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Collapse and Conservation of Shark Populations in the Northwest Atlantic

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Boris Worm, Shelton J. Harley, Penny A. Doherty

Overexploitation threatens the future of many large vertebrates. In the ocean, tunas and sea turtles are current conservation concerns because of this intense pressure. The status of most shark species, in contrast, remains uncertain. Using the largest data set in the Northwest Atlantic, we show rapid large declines in large coastal and oceanic shark populations. Scalloped hammerhead, white, and thresher sharks are each estimated to have declined by over 75% in the past 15 years. Closed-area models highlight priority areas for shark conservation, and the need to consider effort reallocation and site selection if marine reserves are to benefit multiple threatened species.

Human exploitation has propagated across land, coastal areas, and the ocean, transforming ecosystems through the elimination of many species, particularly large vertebrates (1, 2). Only in the past half century, as fishing fleets expanded rapidly in the open ocean, have large marine predators been subject to this intense exploitation. Many species, including tuna, billfishes (3), and sea turtles (4), are of immediate conservation concern as a result. Among the species impacted by these fisheries, sharks should be of particular concern. Despite their known vulnerability to overfishing (5, 6), sharks have been increasingly exploited in recent decades, both as bycatch in pelagic longline fisheries from the 1960s onward (7) and as targets in directed fisheries that expanded rapidly in the 1980s (8). The vast geographic scale of pelagic marine ecosystems constrains our ability to monitor shark populations adequately. Thus, the effect of exploitation on sharks has, for most populations, remained unknown (9). Shark management and conservation have been hindered by the lack of knowledge on their status or even the direction of the population trends.

We present an analysis of logbook data for the U.S. pelagic longline fleets targeting swordfish and tunas in the Northwest Atlantic (Fig. 1). Pelagic longlines are the most widespread fishing gear used in the open ocean. The data set presented is the largest available for this region (214,234 sets between 1986 and 2000 with a mean of 550 hooks per longline set) and includes one of the longest time series for sharks. Six species or species groups were recorded from 1986 onward, and eight species from 1992 onward (Table 1).

For most shark species examined, this is the only data set from which reliable abundance trends can be estimated for the Northwest Atlantic (10). It is also one of the only available sources worldwide from which the effects of exploitation on sharks in the open ocean can be investigated. However, considerable unreporting may occur in logbook data, and missing values cannot be distin-

guished from true zeros (11). To address this problem, we developed a method to model the positive catches using generalized linear models (GLMs) with a zero-truncated negative binomial distribution (12, 13). Our method assumes only that if a positive number of sharks is recorded for a set, then it is approximately correct. We standardized catch per unit effort (CPUE) time series for area, season, fishery variables, and year to obtain indices of abundance. We then performed extensive checks on the robustness of our results and tested the validity of alternative explanations to the observed trends in abundance (13). For each species, the observed direction of the trend was the same in all analyses, and although the magnitude of the declines fluctuated slightly among models, our conclusions are the same irrespective of the model used.

We estimate that all recorded shark species, with the exception of makos, have declined by more than 50% in the past 8 to 15 years (Figs. 2 and 3). Although we expect declines when populations are initially exploited, the shark populations analyzed here had been exploited to varying degrees since the 1960s (14, 15). Because sharks have low maximum intrinsic rates of increase, compensatory responses to ex-

