REPORT

Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico

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Abstract

Historical abundances of many large marine vertebrates were tremendously greater than today. However, while pelagic sharks are known to have declined rapidly in the northwest Atlantic in recent years, there, as elsewhere, little is known about the former natural abundances of these species. Here, we compare initial (1950s) and recent (late-1990s) standardized catch rates of pelagic sharks in the Gulf of Mexico, the area where methods of exploitation between these two periods were most comparable. We estimate that oceanic whitetip and silky sharks, formerly the most commonly caught shark species, have declined by over 99 and 90%, respectively. That the former prevalence of oceanic whitetip sharks in this ecosystem is unrecognized today is clear evidence of shifting baselines. Our analysis provides the missing baseline for pelagic sharks in the Gulf of Mexico that is needed for the rational management and restoration of these species.

Keywords

Fisheries, generalized linear model, marine, overexploitation, pelagic shark assemblage, population, predator, restoration.

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INTRODUCTION

Understanding the full extent and manner in which anthropogenic forces have impacted natural ecosystems requires knowledge of their unexploited state. Although human influences on terrestrial and coastal ecosystems are highly evident (MacPhee 1999; Jackson *et al.* 2001), the open ocean has been regarded as pristine until recently. Precipitous declines in many oceanic species and concomitant fisheries collapses are, however, clear demonstrations that these ecosystems have also been significantly impacted. In particular, large predators are known to structure aquatic ecosystems, but that role may have changed dramatically because of large-scale declines. Estimates for whales, tunas, billfishes and large demersal fishes suggest that as in terrestrial and coastal ecosystems, the former natural abundances of large predators were enormous compared with recent observations (Myers & Worm 2003; Roman & Palumbi 2003). For many species, however, a historical perspective is obscured by a reliance on recent data in analyses. Without this knowledge our baseline of what was natural in the open ocean will continue to shift, and we risk becoming complacent about the rarity of species (Pauly 1995).

In the open ocean, sharks are the remaining pelagic apex predators for which baseline population abundances are unknown. Large pelagic sharks found beyond continental shelves include species which range across entire ocean basins and species whose range is more neritic, here termed oceanic and coastal sharks, respectively. Establishing a baseline for these shark populations is necessary to fully understand how industrial fisheries have impacted them, and thus essential to their informed management and recovery. Sharks are among the least resilient fishes to intense exploitation because of their life histories, which are characterized by a late age at maturity and low fecundity (Musick *et al.* 2000). Populations of different oceanic and coastal shark species in the northwest Atlantic are estimated to have declined by 40–89% since the late-1980s (Baum *et al.* 2003). Despite the magnitude of these losses, we hypothesize that they are likely underestimates because they do not account for changes that occurred during the first several decades of industrial exploitation of these species (i.e. 1957–1985). Moreover, because rates of change are unlikely to have been the same among species, we hypothesize that the composition of unexploited pelagic shark assemblages may have been considerably different than that recognized today.

Quantifying the former natural abundance of pelagic shark populations should be facilitated by the short history of anthropogenic impacts in offshore pelagic ecosystems, relative to that in most other aquatic ecosystems. Beyond continental shelves, these populations were largely protected by their distant location and vast ranges, until the past half century when industrialized fisheries developed in offshore waters to target other large predatory fishes, namely tunas and billfishes. As with other incidental species, however, shark catches were not systematically recorded in these fisheries until recently. Instead, baseline information for the northwest Atlantic is obtained from exploratory surveys that were conducted in the 1950s along the east coast of the United States, in the Gulf of Mexico, and Caribbean, to acquire information for the development of commercial tuna fisheries. Longlines used in these surveys, and in the commercial fisheries that subsequently developed, resemble a transect through the pelagic ecosystem, consisting of a mainline suspended horizontally in the water column by floatlines and buoys, with baited hooks on branchlines attached at set intervals. We focus on the Gulf of Mexico, because unlike in the other regions where target species, fishing methods, and specific locations fished have changed, the initial surveys in this region are similar to contemporary methods of exploitation. We compare shark catch rates in the Gulf of Mexico on pelagic longline gear set to target yellowfin tuna (*Thunnus albacares*) during the 1950s surveys and the late-1990s commercial fishery. Because no sampling of the pelagic community in the Gulf of Mexico has exactly replicated the methods of the 1950 exploratory surveys, this comparison not only required that we standardize catch rates to account for variation in the fishing operation, location, and timing among sets, but that for characteristics of the fishery which have changed over time, we develop a method to incorporate independent estimates of their effects on each species' catchability. Although there will inevitably be some imprecision in our estimates, we believe that establishing a benchmark against which to judge present conditions is critical. Here, we use this approach to estimate the former natural abundance of oceanic whitetip (*Carcharhinus longimanus*), silky (*C. falciformis*), and dusky (*C. obscurus*) sharks in the Gulf of Mexico.

