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Extinction of a shark population in the Archipelago of Saint Paul's Rocks (equatorial Atlantic) inferred from the historical record

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ABSTRACT

Detecting and determining the validity of local extinctions is an important conservation measure in order to uncover management failures. There are quantitative and qualitative methods that estimate extinction probability based on past sighting records. However, because current baselines about species' abundances and distributions in the sea were mostly established after humans had started affecting marine populations, researchers must often rely on historical data to elucidate past environmental conditions. We review early historical records from the Archipelago of Saint Paul's Rocks, together with data from recent expeditions, with the aim of testing the hypothesis that reef sharks (*Carcharhinus* spp.) have become extinct there. Our analyses are based on non-parametric probabilistic tests for extinction and on a qualitative framework to examine and judge as objectively as possible the likelihood of local extinction. Until the mid-20th century, visitors to St. Paul's Rocks invariably commented on the remarkable number of sharks around the Archipelago. These observations contrast with those of expeditions carried out during the last decade, which report no carcharhinid reef sharks while scuba diving in the archipelago, despite many more hours of underwater fieldwork than previous expeditions. All quantitative and qualitative methods conclude that the reef shark *Carcharhinus galapagensis* is locally extinct at St. Paul's Rocks after a sharp decrease in abundance that took place following the commencement of fishing. However, the persistence of occasional individuals of the once locally common *Carcharhinus falciformis* in the vicinity of the Archipelago, as a result of constant immigration of this oceanic species from outside the area, suggest that the population might recover if the present fishing pressure was removed.

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1. Introduction

Human impacts on marine environments have been shown to be greater than previously thought (Jackson et al., 2001; Roberts, 2007). In particular, the effects of unsustainable commercial fishing are highly pervasive, collapsing exploited populations in a matter of decades and producing direct and indirect effects through community food webs (Pauly et al., 1998; Jackson et al., 2001; Worm and Myers, 2003; Ward and Myers, 2005). Depletion of top-predators and large herbivores by intensive fishing has altered the structure and function of marine systems (Bascompte et al., 2005; Mumby et al., 2006; Myers et al., 2007). Moreover, exploitation is considered to be the main factor leading to local extinctions, i.e. extinction that is restricted to local or regional scales, in the sea (Dulvy et al., 2003).

Understanding the full extent and manner in which anthropogenic forces have impacted natural ecosystems requires knowl-

edge of their unexploited state (Baum and Myers, 2004). Unfortunately, most environmental baselines were established after humans had started affecting marine populations (Pauly, 1995). As a result, researchers must rely on historical evidence in order to estimate long-term changes in marine ecosystems (Jackson, 1997; Sáenz-Arroyo et al., 2005a,b, 2006; Roberts, 2007). Over the last decade, researchers from various disciplines have engaged in reconstructing past ecosystem changes. To find historical baselines, they have used a remarkable diversity of data sources, ranging from paleontological and archaeological evidence, to molecular markers, historical records and fisheries statistics (Lotze and Worm, 2009).

The Archipelago of Saint Paul's Rocks (*Arquipélago de São Pedro e São Paulo*), hereafter St. Paul's Rocks, is a remote group of barren islets in equatorial Atlantic Ocean, on the mid-Atlantic ridge (00°55'N; 29°21'W); The Archipelago, which belongs to Brazil, is only 400 m across at its greatest extent, lying approximately 960 km off Cabo de São Roque, north-eastern coast of Brazil and 1890 km south-west of Senegal, West Africa (Fig. 1). The fauna of St. Paul's Rocks is of considerable zoogeographical interest because of its isolation, small size and the presence of endemic species

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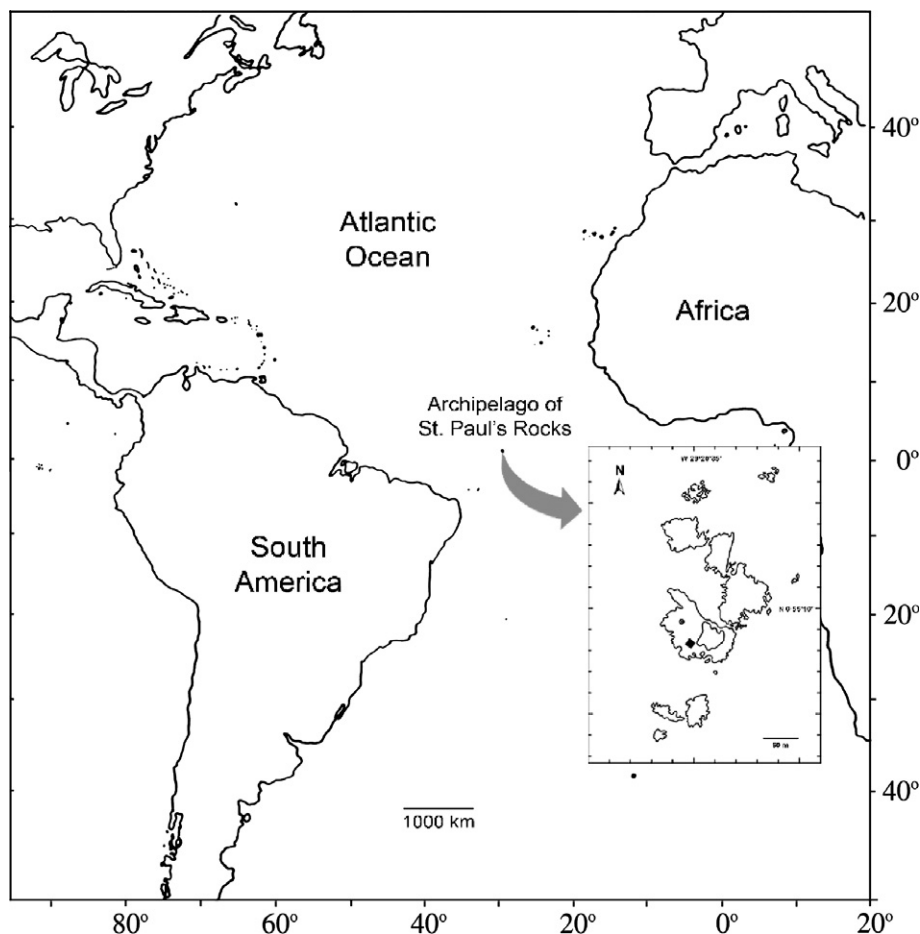


