



Shifting elasmobranch community assemblage at Cocos Island—an isolated marine protected area

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Abstract: *Fishing pressure has increased the extinction risk of many elasmobranch (shark and ray) species. Although many countries have established no-take marine reserves, a paucity of monitoring data means it is still unclear if reserves are effectively protecting these species. We examined data collected by a small group of divers over the past 21 years at one of the world's oldest marine protected areas (MPAs), Cocos Island National Park, Costa Rica. We used mixed effects models to determine trends in relative abundance, or probability of occurrence, of 12 monitored elasmobranch species while accounting for variation among observers and from abiotic factors. Eight of 12 species declined significantly over the past 2 decades. We documented decreases in relative abundance for 6 species, including the iconic scalloped hammerhead shark (*Sphyrna lewini*) (−45%), whitetip reef shark (*Triaenodon obesus*) (−77%), mobula ray (*Mobula* spp.) (−78%), and manta ray (*Manta birostris*) (−89%), and decreases in the probability of occurrence for 2 other species. Several of these species have small home ranges and should be better protected by an MPA, which underscores the notion that declines of marine megafauna will continue unabated in MPAs unless there is adequate enforcement effort to control fishing. In addition, probability of occurrence at Cocos Island of tiger (*Galeocerdo cuvier*), Galapagos (*Carcharhinus galapagensis*), blacktip (*Carcharhinus limbatus*), and whale (*Rhincodon typus*) sharks increased significantly. The effectiveness of MPAs cannot be evaluated by examining single species because population responses can vary depending on life history traits and vulnerability to fishing pressure.*

Keywords: citizen science, eastern tropical Pacific, fisheries, generalized linear mixed models, marine reserve, MPA, sharks, zero-inflated

Modificación del Ensamble de Comunidades de Elasmobranquios en la Isla de Cocos, un Área Marina Protegida Aislada

Resumen: *La presión de la pesca ha incrementado el riesgo de extinción de muchas especies de elasmobranquios (tiburones y rayas). Aunque muchos países han establecido áreas de no-pesca, una escasez de datos de monitoreo implica que todavía no está claro si estas reservas están protegiendo efectivamente a estas especies. Examinamos datos colectados por un pequeño grupo de buzos a lo largo de los últimos 21 años en una de las áreas marinas protegidas (AMP) más vieja del mundo: Parque Nacional Isla de Cocos, Costa Rica. Usamos modelos de efectos mixtos para determinar tendencias en la abundancia relativa, o probabilidad de caso, de doce especies monitoreadas de elasmobranquios compensando la variación entre observadores y de factores abióticos. Ocho de las doce especies declinaron significativamente a lo largo de las últimas dos décadas. Documentamos disminuciones en la abundancia relativa de seis especies, incluidos el tiburón martillo (*Sphyrna lewini*) (−45%), el tiburón de arrecife de punta blanca (*Triaenodon obesus*) (−77%), la manta (*Mobula* spp.) (−78%) y la mantarraya (*Manta birostris*) (−89%); así como disminuciones en la probabilidad de caso de otras dos especies. Muchas de estas especies tienen extensiones de hábitat pequeñas y deberían estar mejor protegidas por una AMP, lo que enfatiza la noción de que las declinaciones de megafauna marina continuarán sin cesar en las AMP a menos de que exista un*

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esfuerzo adecuado de control de pesca. Además de esto, la probabilidad de ocurrencia en la Isla de Cocos de de los tiburones tigre (Galeocerdo cuvier), de las Galápagos (Carcharhinus galapagensis), de punta negra (Carcharhinus limbatus) y ballena (Rhincodon typus) incrementó significativamente. La efectividad de las AMP no puede ser evaluada examinando a una sola especie porque las respuestas poblacionales pueden variar dependiendo de las características de la historia de vida y de la vulnerabilidad a la presión de la pesca.

Palabras Clave: AMP, cero inflación, ciencia ciudadana, modelos lineales mixtos generalizados, Pacífico oriental tropical, reserva marina, tiburones

Introduction

Conservation efforts directed at sharks and rays have increased substantially over the past decade with the recognition that fishing has greatly reduced the abundance of many of these species (Robbins et al. 2006; Dulvy et al. 2014a). Notwithstanding variation in life history characteristics, elasmobranchs tend to be large bodied and to mature late, resulting in lower population growth rates and greater vulnerability to overexploitation than teleost fishes (Hutchings et al. 2012). A consequence of coupling this high vulnerability with excessive fishing pressure is that many elasmobranch species are now considered at a heightened risk of extinction. Currently, 20% of shark and 16% of ray species are listed as threatened (critically endangered, endangered, or vulnerable) by the International Union for Conservation of Nature (IUCN) (Dulvy et al. 2014a). Still lacking, however, are sufficient data to assess the global threat status of many elasmobranch species, and as such, 46% of species on the IUCN Red List are classified as data deficient (Dulvy et al. 2014a). In addition, many elasmobranchs assessed globally lack regional assessments because of a paucity of data. This is true for many reef shark and ray species, especially those inhabiting remote islands or areas with little monitoring or management. Recent analyses suggest, however, that reef sharks have declined enormously in both the Caribbean (Ward-Paige et al. 2010) and the central-western Pacific Ocean (Robbins et al. 2006; Nadon et al. 2012). Lacking time series data, these studies applied space-for-time approaches, where the relative abundance of elasmobranchs was compared across areas differing in intensity of human impacts (Robbins et al. 2006; Stevenson et al. 2007; DeMartini et al. 2008; Nadon et al. 2012).

