ECOLOGY

Shark baselines and the conservation role of remote coral reef ecosystems

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Scientific monitoring has recorded only a recent fraction of the oceans' alteration history. This biases our understanding of marine ecosystems. Remote coral reef ecosystems are often considered pristine because of high shark abundance. However, given the long history and global nature of fishing, sharks' vulnerability, and the ecological consequences of shark declines, these states may not be natural. In the Chagos archipelago, one of the remotest coral reef systems on the planet, protected by a very large marine reserve, we integrated disparate fisheries and scientific survey data to reconstruct baselines and long-term population trajectories of two dominant sharks. In 2012, we estimated 571,310 gray reef and 31,693 silvertip sharks, about 79 and 7% of their baseline levels. These species were exploited longer and more intensively than previously thought and responded to fishing and protection with variable and compensatory population trajectories. Our approach highlights the value of integrative and historical analyses to evaluate large marine ecosystems currently considered pristine.

INTRODUCTION

Climate change and industrial exploitation are radically changing the structure and function of ocean ecosystems (1, 2). However, understanding the magnitude and consequence of this impact is challenged by the relatively brief history of scientific observation and the limited capability of scientific monitoring over large oceanic scales (3, 4). Recognizing what is natural in the ocean is paramount to evaluating how ecosystems respond to human impact, management, and conservation and to set recovery targets. This aspect is particularly pertinent in tropical coral reef ecosystems (5–8), where remote and uninhabited places are often considered models of pristine ecosystems (7, 9), attracting billions of dollars of conservation funds (10).

Recent research has used observations from remote and uninhabited coral reefs to question long-standing tenets of marine community structure (7). Fish assemblages surveyed with scuba diving methodologies (11, 12) have indicated communities dominated by top predators and, in particular, sharks with densities that are exceptionally high and variable (11). They ranged from 218 sharks/km^2 in no-entry marine reserves of the Great Barrier Reef in Australia (13) to 200,000 sharks/km^2 in the uninhabited atolls of the Line Islands (7). These observations led to the hypothesis that marine food webs are arranged as inverted trophic pyramids, where abundance of food web components declines with trophic level (7). However, whether these high densities of sharks observed in remote coral reef ecosystems are natural remains untested. Sharks have been neglected by scientific research for centuries and entered the agenda of research management and conservation only in the last couple of decades (14, 15). For this group, lack of basic data on their ecology and biology is more severe than many other marine taxa (15), and few, if any, historical baselines of abundance exist for sharks in coral reef ecosystems (6).

Theoretical research demonstrated that inverse pyramids are plausible only in rare cases (5). To exist, there need to be extreme combinations of trophic efficiency (TE; how much a predator can transform prey into biomass) and predator-prey mass ratio (PPMR), which are seldom observed in natural marine communities (5). Often, inverse pyramids are actually the result of census biases (11, 12) and a mismatch between the scale of the observations and the scale of the investigated processes (5). Predators can source energy from other adjacent ecosystems and thus have biomass production bases larger than locally observed (12). On the other hand, conventional visual census estimates are often biased because they frequently ignore fish and diver speed, fish size, visibility, and survey time and methodology (11, 12). Considering these factors can reduce shark density estimates by orders of magnitude. For example, in the northern Line Islands, accounting for fish speed downsized estimates of shark density by 95% (from 200,000 individuals/km^2 originally estimated to 9000) (11). Estimates of the same shark population obtained from different survey methodologies have ranged from 5000 to 17,000 individuals/km^2 when obtained with belt transect surveys (11) and from 340 to 680 sharks/km^2 with towed surveys (8). Furthermore, even the latter more conservative estimates are more than an order of magnitude higher than recent independent estimates obtained with mark-recapture models (21.3 sharks/km^2) (16).

Moreover, it is also unclear whether current abundances of reef sharks observed in isolated uninhabited coral reefs are natural or an effect of ecological change induced by fishing elsewhere. Virtually, no place in the ocean is unaffected by human footprint (17). Even uninhabited and remote tropical archipelagos are surrounded by heavily exploited oceanic regions, where large predatory sharks have been fished at very high rates for decades (6, 14, 18, 19). Although sharks commonly found in pristine coral reefs are often considered top predators, they can have foraging behaviors, movement patterns, and morphometric features of meso-predators or upper-level fish consumers (6). These species are expected to benefit from declines of other larger shark species, ranging from coastal to pelagic environments, because of predation or competition release (14, 20).

The Chagos archipelago is one of the most remote coral reef ecosystems in the planet. Located in the Central Indian Ocean (6°S, 71°30′E, Fig. 1), it is part of the British Indian Ocean Territory (BIOT), a UK Overseas Territory, which is composed of seven atolls, a coral reef surface of ~15,000 km^2, and an exclusive economic zone (EEZ) of 640,000 km^2. In 2010, the EEZ became a no-take zone, currently one of the largest marine protected areas (MPA) in the world (21). During the period between the 1780s and 1965, the archipelago had been inhabited by less than 1300 people (22). Then, the area transitioned from under

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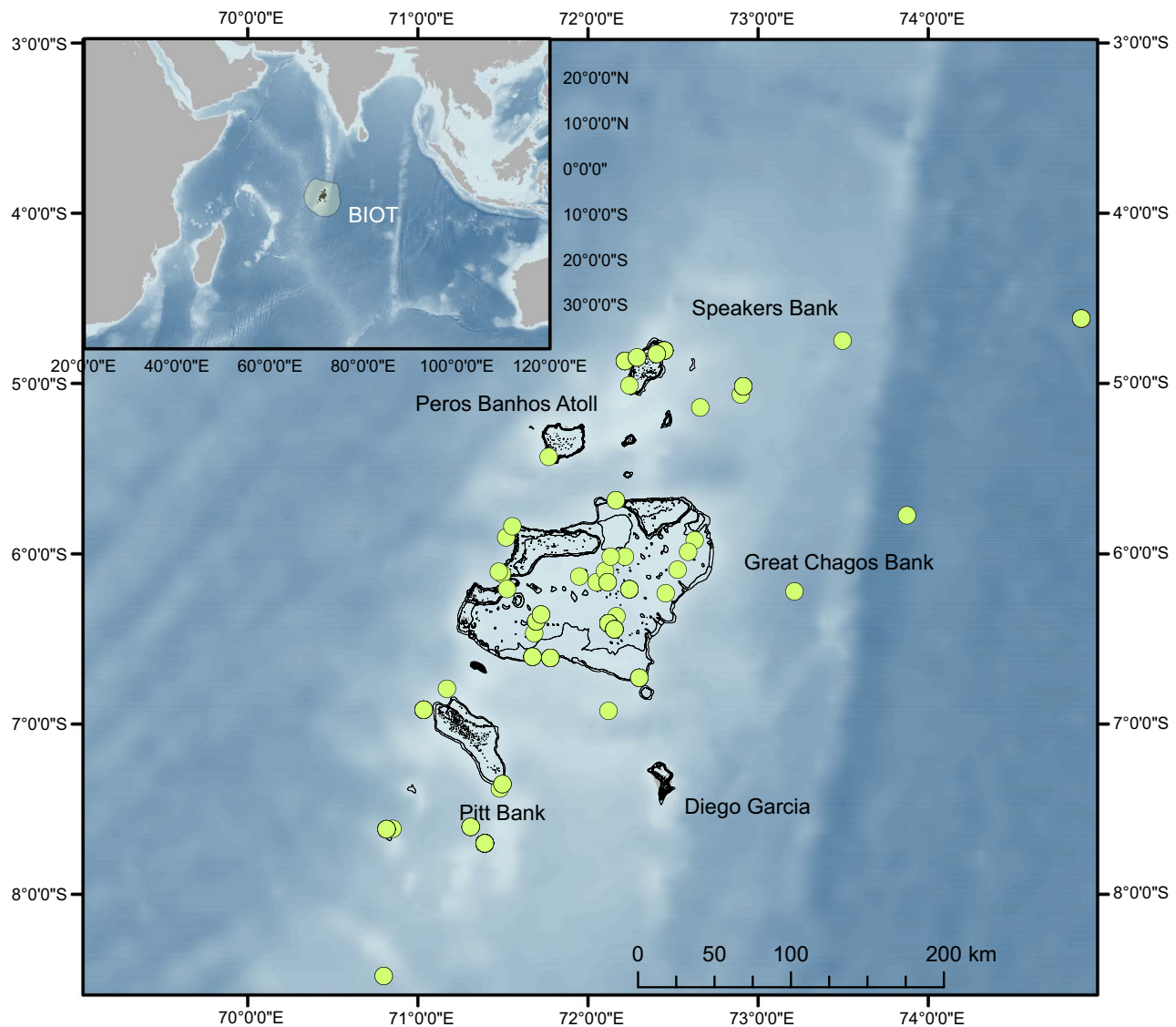*Corresponding author. Email: ferretti@stanford.edu

Fig. 1. The BIOT (green transparent polygon in the inset map) and the Chagos archipelago. Dots are locations of illegal fishing intercepted by the BIOT patrolling vessel, the Pacific Marlin.

the authority of the British colony of Mauritius to direct UK jurisdiction, and between 2000 and 4000 people (military personnel and civilian contractors) remained only on the island of Diego Garcia (with no permanent residence), where a U.S. Navy base and the BIOT office were established (*23*, *24*). After the reserve's establishment, all fishing activities in the BIOT became illegal except for a small recreational fishery around Diego Garcia and subsistence fishing by permitted yacht owners passing through BIOT waters (*25*).