METHODS

Data

Data for the initial exploitation of sharks in the Gulf of Mexico are from the exploratory pelagic longline cruises on the research vessel *Oregon* between 1954 and 1957. During this period, sixteen research cruises were conducted, comprising a total of 170 longline sets. These surveys aimed to determine the distribution of surface tuna in the region, but

quickly focused on the most frequently caught species, yellowfin tuna. Exploratory cruises occurred in all seasons and covered large areas of the Gulf of Mexico in order to determine the distribution of these tuna (Fig. 1). Data were supplemented and cross-checked with cruise summaries (Bullis & Captiva 1955; Wathne 1959; Iwamoto 1965).

The surveys were conducted using standard gear and fishing methods adapted from the Japanese longlining method (Table 1; Shapiro 1950; Murray 1953; Bullis & Captiva 1955; Wathne 1959). Gear was usually deployed before dawn ($n = 145$), and allowed to soak for only a few hours. Gear retrieval usually began mid-morning and lasted for 3–7 h. We retained the longline sets that began in the late morning or afternoon ($n = 25$), because the time of these sets is covered by the longer soak times of sets in the 1990s, but removed the few night sets ($n = 6$).

Recent data are from the scientifically trained observers monitoring US commercial longline vessels between 1995 and 1999. The fleet in the Gulf of Mexico primarily targets yellowfin tuna, but also swordfish and coastal sharks. The target species of the set is identified prior to gear retrieval, and is not based on the catch, but rather on characteristics including time of set, hook depth, and use of lightsticks. For comparison with the 1950s data, we only included data from the most similar sets, those that targeted yellowfin tuna with soak times during the day ($n = 275$ sets from 63 trips; Table 1). These sets occurred in all seasons and were located throughout the northeast and northwest Gulf of Mexico (Fig. 1).

Our comparison between the 1950s and 1990s is contingent upon the similarity of the fishing operations and on our ability to correct for the effects of differences between them. Comparing survey and fisheries data may be tenuous because of the different sampling methods employed, but is possible here because the surveys operated similarly to a fishery, actively searching for and concentrating in areas with yellowfin tuna (Wathne 1959; Iwamoto 1965). The main differences then in comparing the 1950s and 1990s data are the improvements in searching for and targeting yellowfin tuna and the intensified fishing effort, including increases in number of hooks set, hook depth, and soak time (Table 1). Correlations of yellowfin tuna catch rates with each of the commonly caught shark species were all highly non-significant, and yellowfin tuna catch had little effect on our results when included as a model variable (see Appendix S1 in Supplementary Material), thus changes in catch rates of the target species should not bias abundance estimates for sharks. A change between the 1950s and 1990s in the leader material (at the end of the branchlines), from wire to monofilament, has been demonstrated to either increase or have little effect on shark catch rates (Berkeley & Campos 1988; Branstetter & Musick 1993). Other gear changes, such as bait type (e.g. live, frozen) and hook size
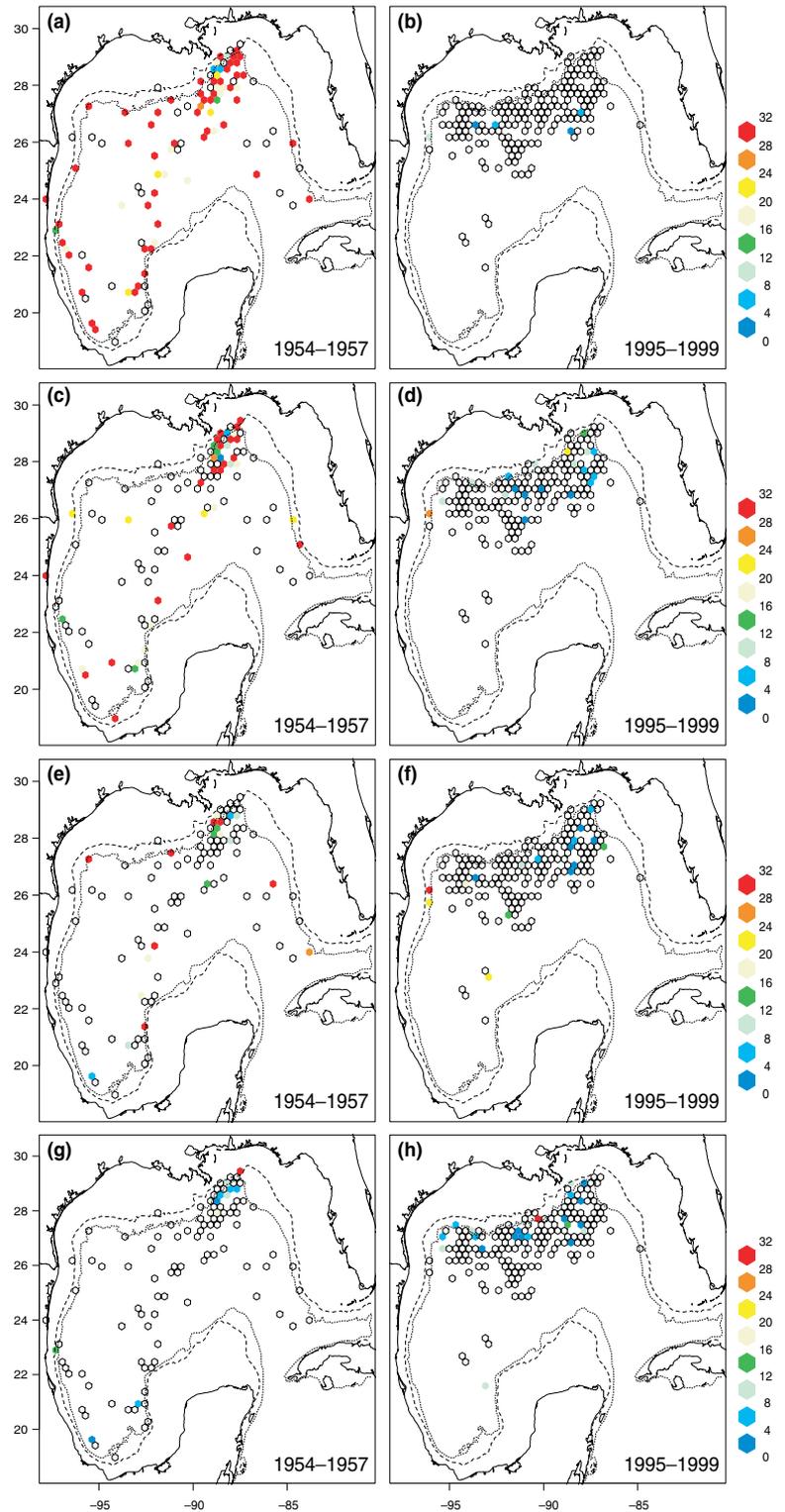
Figure 1 Map of Gulf of Mexico showing unstandardized mean catches per 10 000 hooks on yellowfin tuna targeted sets during the day in the 1950s (a, c, e, g) and the 1990s (b, c, f, h) for oceanic whitetip (a, b), silky (c, d), dusky (e, f) and mako (g, h) sharks. Empty hexagons are set locations where none of the specified shark species was caught. The 200-m and 1000-m coastal isobaths (dotted lines) are shown for reference.

