shark and ray species collected in 27 years (1993–2019) by a dive company. We compared effect sizes for SST and the Oceanic Niño Index across the different species, which vary widely in body size and mobility.

4. Large, mobile species responded strongly but inconsistently to temperature. For scalloped hammerhead sharks *Sphyrna lewini*, 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%). *Mobula* ray occurrence also declined substantially with a few degrees rise in SST, whereas tiger shark *Galeocerdo cuvier* occurrence sharply increased. These species also had divergent responses to the ENSO: *S. lewini* and *G. cuvier* were sighted with greater frequency during La Niña events, and their abundance dropped considerably during El Niño events—over a twofold decline between a strong La Niña and strong El Niño for *S. lewini*. In contrast, *Mobula* rays showed little response to ENSO. The smaller and sedentary *Triaenodon obesus* exhibited the weakest response of all species to both SST and the ENSO, reflecting its lower metabolic rates and mobility.

5. Climate change will continue to impact elasmobranchs, even for smaller and more localized species, with the potential to impact the effectiveness of marine protected areas (MPAs). Our results compel further work on the diversity of elasmobranch responses to environmental change.

1 | INTRODUCTION

Climate change is both gradually rising global ocean temperatures—a 1–3°C change is expected by the end of this century (Collins et al., 2013)—and intensifying the strength and frequency of acute marine heatwaves, such as the El Niño Southern Oscillation (ENSO; Frölicher et al., 2018; Oliver et al., 2018). Marine ectotherms, particularly those in the tropics, tend to occupy their entire fundamental thermal niche, putting them closer to upper physiological limits and forcing them to shift across their range in response to rising temperatures that can precipitously drop physiological performance (Pinsky et al., 2019; Rummer et al., 2014). Long-term shifts in the distributions of many marine fish are expected, both poleward and into deeper waters, in response to gradual changes in ocean temperature and prey availability induced by climate change (Perry et al., 2005; Pinsky et al., 2020), but short-term temperature anomalies, lasting for days or months, now known as marine heatwaves, have also led to rapid range shifts, community re-organization and disruptions to ecosystem function as species track even short-term changes to their habitat (Smale et al., 2019).

The degree to which marine fishes will shift, however, depends on species-specific traits, such as behaviour, body size, metabolic requirements and habitat needs, and will also rely on the local speed of climatic change (Perry et al., 2005; Sunday et al., 2015). Generally, fish species with faster life cycles and earlier maturation, higher mobility, broad latitudinal ranges, higher thermal sensitivity and ecological generalization tend to shift distributions faster and more successfully (Perry et al., 2005; Sunday et al., 2015). Physiological variation associated with differences in size and ecology also drives species-specific responses to ocean temperature changes, and community-wide reorganization is possible as climate change alters the spatial overlap between predators, prey and competitors (Pinsky et al., 2020; Sunday et al., 2015). This variability underscores the need for detailed species and population-specific data to predict how climate change will alter marine fish communities, yet these data are lacking for many taxa outside of Teleostei and other commercially important populations and species.

Many elasmobranch—shark, ray and skate—species are already highly threatened by fishing pressure, but little is known about how they will respond to the additional threat of climate change. On the one hand, low intrinsic rates of growth may predispose elasmobranchs to increased climate change vulnerability (Perry et al., 2005), whereas their overall high mobility suggests the opposite (Sunday et al., 2015). Elasmobranchs must thermoregulate to maintain optimal body temperatures for foraging, digestion, growth and reproduction through regular movements across habitats and depths with differing thermal regimes (Bernal et al., 2012; Ketchum, Hearn, Klimley, Espinoza, et al., 2014; Matern et al., 2000; Nakamura

et al., 2020), suggesting that these species will shift their distributions in response to at least gradual rises in ocean temperatures (Niella et al., 2020). However, short-term temperature anomalies also enhance physiological stress in elasmobranchs (Pegado et al., 2020), with some suggestions that marine heatwaves have led to range expansions in a few species (Beale et al., 2019; Lea & Rosenblatt, 2000; Morales et al., 2019). A combination of changing temperature and prey conditions during the ENSO likely explains why elasmobranch populations also fluctuate as it cycles between its warm water El Niño and cold water La Niña phases (Beale et al., 2019; Wilson et al., 2001). However, little is still known about how elasmobranchs respond to marine heatwaves and their intensification, or how that response varies across species.

Elasmobranchs also display species-specific responses to changes in temperature and prey availability associated with differences in physiology, mobility and ecology (Bernal et al., 2012). Pelagic elasmobranchs maintain high metabolic rates for ram-ventilation and active hunting, and have limited scope to acclimatize to increased temperatures by raising their metabolic rates due to constraints set by gill surface area and the need to swim fast enough to supply sufficient oxygen over the gills (Bernal et al., 2012; Jacoby et al., 2015). As such, more mobile elasmobranchs tend to have narrower thermal sensitivity (Lear et al., 2019). Mobility also enhances access to greater range of conditions, allowing for easier tracking of optimal temperatures (Lear et al., 2019; Pinsky et al., 2020). In contrast, sedentary benthic elasmobranchs maintain lower metabolic rates and have a higher cost of activity compared to ram-ventilating species, reducing both their capacity and need to re-distribute with changing environmental conditions (Whitney et al., 2016). Thus, based on physiology and mobility, there are numerous potential responses of local elasmobranch populations to gradual and acute changes to temperature stress: real population decline due to thermal stress and reductions in prey availability, apparent population decline due to permanent distributional shifts, apparent population fluctuations due to temporary behavioural thermoregulation, or no change due to wide thermal tolerance and a limited need or ability to move.