Shark communities around the Chagos archipelago were considered pristine 40 years ago (*23*). In the 1970s, scuba diving surveys reported sighting rates of 4.2 sharks per dive, most of which were silvertip sharks (*Carcharhinus albimarginatus*) (*26*). After 30 years, the sighting rate declined by >90% to just 0.4 sharks per scientific dive (*23*). Species composition also shifted. From an initial period when silvertip and whitetip reef sharks (*Triaenodon obesus*) were the most abundant species seen, in 1996, gray reef sharks (*Carcharhinus amblyrhynchos*) became the most frequently recorded sharks, followed by tawny nurse (*Nebrius ferrugineus*),

blacktip reef (*Carcharhinus melanopterus*), silvertip, and whitetip reef sharks. By 2006, blacktip and whitetip reef sharks ceased to be seen. Only after the MPA establishment did these species reappear, and average sighting rates increased to 1 to 1.5 sharks per dive (*27*).

A major source of mortality for reef sharks around the Chagos archipelago has been illegal, unreported, and unregulated (IUU) fishing, principally from Sri Lankan fishing vessels (*28*, *29*). These are small-size vessels (<10 m in length), with a capacity of about 5 metric tons, which fish mainly with longlines and gillnets (*29*). Arrest reports indicated that these vessels had been encroaching the area at least since 1996, catching from about 4000 to 25,000 sharks per year (*28*). The impact of these IUU fishing activities before 1996, when patrolling against illegal fishing began, is uncertain. In the surrounding area of the Western Indian Ocean (WIO), sharks have been affected by an international fishing fleet of 22 nations, fishing for tuna and swordfish with longlines and purse seines since the early 1950s (Table 1) (*30*). In particular, longline fleets have caught a substantial amount of sharks,

Table 1. Timeline of exploitation, management, and conservation events with a likely effect on the focal reef shark species around the Chagos archipelago.

Date	Event	Reference
1927	Beginning of industrial exploitation of Mauritian offshore banks including the Chagos archipelago.	(40)
1948	First handline scientific surveys are being carried out in several tropical banks of the WIO including the Chagos archipelago.	(36)
1949	Mauritian bank fishery expands to several banks in the central WIO.	(39)
1952	Longlining was first introduced in the Eastern Indian Ocean and soon spread across the entire ocean.	(32)
1965	The Chagos archipelago is detached from the British colony of Mauritius for joint UK/U.S. defense purposes.	(61)
1967	Indian Ocean Fishery Commission established.	(62)
1971	Construction of a military base started on Diego Garcia.	(24)
1972	The UK government relocated the last few Chagossians from the Chagos archipelago.	(61)
1973	The Taiwanese fleet expanded to target the whole WIO.	(30)
1975	First scuba diving surveys are being carried out around the Chagos archipelago.	(23)
1977	Mauritian bank fishery data became available from the Chagos archipelago.	(39)
1982	The Indo-Pacific Tuna Development and Management Programme (IPTP) was established to manage the rapidly growing industry in the region.	(62)
Mid 1980s	Increasing demand and markets for shark result in growth in shark fishing in the region.	(23)
1989	Total tuna catch in the Indian Ocean exceeds that in the Atlantic Ocean for the first time and has never fallen below it (Pacific tuna catch still exceeds both).	(30)
1991	Establishment of a 200-mile FCMZ.	http://mrag.co.uk/experience/management-british-indian-ocean-territory-fisheries-regime
1996	FCO begins to report illegal fishing vessels incurring in the BIOT.	(28)
1997	The IPTP is replaced by the IOTC whose remit no longer extends into the Western Pacific.	(62)
2000	Start of the fisheries observer program in BIOT.	(58)
2005–2009	Somali piracy results in fishing effort being displaced away from the Somali coast to other areas of the Indian Ocean and an overall 25% reduction in fleet capacity	(63)
9 Nov 2009	Public consultation on establishing a large marine reserve in BIOT opened.	(9)
2009	Maldives ban reef shark fishery within their atolls.	(64)
2010	Maldives completely ban shark fishery within their jurisdictional waters.	(64)
2010	The Maldives extend a national ban on shark hunting, banning shark fishing in all its waters and all shark product exports. This decision was based on evidence that sharks are more valuable as a tourist attraction than as a fishery resource.	(64)
10 Apr 2010	A no-take BIOT marine reserve is established around the BIOT territorial waters, and all fishing activities are banned within the 640,000-km^2 boundary.	(9, 21)

historically as by-catch (31), and since the 1980s and 1990s as target species to supply an increasing international shark fin demand (23). The main shark catches have been large pelagic species such as blue (*Prionace glauca*), mako (*Isurus oxyrinchus*), oceanic whitetip (*Carcharhinus longimanus*), and silky sharks (*Carcharhinus falciformis*), or coastal-pelagic species such as hammerheads (*Sphyrna* spp.) and other requiem sharks (*Carcharhinus* spp.) (32). Reef sharks have also been taken, but in a smaller proportion, although quantifying the true impact of these fisheries on reef sharks is difficult because species-specific shark catches have not been systematically reported in

historical data, and for reef sharks, taxonomic identification is not as reliable as for the other species (33).

Here, we use an integrative and historical approach to reconstructing shark baselines in the Chagos archipelago. With state-space Bayesian surplus production models (SPMs), we combined catch data from illegal fishing operations and monitored industrial fisheries, historical indices of abundance from scuba diving and longline surveys, and ecological theory to estimate standing stock abundance, historical trends, and pristine population estimates of the two most abundant species of reef sharks in the Chagos archipelago: the silvertip and the gray

reef shark. These are the most ubiquitous species occurring in many coral reefs in the planet with partially overlapping ecological niches and different vulnerability to fishing (19, 34, 35). Hence, in a place where the history of human impact and protection is on record almost completely, we made the most of all available sources of historical information to extract long-term population trajectories of these species and used them as indicators of how coral reef shark communities can respond to changes in regimes of historical fishing and protection.

RESULTS

We parameterized the SPMs with information on how many sharks were removed from the system, life histories of the focal species, observed trends in relative abundance, and informed assumptions of how the pristine shark community may have looked before human impact. In evaluating removals, we could only reconstruct shark catches since 1968. From then to 1995, we assumed that sharks were mainly caught by longline offshore fisheries. These were the only fisheries reported to catch reef sharks, and our analyses of contemporary longline surveys suggested that catch rates of silvertip and gray reef sharks were non-negligible (fig. S1). Reconstructed catches indicated that the annual silvertip removal from the area ranged between 21 and 592 individuals (mean, 280; SD, 175), whereas gray reef shark catches ranged between 0 and 96 individuals per year (mean, 18; SD, 29) (Fig. 2).