Given the challenges of controlling fishing pressure, marine protected areas (MPAs) are instead increasingly being used as a conservation measure for sharks (Knip et al. 2012), but to date there has been little evaluation of their efficacy at protecting these large mobile fishes. Comprehensive monitoring of elasmobranch populations relies on fisheries-dependent or research survey data; thus, estimating population trends is difficult in locations with few regulations, no formal data collection, or no fishing activity, including marine reserves (Graham et al. 2010). Insufficient planning or lack of resources for monitoring and enforcement (Claudet & Guidetti 2010) also

commonly creates situations where MPAs are merely paper parks, protected on paper but not in practice (Rife et al. 2013). Studies of the effectiveness of MPAs at conserving elasmobranchs tend to focus on species or life stages with limited ranges that can be protected in even small MPAs (Robbins et al. 2006; Knip et al. 2012).

As one of the world's oldest MPAs, Cocos Island National Park (Isla del Coco; N 05°31'08'', W 87°04'18''), a small (23.85 km²), uninhabited island 550 km from mainland Costa Rica in the eastern tropical Pacific (Fig. 1), presents an opportunity to evaluate the effectiveness of MPAs at conserving elasmobranchs. The waters surrounding Cocos Island provide exceptional habitat for marine organisms due to the island's isolation, associated reef and seamount complexes, and position at the confluence of several major oceanic currents (Garrison 2005). Sea surface temperatures at Cocos Island range from 24 to 30 °C and are affected every 4–9 years by El Niño Southern Oscillation (ENSO) events (Garrison 2005; Sibaja-Cordero 2008), which substantially influence the distribution and abundance of several marine species (Lea & Rosenblatt 2000).

Cocos Island's exceptional biodiversity led to it being designated as a national park in Costa Rica in 1978 (Alvarado et al. 2012). This protection was extended first in 1984, to include the marine environment, and again in 2001 to encompass 22.2 km around the island (Sibaja-Cordero 2008). Although Cocos Island has been protected for over 20 years, with a permanent ranger station in place since 1992, funding for monitoring and enforcement has been limited. Since 2003, however, in conjunction with the Costa Rican Coast Guard, the Mar-Viva Foundation, a regional nonprofit nongovernmental organization (NGO), has patrolled the island (Arias et al. 2014). However, illegal fishing of large elasmobranchs still occurs within the park's waters (Arias et al. 2014). More broadly, sharks and rays are heavily fished both legally and illegally as targets and bycatch throughout the eastern tropical Pacific (Clarke et al. 2013; Dapp et al. 2013). Still, Cocos Island is touted as an example of a successful MPA, and it is known by divers as one of the best locations in the world to view sharks and rays in large numbers (Friedlander et al. 2012; Edgar et al. 2014). What remains unclear, however, is if Cocos Island National Park represents a conservation success or merely a paper park (Rife et al. 2013).

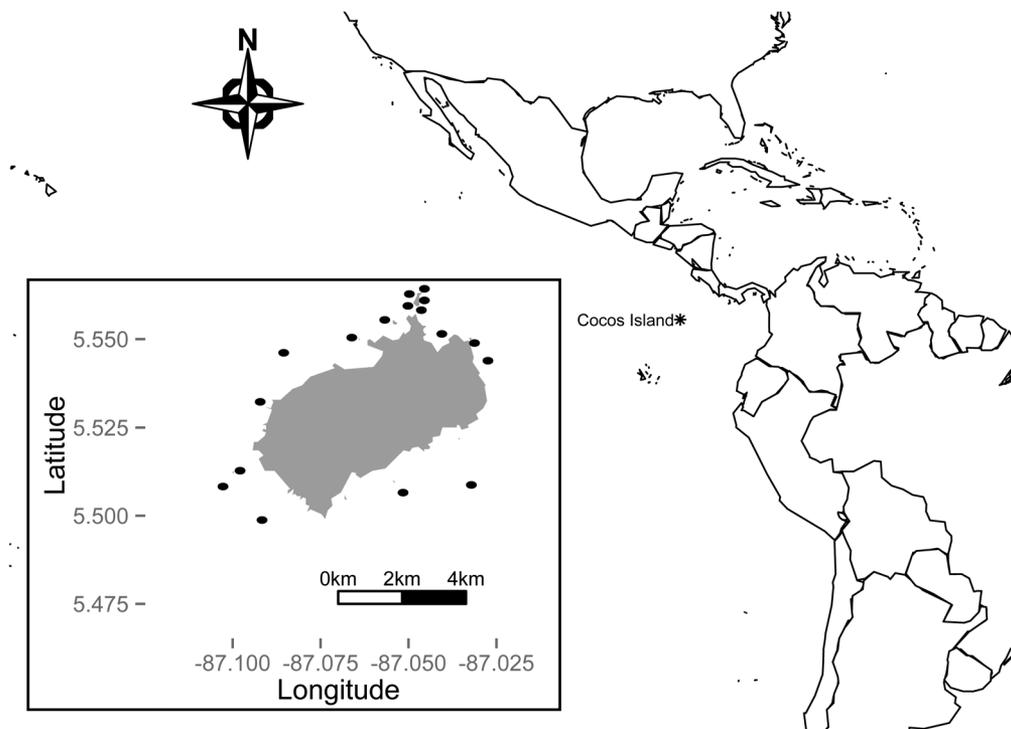


Figure 1. Map of eastern tropical Pacific with inset of Cocos Island, Costa Rica (circles, approximate dive site locations).

We examined standardized time series data of shark and ray observations at Cocos Island, collected systematically by divemasters from a single dive company, Undersea Hunter, on every dive they made between 1993 and 2013. Because there are no fisheries data or systematic research surveys for Cocos Island, these diver-collected data may be used to estimate trends in elasmobranch relative abundance and probability of occurrence. We expect these data to be of higher quality than many citizen science data sets because relatively few highly experienced divers recorded the data and the species studied were large and could be easily identified (Ward-Paige & Lotze 2011; Vianna et al. 2014).