Fig. 1. Location of the Archipelago of Saint Paul's Rocks.

(Lubbock and Edwards, 1980, 1981; Edwards and Lubbock, 1983a; Joyeux et al., 2001; Feitoza et al., 2003; Luiz et al., 2007).

Commercial fishing by Japanese boats commenced at St. Paul's Rocks in 1956 under an agreement with the Brazilian government. Seven years later this was suspended (Oliveira et al., 1997; Vaske et al., 2010). Brazilian fishing boats started exploiting the area sporadically in the 1970s, and since 1988 a commercial fishing fleet from Brazil has been operating continuously (Oliveira et al., 1997; Vaske et al., 2006, 2010). Fishing is carried out from close to the shore (10s of meters from the Rocks) to a few kilometers from the Archipelago. The main species targeted are large pelagic fishes, which comprise 90% of the catch, and include yellowfin tuna (*Thunnus albacares*), wahoo (*Acanthocybium solandri*) and rainbow runner (*Elagatis bipinnulata*) (Oliveira et al., 1997; Vaske et al., 2006, 2010), which are caught mostly by longlines and hand lines. The fleet is composed of small boats (15-m trawlers), which continually take turns to fish, with from one to a maximum of four fishing boats operating simultaneously in the Archipelago every day, all year round (Vaske et al., 2006). Despite not being targeted, significant quantities of sharks were caught by commercial fishing until the 1970s (Oliveira et al., 1997; P. Conolly, pers. comm. to A.J.E.). Nowadays, only oceanic sharks are occasionally caught by longlines (Vaske et al., 2010).

Our study focuses on the drastic reduction of the carcharhinid shark population (historically primarily consisting of the Galapagos shark, *Carcharhinus galapagensis*, and the Silky shark, *Carcharhinus falciformis*; see Edwards and Lubbock, 1982) at St. Paul's Rocks. Both species are large bodied (up to ~300 cm length) and have wide circumtropical distributions (Compagno, 1984), however, they present contrasting behaviour and habitat usage. *C. galapag-*

ensis aggregates around isolated oceanic islands where it is often found in large numbers (Randall, 1963; Edwards and Lubbock, 1982; Compagno, 1984; Wetherbee et al., 1996; Hobbs et al., 2008). It lives close to reefs, has a limited home range, and is considered as resident at the islands where it is found (Meyer et al., 2010). Conversely, *C. falciformis* is an epipelagic species, inhabiting mostly oceanic open waters but occasionally found roaming over reefs (Compagno, 1984). Large bodied sharks have an important ecological role as predators in marine habitats, exerting a strong top-down control over the abundance of other marine organisms (Heithaus et al., 2008). Both species have low reproductive capacity and limited intrinsic rebound potential, and are therefore considered to be susceptible to over-exploitation (Smith et al., 1998; Cavanagh et al., 2003). The major threats for these species are longlines and other bait-fishing activities around islands and seamounts throughout their range (Cavanagh et al., 2003; Afonso et al., 2011; Robbins et al., 2011; Whoriskey et al., 2011).

Expeditions in the 18th, 19th and most of the 20th century that visited St. Paul's Rocks, including those of Charles Darwin on the H.M.S. *Beagle* in 1832 (Darwin, 1845) and of the officers and crew of H.M.S. *Challenger* in 1873 (e.g. Moseley, 1892), invariably commented on the remarkable number of sharks around the Archipelago (Edwards, 1985). These observations contrast with those of expeditions carried out during the last decade by Brazilian field ichthyologists who report no reef sharks, despite many more hours of underwater fieldwork than previous expeditions (Feitoza et al., 2003; Vaske et al., 2005).

Assessing local extinctions is particularly important because they are the warning signs of conservation and management failures and are early steps toward global extinctions (Pitcher, 2001;

Dulvy et al., 2003). Determining the validity of a local extinction is therefore important, and can be instrumental in promoting political will to develop legal protection to prevent further losses.

In order to detect changes in the carcharhinid shark population at St. Paul's Rocks, we compare sighting records before and after the commencement of commercial fishing, based on review of published early travelers' diaries, naturalists' observations and scientific papers that provide casual or formal accounts of the biology of Saint Paul's Rocks. Our aim is to test the hypothesis that sharks of the genus *Carcharhinus* have become extinct at St. Paul's Rocks. Our analyses are based on two approaches using the historical data: (1) from non-parametric probabilistic tests for extinction and estimates of population decline, based on sight records (McPherson and Myers, 2009; Rivadeneira et al., 2009) and (2) under a qualitative framework to examine the historical data and judge as objectively as possible the likelihood that the species have become extinct (Butchart et al., 2006).