Toward the end of the 20th century, the BIOT became increasingly monitored and managed (Table 1). In 1991, the United Kingdom established a 200-mile Fisheries Conservation and Management Zone (FCMZ), and in 1996, fishing fleets could operate only if they were licensed (Table 1). However, between 2000 and 2010, we estimated a higher longline catch for both species, with gray reef shark catches increasing by more than 7 times (mean annual catch, 136.88; SD, 83.27) and silvertip increasing by 1.7 times (mean annual catch, 485.32; SD, 295.24). In 1996, the Foreign and Commonwealth Office (FCO) started to report arrests of illegal fishing vessels encroaching in the BIOT, and from 2006, detailed catch inventories were also included in some of these reports (28, 29). Between 2006 and 2015, the seizure reports documented the catch of at least 4925 sharks. About a half of these catches were nonidentified (reported as miscellaneous sharks), and 15% were reported as unidentified reef sharks. Among the 20 identified species (which included reef, pelagic, and coastal-pelagic sharks), silvertip and gray reef sharks were the most abundant (fig. S2). From these data, we estimated that between 1996 and 2015, 20 to 120 boats entered the area annually and that annual catches for all species ranged from 1745 to 23,195 individuals. Gray reef and silvertip sharks were taken more or less in equal amount: between 402 and 5241 silvertip sharks per year and between 369 and 4471 gray reef sharks per year (fig. S2).

In 1975, scientific scuba diving surveys began in the Chagos archipelago's coral reef ecosystems, providing us with the most suitable source of abundance indices for the stock assessment models. These data indicated an overall 75% decline of detected sharks between the 1970s and 2012, but when disaggregated to the species level, gray reef sharks showed an overall increase (Fig. 2, A and B), while silvertip sharks declined steeply. Because these data were not available at the species level in the 1970s, we reconstructed species proportions (i) by interviewing one of the scuba divers participating in the 1970s' surveys and (ii) independently, from a historical USSR longline survey. From the diver's feedback, we understood that silvertips were perceived to be 5 to 10 times more abundant than gray reef sharks.

Similarly, the USSR survey indicated that gray reef sharks accounted for 3% of all species detected and silvertip sharks accounted for 57% (fig. S1). Both scenarios produced similar trends, although the USSR surveys suggested slightly more pronounced changes over time (Fig. 2, A and B). The USSR surveys were also instrumental in estimating independent trends of abundance indices, confirming that, between 1960 and 1980s, while gray reef shark catch rates increased by 650.51 times [instantaneous rate of change (IRC), 0.31; SD, 0.14], silvertip shark catch rates declined by 81.87% (IRC, −0.08; SD, 0.02; fig. S3).

Finally, we set priors of community composition and shark density under virgin conditions (carrying capacity for the SPM models) with a meta-analysis of published baseline shark densities obtained in other coral reef archipelagos (8) and by looking at the catch composition of historical fishing surveys (36). The meta-analysis indicated that 171.19 reef sharks/km^2 (95% CI, 152.48 to 189.89) (fig. S4) would be expected under natural conditions. With a total possible occupiable coral reef habitat of 15,639 km^2 [Zoological Society of London (ZSL) unpublished data], the Chagos archipelago would thus have hosted 2,677,253 sharks. If we assumed that the relative proportions of sharks in these pristine states were similar to their frequencies of occurrence detected in the historical handline survey in the 1940s (fig. S5) (36), then there would have been 2,363,254 gray reef sharks and 214,841 silvertips (88 and 8% of the catches, respectively), whereas by using ecological theory on the macroecological properties of natural marine food webs (5), we predicted 737,040 gray reef and 452,870 silvertip sharks (fig. S6).

These analyses were used to build informative priors for the stock assessment models, which were run under different scenarios of community structure under baseline conditions and during the 1970s. The most plausible models [according to the widely applicable information criterion (WAIC), Table 2] indicated that, in 2012, the Chagos archipelago had a population of 571,310 (CI, 160,329 to 723,996) gray reef sharks and 31,693 (CI, 9137 to 80,279) silvertip sharks. These abundance levels were 79 and 7%, respectively, of the Chagos archipelago's estimated carrying capacity for these species [K = 727,435 (CI, 642,400 to 815,328) for gray reef sharks and 455,337 (CI, 394,014 to 518,431) for silvertips]. Silvertips were projected to decline sharply between the 1970s and the 1990s (Fig. 3), whereas gray reef sharks showed a steady increase throughout the observed period (Fig. 3).

Our assumptions used to build priors of baseline community composition and density did not significantly influence the shark population estimates, which changed by at most 1.7 times in silvertip sharks (Table 2). For both species, variations across scenarios were smaller than their individual uncertainty (Table 2). More pronounced, instead, was the effect of the baseline scenarios on the carrying capacity's posterior estimates, which changed by more than three times for gray reef sharks using species proportions informed by macroecology ("macroeco" scenario) compared to using proportions informed by empirical catch records of historical catch surveys ("wheeler" scenario; Table 2 and fig. S7).