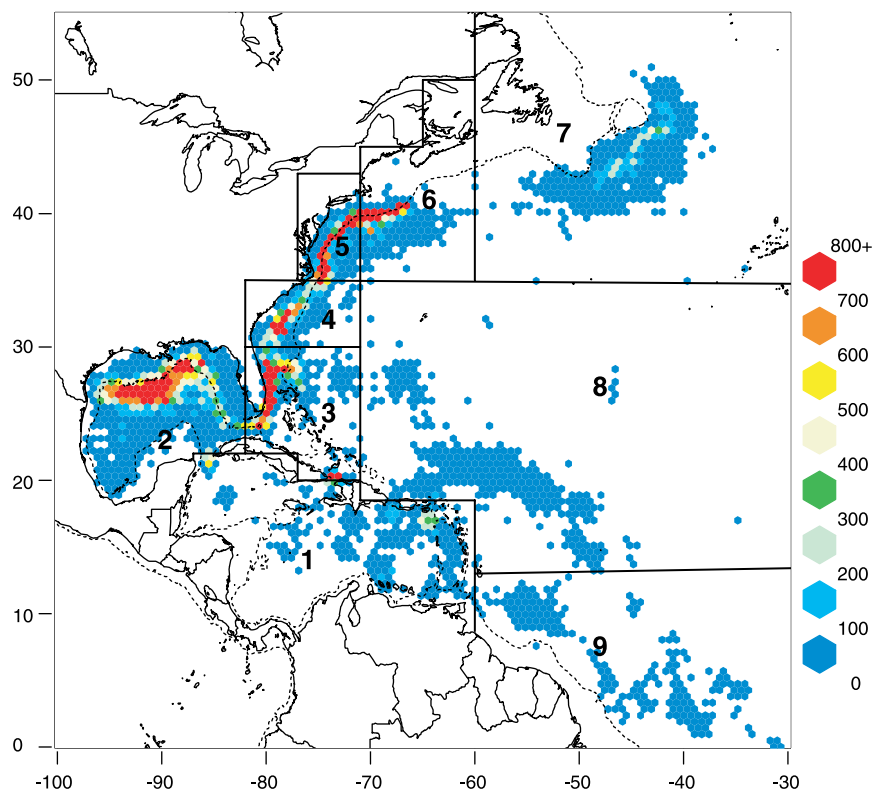


Fig. 1. Map of the Northwest Atlantic showing the distribution of effort in the U.S. pelagic longline fishery between 1986 and 2000, categorized by number of sets (0 to 800⁺), within the nine areas assessed: 1, Caribbean; 2, Gulf of Mexico; 3, Florida East Coast; 4, South Atlantic Bight; 5, Mid Atlantic Bight; 6, Northeast Coastal; 7, Northeast Distant; 8, Sargasso/North Central Atlantic; 9, Tuna North/Tuna South. Areas were modified from the U.S. National Marine Fisheries Service classification for longline fisheries. The 1000-m coastal isobath (dotted line) is given for reference.

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plotation are limited and recovery is expected to be slow (6).

The trend in abundance is most striking for hammerhead sharks; we estimate a decline of 89% since 1986 [95% confidence interval (CI): 86 to 91%] (Figs. 2A and 3A). This group is primarily composed of scalloped hammerheads (*Sphyrna lewini*) (16). The trend for white sharks was an estimated 79% decline (95% CI: 59 to 89%) (Fig. 2B). Catch rates declined in three areas that comprise 80% of its catch (Areas 2 to 4) (Fig. 3B). Since the early 1990s, no white sharks have been reported in Areas 6 and 7, and very few from Areas 5 and 8 (17). The rarity of this species (18) resulted in less precise trend estimates than for the other shark species. Life-history traits have indicated that scalloped hammerhead and white sharks would be among the sharks most vulnerable to over-exploitation (19, 20).

Tiger shark catch rates declined by an estimated 65% since 1986 (95% CI: 58 to 72%) (Figs. 2C and 3C), while the coastal species recorded from 1992 declined by an estimated 61% (95% CI: 55 to 66%) (Figs. 2D and 3D). The latter species, members of the genus *Carcharhinus*, were grouped because they are difficult to distinguish. Individual analysis, however, showed declines for each species (ranging from 49 to 83%). Management of these species has been a contentious issue because of uncertainty in their status (21). We provide strong quantitative evidence to support the argument that these species have declined substantially in the past decade.