To assess the effectiveness of the Cocos Island MPA, we modeled each of the 12 elasmobranch species monitored by Undersea Hunter with a suite of generalized linear mixed models (GLMMs). We classified the monitored elasmobranch species as pelagic sharks (scalloped hammerhead [*Sphyrna lewini*], tiger [*Galeocerdo cuvier*], and silky sharks [*Carcharhinus falciformis*]); reef-associated sharks (whitetip reef [*Trienodon obesus*], blacktip [*Carcharhinus limbatus*], Galapagos [*Carcharhinus galapagensis*], and silvertip sharks [*Carcharhinus albimarginatus*]); bottom-feeding rays (eagle [*Aetobatus narinari*] and marble rays [*Taeniura meyeni*]); and planktivores (whale sharks [*Rhincodon typus*], mobula [*Mobula* spp.], and manta rays [*Manta birostris*]) (Table 1). These species comprise the entire Cocos Island elasmobranch

community, have a taxonomic breadth spanning 4 orders and 6 families, and possess an array of life history traits (Table 1) (Cortés 2012). We hypothesized that pelagic sharks and planktivores have declined at Cocos Island over the past 2 decades because these species have large home ranges and undertake long migrations (Costa et al. 2012), exposing them to fishing pressure both within and outside of the Cocos Island reserve (Bessudo et al. 2011). In response to this pressure, we hypothesized that smaller sharks (whitetips) and bottom-feeding rays (eagle and marble rays), which are preyed on by the large pelagic sharks (Supporting Information), have increased as a result of mesopredator release (Myers et al. 2007). Finally, we hypothesized that reef-associated sharks (blacktip, Galapagos, and silvertip), which spend most of their lives within the Cocos Island MPA, have remained stable or increased.

Methods

Data

Divemasters with Undersea Hunter (<http://undersea-hunter.com/>), a privately owned and operated company, systematically recorded the elasmobranchs observed on each of 27,527 dives conducted between January 1993 and December 2013 ($n = 21$ years) at 17 sites around Cocos Island (Figs. 1 and 2). These data represent one of

Table 1. Elasmobranchs recorded by the Undersea Hunter Dive Company at Cocos Island, 1993–2013.^a

Group	Family	Scientific name	Common name	Global status	ETP status	Size at maturity (cm) ^b	Data type	Frequency of dives present	Max. count on a single dive
Pelagic sharks	Sphyrnidae	<i>Sphyrna lewini</i>	scalloped hammer-head	EN	EN	140–212	count	0.77	1000
	Carcharhinidae	<i>Galeocerdo cuvier</i>	tiger	NT	NE	226–350	binary	0.02	NA
Reef-associated sharks	Carcharhinidae	<i>Carcharhinus falciformis</i>	silky	NT	VU	187–230	binary	0.04	NA
	Carcharhinidae	<i>Triaenodon obesus</i>	whitetip reef	NT	NE	104–109	count	0.97	500
	Carcharhinidae	<i>C. limbatus</i>	blacktip	NT	NE	135–190	binary	0.04	NA
	Carcharhinidae	<i>C. galapagensis</i>	Galapagos	NT	NE	170–236	binary	0.09	NA
Bottom-feeding rays	Carcharhinidae	<i>C. albimarginatus</i>	silvertip	NT	NE	160–199	binary	0.03	NA
	Myliobatidae	<i>Aetobatus narinari</i>	eagle ray	NT	NE	NA	count	0.27	60
	Dasyatidae	<i>Taeniura meyeni</i>	marble ray	VU	NE	100–110	count	0.84	200
Planktivores	Rhincodontidae	<i>Rhincodon typus</i>	whale shark	VU	NE	600–800	binary	0.02	NA
	Mobulidae	<i>Mobula spp.</i>	mobula ray	NA	NA	NA	count	0.07	40
	Mobulidae	<i>Manta birostris</i>	manta ray	VU	NE	400	count	0.04	15

^aInternational Union for Conservation of Nature (2014) threat categories: ETP, eastern tropic Pacific; NE, not evaluated; NT, near threatened; VU, vulnerable; EN, endangered.

^bLength at maturity (a proxy for body size) for sharks (disc width for rays) from Compagno et al. (2005) and IUCN (2014).