appear to have little effect on catch rates of any of the shark species examined. We account for increases in the number of hooks set, hook depth, and soak time in our models. In addition, because the datasets from the 1950s and 1990s represent groupings of 4 and 5 years of data respectively, the effect of any anomalous years, is minimized.

Table 1 Comparison of 1950s and 1990s pelagic longline fishing data from the Gulf of Mexico used in analysis. Mean values ± 1 SD

Descriptor	1950s	1990s
Data source	US Bureau of Commercial Fisheries researchers	US National Marine Fisheries Service observers
Purpose	Exploratory tuna surveys	Commercial fishery
Years	1954–1957	1995–1999
Target species	Yellowfin tuna	Yellowfin tuna
Fishing effort	170 sets, 82 972 hooks	275 sets, 219 461 hooks
Hooks per set	488 ± 251	798 ± 181
Hooks between floatlines	10 ± 1	5 ± 2
Estimated hook depths	72 ± 19 m	110 ± 28 m
Hook type	9/0 Japanese style tuna hook (J-hook)	7/0, 8/0, 15/0, 16/0 primarily J-hook, some circle hooks
Mainline material	132-thread type-E filament nylon (1000lb test)	Nylon monofilament (600–1100lb test)
Branchline material	"Gulf-lay" nylon (11/64″ diameter), 3/32″ diameter 7×7 stainless steel wire leaders	Nylon monofilament (300–450lb test), often with nylon monofilament leaders
Lightsticks	No	No
Bait	Mackerel, herring, squid, menhaden, mackerel scad, Atlantic croaker	Mackerel, herring, squid, sardine, scad
Set time	5:30 a.m. ± 2 h	8:30 a.m. ± 3 h
Retrieval time	10:00 a.m. ± 2 h	7:00 p.m. ± 4 h
Months fished	January–December	January–December

Table 2 Recorded oceanic and coastal shark species and sample sizes in 1950s and 1990s datasets, listed within each category in declining order of abundance in the 1950s

Species		No. caught	
Common name	Latin name	1950s	1990s
Oceanic species			
Oceanic whitetip	*Carcharhinus longimanus*	397	5
Silky	*Carcharhinus falciformis*	158	24
Mako spp.	*Isurus oxyrinchus, I. paucus*	17	24
Coastal species			
Dusky	*Carcharhinus obscurus*	61	30
Tiger	*Galeocerdo cuvieri*	6	18
Blacktip	*Carcharhinus limbatus*	6	0
Hammerhead spp.	*Sphyrna lewini, S. mokarran*	4	8
Sandbar	*Carcharhinus plumbeus*	0	16
Spinner	*Carcharhinus brevipinna*	0	4
Thresher spp.	*Alopias superciliousus, A. vulpinus*	0	4
Atlantic sharpnose	*Rhizoprionodon terraenovae*	0	1
Unidentified sharks			62

Shark species

Pelagic longline fisheries primarily catch oceanic shark species, but also catch coastal shark species when operating in relatively close proximity to land, as in the Gulf of Mexico (Table 2). Of the species caught, we grouped shortfin and longfin mako, bigeye and common thresher, and scalloped and great hammerhead sharks, because these species were sometimes only identified to genus. The high proportion of unidentified sharks in the 1990s data resulted from fishers releasing unmarketable large non-target fishes prior to positive identification by observers (L. Beerkircher pers. comm., Oceanographic Center, Nova Southeastern University, 8000 N. Ocean Drive, Dania Beach, Florida 33004, USA). We account for unidentified sharks in our presentation of unstandardized catch rates and in our models, by distributing them across all shark species caught, except mako sharks, which have high value and are usually retained.