The trends for oceanic sharks have also shown decline. We estimate that thresher sharks—a group composed of the common thresher (*Alopias vulpinus*) and bigeye thresher (*A. superciliosus*)—have declined by 80% (95% CI: 76 to 86%) (Figs. 2E and 3E). Unlike the area examined for other oceanic sharks, the area examined for thresher sharks encompasses the known distribution of their Northwest Atlantic populations (18). Observed declines suggest that these populations have collapsed. The interpretation of trends in abundance for other oceanic sharks is complex because their ranges extend across the North Atlantic. Blue sharks declined by an estimated 60% (95% CI: 58 to 63%) (Fig. 2F). Conflicting patterns between the areas of highest catches (Areas 5 to 7: >90% catches) (Fig. 3F) could indicate density-dependent habitat selection, with blue sharks moving into preferential habitat (Area 7) as the population declined. Abundance of mako sharks (mostly shortfin mako, *Isurus oxyrinchus*) declined moderately (Figs. 2G and 3G). The oceanic whitetip shark declined by an estimated 70% (95% CI: 62 to 75%) (Figs. 2H and 3H). From our data, we cannot infer reliable trends for oceanics across the entire North Atlantic Ocean. However, because oth-

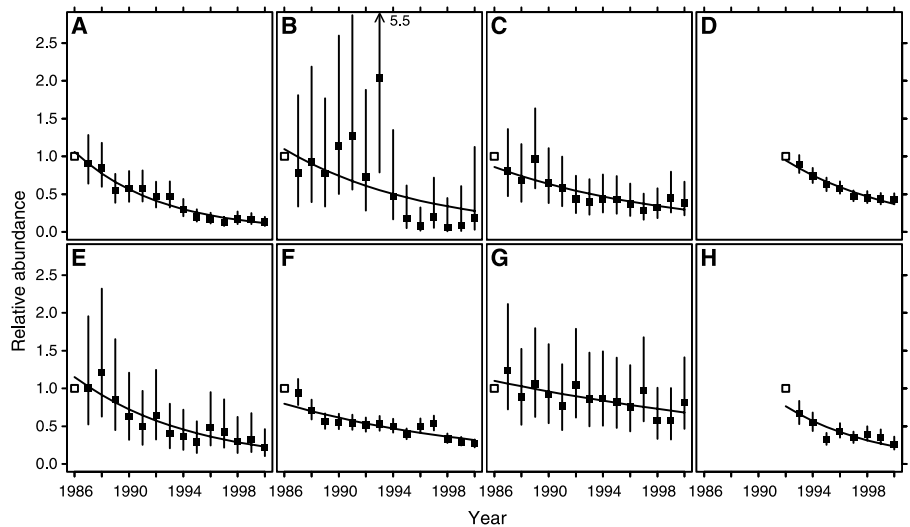


Fig. 2. Declines in estimated relative abundance for coastal shark species: (A) hammerhead, (B) white, (C) tiger, and (D) coastal shark species identified from 1992 onward; and oceanic shark species: (E) thresher, (F) blue, (G) mako, and (H) oceanic whitetip. For each species, the overall trend (solid line) and individual year estimates ($\blacksquare \pm 95\%$ CI) are shown. Relative abundance is initially set to 1, to allow comparisons among species.