Predicting elasmobranch responses to both gradual and acute environmental change requires long-term data on elasmobranchs of differing ecology and movement characteristics in systems affected by both climate-change-induced graduate temperature changes and marine heatwaves. Here, we use 34,342 observations collected in 27 years (1993–2019) of relative abundance (or presence/absence) to investigate the elasmobranch community at Cocos Island, Costa Rica, which is affected by marine heatwaves in the form of regular ENSO events (Lavín et al., 2006) and by climate change—the last decade (2010–2020) in the Eastern Tropical Pacific experienced a rise in mean sea surface temperature (SST) of 0.5–1.0°C compared to 1950–1980 (GISTEMP Team, 2019; Lenssen et al., 2019). Our goals

were three-fold: (a) to identify species-specific responses to gradual temperature change; (b) to identify species-specific responses to acute temperature anomalies, caused by the ENSO and (c) to update population trends for these species, as most were previously revealed to be in decline, save for *C. limbatus* and *G. cuvier* (White et al., 2015). We assessed the relative abundance of four species of shark (scalloped hammerhead shark *Sphyrna lewini*, whitetip reef shark *Triaenodon obesus*, blacktip shark *Carcharhinus limbatus* and tiger shark *Galeocerdo cuvier*) and three species of ray (mobula rays *Mobula* spp., marble ray *Taeniurops meyeni*, spotted eagle ray *Aetobatus narinari*). These species are the most frequently observed at Cocos Island and represent a range of variation in mobility and behaviour that could affect their responses to SST and the ENSO. If thermal sensitivity and shifts in prey availability stimulate movements off island or into deeper waters, we predict counts for all species to decline at both higher SST and warmer phases of the ENSO. We expect the strongest effects for the more migratory and active pelagic species, *S. lewini*, *G. cuvier* and *Mobula* spp. We also expect these effects on *S. lewini* abundance to cause the schooling frequency of *S. lewini* to decline at higher temperatures and during stronger El Niño events. We expect the weakest responses for the benthic species *T. obesus* and *T. meyeni*, which do not rely on ram ventilation and should be less mobile with less aerobic scope for activity. Since elasmobranchs comprise a high percentage of targeted catch and bycatch in both legal and illegal fisheries in Costa Rica (Espinoza et al., 2018; González-Andrés et al., 2020), we predict that population declines will have continued (or started) for at least the highly mobile species most likely to leave the marine-protected area (MPA) around the island, since the last assessment up to 2013 (White et al., 2015). Thus, this time series can be used to investigate how fisheries-impacted populations are affected by both gradual long-term and acute short-term environmental change.

2 | MATERIALS AND METHODS

2.1 | Study site and data

Cocos Island (5.5282°N, 87.0574°W; Figure 1a) has been a no-take MPA in the Eastern Tropical Pacific since 1982, with protection extended to 22.2 km around the Island in 2002 (Alvarado et al., 2012). The island is a hotspot of elasmobranch diversity because of its productive reef and seamount habitats situated at the nexus of multiple currents (Friedlander et al., 2012; White et al., 2015). Together with Malpelo Island in Colombia and the Galápagos Islands in Ecuador, Cocos Island forms an important link in a migration corridor for scalloped hammerhead sharks *S. lewini*; large schools form at seamounts at the island, which draws sharks from across the Eastern Tropical Pacific (Nalesso et al., 2019).

From March 1993 to December 2019 (n = 27 years), experienced dive guides (n = 46) at Undersea Hunter (http://underseahunter. com/), a privately owned and operated dive operation, conducted a total of 34,342 dives on 5,664 different days at 17 sites around Cocos. At the end of each dive, the dive guide recorded the number of sharks or rays, or an estimate when counts were high (e.g. exceeded 100), using standardized data sheets. For three species (*C. limbatus*, *G. cuvier* and *Mobula* spp.), only presence or absence was reliably recorded. Dive guides recorded the presence of manta rays *Mobula birostris* and other *Mobula* species separately, but we combined them to bolster sample size and because of recent taxonomic revisions of *Manta* into the synonymy of *Mobula* (White et al., 2018). Although these dives lacked strict scientific protocol, they had consistent effort (~60 min), dive procedures and depths at each site, which covered the range of shallow water habitat at Cocos Island. Data from all dives were previously transcribed into a single data base (White et al., 2015) and these, plus new data since 2015 already electronically recorded, were checked for errors.

2.2 | Statistical analysis

To assess the influence of both gradual and acute temperature changes on the sightings of these species, and to update their long-term trends (from White et al., 2015), we modelled the effects of SST and the Ocean Niño Index (ONI)—a measure of SST anomaly indicating ENSO conditions—on the abundance (*S. lewini*, *T. obesus*, *A. narinari* and *T. meyeni*) or presence–absence (*G. cuvier*, *C. limbatus* and *Mobula* spp.) of each species using negative binomial generalized linear mixed models (GLMMs) or binomial GLMMs, respectively. This modelling framework allows us to separate the shorter-term effects of climatic factors (i.e. SST and ONI) from other temporal (i.e. longer-term interannual) trends that might be the result of fishing and other factors. These models were found to be appropriate in previous work on these data (White et al., 2015). We ran an additional model on *S. lewini* data, modelling the probability of observing a school (≥50 sharks) during a dive using a binomial GLMM. We assessed zero-inflation for all species with count data using AIC and residual plots (following White et al., 2015), but model fit improved only for *T. meyeni*. Additionally, since *G. cuvier* was seen regularly only after 2006, only data after this year were used in its analyses of the SST and ONI effect, but when estimating percent decline, we used the entire year range to compare our estimates to White et al. (2015).