Modelling change in abundance

We use generalized linear models with a negative binomial error structure and a log link to standardize the catch rates for operational, spatial and temporal variation among longline sets (Venables & Ripley 1999). Thus, for each species s, the observed catch, $C_{s,i}$ on set i is assumed to follow a negative binomial distribution, and the model predicts the mean number of the species that would be caught by a standard longline set, at a standard location and time. We estimate the effect of the fishing period with an indicator variable, I_i, which was defined as 0 if the year was between 1954 and 1957, and 1 if the year was between 1995 and 1999. The exponent of its estimated parameter, e^β, can then be interpreted as the change in abundance between the two fishing periods.

We begin with a basic model of the expected mean catch $\mu_{s,i}$,

$$\log(\mu_{s,i}) = \beta I_{s,i} + q(d_{s,i}) + \beta_{n1}N_{s,i} + \beta_{n2}N_{s,i}^2 + \beta_{w1}W_{s,i} + \beta_{W2}W_{s,i}^2 + \beta_{o1}O_{s,i} + \beta_{o2}O_{s,i}^2 + \log(H_{s,i})$$

where $I_{s,i}$ is the variable for fishing period, $q(d_{s,i})$ is the seasonal cycle described below, the variables for area (degrees latitude north, $N_{s,i}$, degrees longitude west, $W_{s,i}$) and ocean depth $O_{s,i}$ are fit as quadratic terms, and $H_{s,i}$, the number of hooks set is a known value, treated as an 'offset' (McCullagh & Nelder 1989). The seasonal cycle is determined by fitting sines and cosines with periods, j, of 1/2 and 1 year in the model as

$$q(d_{s,i}) = \sum_{j=1}^{2} [\varsigma_j \cos(2\pi j d_{s,i}/365.25) + \sigma_j \sin(2\pi j d_{s,i}/365.25)],$$

where $d_{s,i}$ is the sequential day of the year that set i occurred on, and the estimated parameters are ς_j and σ_j. Including the log hooks as an offset is equivalent to dividing the catch by effort to determine a catch rate, but is used to preserve the probabilistic sampling model for the catch data.

We then develop our model to include independent estimates of the effects of both soak time and hook depth on catch rates of the species being modelled. We use this approach because these variables, both of which are known to significantly influence catch rates of pelagic fishes (Suzuki *et al.* 1977; Uozumi & Okamoto 1997; Ward *et al.* 2003), have changed considerably between the two time periods (Table 1). Estimation of the effect of soak time in particular, if included as a variable in the model, would be largely confounded with the estimates of relative abundance between the two periods, because there is little overlap in this variable between the 1950s and 1990s. Instead, our approach is to include independent estimates of the effect of these variables in the offset of our model. That is, we include more information in the 'offset' than simply the number of hooks, because, for example, if we know that the effectiveness of the hooks in set i is G_i times the average, we can replace the offset, $\log (H_i)$, with $\log (H_iG_i)$.

We use the effect of soak time on catch rates estimated by Ward *et al.* (2003), in which the catchability of species s is defined as a function of soak time, t, in hours, to be $g_s(t) = \alpha_s \exp (\delta_s t)$. Ward *et al.* (2003) used generalized linear mixed models to estimate this effect for five pelagic longline fisheries in the Pacific in which the soak time and catch of each hook were recorded. For each species, we weighted the slope coefficients, δ_s, estimated for the different fisheries by their inverse variance and used the mean value (Table 3). Catch rates of the sharks modelled here increased with soak time, by 1.3–2.2 times after 10 h, the average difference in soak time between the 1950s and 1990s (Table 3). In our datasets, because we do not have records of the catch and soak times of individual hooks, we use data on gear deployment and retrieval times to calculate the shortest and longest soak times of hooks on each set. To include the soak time effect in our model for each species, we assume that the longline is recovered at a constant rate, and integrate over the soak time from the beginning to the end of the haul. We then estimate a mean soak time effect for each species for each set as

Table 3 Modelled species, coefficients for soak time (δ_s) and depth (γ_{s1}, γ_{s2}, γ_{s3}) used to calculate the offset, efficiency of hooks in the 1990s relative to the 1950s for the mean change in soak time and depth respectively, and mean weights in kilograms ± 1SD (sample size)

Species	Soak effect		Depth effect				Weight	
	δ_s	Relative efficiency	γ_{s1}	γ_{s2}	γ_{s3}	Relative efficiency	1950s	1990s†
Oceanic whitetip	0.0458	1.56	−9.886	11.720	−2.188	0.74	86.4 ± 25.9 (370)	56.1 ± 52.2 (30)
Silky	0.0260	1.29	−3.562	−4.423	9.895	0.85	102.3 ± 47.0 (157)	16.7 ± 31.8 (346)
Dusky	0.0778	2.18	−19.048	47.475	−35.911	0.65	154.2 ± 36.9 (61)	60.9 ± 43.5 (65)
Mako spp.	0.0343	1.41	−9.105	26.325	−22.572	0.83	158.2 ± 103.7 (17)	73.6 ± 69.5 (50)

†Weights for the 1990s include data from all pelagic longline tuna targeted sets in the Gulf of Mexico between 1992–1999 because of the otherwise limited sample size.

$$\overline{STE_{s,i}} = \frac{\int_{b_i}^{e_i} g_s(t)dt}{e_i - b_i}$$

where b_i and e_i are the times that the hooks with shortest and longest soak times, respectively, have been in the water.