2. Materials and methods

2.1. Data collection

We accessed historical records of sharks from books, journals and reports from the 18th century to the present. Biological data (opportunistic collections of fish, marine invertebrates, algae, birds and terrestrial arthropods) on St. Paul's Rocks have been derived from occasional fleeting visits by oceanographic vessels which, apart from H.M.S. Challenger, have been primarily intent on non-biological research, and from brief stops by ships carrying polar expeditions to or from Antarctica (Edwards, 1985). Members of the Cambridge Expedition to Saint Paul's Rocks, which visited the Archipelago in 1979, eventually provided a detailed overview of their biology (e.g. Lubbock and Edwards, 1981; Edwards and Lubbock, 1983a,b). All references in the exhaustive bibliography of the natural history of St. Paul's Rocks (Edwards, 1985) were reviewed for information on sharks as were all subsequent published accounts and unpublished records of Brazilian expeditions. Usable shark sightings data were obtained from visits (29) where the marine fauna was remarked upon.

In 1998 the Brazilian Navy established a scientific research station at St. Paul's Rocks. Data from the period after the research station establishment were obtained by interviewing the lead researchers of 13 expeditions made from 1998 to 2009, of which the primary objective was to study the demersal fish fauna. During interviews, the researchers were required to state if they had recorded any sharks during their underwater fieldwork and, if positive, if they are able to identify the species they had sighted. Based on the data derived from historical accounts and interviews we have constructed a sighting record for carcharhinid shark occurrences based on the year of each expedition, the presence or absence of sharks, and the time spent by each expedition at the Archipelago.

Based on behavioral observations, photographs and measurements of three specimens, Edwards and Lubbock (1982) concluded that there were two carcharhinid species present at the Rocks. These were *C. galapagensis*, which was the most common species observed during the daytime, and *C. falciformis*, which was observed close to the Rocks at night (Lubbock and Edwards, 1981).

2.2. Data analyses

The absence of a species in a sighting record does not necessarily mean that it is extinct. Instead it could reflect reduced sampling effort or short-term variation in the abundance of the species (Rivadeneira et al., 2009). In order to address this shortcoming, probabilistic methods have been developed to generate confidence

intervals for the estimated extinction time given the characteristics of a sighting record, which can then be used to evaluate whether a species that has not been sighted for some time is likely to be extinct (Reed, 1996; Roberts and Solow, 2003; Rivadeneira et al., 2009; Elphick et al., 2010). These methods, however, differ in the stringency of their assumptions about the nature of the sampling record. For example, some tests are less complex than others but require a constant sampling effort over time. Other methods make less restrictive assumptions about sampling intensities, but tend to produce large confidence intervals (Rivadeneira et al., 2009).

Rivadeneira et al. (2009) analyzed seven statistical tests according to their restrictive assumptions and performance under different sampling scenarios. They provide a useful guideline to choose among different tests based on the characteristics of the sighting records. For St. Paul's Rocks, these are as follows: (1) the sampling effort is variable over time; (2) sightings arise from sporadic expeditions separated by periods of no effort; (3) sampling has not declined over time; and (4) the locality has been well sampled after the putative extinction date of the species. Two probabilistic tests fit these characteristics and were used to test the hypothesis of extinction for the Galapagos shark at St. Paul's Rocks. These tests were originally described by Marshall (1997) and McCarthy (1998) and were summarized by Rivadeneira et al. (2009). The formulae for each test are, respectively:

$$\sum_{i=T_{n+1}}^{i=T_{ci}} e_i = \lambda \sum_{i=1}^{i=T_n} e_i \quad (1)$$

and

$$\sum_{i=1}^{i=T_{ci}} e_i = \frac{\sum_{i=1}^{i=T_n} e_i}{\alpha^{(1/H)}} \quad (2)$$

For both methods, extinction time corresponds to the time at which the sampling level at the left side of the equations equals the right side of the equation. T_{ci} is the upper bound of the confidence interval of the extinction time, T_n is the time of the last positive sighting, α is the confidence level (0.05), H is the total number of sightings, and e_i is the sampling effort (probability of sampling) in the i th year (Rivadeneira et al., 2009). In Eq. (1) $\lambda = \alpha^{-\frac{1}{(H-1)}} - 1$. The number of days that each expedition spent in the Archipelago of St. Paul's Rocks was used as proxy for sampling effort.

In order to investigate the timing and causes of the population decline of sharks we used a further approach that focuses on estimating population trends rather than verifying extinction (McPherson and Myers, 2009). This method fits a series of generalized linear models that provide multiple estimates of decline under alternate scenarios regarding the appropriate reference period. As in the previous two methods, we treated years in between the expeditions as missing values. Details about the method's assumptions and programming code to implement it in the freely available software R can be found in McPherson and Myers (2009).

Complementing the statistical tests, we have evaluated the likelihood that carcharhinid sharks have become extinct at St. Paul's Rocks using a framework for categorizing the level of confidence that a species is actually extinct based on observational data (Butchart et al., 2006). The framework considers evidence for and against extinction and the time since the species was last reported. Specifically, it is considered as evidence for extinction if: (a) for species with recent last records, the decline has been well documented; (b) severe threatening processes are known to have occurred (e.g. extensive habitat loss, the spread of alien invasive predators, intensive hunting, etc.); (c) the species possesses attributes known to predispose taxa to extinction, e.g. natural rarity and/or tiny range (as evidenced by paucity of specimens relative

Table 1
Historical observations of sharks at St. Paul's Rocks.