Within the models for each species, we included SST, ONI, Julian date (for an overall linear trend), the sine and cosine functions of day of year (1–365, to account for seasonality, Baum & Blanchard, 2010), visibility (continuous estimate) and current strength (categorical from 0 to 5) as fixed effects. We scaled SST and visibility to a mean of zero and a standard deviation of one to be on a similar scale to the ONI. Visibility and current strength were recorded by the dive guides. We retrieved daily mean SST and the ONI data from NOAA: NOAA High Resolution SST data (0.25 degree latitude × 0.25 degree longitude grid) provided by the NOAA/OAR/ESRL PSL, Boulder, Colorado, USA, from their website at https://psl.noaa.gov/, and NOAA ONI data from https://www.cpc.ncep.noaa.gov/data/indices/oni.ascii.txt). We included both SST and ONI in the same model to account for the different types of temperature changes they
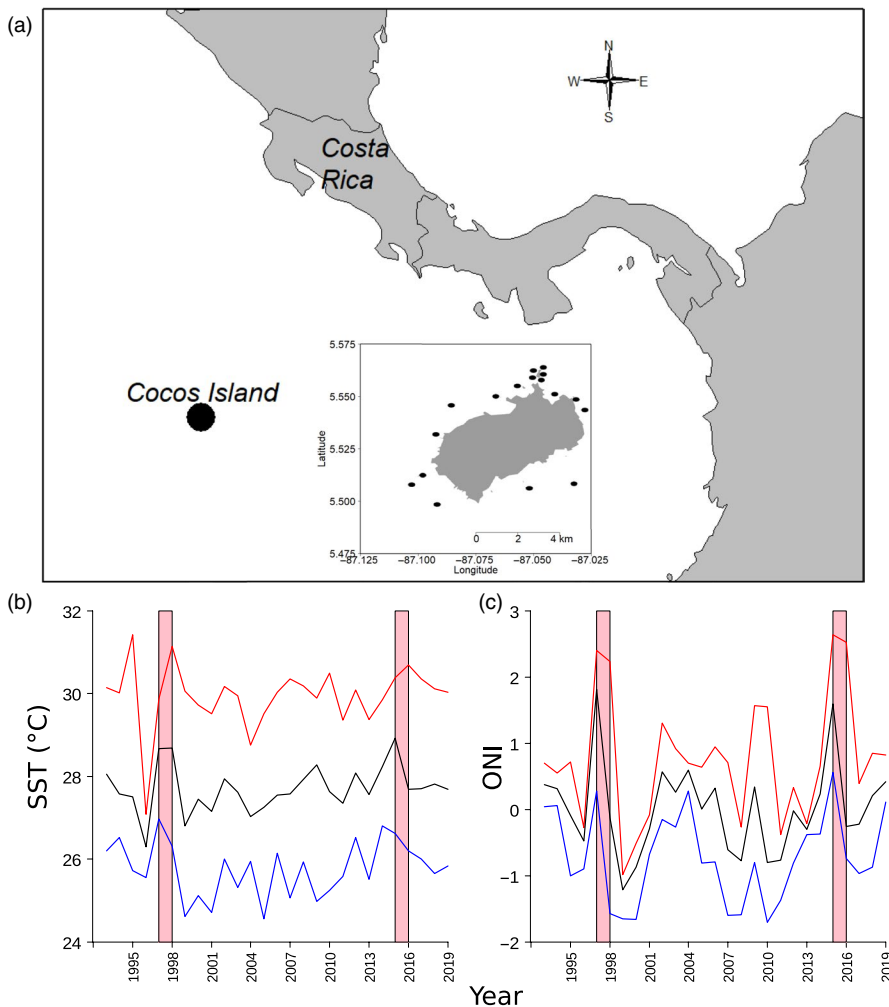
FIGURE 1 (a) Cocos Island with approximate dive sites, and the change in (b) mean, minimum and maximum daily sea surface temperature (SST), and in (c) mean, maximum and minimum Oceanic Niño Index (ONI) at Cocos over the study period. Red rectangles represent the strong El Niño events of 1997–1998 and 2015–2016

represent: the ONI index quantifies the running 3 month mean of SST anomalies in the Niño-3.4 region of the east-central Pacific (NOAA 2020) that also correlates with other oceanographic features in the Eastern Tropical Pacific. In contrast, daily mean SST captures immediate species responses, in terms of their physiology and daily movement that would influence their response to gradual change over decadal time scales. The two data sources were not strongly correlated (rho = 0.34), and correlation direction was not consistent across years. We determined the significance of the SST and the ONI coefficients using Wald's Z-tests (see Table S1). For *G. cuvier* and *A. narinari*, the relationship to ONI appeared nonlinear in plots of data and splines from generalized additive models; likelihood ratio tests determined a significant quadratic and cubic relationship existed with ONI for *A. narinari* and *G. cuvier*, respectively. Random effects accounted for correlations due to dive guide and site. We also included year as a random effect to account for additional interannual variation not explained by SST, ONI or the linear temporal trend.

For each species, we used the SST coefficients to calculate the percent change in abundance or odds of occurrence as SST increased one standard deviation (~1℃) and from 25 to 30℃ (roughly the SST range experienced at Cocos). We also used the ONI coefficient to calculate percent change from a neutral ENSO (ONI = 0) to

a moderate (La Niña: ONI = −1; El Niño: ONI = 1) event and also the percent change between strong La Niña (ONI = −1.5) and strong El Niño events (ONI = 1.5). Including study Julian date as a continuous fixed effect allows us to accomplish two goals. First, we can separate the effects of SST and ONI variables from longer-term trends. In addition, we were able to calculate the percent decline for each species from predicted abundance at the end of 2019 compared to predicted initial abundance at the start of the time series. For *G. cuvier* and *C. limbatus*, only yearly (365-day) percent change was calculated to compare with White et al. (2015). We simulated coefficients for each model from a multivariate normal distribution 10,000 times to generate confidence intervals for each percent change (King et al., 2000). Data are not the property of the authors and cannot be shared, but r-scripts for all analyses and figures are available online (https://doi.org/10.5281/zenodo.4977678; GitHub: github.com/baumlab/Osgood_etal_2021_JAE).

3 | RESULTS

Sea surface temperature varied from 24.6 to 31.4℃, with a mean of 27.8℃, while ONI varied from −1.70 to 2.64 with a mean of

−0.023. Mean, minimum and maximum SST and ONI showed slight increases across the 27 years of the time series (Figure 1b,c).

3.1 | Species responses to temperature

Sphyrna lewini and *T. obesus* were the most frequently observed sharks, counted on 77.7% and 97.2% of dives, respectively, while *C. limbatus* was the least frequently observed species overall (Table 1). *Taeniurops meyeni* was the most frequently observed ray species, with *Mobula* spp. and *A. narinari* observed less frequently (Table 1).

Out of all the sharks, the schooling and mobile *S. lewini* exhibited the strongest response to both types of temperature changes (Figures 2 and 3b; Table S1), with predicted counts declining by 10.3% (95% CI: 8.0%–12.7%) with a 1°C (1SD) increase in SST and

by over a third (40.3%; 95% CI: 32.8%–47.6%) with an increase from 25 to 30°C. Predicted *S. lewini* counts were 105.6% (85.9%–125.9%) higher during strong La Niñas (ONI = −1.5) compared to strong El Niño conditions (ONI = 1.5). Even moderate La Niña conditions (ONI = −1) resulted in predicted *S. lewini* counts rising by 27.2% (23.0%–31.3%) compared to neutral conditions (ONI = 0), whereas moderate El Niño conditions dropped predicted counts by 21.4% (18.8%–23.9%). Additionally, the probability of observing *S. lewini* schools (>50 individuals) declined significantly with increasing SST and ONI (Table S1). Schooling was 11.2% (6.4%–16.0%) more likely at the mean SST than it was even one degree above it, and it was 42.8% (26.9%–57.1%) more likely at 25°C than at 30°C. Moderate El Niño conditions dropped the probability by 23.1% (17.1%–28.6%) compared to neutral ONI values while moderate La Niña conditions increased it by 29.4% (19.6%–38.7%). Schooling was also 118.0%

TABLE 1 The frequency of occurrence (FO), mean count per dive when the species was seen, maximum count observed and temperature preferences from the literature for each studied species