For the effect of depth on catch rates, we use estimates from Myers & Ward (unpublished work available online: http://fish.dal.ca), where the catchability of species s is defined as a cubic function of hook depth D, in kilometres, to be $f_s(D) = \exp(\alpha_s + \gamma_{s1}D + \gamma_{s2}D^2 + \gamma_{s3}D^3)$. Myers & Ward derived the estimates by combining data from three pelagic longline fisheries in the Pacific in which the catch and depth of individual hooks were recorded. Catch rates of each of the shark species modelled declined with depth: the difference in efficiency between hooks at the mean 1990s depth (110 m) and those at the mean 1950s depth (72 m) ranges from 0.65 to 0.85 among species (Table 3). To estimate the depth of hooks on each longline set, we assume that hooks are spaced evenly along the mainline between floatlines and that the shape of the catenary curve formed by the longline, and thus the corresponding depth of hooks, does not vary systematically over the entire set. We then estimate the hook depth at each position using the floatline and branchline lengths, the length of the mainline between floats, and the equation and corrections for the catenary curve (Suzuki *et al.* 1977; Uozumi & Okamoto 1997; Mizuno *et al.* 1999). Our depth estimates are similar to those obtained from depth sounders (Wathne 1959). Estimates for each longline set i result in a vector, $p_i(D)$, which describes the proportion of hooks in the set at depth D. As with soak time, to include the depth effects in our model, for each species we calculate a mean depth effect for each set, using the proportion of hooks in a given set at depth D and the depth effect at each discrete depth $\overline{DE_{s,i}^*} = \sum_D f_s(D)p_i(D)$.

We standardize both the soak time, $\overline{STE_{s,i}^*}$, and depth, $\overline{DE_{s,i}^*}$, effects so that the mean value of each, and hence its mean effect on the efficiency of hooks, was 1. The standardized effects are then included in the offset such that the offset in our basic model is replaced with $\log(H_{s,i}\overline{STE_{s,i}^*,DE_{s,i}^*})$. We demonstrate the effects of soak time and depth on our model estimates in Appendix S1.

Model performance is compared by backward-selection using the Akaike Information Criterion (AIC), which penalizes the deviance by twice the number of parameters p. We then adjust the final model estimates to account for the unidentified sharks in the 1990s. We assume that among the species caught in the 1990s there is no bias in those that are unidentified by observers, such that the species composition of this group should reflect that of the identified sharks (except for mako sharks). Distributing the 62 unidentified sharks among these species proportionally to the abundance of the identified shark species in the 1990s catches increases the total catch of each by 1.56 times. Thus, to account for the effect these sharks would have on our estimates of change in abundance for oceanic whitetip, silky and dusky sharks, we simply reduce our estimated decline by this amount. This is equivalent to removing the amount of effort needed to catch the 'extra' sharks of each species.

Finally, we evaluate the robustness of our results by fitting additional models to test the precision of our soak time effect estimate, the effect of including yellowfin tuna catches as a variable, and the effect of including sets targeting any tuna species, and to examine a reduced area in the Gulf of Mexico, excluding the southern area where there were few sets in the 1990s (see Appendix S1).

Estimating change in size

We estimate the mean size of the species modelled in each time period using data on weights from the 1950s, and lengths in the 1990s applied to length–weight conversions. For the 1990s estimates, we use fork length data from any pelagic longline tuna set in the Gulf of Mexico between 1992 and 1999 to increase the sample size for each shark species. We estimate the weight of oceanic whitetip sharks using fork length to total length conversions (Lessa *et al.* 1999 and unpublished data) and total length to weight conversions (Strasburg 1957). Silky, dusky and mako shark weights are estimated using fork length to weight conversions (Kohler *et al.* 1995). Reported size at maturity is the fork length.

RESULTS

Unstandardized catch rates

Catch rates of sharks were substantially higher in the 1950s than in the 1990s, declining from a mean of 7.30 ($\pm$ 7.94 SD) to 0.92 ($\pm$ 2.51 SD) per 1000 hooks. Sharks comprised on average 17.2% of the total catch on the exploratory pelagic longline sets in the 1950s, but only 2.2% of the total catch on pelagic longline sets in the 1990s. The decline cannot be attributed to increased catches of the target species: yellowfin tuna declined from 57–35% of the total catch between the two time periods.