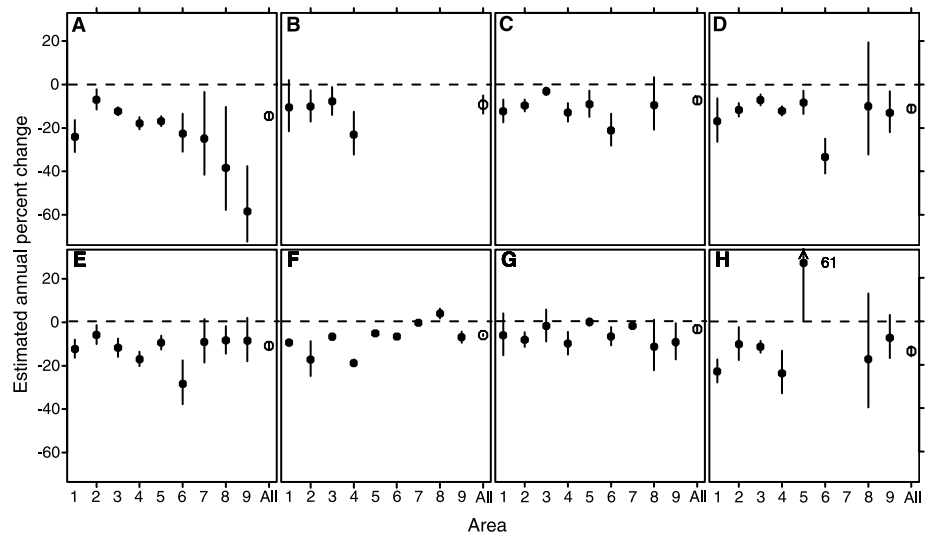


Fig. 3. The estimated annual rate of change, in each area ($\bullet \pm 95\%$ CI) and in all areas combined ($\circ \pm 95\%$ CI), for coastal shark species: (A) hammerhead, (B) white, (C) tiger, and (D) coastal shark species identified from 1992 onward; and oceanic shark species: (E) thresher, (F) blue, (G) mako, and (H) oceanic whitetip. Areas with fewer than 40 observations are excluded.

er longline fleets exert intense fishing effort across the North Atlantic (7), this pattern could well be representative of the entire region.

Our results show that overfishing is threatening large coastal and oceanic sharks in the Northwest Atlantic. The large and rapid declines we document are in addition to substantial historical reductions (2, 22). Overexploitation of elasmobranchs (sharks, skates, and rays) is known to have already nearly eliminated two skate species from much of their ranges (23, 24). The magnitude of the declines estimated here suggests that several sharks may also now be at risk of large-scale extirpation.

Marine reserves have been shown to be effective in rebuilding depleted fish populations (25). In the open ocean this could be different, because animals move across large areas (26), as do fishing fleets (27). We used simple models to analyze the implications of large-scale marine reserves for shark conservation (13). Models were based on empirical data (distribution of fishing effort from log-book data, catch rates per species from scientific observer data) and run under two scenarios that represent the extremes of likely outcomes: (i) after the closure, fishing effort is displaced and changes such that the same total swordfish quota is caught ("constant-quota scenario"); or (ii) fishing effort is dis-