Species	FO	Mean count (excluding zeros)	Max. count	Literature temperature preference	Reference
Galeocerdo cuvier	6.2%	1.4	11	22°C, >30°C	Payne et al. (2018) and Lear et al. (2019)
Sphyrna lewini	77.7%	42.1	1,000	23–26°C	Ketchum, Hearn, Klimley, Peñaherrera, et al. (2014)
Carcharhinus limbatus	4.8%	1.7	40	30°C	Lear et al. (2019)
Triaenodon obesus	97.2%	24.2	500	>26°C	Nadon et al. (2012)
Mobula spp.	9.0%	1.8	40	20–26°C	Couturier et al. (2012)
Aetobatus narinari	22.7%	2.2	60	23–31°C	Bassos-Hull et al. (2014)
Taeniurops meyeni	78.9%	8.5	100		

FIGURE 2 Coefficients and 95% confidence intervals for sea surface temperature (SST) and Oceanic Niño Index (ONI) terms from the generalized linear mixed models for tiger shark *Galeocerdo cuvier*, scalloped hammerhead shark *Sphyrna lewini*, blacktip shark *Carcharhinus limbatus*, whitetip reef shark *Triaenodon obesus*, *Mobula* spp., spotted eagle rays *Aetobatus narinari* and marbled rays *Taeniurops meyeni*. The models for eagle rays had a quadratic term and for tiger sharks had cubic terms for ONI
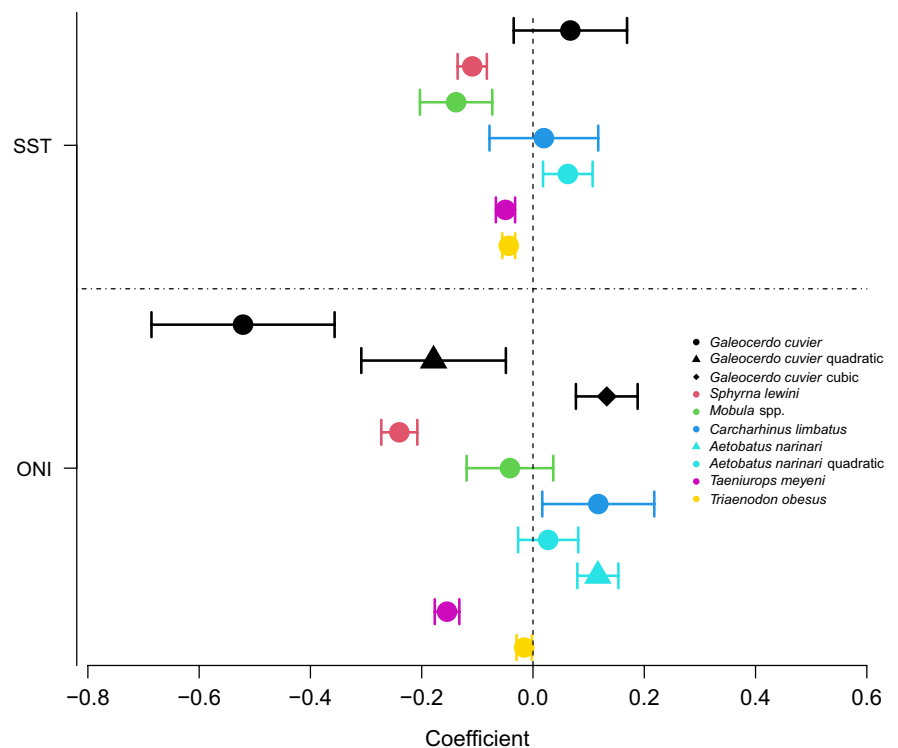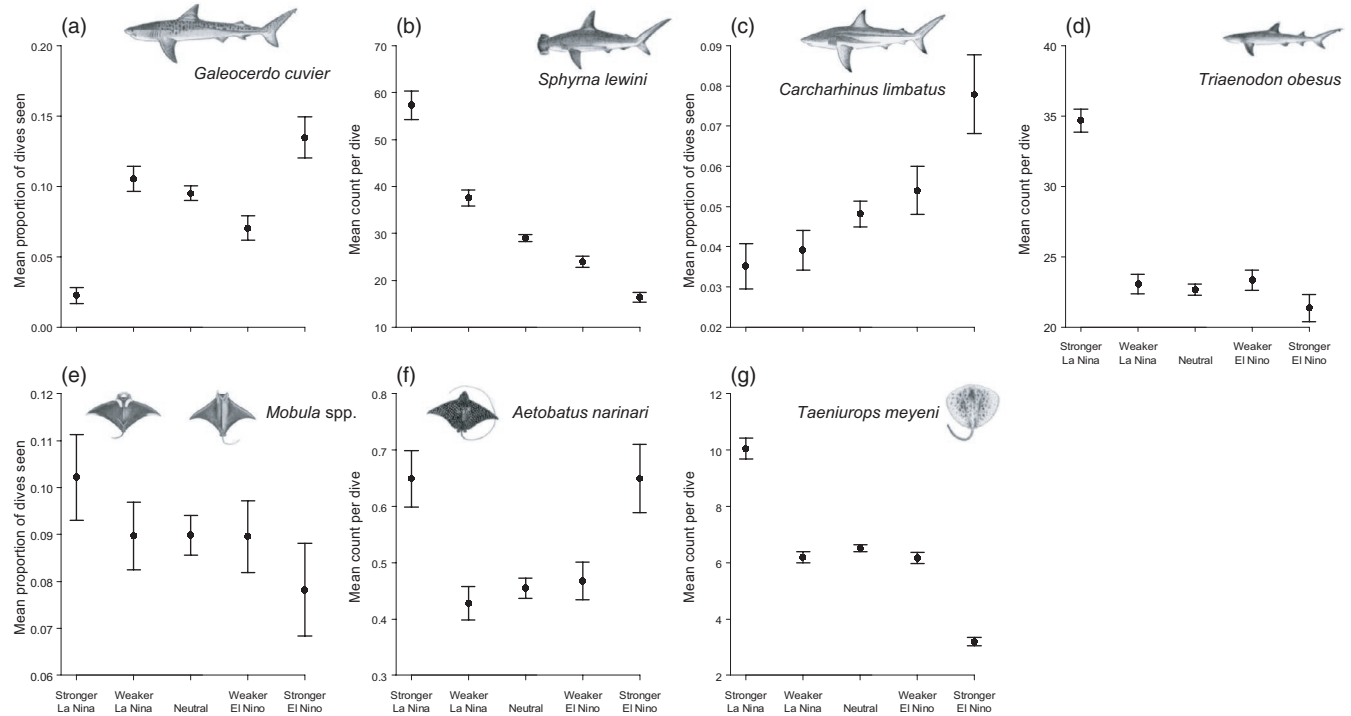
FIGURE 3 The mean count (or mean proportion) observed per dive of (a) tiger shark *Galeocerdo cuvier*, (b) scalloped hammerhead shark *Sphyrna lewini*, (c) blacktip shark *Carcharhinus limbatus*, (d) whitetip reef shark *Triaenodon obesus*, (e) *Mobula* spp., (f) spotted eagle ray *Aetobatus narinari* and (g) marbled ray *Taeniurops meyeni* observed when the ONI indicated a weaker ENSO event (>0.5 for El Niño, <−0.5 for La Niña), a moderate to strong ENSO event (>1 for El Niño, <−1 for La Niña), or neutral conditions (−0.5 < ONI < 0.5). Means were calculated using generalized linear models with either a negative binomial or binomial distribution. Drawings by M. Nikoo

(69.2%–166.3%) more likely during strong La Niña than during strong El Niño conditions.