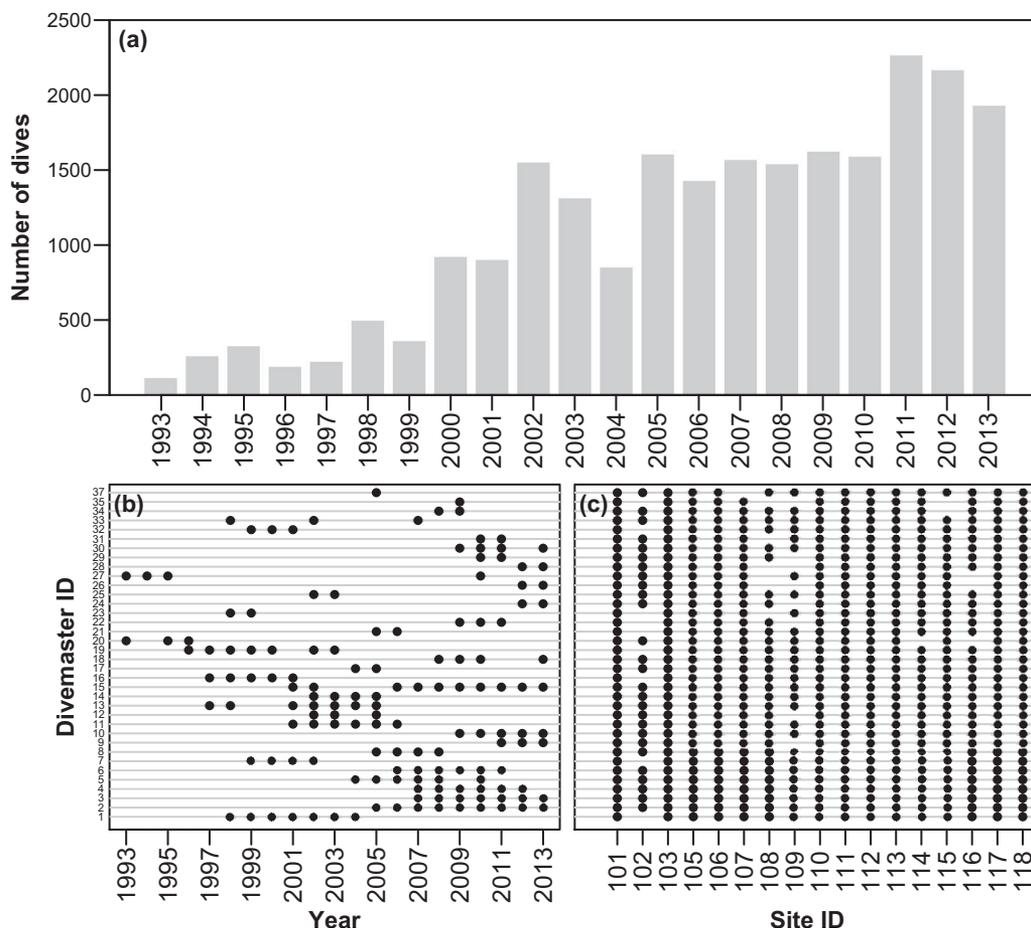


Figure 2. (a) Total number of dives at Cocos Island each year, (b) distribution of observations by individual divemasters over time (circles, particular divemaster recorded at least one dive in that year), and (c) across dive sites (circles, particular divemaster recorded at least one dive at that site).

the longest underwater visual censuses (UVC) for sharks and rays to date and are unique in the eastern tropical Pacific (Ward-Paige & Lotze 2011; Edgar et al. 2014). Although dives were not entirely standardized as in a scientific UVC (e.g., there was no defined field of view), the protocols were consistent throughout the study. Each dive averaged ~60 min and was led by an experienced professional divemaster. Dive depth ranged from 10 to 40 m depending on the site, but depth was consistent within sites. The dive sites encompassed the range of shallow-water environments and hydrographic conditions at Cocos Island. Upon completion of each dive, divers used a standardized data sheet to record the observed numbers of each of the 6 most common elasmobranch species and the presence or absence of 6 less common shark species (Table 1). The number of individuals was recorded when shark and ray numbers were low, and approximations were made when large groups (e.g., upwards of 1000 for scalloped hammerheads) were encountered. We acknowledge that recounting of individual elasmobranchs could have occurred during single

dives, especially when species were seen in large schools. This bias would, however, have been consistent throughout the survey period.

Divemasters also recorded a number of environmental variables (Table 2, Supporting Information). Current strength was measured on a subjective scale from 0 (none) to 3 (strong). Water temperature was recorded by divemasters with their personal dive computers, and because these were not standardized among divers there is likely some measurement error in this variable. Water visibility was estimated in meters by each divemaster. Visibility varied substantially and would have affected how many sharks or rays could be observed during each dive. We expect that any bias created by visibility should hold over the course of a given divemaster's observations. We supplemented these measurements with data from the multivariate ENSO Index (<http://www.esrl.noaa.gov/psd/enso/mei/table.html>).

We transcribed all the data from each of Undersea Hunter's 52 divemasters and compiled them into a single database. We then checked the database to identify and

Table 2. Explanatory variables included in models of shark and ray abundance and occurrence at Cocos Island National Park, 1993–2013.

<i>Variable</i>	<i>Range (min to max)</i>	<i>Description</i>	<i>Fixed (FE) or random effect (RE)</i>
Year	1993 to 2013	year of study	FE
Study day	1 to 7814	Julian day of study (used in seasonality terms, see Methods)	FE
El Niño index	−2.03 to 3.00	multivariate El Niño Southern Oscillation index (see Methods)	FE
Current	0 (none) to 3 (strong)	diver master estimation of current strength	FE
Temperature	13 to 33	surface temperature (°C)	FE
Visibility	2 to 61	water visibility (meters)	FE
Site	17 unique sites	identification number for each dive site	RE
Divemaster	36 unique divers	identification number for each divemaster	RE

correct transcription errors and applied a series of filters to it (Supporting Information). After filtering, 23,391 individual dives (85%) conducted by 36 divers remained for analysis. Marble rays were not recorded for 2013, so only 21,534 records were available for this species.

Modeling Elasmobranch Trends

We modeled each elasmobranch species using a GLMM framework, tailored to each species depending on data type (count or presence-absence) and probability distribution (Tables 1, Supporting Information). Scalloped hammerheads, whitetip reef sharks, and marble rays are common at Cocos Island (Table 1, Figs. 3a, b, and d). For these species, the variance in counts far exceeded the mean (Supporting Information), so we used a GLMM with a negative binomial error distribution to address overdispersion (Zuur et al. 2009). Count data for eagle rays, mobula rays, and manta rays were recorded, but because each of these species was rarely observed (see Supporting Information, Figs. 3c, e, and f), we used zero inflated mixed models with a negative binomial error distribution (Martin et al. 2005). We estimated the zero-inflation parameter for each species and held the parameter constant across dive sites and year. Only presence-absence data were available for the remaining 6 shark species (Table 1), so we used a GLMM with a binomial error distribution for them (Zuur et al. 2009). Mixed effects models were employed for each species, with random effects to account for the nonindependence of observations made by the same diver and at the same dive site (Supporting Information). In addition to explanatory variables recorded by divers or taken from online databases (Table 2), we also included sin and cosine functions of Julian date as explanatory variables to account for seasonality (Baum & Blanchard 2010). For each species, after accounting for environmental variables, diver, and site effects, we used the year coefficient to calculate the percent increase or decrease in relative abundance (for species with count data) or odds of occurrence (for species with only presence-absence data)

annually and over the 21-year study period. All models were implemented in the glmmADMB package (Skaug et al. 2014) in R (R Development Core Team 2013).