Perseverance: December 1799

"Sharks were numerous about the ship, and our people, in attempting to take them, lost a number of hooks and lines, and broke several pair of grains [pronged harpoons]." (Delano, 1817)

HMS Beagle: February 1832

"While our party were scrambling over the rock, a determined struggle was going on in the water, between the boats' crews and sharks. Numbers of fine fish, like the groupars [sic] (or garoupas) of the Bermuda Islands, bit eagerly at baited hooks put overboard by the men; but as soon as a fish was caught, a rush of voracious sharks was made at him, and notwithstanding blows of oars and boat hooks, the ravenous monsters could not be deterred from seizing and taking away more than half fish that were hooked

"At short intervals the men beat the water with their oars all round the boats, in order to drive away the sharks; and for a few minutes afterwards the groupars swarmed about the baited hooks, and were caught as fast as the lines could be hauled up – then another rush of sharks drove them away – those just caught were snatched off the hooks; and again the men were obligated to beat the water." (Fitzroy, 1839)

"The sharks and the seamen in the boats maintained a constant struggle which should secure the great share of the prey caught by the fishing-lines." (Darwin, 1845)

HMS Erebus: November 1839

"One of our party, in attempting to wade across a narrow channel, was taken off his feet by a heavy wave, ... was as frequently carried back by the retiring wave; whilst, unable to afford him the least assistance, we could only look on from the opposite side with the most painful apprehensions of seeing him taken away by one of the numerous sharks that were playing about the cove..." (Ross, 1847)

HMS Challenger: August 1873

"In the evening volunteers for fishing were called for ... Then we caught more sharks, and it was at last discovered that we ought to have been fishing at the surface, and not at the bottom. As soon as we took the sinkers off our lines and allowed the baits to float we began to haul in large fish ... The fish were "Cavalli"... a species of *Caranx* ... Every now and then some one hooked a shark (*Carcharias sp.*), and then there was a tremendous fight, and all the lines in the boat were tangled and fouled ... Sometimes, a tremendous sudden pull was felt at one's line, ... and some big shark went off with hook and bait ..." (Moseley, 1892)

"Excellent and most exciting fishing it was, excepting for the sharks, which were most exasperating, rushing off with the hooks in a hopelessly irresistible manner. ... We also caught numbers of the most unwelcome young sharks." (Campbell, 1876)

SY Scotia: December 1902

"Dec. 10th, St. Paul's Rocks, 0°55'N. 29°22'W. – Sharks innumerable. Secured eight specimens, and took dimensions and weight of each, ... Several fish seen but none caught, as the sharks took every bait." (Wilton, 1908)

"We backed in carefully and Pirie took the first chance to jump as the boat was pulled off. He touched the rock, missed his footing, and fell among the sharks. We had no time to think we had lost our doctor. One doesn't think on such occasions. Every man seized an oar or boat-hook and stabbed and pushed the sharks in the hope of scaring them. Pirie popped up alongside the boat and Davidson caught him by the scruff of the neck from the turmoil of angry sharks ..." (Brown and Murdoch, 1923)

RYS Valhalla: December 1902 and December 1905

"The water round the rocks swarms with sharks ..." (Nicoll, 1904)

"Fishing here presented a somewhat unusual difficulty, for sharks swarmed in incredible numbers, and it was a difficulty task to avoid hooking them instead of more serviceable game; indeed, so numerous were the sharks that, on our return to the ship, we found that during our absence no less than twenty had been caught, all of them at no greater distance than two hundred yards from the shore."

"Several fishes and one bird were dropped into the water during the process of embarkation, and they were immediately taken by sharks, so it was just as well that none of our party slipped into the water."

"Judging from the enormous number of sharks round St. Paul's Rocks, there should be a great supply of food." (Nicoll, 1908).

RYS Quest: November 1921

"On approach to the Rocks it was evident that a considerable swell was running, and the landing was slightly difficult ... Sharks swarmed about the boat."

"The cove in the midst of the Rocks teems with marine life. The floor, which lies at from 6 to 8 fathoms at one end and slopes in to about 1 fathom, is covered with seaweed. Sharks of small size, from 2 to 8 feet in length, swarm in large numbers. It was interesting to note that the fish which maintained a certain level seemed to be unafraid of them, but if they left that level, as for instance when we hooked them and drew them up, the sharks turned and went for them in a flash. We were desirous of obtaining a number of fresh fish for food, but had the greatest difficulty in getting them past the sharks to the surface. We at last adopted the expedient of harpooning the sharks, killing them and throwing them back." (Wild, 1923a)

"We lay to under their lee and dropped a boat. Immediately a countless shoal of sharks came about us, their fins showing above water in dozens on every side. ... The landing of the catch, however, proved not so easy. The little cove swarmed with sharks, which were attracted by the boat, and came about us in scores. ... The moment, however, we hooked one [fish] and started to pull it up, the sharks turned like a streak and went for it with such voracity that we had the greatest difficulty in getting it to the surface. What was worse, they frequently bit through the lines and took the hook also. ... On one occasion I succeeded in getting a fish clear of the water, and thinking for once I had eluded the sharks, was in the act of swinging it aboard when there was a flash of something white, an ugly snout broke water, and I was left gazing stupidly at half a head. ... Indeed, it was not safe to put a hand over the gunwale, for immediately a head rose towards it." (Wild, 1923b)

Meteor: 10 May 1925

"A shoal of sharks surrounded the ship, sometimes more than twenty, and after a short time we have one of these most hated enemies of the sailors on the fishing line to the joy of the crew." [This was then cut up and thrown to the other sharks.] (Speiss, 1928)^a