In the 1950s, oceanic whitetip and silky sharks were the second and fourth most commonly caught fishes on the pelagic longline surveys. Both species were found throughout the Gulf of Mexico: the oceanic whitetip shark was caught on 64% of sets, the silky shark on 35% of sets (Fig. 1a–d). Oceanic whitetip sharks accounted for 61% of all sharks caught, while silky sharks accounted for 24%.
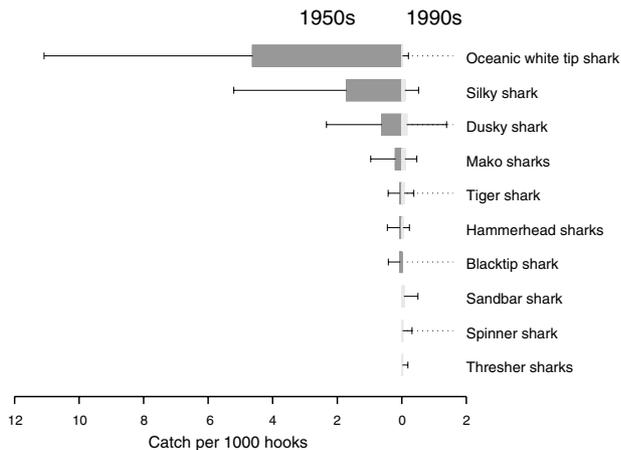
Figure 2 Mean catch rates (±SD) of each shark species recorded in the 1950s data and/or 1990s data. Catch rates are unstandardized for changes in spatial, temporal and operational variation. Species are listed in declining order of abundance in the 1950.

Figure 3 The estimated change in abundance (±95% CI) between the 1950s and 1990s of oceanic whitetip (OCS), silky (FAL), dusky (DUS) and mako (MAK) sharks. A value of 1 indicates no change in abundance, a value of 10 indicates a 10-fold, or 90%, decline.

Between the mid-1950s and the 1990s, catch rates of oceanic whitetip and silky sharks declined from an average of 4.62 (±6.47 SD) and 1.71 (±3.49 SD) per 1000 hooks, to only 0.02 (±0.18 SD) and 0.10 (±0.42 SD) per 1000 hooks, respectively (Fig. 2). These two species, which together comprised on average almost 15% of the total pelagic longline catch in the 1950s, accounted for only 0.3% of the total catch in the 1990s. Catch rates of the next most commonly caught shark in the 1950s, dusky shark, were also substantially lower in the 1990s (Fig. 1e, f), declining from a mean of 0.61(±1.72 SD) to 0.16(±1.24 SD) (Fig. 2). Despite the decrease, dusky sharks had the highest catch rate among sharks in the 1990s. Mean catch rates of oceanic whitetip (0.04), silky (0.17) and dusky (0.21) sharks still show substantial declines when their total catches in the 1990s are adjusted to include a proportion of the unidentified sharks.

Catch rates of all other shark species caught in either time period were low. Catch rates of mako sharks declined from 0.19 (±0.77 SD) in the 1950s to 0.09 (±0.37 SD) in the 1990s (Figs 1g, h, 2). The 1950 surveys caught only three other shark species: blacktip, tiger and hammerhead sharks (great hammerhead (*S. mokarran*) and two sharks identified only to the genus *Sphyrna*), each of whose mean catch rate was less than 0.06 per 1000 hooks. The blacktip shark was not recorded by observers in the 1990s, while catch rates of tiger and hammerhead sharks were similar (Fig. 2) or slightly higher when adjusted for unidentified sharks. Of the shark species unique to the 1990 data, the mean catch per 1000 hooks of sandbar sharks was 0.07 (0.11 when adjusted for unidentified sharks), while those of spinner and thresher sharks were less than 0.03, even when adjusted.
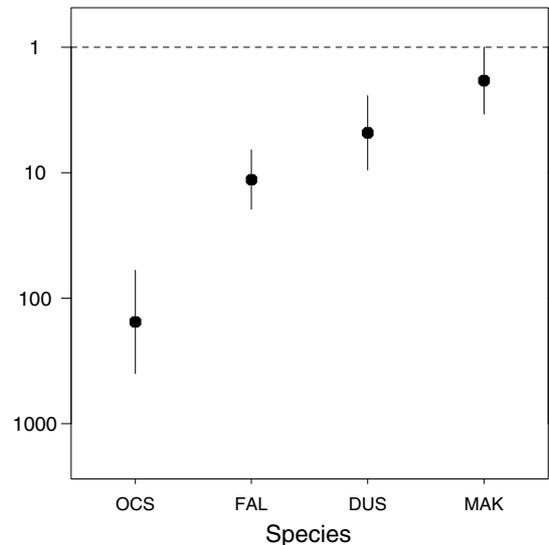
Abundance and size estimates

Model estimates indicate that the abundance of oceanic and coastal sharks declined substantially between the 1950s and late-1990s. The most commonly caught shark species in the 1950s, the oceanic whitetip shark, is estimated to have declined by more than 150-fold, or 99.3% (95%CI: 98.3–99.8%), during this time (Fig. 3). We estimate over a 10-fold decline, 91.2% (95% CI: 84.8–94.9), in silky shark abundance and almost a 5-fold decline, 79.2% (95% CI: 58.8–89.5%), in dusky shark abundance (Fig. 3). Mean estimated declines in our robustness analysis were very similar for oceanic whitetip and silky sharks (within 1 and 2% respectively), but ranged from 70.6–87.2% for dusky sharks (see Appendix S1). Fishing period (1950s, 1990s) was the most important explanatory variable for each of these species in all models (Appendix S2 in Supplementary Material).