We also considered the possibility that our catch reconstruction underestimated the actual removal of reef sharks from the area, especially for the period before 1996 when reports of illegal fishing vessel incurring in the BIOT were not available. To test this aspect, we included a multiplicative factor (ψ) on the reconstructed catch series, assuming that our catch reconstruction was censored, and thus there was an unobserved amount of catches that had to be estimated from the data. Results suggested that in all scenarios, the catch estimated for the period before 1996 would have been underestimated by a factor of 184.6 for
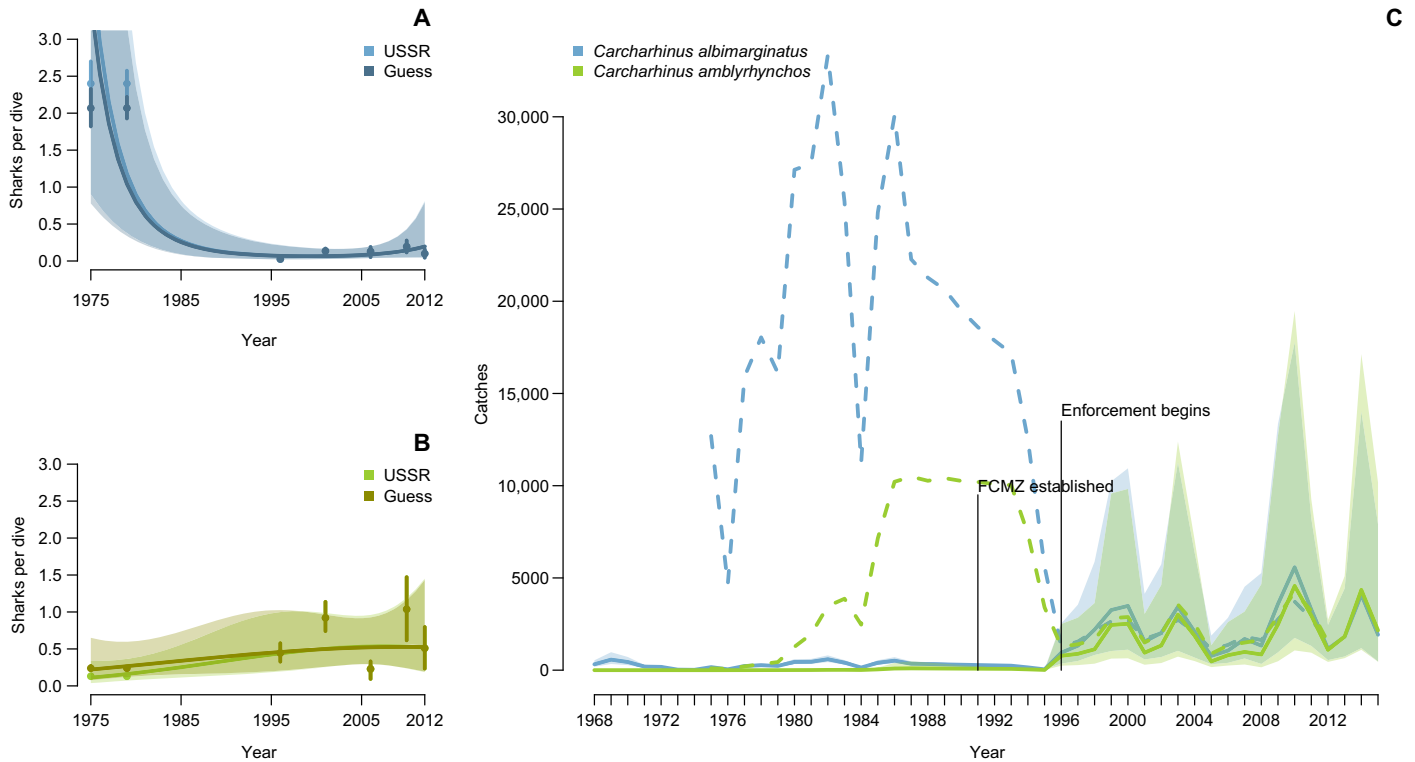
Fig. 2. Abundance indices and estimated catches of silvertip and gray reef sharks in the Chagos archipelago. Time series of the indices of abundance obtained from scuba diving surveys for silvertip (**A**) and gray reef sharks (**B**). Trend lines in (A) and (B) were predicted for illustrative purposes by fitting a weighted quadratic regression ($O_t = year + year^2 + \epsilon$). Shown are trends both within the USSR and guess scenario of community structure for the 1970s when species-specific indices were unavailable (see the text). (**C**) Estimated total catch of species from longline and IUU fisheries in the BIOT. Dashed lines are posterior means of estimated catches during the period 1975 to 1995 under a scenario of censored catch records (that is, in this period, our catch reconstruction for the two species was a gross underestimation; see Results). The posterior means of estimated catches referred to the best models for each species respectively.
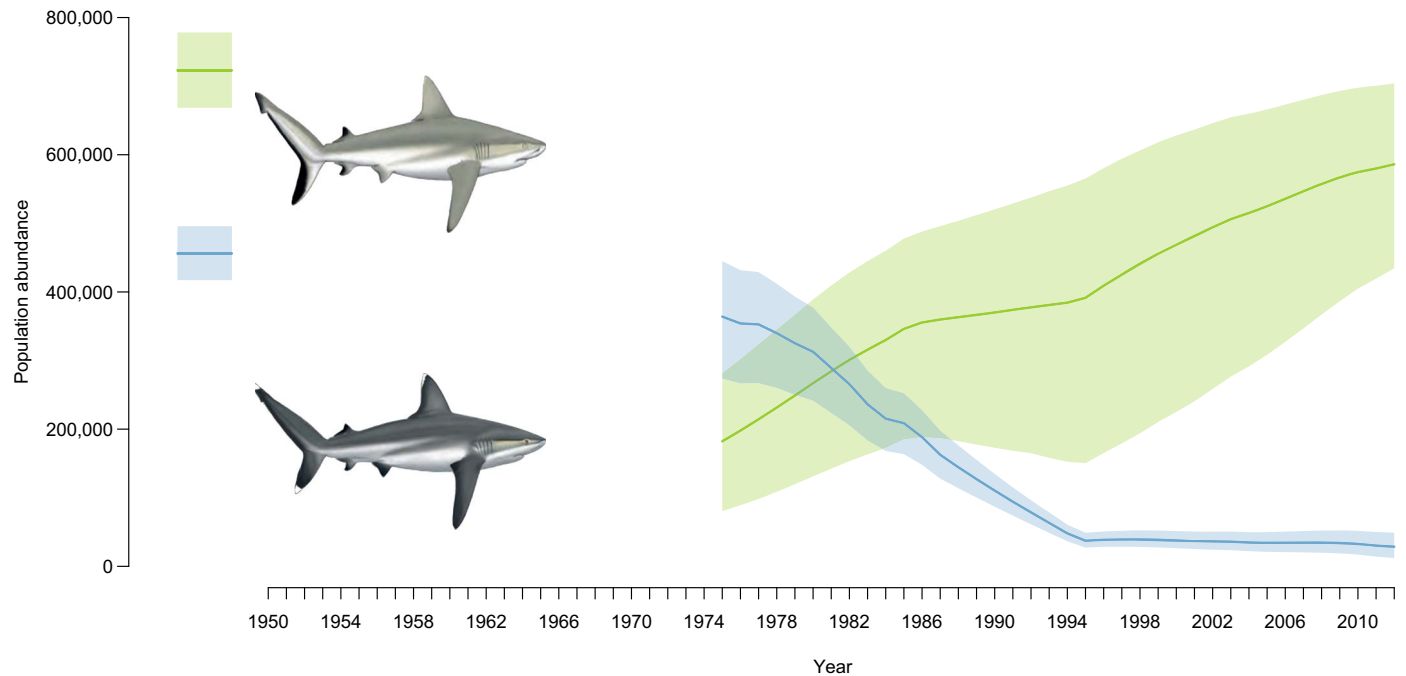

Fig. 3. Population trends of gray reef (green) and silvertip sharks (blue) as estimated by the SPMs. Trajectories are drawn only for periods when O_t and C_t data exist and overlap. Lines are mean population estimates and transparent polygons are 80% credible intervals (CI). Carrying capacity is represented by the initial flat line and CI before 1948 (that is, we estimated that population baselines occurred sometime earlier than 1948 for both species).

Table 2. Summary statistics for the posterior estimates of population abundance (PopEs), carrying capacity (K), maximum population growth rate (r), coefficient q, and catch factor (ψ) under different modeling scenarios. BS, baseline; SS, seventies scenario. The SDs of the posterior distributions are shown in parentheses. Model fit is indicated by its relative WAIC.

	Species	BS	SS	PopEs	K	r	q	ψ	WAIC
1	Silvertip shark (STS)	Macroeco	Guess	31,693 (18,513)	455,337 (31,780)	0.045 (0.001)	4.0×10^{-6} (1.4×10^{-6})	0.0155 (0.0031)	2330.21
2	—	—	USSR	28,623 (17,057)	456,142 (30,553)	0.045 (0.001)	4.4×10^{-6} (1.6×10^{-6})	0.0152 (0.0029)	2444.74
3	—	Wheeler	Guess	20,122 (13,336)	216,709 (15,059)	0.045 (0.001)	6.2×10^{-6} (2.3×10^{-6})	0.0344 (0.0079)	2632.70
4	—	—	USSR	18,595 (12,381)	217,439 (14,784)	0.045 (0.001)	6.6×10^{-6} (2.5×10^{-6})	0.0343 (0.0081)	2341.33
5	Gray reef shark (GRS)	Macroeco	Guess	586,114 (154,059)	722,930 (42,733)	0.125 (0.005)	2.0×10^{-6} (3.2×10^{-6})	0.0058 (0.0054)	2042.31
6	—	—	USSR	571,310 (124,915)	727,435 (43,353)	0.125 (0.005)	1.6×10^{-6} (1.6×10^{-6})	0.0075 (0.006)	1788.60
7	—	Wheeler	Guess	439,654 (355,158)	2,330,047 (164,414)	0.124 (0.005)	4.4×10^{-6} (3.1×10^{-6})	0.0038 (0.0026)	2708.90
8	—	—	USSR	645,275 (344,663)	2,325,847 (162,766)	0.123 (0.005)	2.4×10^{-6} (1.6×10^{-6})	0.0045 (0.003)	2359.70

gray reef sharks and by a factor of 40.3 for silvertip sharks (Table 2 and Fig. 2C).

DISCUSSION

Reconstructing community and population baselines for marine animals is one of the most challenging objectives in ecology and conservation. It is difficult because there are few places on Earth that are unaltered by humans (*17*), and for most marine locations, scientific data became available long after initial human impacts (*4, 37*). Furthermore, the ecosystem consequences of this impact often go beyond the spatial and biological boundaries of this perturbation (*14, 20*). Therefore, even in remote and uninhabited marine locations, it is unclear whether ecosystems are pristine or are the results of historical or indirect ecological changes triggered elsewhere.

In the Chagos archipelago, scientific surveys predated industrial exploitation in inshore and offshore waters, and for 40 years, fisheries statistics and scientific monitoring data were available before and after the establishment of one of the largest MPAs in the planet. These data were sparse and heterogeneous but enabled us to estimate the abundance of local reef sharks across temporal and spatial contrasts of fishing exploitation and reconstruct their abundance under pristine conditions. Our models indicated that the recent abundance of these species (in 2012) was a fraction of their estimated baseline abundance, although both displayed complex decadal trajectories of population abundance, likely driven by alternate phases of fishing exploitation and protection in coastal and pelagic environments.