Model Evaluation, Selection, and Robustness

Following our tailored modeling approach, we used a unified approach for model diagnostics and model selection for each species. We examined the Pearson residuals plotted against model predictions and time (Supporting Information). We selected covariates for each species by first running all possible combinations of explanatory variables ($n = 64$; excluding interaction effects) in the MuMIn package (Barto 2013). We defined competitive models as those within 2 Akaike information criterion (AIC) of the best model (Supporting Information). If several models fell within 2 AIC of the best model, we used a model averaging approach (Zuur et al. 2009) to generate parameter estimates.

To test the robustness of our models and specifically the estimated year effect, we conducted 2 sensitivity analyses. First, we modeled each species as described above but used a subset of the data that included only the 5 most experienced divers. Second, we used a subset of data that included only the 5 most commonly visited sites. For both sensitivity analyses, results changed little from those obtained with the complete data set (Supporting Information).

Results

At least one shark or ray was seen on almost every dive (99% of $n = 23,391$ dives), with a total of 1,411,187 individuals recorded between 1993 and 2013 (Table 1, Supporting Information). Whitetip reef sharks were by far the most common elasmobranch observed at Cocos Island. They were observed on 97% of dives (average 25.6 [SD 25.8] per dive). Scalloped hammerheads and marble rays were also commonly seen (on 77% and 84% of dives, respectively; average 34.0 [SD 68.3]

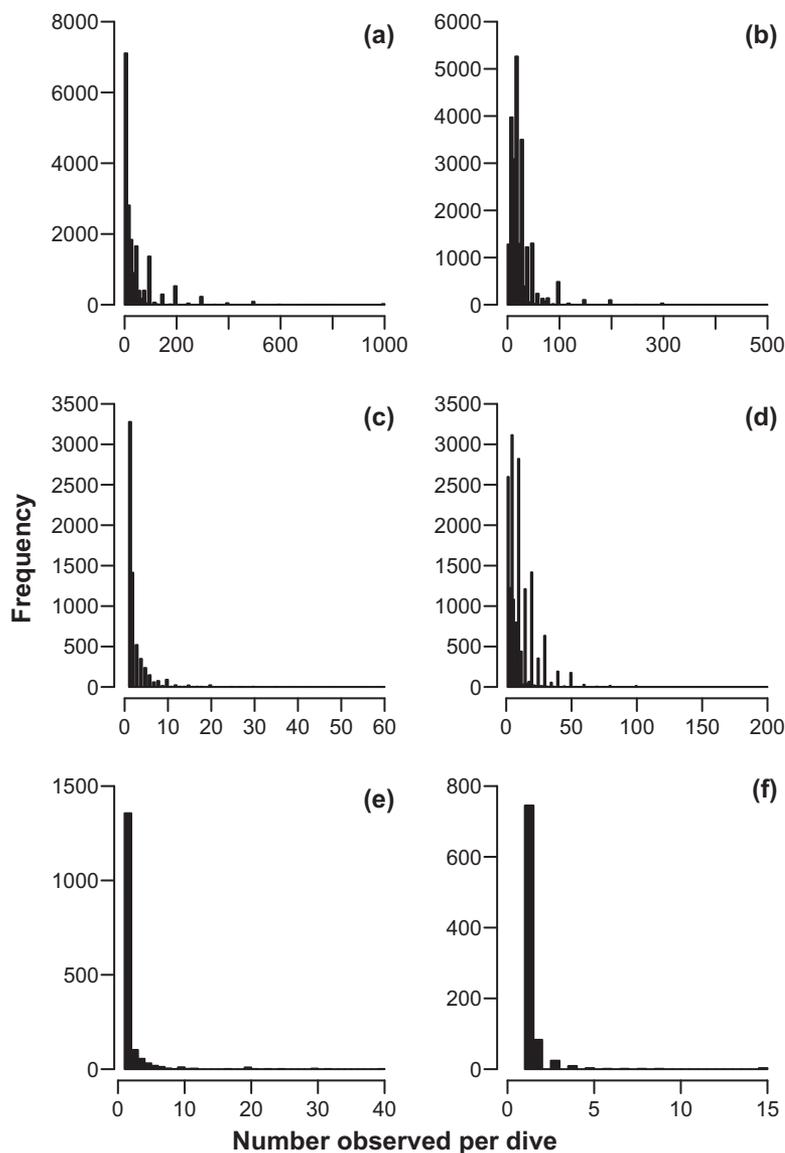


Figure 3. Frequency of the number of (a) scalloped hammerheads sharks, (b) whitetip reef sharks, (c) eagle rays, (d) marble rays, (e) mobula rays, and (f) manta rays recorded on each dive (zeros are excluded, but see Supporting Information for full frequency distribution).

and 8.5 [SD 9.8] individuals/dive, respectively). At least one of the 6 sharks species for which only presence or absence was noted was reported on 20% of dives.

Although the statistical significance of the explanatory variables varied across species, the temporal trend (as indicated by the year effect) was significant ($p < 0.001$) for each species (Table 3). Eight of 12 elasmobranch species declined significantly over the 21 years. Generally, relative abundance of each species was also highly influenced by ENSO activity, seasonality, and water temperature (Table 3). Although imperfect, residual analyses indicated that the assumptions underlying our modeling approach were justified (Supporting Information). In addition, by examining subsets of the data, we determined that the year estimates for each species were robust (Supporting Information). We retained diver identity and site

identity in every model as random effects to account for the nonindependence of observations within each group.