We estimate that there has been less of a decline in mako shark abundance (45, 95% CI: 0.02–70.6%; Fig. 3). However, in the final model for mako sharks, fishing period explained less variance than ocean depth, and in general estimates for this species group are much less precise than for the other modelled species because of the lower sample size (Appendix S2). The change in abundance of each of the other shark species was poorly determined because of their rarity in the pelagic longline catches.

The mean weight of each of the modelled species is also estimated to be much lower than in the 1950s (Table 3). The average size of oceanic whitetip sharks is near the size at maturity. The mean size of other species is now below the

size at maturity: dusky sharks mature at 230 cm (Kohler *et al.* 1995) and now average 165 cm, shortfin mako sharks mature at over 180 cm (Kohler *et al.* 1995) and now average 171 cm, and in the most extreme case, silky sharks, which mature at about 180 cm (Kohler *et al.* 1995) now average only 97 cm.

DISCUSSION

Pelagic shark species are estimated to have declined precipitously in the Gulf of Mexico since the onset of industrialized pelagic fisheries. The shark species that were initially most commonly caught underwent the greatest declines. In particular, the oceanic whitetip shark, the most prevalent shark in the 1950s, is estimated to have declined by over 99%. Silky and dusky sharks are estimated to have declined by 91 and 79%, respectively. Our results for oceanic whitetip and silky sharks are very robust, and although the magnitude of the declines fluctuated among models of dusky sharks, each model estimates that this species has also declined substantially.

Differences in the magnitude of declines among shark species have altered the composition of the Gulf of Mexico's pelagic shark assemblage. Whereas in the 1950s, catches of oceanic whitetip sharks accounted for over 60% of sharks captured, by the 1990s this species comprised only 2% of shark catches. The oceanic whitetip has not been replaced by other shark species, but rather the remaining catches are comprised of other depleted species, dusky, silky, and mako sharks, and by several species that were either extremely rare or not caught at all in the 1950s. The rarity of these latter species is because of the location of the pelagic longline fishery, which operates almost entirely beyond the continental shelf (Fig. 1), at the margins of their distributions. Catches of new shark species in the 1990s may be an artefact of the increased sample size or increased depth of sets (e.g. sandbar sharks), although it is also possible that their distribution may have expanded offshore to occupy niches left by the pelagic sharks that have declined. The disappearance of blacktip sharks from catches suggests a decline in this species.

Mean sizes for each modelled species are now at or below the size at maturity, which may accelerate declines and cause local extinction. Decreased sizes are often observed in heavily exploited species because fishing gear usually targets the largest individuals, but declines below sizes at maturity are of particular concern. Although a change in pelagic longline gear from wire to monofilament leaders was partially intended to reduce catches of large incidental species, studies comparing wire and monofilament have found very similar mean shark catch rates and sizes, notably documenting mean lengths of silky sharks below the size at maturity on both gear types (Berkeley & Campos 1988;

Branstetter & Musick 1993). Indeed, large fishes are still caught on the latter gear type: the mean size of the target species in the Gulf of Mexico was higher than that of oceanic whitetip, silky and dusky sharks in the 1990s, suggesting that the mean sizes of these shark species reflect real declines.

The magnitude of the shark declines estimated here reflects both the life histories and levels of exploitation of these species. Along with other elasmobranchs, sharks are generally more vulnerable to overexploitation than teleost fishes, because their slow growth, late maturity and low fecundity result in low intrinsic rates of increase. Declines estimated here range from being less (dusky sharks) to an order of magnitude greater (oceanic whitetip sharks) than those estimated for pelagic teleost predators (Myers & Worm 2003). However, intrinsic rates of increase decline in order from oceanic whitetip, silky to dusky sharks (Cortes 2002), opposite to the estimated magnitude of their declines. We attribute this to differences in the distribution of these species, which have translated into different exploitation rates. The oceanic whitetip is primarily an offshore species whose entire population has been vulnerable to intense pelagic longline fishing effort for over four decades (Compagno 1984). In contrast, silky sharks are more abundant offshore near land than in the open ocean and have nursery areas along the outer continental shelf edge, and dusky sharks only range into offshore waters adjacent to continental shelves (Compagno 1984; Branstetter 1987). Thus, these two species have lower catch rates in pelagic longline fisheries and their populations have been partially protected from pelagic longline fishing effort. Directed shark fisheries that catch these sharks developed only in the 1980s.