It has been frequently assumed that the Chagos archipelago was nearly pristine when scuba diving surveys were first carried out in the area in 1975 (*23*). The impact of historical settlements in the archipelago was thought to be minimal, and industrial exploitation offshore was deemed to be in a very germinal stage to affect reef shark populations (*23*). Here, we estimated that silvertips were, in 1975, 3.68 times more abundant than gray reef sharks and at 79% of their estimated carrying capacity. Gray reef sharks, in turn, were already at 13% of their predicted abundance under baseline conditions. These abundance levels were radically different from expectations from ecological theory (fig. S6) and from what historical fisheries surveys recorded in 1948 (fig. S5) (*26, 36*).

Local inhabitants have been in the Chagos archipelago at least since 1744, when the area was first explored by French navigators (*38*). These

people were mainly workers of coconut plantations (*23*), subsidizing their dietary needs with imported rice and other agricultural products of the islands. However, they also exploited local marine life, causing population depletions and local eradications of large marine animals as early as the mid 19th century (*38*). Early explorers reported that seals, "walruses" (probably dugongs, *Dugong dugon*), and large numbers of green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles occurred in the Chagos archipelago before the second half of the 19th century (*38*). Seals and dugongs disappeared from the archipelago in the mid 19th century, and although the area remains a globally significant breeding site for both green and hawksbill turtles, these animals were heavily exploited for their shells and meat (*38*). How much these coconut plantation workers affected local shark populations is unclear. However, independent historical reconstructions predicted that, between 1950 and 1972, about 46 to 93 metric tons of finfish were taken annually by subsistence fishing in the archipelago (*24*). Although this fishery may have not targeted sharks specifically, previous studies have shown that sharks can be intentionally killed in similar subsistence coral reef fisheries to increase catch rates of more profitable bony fishes (*8*).

In addition, the Chagos archipelago was one of the sectors exploited by a Mauritian semi-industrial handline fishery that began exploiting several banks of the WIO at the end of the 18th century (*39*). Catch data from this fishery in the Chagos archipelago only became available in 1977 and indicated that, until 1994, annual fish catches ranged from 32 to 305 metric tons. However, this fishery may have operated in the Chagos banks at least since the late 1940s, when Wheeler and Ommanney (*36*) published the results of their exploratory fishing survey, giving new impetus for a region-wide exploitation (*39*). Again, information on the impact of this fishery on sharks is scant. Bank fishers targeted coral reef–associated fish such as lethrinids, serranids, lutjanids, siganids, and carangids, with light handlines (*40, 41*), but sharks caught on the spot were used as bait, and results from the exploratory handline surveys suggested that a substantial number of sharks could be caught as well (about 16% of the total fish catch in number) (*36*). Furthermore, fishers operating on other WIO banks were seeing declines of shark populations, which they attributed to targeted exploitation by foreign fishing vessels. Therefore, although we cannot be sure of the impact of the bank fishery on shark populations around the Chagos archipelago, anecdotal evidence suggest that reef sharks were being depleted across the WIO (*41*). Thus, it cannot be excluded that subsistence fishing by local Chagossians

and the Mauritian bank fishery had affected the reef shark community around the Chagos archipelago much earlier than when scuba diving surveys began to be carried out in the area (40).

The radical differences in population abundance estimates between baseline reference points and the 1970s, and eventually the complementary population trajectories estimated between 1975 and 2012, were possibly driven by alternate phases of fishing exploitation and protection, inshore and offshore within the BIOT, and the species' susceptibility to these changing exploitation regimes, given by their intrinsic vulnerability and spatial ecology. We saw three overlapping stages of exploitation regimes:

(1) Historical inshore phase. Since the initial settlement, the Chagos archipelago went through an initial phase of subsistence inshore fishing operated by locals and, toward the mid 20th century, even a short period of semi-industrial exploitation operated by the Mauritian bank fishery. This exploitation phase would have more strongly affected the inshore and more reef-associated gray reef sharks (19). In 1972, local Chagossians were relocated because of the transition of the archipelago to UK jurisdiction, and the Mauritian bank fishery ended its operations in 1994.

(2) Offshore phase. In the second half of the 20th century, the Chagos archipelago became exposed to industrial exploitation offshore from high-seas fisheries, over time becoming increasingly more impactful for sharks (32). These high-seas fisheries would have posed a larger threat to silvertip sharks than to gray reef sharks, because silvertips use offshore waters more extensively (19, 35, 42) and have been demonstrated to be vulnerable to these fisheries around other coral reefs of the Indian Ocean and the Pacific Ocean (34, 35).

(3) Protection phase. Since 1991, in the BIOT, there has been a period of increasing fisheries monitoring, restrictions, and protection for sharks, culminating in 2010 with the total closure of the area to fishing (Table 1). In this period, we estimated the largest reef shark removal, mostly driven by poaching. Catches of the two species were predicted to be an order of magnitude higher than in the 1968 to 1987 period (Fig. 2), with little difference before and after the MPA creation. Results of our models suggested that such a low exploitation regime before 1996 was likely an artifact of missing catch statistics, mainly during the 1980s and 1990s in the offshore fishing period (Table 2 and Fig. 2). However, although these unobserved catches would explain the steep decline of silvertips, they were not enough to have an impact on the population of gray reef sharks, which are three times more productive than silvertips (in terms of r_{max}, Table 2).

Historical accounts of exploitation and protection regimes, such as those we documented here, are still rare in the literature but may have occurred in many other remote archipelagos across the planet. Since the beginning of industrial fishing, access to pelagic environments or unmonitored jurisdictional waters of many remote coral reef ecosystems has been trivial for globally ranging fishing fleets (43). High-seas fisheries have been recorded to affect shark communities globally, but most of their shark catches are unreported (14, 44). In addition, the history of settlement and inshore exploitation for many of these isolated tropical archipelagos has not yet been described or may be much longer than what is available from scientific record. In the Chagos archipelago, this history unfolded for at least 200 years before the first scientific monitoring programs began. These scientific data documented severe depletion of local shark communities (23), and by comparing and integrating them with more historical observations, we showed that shark populations were far from being pristine even in the initial years of this scientific monitoring stage. A historical perspective is therefore crucial when interpreting patterns of shark abundance and composition in remote coral reefs. In these ecosystems, high abundances of reef sharks are often celebrated as conservation opportunities or victories (45). However, ensuring that we clearly understand whether these states are truly natural or an effect of ecosystem change is paramount to avoid not only misguiding management, conservation, and recovery plans but also wasting already limited resources for these goals (46). Controlling for historical shifts in fishing exposure for the diverse and variably vulnerable range of shark species occurring in these systems can help correctly identify ecosystem baselines (5, 8), characterize the functional role of sharks in coral reef ecosystems (6), and consequently evaluate the ecological and conservation role of large MPAs and shark sanctuaries around the world.

Together with a historical perspective, observations coming from remote coral reefs need to be properly handled statistically and integrated within a population and community dynamics' framework (5, 11, 12, 16). Often, this has the effect of substantially reducing initial estimates of shark abundance and verifying whether these indices are plausible ecologically. Our standing stock estimates for the gray reef shark were comparable in magnitude to the shark densities recently estimated in Palmyra, another remote large marine reserve (36.5 gray reef sharks/km^2 in the Chagos archipelago compared to 21.3 sharks/km^2 in Palmyra) (16) and a rare place where shark stock assessment is also available. Here, population indices were obtained from analyses that explicitly addressed the statistical nature and spatial process of the field observations. They downsized previous estimates (7, 8, 11) by orders of magnitude and empirically disproved the occurrence of inverted trophic pyramids (16). However, because no temporal trends were detected in 5 years of observations, these shark densities were inferred to represent population baselines. In light of our results, we propose that even this conclusion is uncertain. Carrying capacity was not directly assessed and the multiannual shark densities estimated could also be coherent with a longer-term increasing population trajectory. In the Chagos archipelago, we estimated shark populations far from their carrying capacity despite no previously detected trends in shark indices of abundance between 1975 and 1979 (23). Gray reef sharks were recovering from a strongly altered status, whereas silvertip sharks were rapidly declining from a historical status of dominance. After 37 years (in 2012), gray reefs reached population densities higher than those in Palmyra but still at 79% of the estimated baseline level.