The highly mobile *G. cuvier* also had a strong response to ONI (Figures 2 and 3a; Table S1), but showed a non-significant trend with SST in the opposite direction compared to other sharks. However, similar to *S. lewini*, the probability of observing *G. cuvier* declined by 25.1% (18.2%–31.7%) during weak, and 43.3% (32.5%–53.4%) during moderate, El Niño conditions. Despite increasing by 22.1% (12.1%–32.2%) during weak La Niña conditions, when compared to neutral conditions (Figure 3a), moderate La Niña conditions only increased predicted occurrence by 23.3% with the 95% confidence interval including zero (−1.2%–49.5%). Their predicted probability of occurrence was also higher, by 95.0% (12.4%–188.0%), when ONI was at −1.5 than at 1.5, but due to the cubic relationship fit to accommodate the high frequency of *G. cuvier* observations during the strong 2015/2016 El Niño (Figure 3a), predicted probability of occurrence was nearly the same, only 3.8% (−77.0%–100.1%) higher during the strongest El Niño conditions (ONI = 2) compared to similarly strong La Niña conditions (ONI = −2).

The remaining two sharks *C. limbatus* and *T. obesus* showed weaker responses to temperature changes. The probability of observing *C. limbatus* increased with SST, but not significantly (Figure 2; Table S1). Moreover, it shrank only by 5.7% (0.99%–10.4%) during weak La Niña conditions and grew by 6.0% (0.8%–11.4%) during weak El Niño conditions compared to when the ONI was neutral

(Figure 3c; Table S1). It was also 41.9% (0.81%–87.1%) higher during strong El Niño compared to strong La Niña conditions. The sedentary *T. obesus* had the weakest response to temperature of any shark (Figures 2 and 3d): its predicted counts declined significantly with rising SST and ONI (Table S1), but by 4.3% (3.1%–5.4%) with a 1℃ rise in SST and by 1.6% (0.2%–2.9%) with an increase from neutral to moderate El Niño conditions. Counts of *T. obesus* declined by 18.6% (14.1%–23.1%) with an increase from 25 to 30℃. Similarly, *T. obesus* predicted counts were 4.8% (0.5%–9.2%) higher during a strong La Niña compared to a strong El Niño, and did not change greatly under weaker ENSO conditions (Figure 3d).

All rays were also significantly affected by SST, but ONI only significantly affected the counts of *T. meyeni* and *A. narinari* (Figures 2 and 3e–g; Table S1). The probability of spotting *Mobula* spp. decreased by 11.2% (6.0%–16.3%) as SST increased by 1℃, and by 42.5% (26.4%–57.4%) as SST increased from 25 to 30℃. The predicted counts of *T. meyeni* also declined, by 4.8% (3.2%–6.5%) and 20.7% (14.1%–27.0%) over the same respective ranges. The ONI also affected *T. meyeni*, mostly due to a strong effect of moderate to strong ENSO events on their relative abundance (Figure 3g): when conditions shift from neutral to a moderate La Niña or El Niño, predicted counts of *T. meyeni* increased by 16.7%% (14.1%–19.3%) or declined by 14.3%% (12.4%–16.2%), respectively. Similarly, a predicted 73.6% (61.2%–86.1%) increase would occur switching from a strong El Niño to strong La Niña conditions. In contrast, the

predicted counts of *A. narinari* grew with increasing SST, by 6.5% (1.7%–11.2%) with a 1°C increase and 34.1% (6.7%–62.6%) from 25 to 30°C. The counts of *A. narinari* had a significant quadratic relationship to ONI driven by a positive effect of moderate to strong ENSO events, regardless of whether they were La Niña or El Niño conditions (Figures 2 and 3f); predicted counts were only 1.6% (−1.5%–4.6%) and 4.4% (1.6%–7.2%) higher during weak La Niña and weak El Niño conditions, respectively, but were also 9.3% (1.6%–17.2%) and 15.5% (8.9%–22.3%) higher during each of moderate La Niña and El Niño conditions. *Aetobatus narinari* counts did not differ between strong La Niña and strong El Niño conditions (Figure 3f).

3.2 | Population trends

Declines continued for the five species that had been declining in the analysis of data up to 2013 by White et al. (2015; Figure 4; Table S3). However, the magnitudes of each decline differ in our new analysis: declines of *T. obesus* and *Mobula* spp. eased such that we now estimate there has been only a 59% and 68% decline for each over the entire time period, respectively. In contrast, the declines of *S. lewini*,

T. meyeni and *A. narinari* became increasingly severe: from declines of 45%, 73% and 34% in White et al. (2015), respectively, to declines of 75%, 82% and 77% for these three species over the 27-year period (Table S3). Increases observed by White et al. (2015) for both *C. limbatus* and *G. cuvier* have since reversed such that in recent years both species have been declining (Figure 4a,c; Table S3). However, across the entire 27-year period, both species still showed an overall increase.