Albatross: 1948

"There was no need to swim for the shore, which was perhaps just as well, considering the throng of eager and probably very hungry sharks which expectantly crowded around the boat, viciously snapping at our oars! The main island, about 300 feet long, on which we landed – the other islands were inaccessible owing to the swell and the sharks – had the remnants of a small lighthouse on its highest rock, ..." (Pettersson, 1954)

USS Atka: March 1955

"The numerous sharks, which swarm in the waters of the cove and around the Rocks, speedily attack hooked fish and either snatch the whole fish off the line or leave only a half fish or head on the hook for the fisherman. On the ATKA, the chief medical corpsman hooked a beautiful tuna-like fish from the fantail several hundred yards off the Rocks, but when he hauled in his catch all that remained was an enormous head fully a foot high ..." (Tressler et al., 1956)

R.V. Chain: March 1963; *R.V. Atlantis II*: 1966

"Not merely has the shark population – as noted during both our 1963 and 1966 visits – diminished to a point that permits ready retrieval of fish hooked close to the islands, quite contrary to the experiences of the men on 'Beagle' or on 'Challenger', and even permits a toothsome geologist or two to fall into the lagoon and come up swimming with his rocks in his hands." (Bowen, 1966)

"Many small sharks were seen, although only one large one was noticed by anyone in our party. There were fewer sharks than reported by earlier visitors." (Masch, 1966).

RRS Bransfield: May 1971

"... the ship's launch was used to catch fish just off-shore from the Rocks. ... Difficulty was experienced in obtaining these specimens as fish once hooked were frequently taken by marauding sharks before they could be brought on board." (Smith et al., 1974).

Table 1 (continued)*Cambridge Expedition: September 1979*

"... at night there always seemed to be 5–20 or more sharks around our boat (as observed from the deck and on one occasion from a cage lowered beneath the boat). Most of the sharks are relatively small (1–1.5 m T.L.). ... Sharks are rarely seen away from the Rocks during the day, but at night considerable numbers swim close to the surface. We often heard or saw splashing at night that seemed to involve sharks, and it appeared that the sharks were attempting to feed on the flying fishes; ..." (Lubbock and Edwards, 1981)

"During the first two days at the rocks, divers were frequently surrounded by ten to twenty or more *C. galapagensis*. Subsequently sharks became significantly less common during daylight hours, although still numerous at night when at least five or six and sometimes up to twenty sharks (presumably both *C. falciformis* and *C. galapagensis*) could be seen around our boat. It was notable that during the day sharks hardly interfered with line fishing activities and were only rarely seen at the surface. ... suggest that the shark population may have declined somewhat in recent years; our observations are in agreement with such a conclusion. In this respect it is perhaps worth noting that the Rocks have recently been subject to occasional visits by Brazilian fishing boats; one of these recorded capturing two tons of sharks by accident in one evening while fishing for commercial species (P. Conolly, pers. comm.)."

"The carcharhinid population is still relatively dense, although there is some evidence of a decline in recent years perhaps as a result of increased fishing activity." (Edwards and Lubbock, 1982)

Segredos Submersos Expedition: November 1993

"All dives we made were magnificent, but the lack of sharks was noticeable."

"We carried luparas (sticks with explosive tips) and electric end sticks in order to repel the sharks we expected to find, ... truly, we never had to use these."

"Yet over the plateau, I saw two sharks swimming in circles ... they seemed to be in courtship behavior and were two meters length."

"... on afternoon we dove at the same plateau that we sought these two sharks in the morning ... we went to 33 m depth and nothing of sharks."

"... as we did not find the multitude of sharks we expected, we give up to descend the cage, even the luparas and the electric sticks were left on board during the subsequent dives." (Meurer, 2004)^a

^a Translated from the original German (Speiss, 1928) and Portuguese (Meurer, 2004) respectively.

Table 2

Sighting records from 1799 to 2009 of *Carcharhinus* sharks at St. Paul's Rocks. Estimations of the magnitude of population decline follow McPherson and Myers (2009). (NB: A magnitude of decline in abundance of 20 indicates a 20-fold decline i.e. population at one 20th, and is thus equivalent to a 95% decline.)

Date	Sighting	Sampling effort (days)	Estimated magnitude of decline (median and 95% CI)	References
1799, December	Yes	0.2	5.2 (1.3–31.2)	Delano (1817)
1832, February	Yes	0.4	5.4 (1.3–22.1)	Fitzroy (1839) and Darwin (1845)
1839, November	Yes	0.75	6.7 (1.4–31.1)	Ross (1847)
1873, August	Yes	2	7.6 (1.5–37.6)	Campbell (1876) and Moseley (1892)
1902, December	Yes	0.8	7.6 (1.6–33.2)	Brown and Murdoch (1923), Wilton (1908) and Nicoll (1908)
1905, December	Yes	0.5	9.3 (1.7–50.1)	Nicoll (1904, 1908)
1921, November	Yes	0.5	10.3 (1.8–58.5)	Wild (1923a,b)
1925, May	Yes	0.5	14.1 (2.1–96.4)	Speiss (1928)
1948	Yes	0.5	19.8 (2.2–174.1)	Pettersson (1954)
1955, March	Yes	0.25	25.5 (2.3–280.8)	Tressler et al. (1956)
1963, March	Yes	0.3	31.4 (2.2–437.8)	Masch (1966)
1966, April	Yes	1.25	39.0 (2.1–707.8)	Bowen (1966)
1971, May	Yes	0.12	51.2 (1.9–1357.4)	Smith et al. (1974)
1976	Yes	3	64.1 (1.6–2602.2)	L. Davidson (pers. comm.)
1979, September	Yes	8	78.7 (1.3–4741.5)	Lubbock and Edwards (1981) and Edwards and Lubbock (1982)
1993, November	Yes	7	NA	Meurer (2004) and E. Meurer (pers. comm.)
1998, August	No	10	NA	C.R. Rocha (pers. comm.)
1999, April	No	20	NA	L.A. Rocha (pers. comm.)
1999, November	No	10	NA	O.J. Luiz (pers. observation)
2000, April	No	15	NA	C.A. Rangel (pers. comm.)
2000, August	No	20	NA	B.M. Feitoza (pers. comm.)
2001, August	No	15	NA	B.M. Feitoza (pers. comm.)
2002, September	No	15	NA	C.A. Rangel (pers. comm.)
2006, January	No	15	NA	O.J. Luiz (pers. observation)
2007, April	No	15	NA	B.M. Feitoza (pers. comm.)
2007, May	No	15	NA	B.M. Feitoza (pers. comm.)
2008, February	No	3	NA	B.M. Feitoza (pers. comm.)
2008, April	No	15	NA	C.E. Ferreira (pers. comm.)
2009, June	No	15	NA	C.E. Ferreira (pers. comm.)