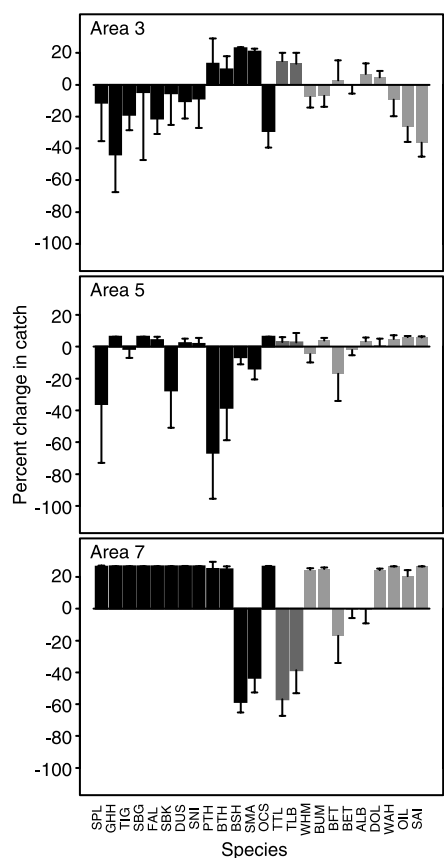


Fig. 4. Results from closed-area model showing predicted changes in catch as caused by year-round longline closure of Areas 3, 5, and 7. Remaining areas are shown in fig. S2. Results for the constant-quota (above and fig. S2) and constant-effort (fig. S3) scenarios were similar. Negative values refer to reductions in catch. Error bars are 95% bootstrap confidence intervals, accounting for the uncertainty in the observer estimates of species composition. Black bars represent sharks (SPL, scalloped hammerhead; GHH, great hammerhead; TIG, tiger; SBG, bignose; FAL, silky; SBK, blacktip; DUS, dusky; SNI, night; PTH, common thresher; BTH, bigeye thresher; BSH, blue; SMA, shortfin mako; OCS, oceanic whitetip), dark gray bars represent sea turtles (TTL, loggerhead; TLB, leatherback), and light gray bars represent finfish (WHM, white marlin; BUM, blue marlin; BFT, bluefin tuna; BET, bigeye tuna; ALB, albacore tuna; DOL, common dolphin; WAH, wahoo; OIL, oilfish; SAI, Atlantic sailfish). See table S2 for scientific names and conservation status.

Table 1. Examined shark species, categorized as large coastal or oceanic according to the U.S. Fishery Management Plan (FMP) for Sharks of the Atlantic Ocean (35). These species are also caught in U.S. commercial and/or recreational shark fisheries.

Species	Latin name	Year first recorded	Total number recorded
<i>Large coastal species</i>			
Hammerhead spp.	<i>Sphyrna lewini</i> , <i>S. mokarran</i> , <i>S. zygaena</i>	1986	60,402
White	<i>Carcharodon carcharias</i>	1986	6,087
Tiger	<i>Galeocerdo cuvieri</i>	1986	16,030
Coastal spp.	<i>Carcharhinus altimus</i> , <i>C. brevipinna</i> , <i>C. falciformis</i> ,* <i>C. limbatus</i> , <i>C. obscurus</i> , <i>C. signatus</i>	1992	80,480
<i>Oceanic species</i>			
Thresher spp.	<i>Alopias superciliosus</i> , <i>A. vulpinus</i>	1986	23,071
Blue	<i>Prionace glauca</i>	1986	1,044,788
Mako spp.	<i>Isurus oxyrinchus</i> , <i>I. paucus</i>	1986	65,795
Oceanic whitetip	<i>Carcharhinus longimanus</i>	1992	8,526
Porbeagle	<i>Lamna nasus</i>	1992	829

*The silky shark (*C. falciformis*) is biologically an oceanic species, but is classified in the FMP as a large coastal.

placed but remains constant overall (“constant-effort scenario”). Area 7 has been closed since July 2001 to reduce bycatch of endangered sea turtles (28). We examined the effects of closing this area and each of the remaining areas (Fig. 1) in turn on catches of 13 examined shark species, and on 2 turtle and 10 finfish species of concern (29–31).

Model results show that marine reserves can indirectly cause harm if fishing effort is merely displaced. For example, the closure of Area 7 meets its objective in reducing sea

turtle bycatch and also protects sharks of lower conservation concern: blue and mako sharks. However, this closure increases catch of almost every other species (Fig. 4), because effort is redistributed to areas of higher species diversity. In contrast, closure of Area 3 would afford protection to most coastal shark species, including the hammerheads, but catch rates of oceanic sharks and sea turtles would increase (Fig. 4). Closure of Area 5 would be needed to protect thresher sharks (Fig. 4). Clearly, if marine reserves are

to be effective, their placement is of critical importance, and conservation initiatives must explicitly consider impacts on the whole community of species. Emphasis on single-species conservation, without controlling effort, simply shifts pressure from one threatened species to another and may actually jeopardize biodiversity.

We have presented strong quantitative evidence showing large declines in many coastal and oceanic shark species over a short period. Our results indicate that they should be given conservation attention equal to that given other threatened large marine predators. Given that in all oceans, longline and other pelagic fisheries are intense and catch many of the same shark species (7), serious declining trends in Northwest Atlantic shark abundances may be reflective of a common global phenomenon. Because consumers exert important controls on food web structure, diversity, and ecosystem functioning (32, 33), pervasive overfishing of these species may initiate major ecological changes. However, our analysis shows that marine reserves are not a panacea for overexploitation. Instead, we suggest that carefully designed marine reserves in concert with reductions in fishing effort (34) could hold promise for safeguarding sharks and other large pelagic predators from further declines and ecological extinction.