4 | DISCUSSION

Overall, as we predicted, both SST and the ENSO cycle of marine heatwaves and cooling had substantial impacts on elasmobranch relative abundance at Cocos Island (Figures 2–4). However, there was substantial variation between species. For four of the seven species, the relative abundance of the examined elasmobranchs declined with rising SST and during marine heatwaves, as expected given that tropical ectotherms live near their upper thermal limits (Bernal et al., 2012; Rummer et al., 2014) and respond rapidly to even a few degrees of warming (Magel et al., 2020).
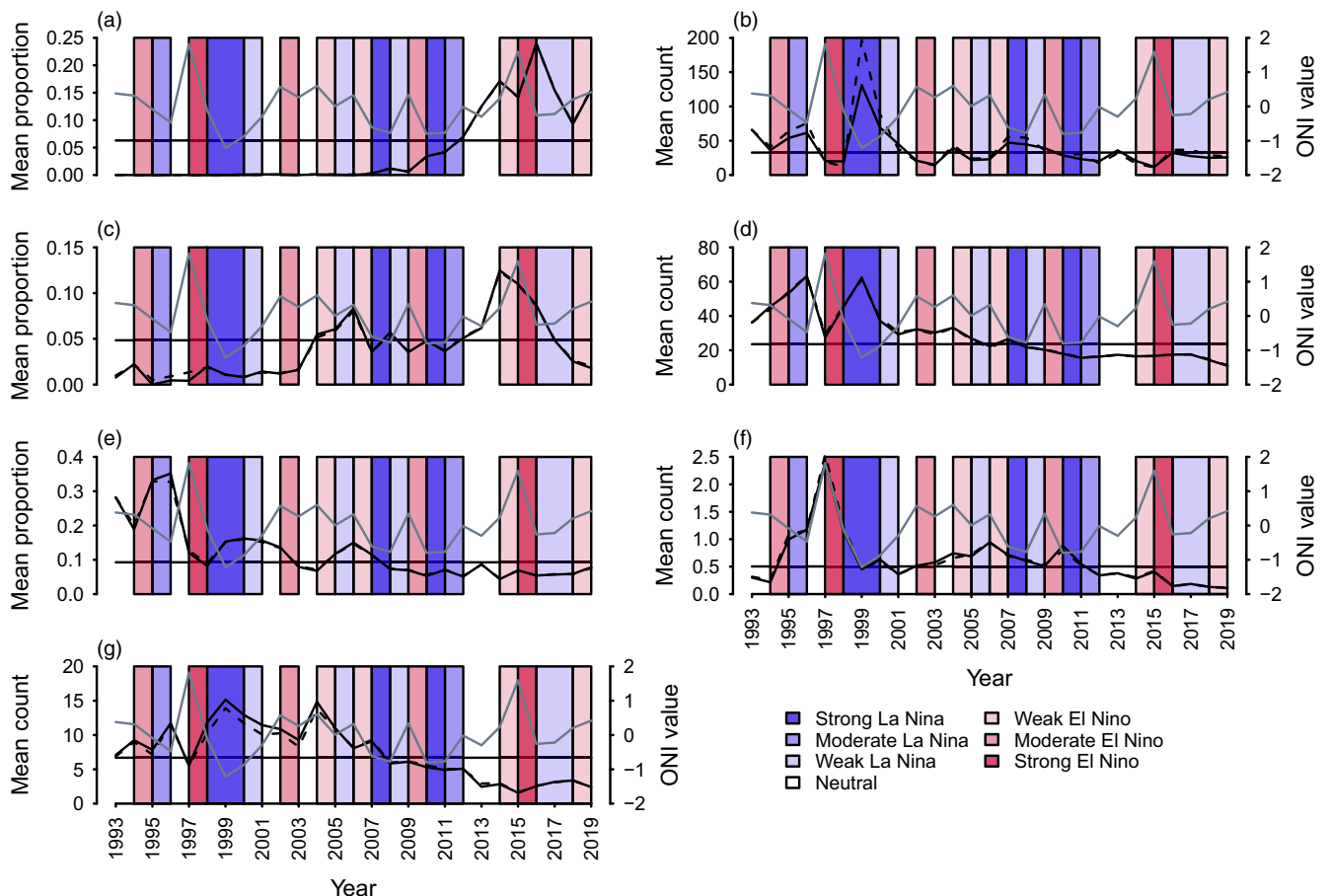

FIGURE 4 The mean (solid black line) count or frequency of occurrence, mean (dotted black line) predicted value from a GLMM and mean ONI value (solid grey line) by year for each species. (a) Tiger shark *Galeocerdo cuvier*, (b) scalloped hammerhead shark *Sphyrna lewini*, (c) blacktip shark *Carcharhinus limbatus*, (d) whitetip reef shark *Triaenodon obesus*, (e) *Mobula* spp., (f) spotted eagle rays *Aetobatus narinari* and (g) marble rays *Taeniurops meyeni*

Contrasting with our original predictions, the relative abundance of *G. cuvier* and *A. narinari* increased at higher temperatures, although only the latter was significant. *Carcharhinus limbatus* showed no relationship to SST at all and was the only species to respond negatively to La Niña conditions, reflecting the variation in thermal tolerance and ecological requirements amongst elasmobranch species. Cocos Island's coral cover was little affected by the recent 2015–2016 El Niño (Alvarado et al., 2020), suggesting that changes in habitat quality were not responsible for these effects. Because we were also able to isolate SST and El Niño effects from other longer-term trends (e.g. fishing) by incorporating Julian day and year as covariates in the model, we expect that the observed changes reflect direct responses to temperature. However, since El Niño heatwaves also reduce primary and secondary productivity in the Eastern Tropical Pacific, local declines in abundance could be associated with shifting prey distributions (Lavín et al., 2006; Pennington et al., 2006; see Section 4.2 for further discussion of how these findings might interact with fisheries exploitation in the area).

4.1 | Interspecific differences

The magnitude of responses to temperature changes varied across species, with larger, more mobile *S. lewini* and *Mobula* spp. showing the strongest responses to SST. The large *G. cuvier* also responded strongly to SST, but with wide uncertainty reflecting its rarity in the time series. The species-specific effects of the ENSO were less clearly delineated, but differences associated with mobility still occurred, especially between the mobile *G. cuvier* and *S. lewini* and the less mobile *T. obesus*. Interspecific variation in responses may reflect differences in body size and mobility that could influence physiological tolerance to temperature changes, energetic requirements and the ability for behavioural thermoregulation and migration (Bernal et al., 2012; Lea et al., 2018).