Pelagic Sharks

We estimated that the relative abundance of scalloped hammerhead sharks at Cocos Island has declined by 45% (95% CI 39%–50%) since 1993 (Table 3, Fig. 4a). However, the temporal trend was not a simple exponential decay; rather, there was a major increase in hammerhead shark observations in 1999–2000, the La Niña years that followed the major El Niño event of 1997–1998 (Fig. 4a). Rerunning the models without data from the El Niño years suggests a more modest decline, of 19% (95% CI 9%–28%), for scalloped hammerheads since 1999. Silky sharks are also estimated to have declined: the odds of

Table 3. Top model and model type for count or occurrence of each species of elasmobranch.

Group	Common name	Top model ^a	Model type ^b
Pelagic sharks	scalloped hammerhead	Year* + ElNiño* + Visibility* + Current* + Temp* + sinO* + cosO*	GLMM, count
	tiger	Year* + ElNiño + Visibility + Current + Temp + sinO + cosO	GLMM, binary
	silky	Year* + ElNiño + Visibility + Current* + Temp* + sinO* + cosO*	GLMM, binary
Reef-associated sharks	whitetip reef	Year* + ElNiño* + Visibility* + Current* + Temp* + sinO* + cosO*	GLMM, count
	blacktip	Year* + ElNiño + Visibility* + Current + Temp + sinO + cosO	GLMM, binary
	Galapagos	Year* + Visibility* + Current* + Temp + sinO* + cosO*	GLMM, binary
Bottom-feeding rays	silvertip	Year* + ElNiño + Visibility* + Current* + Temp + sinO + cosO	GLMM, binary
	eagle ray	Year* + ElNiño* + Visibility* + Current* + Temp* + sinO + cosO*	ZI GLMM, count
	marble ray	Year* + ElNiño* + Visibility* + Current* + Temp* + sinO + cosO*	GLMM, count
Planktivores	whale shark	Year* + ElNiño* + Visibility* + Current + Temp + sinO* + cosO*	GLMM, binary
	mobula ray	Year* + ElNiño + Visibility* + Current* + Temp* + sinO* + cosO*	ZI GLMM, count
	manta ray	Year* + ElNiño* + Visibility + Temp + sinO + cosO	ZI GLMM, count

^aAsterisk indicates statistical significance, $p < 0.001$.

^bAbbreviations: GLMM, generalized linear mixed model; ZI, zero-inflated. Each model also includes the random effects of site and divemaster.

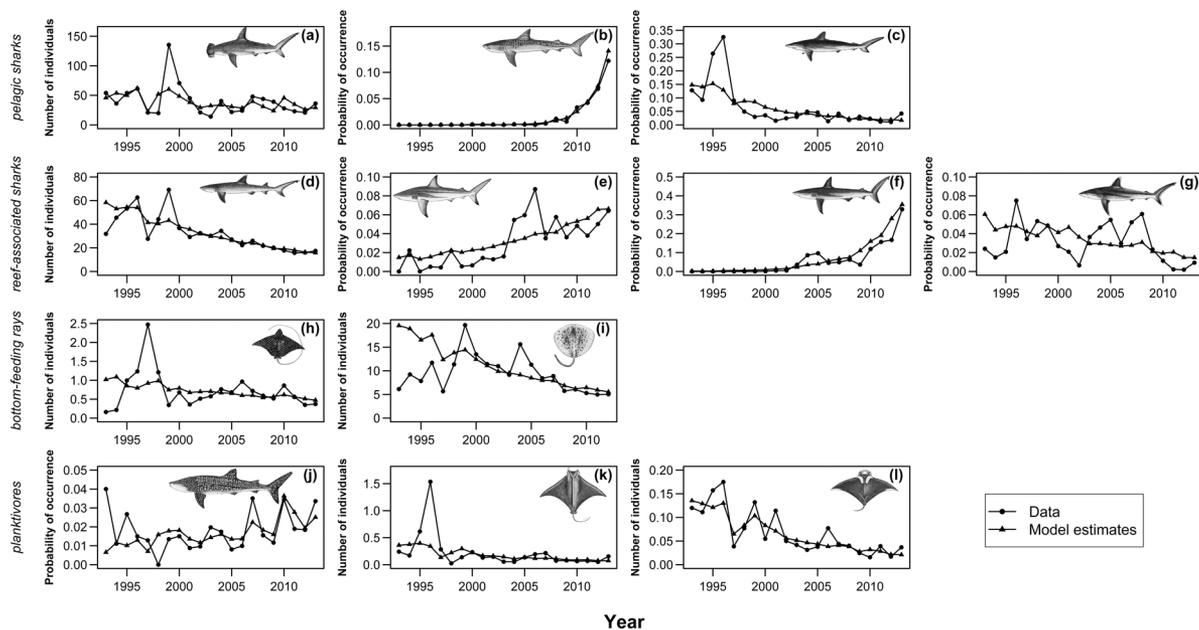


Figure 4. Observed data and model estimates of mean yearly number of individuals or mean probability of occurrence for (a) scalloped hammerhead sharks, (b) tiger sharks, (c) silky sharks, (d) whitetip reef sharks, (e) blacktip sharks, (f) Galapagos sharks, (g) silvertip sharks, (h) eagle rays, (i) marble rays, (j) whale sharks, (k) mobula rays, and (l) manta rays at Cocos Island, 1993–2013.

occurrence of silky sharks declined by 91% over the 21 years (95% CI 87%–93%) (Fig. 4c). Apart from the temporal trend, silky shark occurrence was also positively associated with stronger currents, lower water temperature, and the wet season (June–November). In contrast, the odds of occurrence of tiger sharks increased by 79%/year (95% CI 69%–89%) (Fig. 4b), driven largely by the fact that this species was not observed by divemasters at Cocos until 2000 and have since increased such that they are now typically observed on 12% of dives. Tiger shark occurrence was not strongly associated with any environmental variable in our models.