Whether the history of exploitation in the Chagos archipelago triggered ecological consequences such as meso-predator releases and trophic cascades (14, 20) could not be tested. We could not test whether the gray reef shark recovery was only attributable to a reduction of fishing mortality and not to an increase in survival or overall fitness caused by the overexploitation of other shark predators (for example, bull, tiger, hammerhead, or oceanic whitetip sharks) or competitors (like the silvertip sharks) from the BIOT marine reserve's boundaries (33). In addition, unknown at this time are the impacts on these patterns of environmental variation detected in the Indian Ocean (47). Detecting these processes is possible only by combining multiple data sets spanning decades or entire oceanic regions (3) and analyzing them in the context of a quasi-experimental framework (3). Here, we adopted such an integrative approach with all historical data sets we could find in the region by extracting from them as much information as possible and borrowing information from other systems. Moreover, we exploited the Chagos archipelago's temporal and spatial contrasts in exploitation and protection regimes to interpret the emerging patterns in shark abundance. However, the available data (indices of abundance, catch statistics, and other priors of baseline structure) were

too scant, uncertain, and of limited resolution to increase the number of parameters we could reliably estimate in the Bayesian SPM used. Nonetheless, integrative analyses such as these are essential to reconstruct and conserve baselines of animal populations. Iterative in nature, they identify information gaps and lay the ground for future work. In the Chagos archipelago, our analyses provided a different view of baselines previously assumed for the system, shed new light on how they responded to human impact, and confirmed that management strategies involving both site protection and fisheries management in surrounding regions may be the best options to protect these sites (19). More effort is now needed to increase the resolution of the catch data and historical information for reducing uncertainty on the reconstructed population estimates and to explain the multiple drivers affecting them.

Remote coral reefs offer rare opportunities to reconstruct ecosystem baselines (8, 16). However, shark community dynamics and their stressors unfold over spatial and temporal scales larger than any extant large MPA and conservation program ever established (6, 12, 14, 18, 19). These scales make the term remote inappropriate for many distant coral reef ecosystems. In these locations, selective exploitation and protection can alter shark baselines in ways difficult to characterize unless field observations are properly handled statistically (11, 12, 16), incorporated within a population and community dynamics' framework, and interpreted with a historical perspective. This approach promises to reveal important insights into the abundance, structure, and function of shark communities in coral reef ecosystems around the world and thus identify true pristine ecosystems to protect or set as conservation targets.

MATERIALS AND METHODS
Surplus production models
We estimated historical and current population abundances of gray reef and silvertip sharks by using Bayesian state-space SPMs (48). These are convenient stock assessment models with minimum data requirements and therefore instrumental in data-limited scenarios. With a time series of observed abundance indices (O_t) and a time series of estimated catches ($\hat{C}_t$), we can assume that the observed indices are lognormal deviates from an underlying true index of abundance U_t (unobserved), which is, in turn, proportional to the population abundance (N_t, number of individuals) by a constant q: $O_t \sim \ln \mathcal{N}(\ln U_t = \ln (qN_t), \sigma_O^2)$, where σ_O^2 is the observation error. N_t is therefore U_t/q, and also, by taking the Schaefer function (49)

$$N_t = N_{t-1}\left[1 + r\left(1 - \frac{N_{t-1}}{K}\right)\right] - C_{t-1} \quad (1)$$

where r is the maximum population growth rate, K is the carrying capacity, and C_t are catches. By rearranging the equation in terms of O_t

$$\frac{O_t}{q} = \frac{O_{t-1}}{q}\left[1 + r\left(1 - \frac{\frac{O_{t-1}}{q}}{K}\right)\right] - C_{t-1} \quad (2)$$

the model can be a state-space model with an observation error σ_O^2 and a process error σ^2 on N. Here, we adapted the model framework of Meyer and Millar (48) to our case by modeling C_t also as a state-space model with an additional parameter ψ, which would rescale the estimated $\hat{C}_t$ for years when we had little confidence on the catch estimations (that is, before 1996, see the "Total catch" section).

Hence, if we rescale N_t as a proportion of the carrying capacity [$P_t = N_t/K$, to speed Markov Chain Monte Carlo (MCMC) chain mixing (48)], the state equations are

$$P_1 \big| \sigma^2 = e^{u_1}$$

$$P_t \big| P_{t-1}, K, r, \sigma^2 = \left(P_{t-1} + rP_{t-1}(1 - P_{t-1}) - \frac{\hat{C}_{t-1}}{K}\right)e^{u_t} \quad (3)$$

$$t = 2, \dots, N$$

$$O_t \big| P_t, q, \sigma_O^2 = qKP_t e^{v_t} \quad (4)$$

$$t = 1, \dots, N$$

Model priors
Below, we describe how we set priors for r, K, and q, and modelled the estimated catches $\hat{C}_t$. For the process error u_t, we used the model $u_t \sim \mathcal{N}(1,\sigma)$, where $\sigma \sim \mathcal{N}(0, 0.02)$. For the observation error v_t, we used the model $\mathcal{N}(0,\tau)$, setting τ to $\mathcal{N}(0,\sigma_O)$ (restricting to positive values), where σ_O is the mean of observed σ_{O_t}.

Maximum population growth rate
To generate a prior distribution of r_{max}, we use a predictor based on life histories and a stochastic approach that sampled input life histories from set distributions. The predictor of r_{max} was a value twice the population rebound potential calculated following Smith *et al.* (50) and using 1.5 times the estimated natural mortality (51). For this method, we needed natural mortality (M), age at maturity (t_{mat}), longevity (t_{max}), fecundity (b), and reproductive frequency (τ; that is, years between litters) of the species. For M, we used a life-history invariant method using t_{max} (life span), $M = 4.899 * t_{max}^{-0.916}$ (52), a method shown to outperform all other mortality predictors based on life histories and to be robust for low-productive species, such as sharks (52). Source life histories were taken from the literature and www.fishbase.org through the rfishbase package (tables S1 and S2). When not available, they were predicted from empirical relationships from other available life histories (hereby, we will use the notation $\hat{\theta}$ to indicate a predicted life history θ). We sampled input life histories as follows:

(1) Age at maturity (t_{mat}) was sampled from a uniform distribution with limits equal to the range of the available values (table S1).

(2) Fecundity (b) was not available for the silvertip shark. Thus, we calculated it from published litter size (ls) and reproductive frequency (τ), $b = \frac{ls}{2\tau}$. From a set of published ls values, we used their mean and SD to generate 1000 random draws of ls from a normal distribution. Then, we used these draws to calculate a distribution of b values and the corresponding means and SD. For gray reef sharks, we generated 1000 b values from a normal distribution with μ_b equal to the available published value and SD $\sigma_b = 0.30 * \mu_b$. Cortés (53) observed that the reported fecundity's SDs range between 20 and 40% of their mean.

(3) t_{max} was sampled from a triangular distribution with a mode equal to the maximum available value, a lower limit equal to our minimum available value, and an upper limit equal to 30% of the mode. This is a modification of the approach used by Cortés (53).

Once we had all the source life-history distributions, we resampled them 1000 times, and for each draw, we calculated the corresponding

r_{max}. Then, we built a lognormal prior of r_{max} by taking the log of the values and calculating the mean and SD.

Carrying capacity
Priors for carrying capacity were constructed by estimating shark density (that is, all shark species) and community composition under baseline conditions.

Baseline shark density
Nadon et al. (8) predicted the density of reef sharks under baseline conditions (absence of humans) from 46 individual U.S. islands, atolls, and banks in the Pacific Ocean, across a wide range of temperature and productivity regimes. We extracted these estimates and calculated a random effects meta-analytical average to have a prior estimate of the average number of sharks per square kilometer expected under unfished conditions

$$\bar{x}^* = \frac{\sum x_i w_i^*}{w_i^*}$$

$$w_i^* = 1/v_i^*$$

$$v_i^* = se_i^2 + \tau^2$$

$$\tau^2 = \max\left(0, \frac{Q - df}{C}\right) \tag{5}$$

$$df = n - 1$$

$$C = \sum w_i - \frac{\sum w_i^2}{\sum w_i}$$

$$Q = \sum w_i (x_i - \bar{x})^2$$

where $\bar{x}^*$ is the meta-analytical mean, w_i^* is the random effects weight for study i, v_i^* is the random effects variance of study i, Q is the homogeneity coefficient, and τ^2 is the super-population variance. The shark density prior was generated by randomly sampling 1000 values from a normal distribution $N(\mu = \bar{x}^*, \sigma = se(\bar{x}^*))$.

Baseline community composition
To estimate species proportions under virgin conditions, we used a historical data set and a theoretical approach based on macroecological theory.