The three most mobile species—*S. lewini*, *G. cuvier* and the *Mobula* rays—which had the strongest response to SST are all large, pelagic and obligate ram-ventilators that occupy large home ranges and can migrate 100s to 1000s of kilometres in a few months (Couturier et al., 2012; Ferreira et al., 2015; Hearn et al., 2014; Ketchum, Hearn, Klimley, Peñaherrera, et al., 2014). *Sphyrna lewini* and *G. cuvier* are also active apex predators with high metabolic rates: *S. lewini* has one of the highest metabolic rates among elasmobranchs, higher than even some endothermic sharks (Lowe, 2001, 2002). *Galeocerdo cuvier* closely tracks changes in thermal habitat to tightly control its body temperature and optimize swimming performance (Payne et al., 2018), and thus the insignificance of its increase with SST reflects wide confidence intervals stemming from its rarity at the beginning of the time series. Cranial retia in *Mobula* rays suggest these species also maintain high metabolic rates that could increase their sensitivity to high temperatures (Alexander, 1996). For these species, the observed changes in response to both gradual temperature change

and marine heatwaves likely reflect distributional changes, both horizontally and vertically, to track spatial changes in temperature and prey availability (Ketchum, Hearn, Klimley, Espinoza, et al., 2014; Payne et al., 2018). For instance, both *S. lewini* and *G. cuvier* use depth to thermoregulate and make long-distance movements associated with seasonality and temperature changes (Ketchum, Hearn, Klimley, Espinoza, et al., 2014; Ketchum, Hearn, Klimley, Peñaherrera, et al., 2014; Payne et al., 2018). The appearance of *S. lewini* off California during the 1997–1998 El Niño suggests some latitudinal shifts occur, at least for this species (Lea & Rosenblatt, 2000).

The high energetic requirements of *S. lewini* and *G. cuvier* may also explain why counts of both species generally increased during La Niña conditions—over twofold for *S. lewini* during strong La Niña events—as they might have been responding to shifting prey distributions in addition to changes in SST (Duncan, 2006; Lavín et al., 2006; Lea et al., 2018). This could explain the contrasting response of *G. cuvier* to ONI compared to SST. *Galeocerdo cuvier* exhibited a cubic relationship with ONI, with observations most likely during the strongest El Niño events and least likely during the strongest La Niña events (Figure 3a). However, since *G. cuvier* occurrence sharply increased during the time series, it was only at the island for the strong La Niña of 2009–2010, while still rare, and the strong El Niño of 2015–2016, at the peak of its interannual trend (Figure 4). Outside of these two strong events, *G. cuvier* occurrence decreased linearly with rising ONI. Thus, the cubic relationship could represent overfitting to the extreme events in these years, with the effect of strong ENSO events still confounded with its positive yearly trend. More strong ENSO events need to be observed to solidly probe *G. cuvier's* response to ONI at the island.

Contrary to predictions, the occurrence of *Mobula* rays changed little during ENSO events at Cocos, although the El Niño is known to alter the distribution of their zooplankton and larval fish prey (Lavín et al., 2006). Despite being pelagic and mobile in the water column, *Mobula* rays, even the large *M. birostris*, may be more resident and not as migratory as often as expected (Stewart et al., 2016). Ultimately, the absence of *Mobula* aggregations at Cocos suggests that the lack of an ENSO response may stem from their rarity and a lack of importance of Cocos Island, at least their foraging ecology.

In contrast to the larger, more pelagic species, *T. obesus* is a small and inactive shark that spends approximately 30% of its time resting while ventilating through buccal pumping (Barnett et al., 2012; Whitney et al., 2007). These traits would lower its metabolic rate, while increasing its metabolic cost of activity, limiting both the ability and need for this species to shift habitats in response to thermal changes (Whitney et al., 2007, 2016). On other Pacific reefs, *T. obesus* abundance also does not vary greatly with temperature (Nadon et al., 2012), and although long-range dispersal does happen on occasion, *T. obesus* spends most of its life resident within a few kilometres of specific aggregation sites (Barnett et al., 2012).

This study represents the first examination of temperature effects on the benthic ray *T. meyeni* in the wild. This species had a weak

response to SST compared to *Mobula* rays, but a greater response than the more intermediate ones of *A. narinari* or *C. limbatus*, despite the higher mobility of these species (Figure 2). *Taeniurops meyeni's* stronger response to SST than *T. obesus* likely reflects the genus' narrow thermal niche and limited ability to acclimatize (Dabruzzi et al., 2013). Surprisingly, this ray's abundance also changed sharply during stronger ENSO events, with a slightly weaker response than the highly mobile *G. cuvier* and *S. lewini* (Figures 2–3). Its strong negative response to the ENSO is puzzling, and we can only speculate that perhaps it is tracking long-term cycles in temperature during the ENSO.

Contrasting with most of the other elasmobranchs we examined, *C. limbatus* and *A. narinari*, both showed increases with SST and El Niño conditions. These two species prefer high temperatures (Bassos-Hull et al., 2014; Lear et al., 2019), and are generally more resident species than the larger sharks and rays, with smaller home ranges and movements typically restrained to local reefs or sandflats (Ajemian & Powers, 2014; Yates et al., 2016). Thus, both species could be more tolerant of temperature extremes (Lear et al., 2019), and in fact, the positive effect of SST on *C. limbatus* occurrence was weak at Cocos. *Carcharhinus limbatus* sometimes spends time above its thermal optimum, likely to avoid predators or take advantage of foraging opportunities (Lear et al., 2019). Small myliobatid rays also use warm waters to increase metabolic rates while foraging (Ajemian & Powers, 2014; Matern et al., 2000), and *A. narinari* may be doing the same at Cocos.

The increase in relative abundance of both *C. limbatus* and *A. narinari* during El Niño events could reflect these species' temperature preferences, as well as avoidance of predation and competition from large sharks (Bond et al., 2019). The quadratic response of *A. narinari* to the ENSO could reflect a combination of it avoiding predation when large sharks, such as *S. lewini*, are scarce during the El Niño, and shifts in prey availability during the La Niña. Research on *A. narinari* in the Pacific is, however, lacking so these explanations are uncertain. Research is also scarce for *C. limbatus*, but since it is not as common at Cocos as other elasmobranchs, perhaps its increase during El Niño events represents a latitudinal shift from hotspots elsewhere in the Pacific as it tracks preferred temperatures or reduced competition from the larger sharks. More research is needed on the thermal preference of both species, particularly adult *C. limbatus* in oceanic habitat, and on changes to fish and invertebrate communities at Cocos during ENSO events, to draw more definite conclusions on how temperature and the ENSO affect the physiology and migration of these two species.

The occurrence of *G. cuvier* at Cocos also increased with rising SST, but with large uncertainty seen in 95% confidence intervals including zero. The optimal temperature of *G. cuvier* is over 30°C in the Gulf of Mexico (Lear et al., 2019), reflecting the response at Cocos, but does vary by location, being closer to 22°C in Hawaii (Payne et al., 2018), possibly through acclimatization or adaptation. Thus, *G. cuvier* thermal tolerance seems adaptable and broad on a global level (Ferreira et al., 2015), possibly related to its large size (Nakamura et al., 2020), and we saw indications of that broad tolerance at Cocos.