to collecting effort), or congeners that may have become extinct through similar threatening processes, and (d) recent surveys have been apparently adequate given the species' ease of detection, but have failed to detect the species. Evidence against extinction is considered if: (a) recent field work has been inadequate (any surveys have been insufficiently intensive/extensive, or inappropriately timed; or the species' range is inaccessible, remote, unsafe or inadequately known); (b) the species is difficult to detect (it is cryptic, inconspicuous, nocturnal, nomadic, identification is difficult, or the species occurs at low densities); (c) there have been reasonably convincing recent local reports or unconfirmed sightings; and (d) suitable habitat remains within the species' known

range, and/or congeners may survive despite similar threatening processes (Butchart et al., 2006). By explicitly laying out and classifying evidence for and against local extinction under this framework (see Table 3), we then make the judgment of species extinction based on qualitative historical observations as objectively as possible.

3. Results

Excerpts from historical observations of sharks at St. Paul's Rocks are presented in Table 1. Travelers and naturalists from

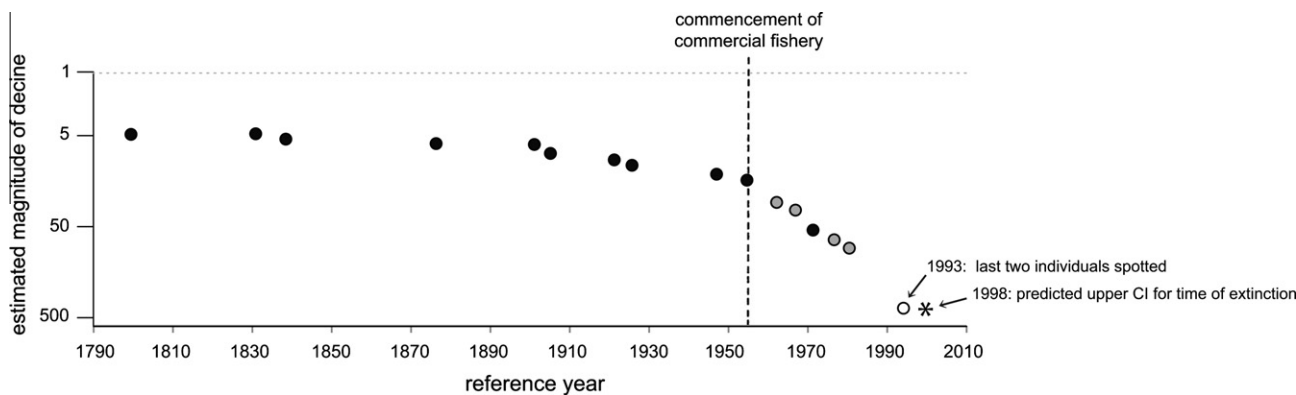


Fig. 2. Plot of the temporal distribution of sightings of reef sharks (*Carcharhinus* spp.) at St. Paul's Rocks and estimates of declines for any given reference year between 1799 and 2010. Grey circles denote sightings where a reduction in the population size of sharks was noted by the observers. The dashed line marks the year when commercial fishing at the Archipelago was first documented. The asterisk marks the upper bound of the 95% confidence interval for the local extinction time. The open circle indicates the timing of the last sighting of reef sharks at St. Paul's Rocks and does not indicate magnitude of decline.

the 18th to the 20th centuries frequently quoted the abundance of sharks in the St. Paul's Rocks as 'innumerable', 'countless' or 'so numerous'. Among the expressions that they used to communicate what they had seen were variations of 'water swarms with sharks' or 'sharks swarmed in incredible numbers' (Delano, 1817; Ross, 1847; Wilton, 1908; Nicoll, 1904, 1908; Wild, 1923b; Tressler et al., 1956). Several accounts considered landing on the islets as a dangerous endeavor because the abundance of sharks (Ross, 1847; Nicoll, 1908; Brown and Murdoch, 1923; Wild, 1923a; Pettersson, 1954). The overall impression is that sharks occurred there at unusually high densities, similar to those remarked on by 18th and 19th century travelers at remote Pacific locations such as Cocos Island, Revillagigedo Islands and Palmyra atoll (Colnett, 1798; Fanning, 1833; summarized in Roberts (2007)).