(1) Historical data set. In 1948, the British colonial government undertook exploratory fisheries surveys in different tropical archipelagos of the Indian Ocean including the Chagos archipelago (36). Of 1281 hours of handlining carried out in different stations around the Chagos archipelago, the authors recorded 88% of gray reef sharks and 8% of silvertip sharks (that is, gray reef sharks on the order of seven sharks per hour of handlining and one silvertip shark every 40 min). We assumed that this catch composition was indicative of the species composition of the sampled shark community. Because we did not have information on the level of uncertainty around these percent values, we assumed an associated SE of 4%. We will call this approach the Wheeler scenario.

(2) Macroecological theory. In size-structured ecological communities, density is predicted to scale with body mass according to

$$N \propto M^{-0.75 + \log_{10}(TE)/\log_{10}(PPMR)} \tag{6}$$

where N is the density of size classes, M is the mean body mass of such a class, TE is transfer efficiency, and PPMR is the average predator-

prey mass ratio (54). We used this function to calculate the expected density for each species. As a proxy of body mass, we used the species' maximum weight (W) estimated from total length (TL), $W = aTL^b$ (data and methods for estimating species' maximum weight are detailed in the Supplementary Materials). For TE and PPMR, we used values commonly found in marine communities and published in Trebilco et al. (5). We then calculated a prior distribution of species densities by randomly selecting 1000 values of a, b, TE, and PPMR from appropriate statistical distributions. For a and b, we used a lognormal distribution $\ln\mathcal{N}(\mu, \sigma)$, where μ and σ were calculated from the logarithm of empirical values extracted from shark species in fishbase. For TE, we used a normal distribution $\mathcal{N}(\mu = 0.1, \sigma = 0.058)$, and for PPMR, we used a uniform distribution $\mathcal{U}(100, 3000)$ [the distribution parameters were taken from Trebilco et al. (5)]. We will call this approach the macroeco scenario.

We then build a prior of K by multiplying the values of shark density ($\bar{x}^*$) obtained from the meta-analysis by the extension of coral reef habitat in the Chagos archipelago. Total surface of coral reef habitat was extracted from Andrefouet et al. (55). Finally, we multiplied the obtained total number of sharks by the estimated relative proportions (f_i) of the focal species in the unobserved virgin community.

Abundance index
For observed indices of population abundance O_t, we used shark sightings recorded in visual census surveys carried out in the Chagos archipelago between 1976 and 2012 (23, 27). Species-specific sightings per hour of scuba diving [hereby referred to as sightings per unit of effort (SPUE)] were available from 1996 to 2012. We extracted mean annual SPUE (O_t) and confidence intervals from Graham et al. (27). O_t SEs were estimated from the reported CIs by assuming a normal distribution (that is, $\left|\frac{CI_{0.025|0.975} - \mu}{1.96}\right|$). Because the published data referred to all sharks, we extracted species-specific O_t by extracting the annual proportions of the species reported by Graham et al. (27). In these data, species-specific proportions were absent for the 1970s. We estimated these proportions from the following:

(1) An exploratory scientific longline survey carried out throughout the Indian Ocean by the Soviet Union (33). From this survey, we selected the longline sets deployed in the sector between 0° to 25°S and 55° to 75°E. In this area, we assumed that the longline sets sampled habitats similar to those in the Chagos archipelago. We fit generalized linear models (GLMs) with negative binomial distributions to the catch data to obtain standardized catches per unit of effort (CPUE) (56). Model selection was done by taking an information theoretic approach (details on the standardization process is indicated in the Supplementary Materials) (57), and from a final set of plausible models, we estimated an average model to predict species-specific CPUEs in areas deemed to encompass reef habitats (that is, close to the coast, for bottom depths equal to 70 m, and hook depths of 50 m) (fig. S1). From the standardized CPUEs, we calculated the frequency of occurrence f_i of each species in 1975 as $f_i = \frac{\widetilde{cpue_i}}{\sum_{i=1}^n \widetilde{cpue_i}}$, where n is the number of species for which we could predict a standardized index of abundance, and $cpue_i$ is the number of sharks caught per 1000 hooks deployed for species i. The prior distribution of relative proportion was estimated by randomly sampling 1000 values from a normal distribution $N(\mu = \widetilde{cpue_i}, \sigma = se(\widetilde{cpue_i})$. For each draw, we calculated the relative proportion of species and thus we built a distribution of 1000 relative proportions. The shapes of the generated distributions were skewed and thus we parameterized them with a beta distribution. Hence, from the mean and SD of the generated

distributions, we calculated the α and β from the mean (μ) and SD (σ²) of the empirical distribution rescaled to its maximum value (so that the empirical distribution ranged from 0 to 1); that is, $\alpha = (\frac{1-\mu}{\sigma^2} - \frac{1}{\mu}\mu^2)$ and $\beta = \alpha(\frac{1}{\mu} - 1)$. We will call this approach the "USSR" scenario.

(2) We asked C. Sheppard, one of the scientists participating in the early surveys, about the proportions of sharks he saw. In an earlier publication, he and other coauthors (26) reported that silvertip sharks were the most abundant species seen by scuba divers in the 1970s but did not specify the exact magnitude of this abundance. Hence, when we asked whether they could remember a more precise estimate of the species' relative abundance, they reported that silvertip sharks and whitetip sharks were about 5 to 10 times more abundant than gray reef sharks. Therefore, we assumed that, on average, silvertips and whitetip reef sharks were 7.5 and 6.5 times more abundant than gray reef sharks, respectively, and the remaining shark species accounted for 1% of the sightings. Solving a system of equations with these conditions, it was found that silvertip and gray reef sharks accounted for 49.5 and 5.72% of the sightings. This approach will be called the "guess" scenario.

The information elicited from the divers also gave us the opportunity to model the two species jointly. There is important information to be gained by modeling the species jointly. Our qualitative information that there are roughly 5 to 10 times more silvertips than gray reefs in 1975 amounts to a constraint

$$\frac{N_{1,\,silvertip}}{N_{1,\,gray\,reef}} = \frac{P_{1,\,silvertip} \cdot K_{silvertip}}{P_{1,\,gray\,reef} \cdot K_{gray\,reef}} \approx 5-10 \qquad (7)$$

We model this approximation by a normal distribution centered at 7.5 with an SD of 1.5. Given the uncertain information about carrying capacities and proportions of carrying capacities (P_1), we expected this constraint to increase the precision of our posterior inferences. The joint modeling would ensure that inferred parameter values are compatible not only with the species-specific statistics (for example, observed indices O_t) but also with cross-species statistics such as the ratio of observed abundances between the two species.

To explore the effect of this constraint, we run the models both separately, for each species, and jointly. In the separate analyses, we specified independent priors

$$P_{1,\,silvertip} \sim \mathrm{Unif}[0.5,1] \qquad P_{1,\,gray\,reef} \sim \mathrm{Unif}[0,0.5] \qquad (8)$$

In the joint analyses, we used a dependent prior

$$P_{1,\,silvertip} \sim \mathrm{Unif}[0.5,1] \quad P_{1,\,gray\,reef} = \frac{P_{1,\,silvertip} \cdot K_{silvertip}}{\rho \cdot K_{gray\,reef}} \quad \rho \sim N(7.5,1.5) \qquad (9)$$

We also decided to conduct a joint analysis for the USSR scenario. In this case, the qualitative information provided to us by the divers is possibly at odds with the USSR survey, but an advantage of Bayesian modeling is the ease with which it can integrate different and even conflicting pieces of information. Ultimately, both the diver's guess and the USSR survey provide only noisy approximations to reality. The model then compromises between these two sources of information to achieve inferences most compatible with the data and our prior knowledge. Thus, when gathering data from multiple sources,

one does not need to decide on a single definitive source, but can use all the data and let the model decide to what extent it trusts each source.

Coefficient q
The coefficient q relates the indices of abundance (O_t) to the population size ($O_t = q * N_t$). We had no information about this value. Therefore, we built an uninformative prior according to a uniform distribution $\mathcal{U}(0.000001, 0.001)$. The limits of the distribution were set using plausible values gauged by comparing the estimated priors of carrying capacity and the O_t. We used a range that would have underlined populations from a few thousand to millions of sharks.