4.2 | Conservation implications

Although the trends associated with temperature and marine heatwaves likely reflect primarily distributional change rather than overall population declines, the decadal declines continued for most species, suggesting impacts of ongoing fisheries exploitation (Figure 4). Permanent distributional changes due to climate change may also have contributed to the decline, especially by increasing exposure to fisheries (Bruno et al., 2018; Maxwell et al., 2020). In addition, the previously observed increases of *C. limbatus* and *G. cuvier* have since halted and appear to have declined since 2015 (Figure 4), although continued monitoring is required to assess whether these declines are real or instead represent natural variability or population movement. Ongoing fisheries exploitation likely affects the entire elasmobranch community at Cocos, especially the larger and more pelagic *S. lewini*, *G. cuvier* and *C. limbatus*, which are more likely to be caught in the pelagic longlines dominating the region's fishing (Espinoza et al., 2018; Friedlander et al., 2012; González-Andrés et al., 2020). However, any effects from fisheries exploitation will likely not be evident in abundance datasets until years later. Within the waters of Cocos Island, González-Andrés et al. (2020) used park ranger log books to show that illegal fishing activity was correlated with yellow fin tuna *Thunnus albacares* and silky shark *Carcharhinus falciformis* abundance, but was not correlated with any species from our study. Dapp et al. (2013) examined the catch rates of marine megafauna for the Costa Rican longline fishery in general, including near Cocos Island. Of the species found in our study, *S. lewini*, *Mobula* spp. and *A. narinari* were caught at the highest rates. Smaller and less mobile species, such as *T. obesus* and *T. meyeni*, were not caught in these longlines (Dapp et al., 2013).

The gradual rise in mean and minimum SST during the time series may have contributed to the declines observed by forcing distributional shifts or reducing the fitness of the less mobile species. For instance, *T. obesus* exhibited large declines despite its lower mobility and lower catchability on longlines, and so the small negative effects of SST may have impacted its population fitness. However, the sharp declines in *A. narinari* relative abundance and its positive relationship to SST—being most abundant above 30°C—suggest fishing could be impacting their populations despite a generally high residency and site fidelity (Ajemian & Powers, 2014). We hypothesize that climate change and fisheries exploitation may be interacting to affect long-term trends. Climate change may affect species distributions, which would, in turn, affect the catch rates of certain species by pushing them beyond the boundaries of the MPA more frequently (Bruno et al., 2018; Maxwell et al., 2020; Pinsky et al., 2020). Ultimately, more fisheries data, combined with species movement information, from across the Eastern Tropical Pacific are needed to assess the extent to which these long-term trends reflect distributional shifts versus real population declines, and how much climate change will influence fisheries exploitation (Niella et al., 2020). Combined, these effects may alter the effectiveness of the Cocos Island MPA overall, especially for more mobile species (Bruno et al., 2018; Maxwell et al., 2020).

Regardless, these varied environmental effects on the elasmobranchs at Cocos Island suggest that climate change—through gradual rises in SST and more intense and frequent marine heatwaves like ENSO events—will have consequences for chondrichthyan ecology and conservation. The Cocos MPA is an important landmark for sharks navigating from the islands of the Eastern Tropical Pacific to the coasts of Central and South American during seasonal migrations (Ketchum, Hearn, Klimley, Peñaherrera, et al., 2014; Nalesso et al., 2019). Our results suggest climate-induced changes in temperature and productivity could alter these migration patterns and the connectivity these elasmobranchs provide to the ecosystems of the eastern Pacific. Although connectivity with other ecosystems could also be enhanced as range expansions and distributional shifts occur in response to expanding thermal habitat and changing currents removing barriers to dispersal (Niella et al., 2020). It has, for example, been suggested that El Niño events are the likely cause of recent range expansions of even the less mobile *T. obesus* into Rapa Nui in Chile (Morales et al., 2019). In our own time series, *G. cuvier* was only regularly observed after the La Niña events of 2005/2006, suggesting the ENSO may already be altering the predation ecology of Cocos.

4.3 | Citizen science implications

If shifting distributions and migration patterns are responsible for the effects we observed, climate change and ENSO intensification will have consequences for both dive tourism and citizen science at Cocos, and likely elsewhere, where large migratory sharks are popular. Schools of *S. lewini*, an important draw for the dive industry at Cocos (Friedlander et al., 2012), declined in frequency with only a few degree changes in SST as well as during strong El Niño events. Such changes in the location of 'hotspots' of high abundance also threaten to mask real trends with distributional shifts if the same sites are continuously dived (Fournier et al., 2019), thus reducing the reliability of dive tourism at Cocos for monitoring of real population trends. Considering temperature and indices of marine heatwaves explicitly in modelling helps reduce uncertainty, but we cannot statistically account for climate-induced long-term shifts in effort, especially over large spatial scales.

5 | CONCLUSIONS

Several elasmobranch species responded strongly to both gradual temperature changes and acute temperature anomalies, likely due to metabolic constraints and effects on prey availability, with many of these species declining during warmer temperatures and marine heatwaves. Such change occurred with only a few degrees rise in temperature. However, we have shown the response of elasmobranchs to climate change will be complex and varied, underscoring the need to study the thermal physiology of all these species. The energetic requirements of more elasmobranch species, and the effects of temperature on their populations, need additional research attention to assess just how climate change will affect elasmobranch communities. As both SST and ENSO events are predicted to intensify during the coming century, elasmobranch communities will fluctuate, as local abundances change in accordance to species-specific thermal tolerance and capacity to move. We also observed ongoing declines in the relative abundance of many species of elasmobranch at Cocos Island. These declines, likely fisheries-induced, have the potential to interact with future climate change impacts to drastically alter the elasmobranch community across the Eastern Tropical Pacific. Mobile MPAs may work to mitigate climate change impacts on mobile species on the high seas (Maxwell et al., 2020), but the critical seamount habitat at Cocos will not shift with rising temperatures. For these species, there are few substitutes for reducing global emissions and supporting enforcement of the current MPA and stronger fishing regulations outside it. As climate change strengthens, it will interact with exploitation, underscoring the need to understand the links between thermal sensitivity and species traits to predict future changes to the ecology of diverse marine communities.

CONFLICT OF INTEREST

All authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

G.J.O., E.R.W. and J.K.B. conceived the idea; G.J.O. and E.R.W. collated and cleaned the data; G.J.O. designed the study and analysed the data; G.J.O. and J.K.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are not the property of the authors and cannot be shared, but r-scripts for all analyses and figures are available online (https://doi.org/10.5281/zenodo.4977678 (Osgood et al., 2021); GitHub: github.com/baumlab/Osgood_etal_2021_JAE).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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