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 36. We thank NOAA-NMFS for data; J. Cramer, L. R. Beerkircher, and J. Musick for advice; W. Blanchard, L. Gerber, and M. Ortiz for technical assistance; H. Keith for initial closed-area model implementation;

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Supporting Online Material
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 Methods
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Selective Trafficking of Non-Cell-Autonomous Proteins Mediated by NtNCAPP1

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In plants, cell-to-cell communication is mediated by plasmodesmata and involves the trafficking of non-cell-autonomous proteins (NCAPs). A component in this pathway, *Nicotiana tabacum* NON-CELL-AUTONOMOUS PATHWAY PROTEIN1 (NtNCAPP1), was affinity purified and cloned. Protein overlay assays and in vivo studies showed that NtNCAPP1 is located on the endoplasmic reticulum at the cell periphery and displays specificity in its interaction with NCAPs. Deletion of the NtNCAPP1 amino-terminal transmembrane domain produced a dominant-negative mutant that blocked the trafficking of specific NCAPs. Transgenic tobacco plants expressing this mutant form of NtNCAPP1 and plants in which the *NtNCAPP1* gene was silenced were compromised in their ability to regulate leaf and floral development. These results support a model in which NCAP delivery to plasmodesmata is both selective and regulated.

In plants, the trafficking of NCAPs that are involved in the regulation of plant development is thought to occur through plasmodesmata (1–6). However, little information is available concerning the manner in which such NCAPs enter this cell-to-cell translocation pathway (5, 6). To identify potential components in this pathway, we used the NCAP CmPP16 (7) as bait for the affinity purification of interaction partners contained within a plasmodesmal-enriched cell wall protein (PECP) fraction (8–10) prepared with tobacco BY-2 cells [fig. S1, A and B (11)]. A resultant highly enriched 40-kD protein was identified (Fig. 1, fig. S1C), cloned, and named NtNCAPP1 (GenBank accession number AF307094; hereafter called NCAPP1) [fig. S2 (11)].

The specificity of the interaction between NCAPP1 and CmPP16 was tested using a protein overlay approach (11). Native NCAPP1 (contained within the PECP preparation) interacted with only a very small subset of the proteins present in the PECP fraction (Fig. 2A). Furthermore, fractions enriched for cytoplasmic proteins exhibited

only minimal interaction with NCAPP1 (Fig. 2B). A reciprocal experiment in which the PECP fractions were probed with the CmPP16 bait confirmed the specificity of the interaction between native NCAPP1 and CmPP16 (Fig. 2C). As the CmPP16 is an endogenous NCAP located within the phloem sap (7), we next used fractionated phloem sap (11) in an overlay with PECP and, as anticipated, detected a strong signal in the region corresponding to the CmPP16 (Fig. 2D). A range of other phloem proteins also interacted positively with NCAPP1, consistent with observations that various phloem components can traffic through plasmodesmata (12). These results confirmed that the NCAPP1 enrichment achieved in our affinity chromatography experiments (Fig. 1) was due to its specific interaction with the CmPP16 bait. The presence of a range of NCAPP1-interacting proteins in the phloem sap suggests that NCAPP1 (and other isoforms) may be central to NCAP trafficking in general.

Subcellular localization of NCAPP1 was examined by expression of fluorescently tagged NCAPP1 in BY-2 cells (Fig. 3). In contrast to the fluorescence pattern observed with free EGFP (enhanced green fluorescent protein) (Fig. 3A), NCAPP1-EGFP accumulated at the cell periphery (Fig. 3B). Similarly, fluorescence associated with CmPP16-RFP was highest at the periphery of BY-2 cells (Fig. 3C). A role for the predicted NH₂-

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