Total catch
To evaluate the source of fishing mortality for sharks in the BIOT, we reviewed published primary and gray literature reporting the number and kind of fishing fleets operating in the area. From these fleets, we identified those capable of generating fishing mortality for reef sharks.

Catch from seizure reports
IUU fishing is considered the main source of fishing mortality for reef sharks in the BIOT (23). We estimated C_t for the period 1996 to 2015 by using seizure reports of the fishery patrolling vessel (FPV, fig. S8). The Marine Resources Assessment Group (MRAG) and UK FCO compile these reports when illegal fishing operations are detected and intercepted inside the BIOT. Catch reports were only available from 2008 to 2015 and included 56 IUU operations (Fig. 1). Arrest records were available since 1996 (29). From these data, we calculated the expected number of sharks caught by each boat for each species for each year (fig. S8). Because seizure reports were often incomplete (that is, missing catch records for all or some species), we fitted a GLM with truncated negative binomial distribution (TNBD) (56) to the positive catches and predicted the expected number of annual shark catches per vessel for the period 2008 to 2015 (see the Supplementary Materials for details). Using the TNBD was instrumental to overcome the problem of identifying true zeros and missing values in the catch data. To extend the series to 1996, we assumed that between 1996 and 2008, catches were equal to the average in the period 2008 to 2015.

Finally, we predicted the total annual number of sharks caught by multiplying the average catch rate of sharks per boat per year by the predicted number of boats that would have entered the BIOT (including those that were undetected). These were calculated by multiplying the number of boats arrested on record by 10, as previous estimates suggested that about 10% of the boats incurring in the area are successfully intercepted by the FPV (Supplementary Materials) (23).

Catch from longline fishing
(1) 1968 to 1989. In addition to the IUU catches, we also calculated those coming from the longline fishery that operated in BIOT before the reserve's establishment in 2010. We calculated the likely number of reef sharks caught by this fishery over the considered period by multiplying species-specific CPUEs recorded in the area by the total number of hooks deployed locally by the fishery. Standardized CPUEs were obtained from the USSR surveys by using the methods described above. To predict total catch around the Chagos archipelago, we first predicted species-specific CPUE for the average bottom depth, set depth, distance from the 30-m isobaths, and the set's soak time of all the survey sets deployed in the sector around BIOT. We reasoned that the empirical distribution of these experimental sets might have represented a reasonable approximation of where longline-fishing fleets operated in the area. Total number of hooks deployed in this area was extracted from the online catch and effort database published by the Indian Ocean Tuna

Commission (*30*). This database stratifies data in 5° geographic cells. We selected only the cells overlapping with the BIOT (that is, nine cells going from 65° to 80°E and 0° to 10°S). We then obtained the number of hooks likely deployed in the BIOT by prorating the total number of hooks recorded in this 9° cell window with the ratio between the ocean surface of the BIOT (~545,000 km^2) and the total surface of the selected nine-cell square. In this way, we calculated the catches from 1968 to 1989, which is the period for which the standardized catch rates were available.

(2) 1993 to 2010. Before the establishment of the MPA, a licensed longline fishery for bigeye tuna and yellowfin existed within the BIOT. Vessels fishing within the FCMZ (that is, the BIOT's EEZ) were required to submit comprehensive logbook data. The historical longline logbook records from within the BIOT pertain to the period July 1993 to May 2010. Data were collated by the MRAG who, on behalf of the UK government, granted and managed fishing licenses within BIOT during that period (*9*). For every fishing event (longline set), data on date, location (latitude/longitude), number of hooks deployed, and catch composition to the species level were available. However, sharks were lumped in the general group "elasmobranchs." Therefore, from these data, we could extract only fishing efforts (number of hooks deployed). Independent analyses on an observer survey estimated that shark CPUE was about 3.6 individuals per 1000 hooks between 2000 and 2003 (*58*) and that reef sharks accounted for 7% of all sharks caught. The proportions on gray reef and silvertip sharks were not reported. Therefore, we used the empirical CPUE proportions we estimated for the USSR survey in 1987 (the most recent year in the survey, that is, gray reef shark CPUE accounted for 22% of the reef sharks and silvertips accounted for 78% of the catches). Catches for missing years between the historical and the most recent period were estimated by linear interpolation.

Dealing with catch reconstruction uncertainty

We acknowledge that (i) the reconstructed catch series, $\hat{C}_t$, are noisy estimates of the true C_t and (ii) our reconstruction may be severely downward biased in the period before 1996 because of the lack of seizure reports or unmonitored historical shark catches. Our model tries to accommodate both sources of error. First, we assume that, on the log scale, our reconstruction is a normal deviate from the true C_t

$$\begin{aligned} \hat{C}_t \sim \psi C_t e^{w_t} & \quad \text{if } t < 1996 \\ \hat{C}_t \sim C_t e^{w_t} & \quad \text{if } t \geq 1996 \end{aligned} \qquad w_t \sim N(0, (\log \mathrm{Cse})^2) \quad (10)$$

where log Cse is the SE of our catch estimates and is reflecting this unobserved fraction of catches. Before 1996, we expected a certain amount of censoring because of no monitoring by the BIOT patrolling boat. After 1996, we assume that we had a reasonable estimate of shark removal.

Then, we assumed that the yearly catches, C_t, varied about two period-specific averages, one ($e^{\mu_{\mathrm{catch}} + \delta_{\mathrm{catch}}}$) for the period before 1996 when we believe monitoring was laxer and another one ($e^{\mu_{\mathrm{catch}}}$) for the period after when the patrolling vessel was actively monitoring the area and reporting illegal fishing events

$$\begin{aligned} C_t \sim e^{\mu_{\mathrm{catch}} + \delta_{\mathrm{catch}}} e^{z_t} & \quad \text{if } t < 1996 \\ C_t \sim e^{\mu_{\mathrm{catch}}} e^{z_t} & \quad \text{if } t \geq 1996 \end{aligned} \qquad z_t \sim N(0, \sigma_{\mathrm{catch}}^2) \quad (11)$$

where $\sigma_{\mathrm{catch}}^2$ represents the variability of the catches across years in the same period.

Because these means are location parameters, we used noninformative uniform priors for both $\mathcal{U}(0, \infty)$. For the parameter ψ, we used a uniform prior on $\psi \sim \mathcal{U}(0, 1)$, and for $\sigma_{\mathrm{catch}}^2$, a Cauchy distribution with median 0 and scale 1 (restricted to positive values).

Model fitting

For each species, we ran the stock assessment models under four different scenarios (Table 2) and with both the separate and joint modeling approach (results of the joint modeling are reported in the Supplementary Materials). These scenarios reflected different assumptions about the baseline structure of the shark community and relative proportions of shark abundance in the 1970s. Model fitting was done in Stan using the R package rstan. For each model, we ran Stan with four Markov chains, each with a warm-up phase of 20,000 iterations, followed by 200,000 additional iterations, which were kept for analysis after appropriate thinning (by every 200 iterations). We assessed convergence using the Gelman-Rubin $\hat{R}$ statistic (*59*) and by visual inspection of various parameter trace plots. We also calculated the WAIC for each model to assess model performance across the different scenarios and modeling structure (that is, separate and joint modeling) (*60*). Model output including scripts, data, and samples from the posterior distributions are included as R data files in the Supplementary Materials.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/3/eaaq0333/DC1

Supplementary Materials

fig. S1. Standardized CPUEs of elasmobranchs detected in the USSR surveys.

fig. S2. Summary of shark catches from seizure reports.

fig. S3. Parameter estimates of the models standardizing the USSR surveys' CPUE.

fig. S4. Meta-analysis of baseline shark densities.

fig. S5. Handline survey's CPUE.

fig. S6. Baseline community composition as estimated from ecological theory.

fig. S7. Posterior means and credible intervals of shark population abundances.

fig. S8. Catches of vessels intercepted by the BIOT patrolling vessel.

fig. S9. Geographic distribution of the USSR longline sets.

fig. S10. Pictures of seized shark catches, a BIOT patrolling vessel, and a typical illegal fishing boat entering the BIOT.

table S1. Input life histories for *Carcharhinus amblyrhynchos*.

table S2. Input life histories for *Carcharhinus albimarginatus*.

table S3. Summary statistics of the SPMs.

Model output files

Reference (*65*)

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Shark baselines and the conservation role of remote coral reef ecosystems

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