The near disappearance of oceanic whitetip sharks from the Gulf of Mexico is a clear example of our shifting baseline in marine ecosystems (Pauly 1995). This species was initially described as the most common pelagic shark beyond the continental shelf in the Gulf of Mexico (Wathne 1959; Bullis 1961). Between two and three to as many as twenty-five oceanic whitetip sharks were usually observed following the vessel during longline retrieval on the exploratory surveys, and the abundance of these sharks was considered a serious problem because of the high proportion of tuna they damaged (Bullis & Captiva 1955; Backus *et al.* 1956; Wathne 1959). In contrast, recent papers on pelagic sharks have either not mentioned the oceanic whitetip or have dismissed it as a rare species, with no recognition of its former prevalence in the ecosystem (e.g. Witzell 1985; Anderson 1990; Russell 1993; Gonzalez Ania *et al.* 1997; Brown 1999). The oceanic whitetip shark is assessed by the World Conservation Union only as lower risk/near threatened (IUCN 2002). Similarly, the extent of declines in the once abundant silky shark has not been recognized (e.g.

Branstetter 1987; Russell 1993; Beerkircher *et al.* 2003). How did declines in these conspicuous predators go undetected? Population collapses of many coastal shark species were noted because of declining catches in the fisheries targeting them (e.g. Ripley 1946; Olsen 1959; Parker & Stott 1965; Holden 1968), but oceanic sharks have never been the primary target of commercial fisheries in the Gulf of Mexico and thus have received little research and management attention despite their high levels of exploitation. Consequently, dusky sharks, which are caught in the directed US coastal shark fishery, are listed as a candidate species for the US Endangered Species Act because of their high susceptibility to overexploitation, while oceanic whitetip and silky sharks have been overlooked.

Taken together, our model estimates indicate that the overall shark assemblage in the Gulf of Mexico's offshore waters declined considerably during this time period. Estimating the precise change in abundance of this assemblage is difficult, however, given that catchability on pelagic longlines may differ among species. The estimated total decline in the assemblage would be about 92% if species' catchabilities were equal, such that the prevalence of each species was indicative of their abundance in the sampled area. But even if the catchability of any of the four modelled species was an order of magnitude different than the other species (e.g. oceanic whitetip sharks 10× more catchable and hence less abundant) the total decline in the shark assemblage would still be about 82%. Although the ecosystem impacts of overexploitation in the open ocean remain largely unexplored, consumers like sharks often exert important controls on food web structure, diversity and ecosystem functioning (Paine 2002; Worm *et al.* 2002). Altering entire assemblages of large predators significantly may have had a considerable impact on the pelagic ecosystem.

Our results represent snapshots of the Gulf of Mexico's pelagic shark assemblage in the 1950s and in the 1990s, thus it is not clear when during this period the declines occurred. Evidence that in other areas marine predators declined on average 80% within the first 15 years of industrial exploitation (Myers & Worm 2003) suggests that shark populations (particularly oceanic species) could have been reduced rapidly following initial exploitation in the Gulf of Mexico. Although this may be the case, shark populations in the Gulf of Mexico have not stabilized, but rather recent analyses indicate that these species continued to decline in the 1990s (Baum *et al.* 2003). Using independent data from that examined here, Baum *et al.* (2003) estimated that in the Gulf of Mexico, oceanic whitetip, dusky and silky sharks declined by about 10% per annum between 1992 and 1999. Combined with our results, this suggests that each of these species is under a serious risk of extirpation in this region.

The precipitous declines documented here may be reflective of a general phenomenon for oceanic sharks. Early research surveys described the oceanic whitetip as the most common pelagic shark throughout the warm-temperate and tropical waters of the Atlantic and Pacific (Mather & Day 1954; Strasburg 1957), but as in the Gulf of Mexico current pelagic fisheries in these oceans apparently catch very few of this species (Williams 1999; Matsunaga & Nakano 2000; Matsushita & Matsunaga 2002). Considering that oceanic sharks are heavily exploited throughout the world's oceans, and that these fishes are more vulnerable to collapse than the teleost fishes recently estimated to have declined by a factor of ten (Myers & Worm 2003), it is quite possible that declines estimated for the Gulf of Mexico have occurred elsewhere. In most other regions, it will not be possible to quantify the former natural abundance of these species because of changes in methods of exploitation over time, and because much of their exploitation occurs in international waters and is incidental to other target species such that there has been little monitoring of their catches. As with many marine organisms (Casey & Myers 1998; Dulvy *et al.* 2003), we may therefore fail to detect the risk of local extinctions of oceanic shark populations until after the fact.

This study contributes to the growing awareness that human impacts on natural ecosystems extend to our oceans, and that retrospective analyses are essential to understand the full magnitude and nature of these impacts (Jackson 2001; Jackson *et al.* 2001). The perception of what was natural in the open ocean has clearly changed over a very short period (less than half a century), and our results suggest that it may be particularly easy for baselines of incidentally harvested species to shift because they are usually poorly monitored. We provide the first estimates of baseline abundances for pelagic sharks in the open ocean, demonstrating that these species were enormously more abundant than today. Our results strongly imply that oceanic whitetips are ecologically extinct in the Gulf of Mexico, but also provide a benchmark needed to set clear goals for their restoration.

the Pelagic Fisheries Research Program (R.A.M.), and the Future of Marine Animal Populations project of the Sloan Foundation Census of Marine Life (R.A.M.).

SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE564/ELE564sm.htm

Appendix S1 Additional model details
Appendix S2 Model output

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