The former abundance of sharks is also illustrated by descriptions of fishing practices made by the crew of early expeditions. The quantity and the voracity of sharks were considered a nuisance to fishing because they usually seized and took away fish that were hooked (Fitzroy, 1839; Wild, 1923b; Tressler et al., 1956; Smith et al., 1974), broke gear, tangled lines, and snatched bait and hooks (Delano, 1817; Moseley, 1892; Wilton, 1908; Wild, 1923b). Sharks were considered an unwelcome catch, being less valuable as food than some bony fish species. Nevertheless, sharks were constantly caught due to the fervor with which they took bait and hooked fish, making it almost impossible to catch other fish (Campbell, 1876; Moseley, 1892; Nicoll, 1908).

Visitors in the second half of the 20th century were the first to note a decline in shark numbers. Two geological expeditions in 1963 and 1966 commented on the apparent decline in shark

Table 3
Evaluation of the qualitative evidence for and against local extinction using the framework of Butchart et al. (2006).

	Observational data
<i>Types of evidence for extinction</i>	
• For species with recent last records, the decline has been well documented	Yes. Observations made during expeditions in the latter part of the 20th century specifically commented on the decrease in shark numbers compared to early accounts
• Severe threatening processes are known to have occurred	Yes. Records of commercial fishing start a few years before the reduction in shark abundance was noticed for the first time. Commercial fishing efforts then intensified while carcharhinid sharks became less common, and eventually ceased to be recorded at the Rocks
• The species possesses attributes known to predispose taxa to extinction	Yes. The vulnerability of sharks to over-exploitation is well-known and characterized by life-history attributes like slow growth, late attainment of sexual maturity, long life spans and low fecundity (Stevens et al., 2000)
• Recent surveys have been apparently adequate given the species' ease of detection, but have failed to detect the species	Yes. Recent expeditions, made after 1993, have involved over six times the total sampling effort between 1799 and 1993 (~26 days)
<i>Types of evidence against extinction</i>	
• Recent field work has been inadequate	No. A series of expeditions whose primary objective was to study the demersal fish fauna were carried out during the last decade
• The species is difficult to detect	No. The Galapagos shark is large and conspicuous. It lives close to shore and has a small range (Meyer et al. 2010), making it easily detectable by SCUBA divers. Early expeditions generally detected the sharks within minutes of arrival
• There have been reasonably convincing recent local reports or unconfirmed sightings	No
• Suitable habitat remains within the species' known range, and/or allospecies or congeners may survive despite similar threatening processes	Appropriate habitat remains for <i>C. galapagensis</i> but it is unlikely that individuals remain undetectable due to the small shallow water area (~0.5 km ² <60 m deep) of the Archipelago, which allowed it to be thoroughly surveyed during recent expeditions. The epipelagic congener <i>C. falciformis</i> was also observed to live at the Rocks as evidenced by specimens collected (Edwards and Lubbock, 1982), but since 1993, no carcharhinid has been recorded during underwater field surveys. The continued catch of occasional <i>C. falciformis</i> on longlines of boats fishing nearby the Archipelago are probably due to open sea strays

numbers since the 19th century, noting that the sharks did not interfere with fishing (Masch, 1966; Bowen, 1966). Members of the Cambridge Expedition to St. Paul's Rocks in 1979 also commented on the apparent decrease in the shark population (Lubbock and Edwards, 1981; Edwards and Lubbock, 1982), but still reported 10–20 *C. galapagensis* surrounding them during dives.

The last confirmed sighting of Carcharhinidae sharks at the Archipelago was made in 1993, when two individuals were video recorded underwater (Meurer, 2004; E. Meurer, pers. comm.). In the period between 1998 and 2009, 13 expeditions primarily focused on studying the demersal fish assemblage failed to detect any *Carcharhinus* spp. despite approximately 500 h of underwater fieldwork over 183 days (compared to the 16 records from previous visits which collectively total only 26 days).

Analysis of the sighting record (Table 2) using Eqs. (1) and (2) indicate the upper bound of the 95% CI for extinction time occurring at 1998 (Fig. 2). Both statistical methods suggest that for the relatively large and obvious carcharhinid sharks at this small isolated locality, only about 6 days of dedicated sampling effort would be needed to indicate local extinction. The analysis of population trends shows relative stability followed by sharp decline in abundance that coincides with the commencement of fishing (Fig. 2).

The qualitative analysis of the historical records and recent surveys under the framework proposed by Butchart et al. (2006) give support for the four main types of evidence for local extinction of *C. galapagensis* and *C. falciformis* at the Archipelago (Table 3). On the other hand, there is no support for the four types of evidence against extinction except in the case of *C. falciformis*, which is occasionally caught by fishing boats nearby although no longer seems to frequent the reefs of St. Paul's Rocks.

4. Discussion

The review of historical accounts from St. Paul's Rocks shows that carcharhinid sharks were abundant there until approximately 50 years ago. The occurrence of such large numbers of sharks around oceanic islands is not an uncommon feature in the reports of the 18th and 19th century's ocean explorers (Sáenz-Arroyo et al., 2006; Roberts, 2007; see Supplemental data in Sandin et al. (2008) and Ward-Paige et al. (2010)). In fact, it appears to have been normal. Today, only a few places in the world, such as the northwestern Hawaiian Islands (Friedlander and DeMartini, 2002), Kingman and Palmyra Atolls in the northern Line Islands (Sandin et al., 2008), and some no-entry zones in the Great Barrier Reef (Robbins et al., 2006), have shark densities that approach those described in historic accounts. These places can provide the best baselines we have for estimating ecological changes in areas where top predators have been depleted.