Reef-Associated Sharks

Both whitetip reef and silvertip sharks declined significantly over the study period. Whitetip reef shark counts decreased by 77% (95% CI 76%–78%) (Fig. 4d). Although whitetip reef sharks are year-long residents of Cocos Island, their relative abundance showed seasonal trends. More whitetips were observed in the wet season when there was more precipitation and sea surface temperatures were relatively low. Fewer whitetips were observed during El Niño events. The odds of occurrence for silvertips declined by 87% over the study period (95% CI 81%–91%) (Fig. 4g). Silvertip sharks were more

commonly observed at lower current strengths and when water visibility was poor. The sharpest declines in silver-tip occurrence came after 2007.

In contrast, the odds of occurrence for either Galapagos or blacktip sharks increased over time. The odds of Galapagos occurrence increased by 33%/year (95% CI 30%–34%) (Fig. 4f). Galapagos sharks were not observed at Cocos Island before 2000, and since 2008 the probability of Galapagos occurrence increased greatly (Fig. 4f). In general, Galapagos shark presence increased with increasing current strength, water visibility, and during the wet season. Blacktip sharks were present at Cocos at the beginning of the survey and exhibited a modest increase in their odds of occurrence of 9%/year (95% CI 8%–10%) (Fig. 4e). Blacktip occurrence increased with increasing water visibility, but it was not correlated with other variables we examined.

Bottom-Feeding Rays

We estimated that both species of bottom feeding rays declined at Cocos Island over the past 2 decades. Marble ray relative abundance decreased by an estimated 73% (95% CI 71%–75%) from 1993 to 2012 (Fig. 4i). Marble ray relative abundance decreased with increasing El Niño activity and water temperature, but it was positively associated with stronger currents, greater visibility, and the wet season. Eagle ray relative abundance also decreased by an estimated 34% (95% CI 23%–43%), but as with scalloped hammerheads, the individual year estimates did not match the overall declining trend well. Specifically, between 1995 and 1997, the number of eagle rays observed increased (Fig. 4h). These increases may have been driven by ENSO activity, which was significant for this species. In addition, more eagle rays were observed when current strength, water visibility, and water temperature were high.

Planktivores

Whale sharks have been observed each year at Cocos Island, typically between May and August. The odds of occurrence for whale sharks has increased by 4.5%/year (95% CI 3.3%–5.7%) (Fig. 4j). Whale sharks were less commonly seen in years of high El Niño activity and more commonly seen during the wet season. In addition, peaks in whale shark presence occurred every 3 years (Fig. 4j).

Mobula and manta rays were observed only occasionally at Cocos Island. Mobula ray relative abundance decreased by 78% (95% CI 72%–84%) (Fig. 4k). Increased relative abundance of mobula rays was related to lower El Niño activity and water temperature. Further, more mobula rays were seen on dives with strong currents and good water visibility. Manta ray relative abundance declined a similar amount, 89% (95% CI 85%–92%), over 21

years (Fig. 4l). High manta ray abundance was correlated with lower El Niño activity.

Discussion

Overall, we estimated that 8 of 12 elasmobranch species observed at Cocos Island declined significantly from 1993 to 2013. Six of these were declines in relative abundance, while the remaining 2 were declines in probability of occurrence. The 4 remaining species increased in the odds of their presence and were among the larger-bodied sharks at Cocos Island. Large citizen-science collected data sets require careful scrutiny to ensure quality and consistency among observers. Results based on the effects of divemaster-recorded environmental variables should be interpreted cautiously because these variables were not always standardized, as would be the case in a scientific survey. However, our analysis of this data set showed that individual divemasters had little influence on the number of sharks observed, and our parameter estimates for time trends were robust when using only a subset of the divemasters (Supporting Information). These results are in accordance with previous research indicating the effectiveness of using diver-collected data to assess trends in marine megafauna (Ward-Paige & Lotze 2011; Vianna et al. 2014).

We hypothesized that large-bodied wide-ranging pelagic sharks and planktivores would experience declines, primarily as a result of overfishing. The temporal trends for 4 of the 6 species within this category, including the iconic scalloped hammerhead, were in accordance with this hypothesis. The scalloped hammerhead is considered endangered within the eastern tropical Pacific, where it is caught as bycatch in at least Mexico, Costa Rica, and Ecuador (Baum et al. 2007; Kyne et al. 2012). Scalloped hammerhead sharks are known to move among the major offshore islands in the region: Cocos, Galapagos, and Malpelo (Bessudo et al. 2011). Although each of these islands is designated as an MPA, scalloped hammerheads are still caught both illegally within these protected areas and legally outside them (Kyne et al. 2012). Thus, substantial declines in this species are not surprising. In addition to water temperature and seasonality (Ketchum et al. 2014), our models also revealed the importance of El Niño activity in driving the relative abundance of scalloped hammerheads at Cocos Island. During El Niños, scalloped hammerheads are thought to shift their distribution, either into deeper waters (Bessudo et al. 2011) or away from the equator (Lea & Rosenblatt 2000).

Silky shark, the other large pelagic shark that declined significantly, is the most commonly caught shark species in the eastern Pacific's tuna purse seine fisheries (Watson et al. 2009). Although silky sharks are listed as near threatened globally, they are considered

vulnerable in the eastern tropical Pacific because of directed fishing for their fins and bycatch (Watson et al. 2009; IUCN 2014). From 1994 to 2004, capture rates of silky sharks as bycatch in purse seine fisheries in this region are estimated to have fallen by 50% (Minami et al. 2007). Although we examined silky shark presence instead of counts, our results indicate a similar dramatic decline.

Worldwide, mobula and manta rays are threatened by overfishing (Ward-Paige et al. 2013; IUCN 2014). The population status of these species has been uncertain in the eastern tropical Pacific, but our results indicate dramatic declines in relative abundance of 78% and 89%, respectively. These declines likely stem from the multi-nation fisheries in the eastern tropical Pacific because both tend to have a large home range and low rebound potential (Dulvy et al. 2014b).

Contrary to our initial prediction, tiger sharks showed significant increases in their odds of occurrence over time, arising from the abrupt increase observed since 2007 (Fig. 4b). It is possible that within this system of strong fishing pressure, tiger sharks have an advantage over other elasmobranch species because of their relatively high intrinsic rate of increase (Hutchings et al. 2012) and high post-hooking survival rate (Gallagher et al. 2014). Tiger shark population increases have been documented recently in the northwestern Atlantic (Baum & Blanchard 2010) and South Africa (Dudley & Simpfendorfer 2006). In the latter case these increases were attributed to competitive release. However, the abrupt increase in tiger shark observations at Cocos Island beginning in 2007 suggests that tiger sharks have simply moved to Cocos Island and established long-term residency there. Even though tiger sharks are a pelagic species capable of long migrations, recent evidence suggests that some individuals may display year-round residency at isolated reefs (Werry et al. 2014). The estimated increase should thus be interpreted cautiously because it may better reflect tiger shark movement than population trends.

Also contrary to our initial hypothesis, we observed a slight increase in the odds of occurrence for whale sharks at Cocos Island. There is, however, large interannual variability for this species; its odds of occurrence at Cocos Island appeared to spike every 3 years (Fig. 4j). This suggests that Cocos may be a stopover for whale sharks moving to feeding or mating grounds (Hearn et al. 2013). Our results are in contrast to documented whale shark declines elsewhere in the world, which have resulted primarily from overfishing (IUCN 2014). Although whale sharks are protected under several international agreements, this species has continued to decline in many places (IUCN 2014).

We had expected that smaller sharks (whitetip reef) and bottom-feeding rays (eagle and marble rays) would experience increases in their relative abundance

because of mesopredator release, but all 3 species instead declined greatly in relative abundance. This is likely due to a combination of other predators (Galapagos, tiger, and blacktip) increasing in presence, thereby changing species interactions, and illegal fishing activity within the Cocos Island MPA (Baskett et al. 2007; Arias et al. 2014).

We initially hypothesized that reef-associated sharks (blacktip, Galapagos, and silvertip), because of their high site fidelity, would be better protected by the Cocos Island MPA. Our results are consistent with this hypothesis for both blacktip and Galapagos sharks, but silvertip sharks declined over time. Silvertip sharks may be in direct competition with blacktip and Galapagos sharks, which may explain why the latter 2 species increased at the same time as the recent severe declines in silvertip sharks occurred (Figs. 4e, f, and g). Additionally, increases in the presence of blacktip and Galapagos sharks could be due to the Cocos Island MPA working effectively for these largely reef-restricted species.

Despite substantial declines in 8 shark and ray species we documented, Cocos Island continues to be hailed as an example of a successful MPA and a world class location for viewing large numbers of elasmobranchs (Friedlander et al. 2012; Edgar et al. 2014). This suggests a problem of shifting baselines, with recreational divers failing to recognize how much of the megafauna at Cocos Island already has been lost. Moreover, while many divers are excited by the increasing number of some larger elasmobranch species (i.e., tiger, blacktip, Galapagos, and whale sharks), these shifts reflect the changing community assemblage that has occurred at Cocos Island over the past 21 years and are not necessarily an indication of the MPA's effectiveness (Baskett et al. 2007). It is unclear if the current dynamics of the Cocos Island elasmobranch community are simply indicative of a long transient response following creation of the MPA (White et al. 2013). Although management efforts have increased in the past decade, illegal fishing still occurs within the island's waters (Arias et al. 2014). It is unclear if the Cocos Island MPA is even properly designed (Botsford et al. 2003) to protect such large and wide-ranging species (Hooker & Gerber 2004; Grüss 2014). Conservation efforts at Cocos Island cannot be focused simply on expanding the protected area (Arias et al. 2014); rather, efforts should be put toward increasing enforcement and management (Kelaher et al. 2015). Costa Rica's efforts to increase their MPA coverage are admirable, but the establishment of MPAs cannot be the end point. Explicit plans and dedicated funding for monitoring and enforcement must be in place to prevent the creation of a network of paper parks. These plans need to include using both theory about MPAs and empirical data (White et al. 2011). Further, there must be stronger penalties for noncompliance with MPA rules to offset the potential gains of illegal fishing (Arias et al. 2014). We found that data collected

by divemasters can be a reliable way to discern trends in relative abundance. We recommend that monitoring and enforcement of Costa Rica's MPAs be increased substantially and that international environmental NGOs and foundations contribute to these efforts. Such efforts are urgently required if Cocos Island is to recover its elasmobranch populations and claim its status as a truly successful MPA.

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Supporting Information

Additional background information and methods, a table of consumer-prey relationships (Appendix S1), a figure of dive effort over time at each dive site (Appendix S2), distributions of the measured environmental variables (Appendix S3), species specific record information (Appendix S4), distributions of counts for each species (Appendix S5), distribution of counts for each species for each individual divemaster (Appendix S6) and each dive site (Appendix S7), residual plots for each species (Appendix S8), tables with ranking of the top models for each species (Appendix S9), and tables of the top models for subsets of data (Appendix S10), and tables of model averaged coefficients (Appendix S11) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of material) should be directed to the corresponding author.

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