Our analyses of the data from recent and historical observations provide strong evidence that the once extremely abundant carcharhinid reef sharks (especially *C. galapagensis*) are now extinct in the remote Archipelago of Saint Paul's Rocks. Shark populations worldwide have been depleted by overfishing (Worm and Myers, 2003; Robbins et al., 2006; Dulvy et al., 2008), but apparently persist at high abundance at a few remote and uninhabited islands and atolls (Stevenson et al., 2007; DeMartini et al., 2008; Sandin et al., 2008). However, our results support the claim of Anderson et al. (1998) (see also Graham et al., 2010) that a locality, even if isolated and uninhabited, is not necessarily safe from overfishing. In those localities where shark density is regarded as relatively undisturbed, protection from illegal fishing is well enforced. Thus, a combination of isolation, low human density, and effective protection seems to be necessary to maintain shark populations in their natural state.

Fishing is the factor that stands out as the agent of *Carcharhinus* spp. extinction at St. Paul's Rocks. The decline in the number of sharks coincided with the commencement of commercial fishing, after a period of more than 150 years when sharks were documented to be very abundant (Fig. 2). This is not surprising given the vulnerability of sharks to exploitation because of their life-history strategy, characterized by large size, long life-span, low rate of reproduction, late maturity, slow growth, and low natural mortality (Stevens et al., 2000). Also, they are positively attracted to certain types of fishing gear (baited hooks). During roughly the same period, populations of sharks in much larger geographic areas, like the Gulf of Mexico (Baum and Myers, 2004) and the Mediterranean Sea (Ferretti et al., 2008), were reduced by more than 90% due to commercial fishing. Sharks are vulnerable to even light fishing pressure by artisanal and subsistence fishers on remote islands (DeMartini et al., 2008). Clearly, a continuous and spatially concentrated fishing effort in such a small area as St. Paul's Rocks is incompatible with shark survival.

The ecological effects of removal of sharks and other top-predators have important consequences for the stability of marine ecosystems (Myers et al., 2007; Heithaus et al., 2008; Ferretti et al., 2010). A well-known phenomenon is the top-down trophic cascade that may occur after the release of prey from predatory control (reviews in Heithaus et al. (2008) and Baum and Worm (2009)). Due to the lack of quantitative data on past densities of reef fish at St. Paul's Rocks, it is difficult to infer whether such cascade effects have occurred there.

However, possible evidence of trophic cascades are brought to light from the assessment of Lubbock and Edwards (1981), that was made in a period when the sharks were declining, thought still very common. In 1979, they found that the moray eel *Muraena pavonina* was moderately common, usually found inside holes, crevices and occasionally in macro-algae beds (Lubbock and Edwards, 1981). Today, *M. pavonina* is one of the most abundant species there (Ferreira et al., 2009) and, uncharacteristically for moray eels, regularly observed swimming away from shelter during daylight (Luiz, 2005). Even if populations of meso-predators, such as carangids and moray eels, have not changed significantly, given the previous high abundance of sharks it is likely that now they spend more time foraging and/or forage over larger areas than before, when the risk of predation by sharks was higher (i.e. risk effects; Heithaus et al., 2008; Madin et al., 2010). This raises concerns about the conservation status of the small fishes that meso-predators prey upon, particularly endemic species, which may be threatened with global extinction. Four endemic species of fish are known from the Archipelago (Lubbock and Edwards, 1980, 1981) and at least two other endemic species are awaiting formal description, from which nothing is known about their population dynamics and vulnerability to human impacts. The small endemic basslet *Anthias salmopunctatus*, for instance, was common on rocky faces below 30 m depth in 1979 and usually found in small shoals (Lubbock and Edwards, 1981) but is now extremely rare (Luiz et al., 2007).

Because most detailed scientific studies in the sea have been carried out after humans significantly modified it (Jackson et al., 2001), it is often necessary to use historical data to reconstruct the past abundances of marine organisms (Lotze and Worm, 2009; McClenachan, 2009). A recent review has found that the application of historical contrasts is responsible for the detection of 80% of all known extinctions in the sea (Dulvy et al., 2003). However, despite its value, historical data are often descriptive and opportunistic, challenging our capacity to apply quantitative analyses to them (Roberts and Solow, 2003; Monte-Luna et al., 2009). Thus, whenever possible, historical data should be analyzed by a set of different methods in order to provide sound inferences of species declines (Roberts and Kirchner, 2006). This is especially

important when inferring extinctions because to consider a species as extinct prematurely could undermine potential last-minute conservation action and contribute to its demise (Collar, 1998). It could also increase the danger of conservationists 'crying wolf' too often, reducing public confidence in the accuracy of extinction designation, and be used to question the integrity of conservation practices (Roberts and Kirchener, 2006; Monte-Luna et al., 2007). On the other hand, the failure to detect real extinctions can hinder our understanding of factors that lead to them and hinder our ability to prevent further losses.

In this study we use of a combination of different methods, two quantitative and one qualitative, to estimate the likelihood of local extinction for sharks of the genus *Carcharhinus*, plus a quantitative method to analyze trends in population stability and decline. All conclude that reef sharks (*Carcharhinus* spp.) are locally extinct at St. Paul's Rocks and that a sharp shift from a relative stability in shark abundance toward a declining trend occurs roughly at the same time as fishing commenced. However, the persistence of occasional individuals of the once locally common *C. falciformis* in the vicinity of the Archipelago, as a result of constant immigration of this oceanic species from outside the area, suggest that if the present fishing pressure was removed then the population might recover.

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