

## Cascading effects of the loss of apex predatory sharks from the coastal ocean

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### 20 **Abstract**

Impacts of chronic overfishing are evident in population depletions worldwide yet indirect community and ecosystem effects, mediated by the removal of apex predators, remain  
25 unpredictable. As abundances of all eleven great sharks that consume elasmobranchs plummeted over the past 35 years, 12 of 13 species of their elasmobranch prey increased tremendously in coastal northwest Atlantic ecosystems. Effects of this community restructuring have cascaded from one mesopredator, cownose ray, downwards: its order of magnitude increase resulted in sufficient predation pressure to render rare its bay scallop prey, terminate a century-long scallop  
30 fishery, and apparently inhibit recovery of other depressed bivalve populations. Analogous ecosystem transformations may be a predictable consequence of perturbations that eliminate the function of an entire consumer **trophic level**.

**One-sentence summary:** Concurrent with overexploitation of great sharks, abundances of their  
35 elasmobranch mesopredator prey have increased tremendously: order of magnitude enhancement of one mesopredator, the cownose ray, cascaded down the food web to induce a crash in its bay scallop prey and subsequent termination of a century-long scallop fishery.

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**Total word count** (abstract, main text, references, and figure captions) = 3464

40 ~~Anthropogenic perturbations to ecological communities are often initiated with the removal of~~  
~~top predators (1, 2).~~ The potential impacts on ecosystem structure and function of eliminating apex  
predators, including mesopredator-release (Crooks, Shepherd) and trophic cascades (Paine,  
Terborgh, Pace), can be far-reaching because of the strong influence predators may exert on their  
prey populations (Duffy). ~~Subsequent impacts on ecosystem structure and function, including~~  
45 ~~mesopredator release (3, 4) and trophic cascades (Paine, 5, 6), can be far-reaching because of~~  
~~the strong influence predators exert on their prey populations.~~ In the ocean, the most pervasive  
human activity, fishing, concentrates disproportionately on extraction of predators, particularly  
those at the top of the food web (Pauly). Consequently, the abundance of apex predators has  
been greatly reduced in marine ecosystems worldwide, eliciting concern about not only their  
50 conservation but also indirect ecosystem effects that might ensue from their removal. Yet, while  
top-down effects are relatively well understood in rocky intertidal, coral reef, and kelp forest  
ecosystems (Estes, Paine, Jackson), their importance and prevalence in other oceanic ecosystems  
remain unclear. Evidence of oceanic trophic cascades is limited (8-11), and some have argued  
that in complex marine food webs, with many interacting species and opportunities for functional  
55 redundancy, top-down effects may be attenuated (Strong, Jennings). ~~Here we explore the~~  
~~consequences of overexploitation of an entire trophic level of apex consumers, which induces~~  
~~strong top-down influence on species at lower trophic levels.~~

Fundamental constraints on studying apex predators, sampling vast marine ecosystems, and  
conducting controlled experiments in the sea have limited our capacity to predict indirect effects of  
60 marine predator removal or (in many cases) even to identify those that have occurred. This gap in  
understanding presents a critical challenge to mitigating human impacts and restoring marine  
ecosystems. To meet this challenge, we employed the two most powerful empirical methods in  
ecology, meta-analysis of multiple independent data sets and controlled experimental hypothesis  
testing replicated over space and time, using a unique compilation of research surveys, fisheries  
65 and landings data, and predator exclusion experiments, to investigate the consequences of the  
functional elimination of apex predatory sharks from the coastal ocean.

70 Large sharks (>2m) are top predators of global conservation concern. ~~Distributed~~  
~~circumglobally,~~ these species range from inshore coastal to oceanic habitats, and most are  
distributed circumglobally. Exploitation of large sharks has intensified worldwide in recent  
decades, driven by an upsurge in demand for shark fins and meat (13), and bycatch in many  
fisheries. Data to assess the direct impacts of exploitation on the great sharks are sparse, but  
where available, consistently indicate that they have been driven to ~~unprecedented~~ low levels (13-  
15). Whether functional elimination of these species also induces indirect ~~ecosystem-community~~  
effects, however, is an open question (15).

75 We hypothesized that weakened top-down control by the entire trophic level formed by large  
sharks could ~~trigger community-level changes through the~~ release of their elasmobranch  
mesopredator prey ~~from predation from predation, and, and that this effect of increasing~~  
mesopredators that associated effects that might cascade to lower trophic levels (Polis 2000. ~~We~~  
80 ~~reasoned that because~~). Because elasmobranch mesopredators (rays, skates, and small  
sharks) are of a substantial size, even as juveniles, and are thus consumed almost exclusively by  
large sharks (16; Table S1), we inferred that this group of prey species would include those most  
likely to be affected by the losses of these apex predators, the loss of the great sharks would  
most likely affect them. Moreover, interannual population variability in these species is minimal  
85 because of their ~~very~~ low reproductive rates, such that changes effected by predator removal  
should be detectable in time series data. We focused on the eastern seaboard of the United  
States, from Cape Cod (41.5°N) to Cape Canaveral (28°N), a region that encompasses the  
primary latitudinal range of the Northwest Atlantic's great sharks and the elasmobranch species  
they consume. ~~We predict that shark removal will have a community-scale effect on their prey, e.g.~~  
90 ~~small elasmobranchs (Polis 2000).~~

To test our hypothesis, we first analyzed temporal population trends from multiple data sets,  
both separately and combined in random effects meta-analysis (16) to yield a synthetic estimate of  
overall rate of change in abundance of each species. We extracted from an earlier study (14) of

95 the largest shark data set for the northwest Atlantic (logbook reports from the U.S. pelagic longline  
fishery) results for those 10 analyzed species of the 11 great sharks known to consume  
elasmobranchs. We tested the robustness of the results by analyzing scientific observer data from  
the same fishery using generalized linear mixed models. We then assembled all available  
scientific research surveys with species-specific data that began prior to 1990 and were conducted  
100 using a consistent standardized methodology throughout the survey period (16). Eighteen  
independent surveys, which together cover the eastern US coast (Fig. S1), met these criteria  
(Table S2; mean time span = 27 years). One, the UNC survey, conducted annually since 1972 off  
Cape Lookout, represents (to our knowledge) the longest continuous shark survey globally, and  
until now has never been analyzed. We conducted chose 1970–2005 as a baseline year because  
105 most of the surveys only when back to 1970, and we analyzed data records through 2005, where  
available. F..... We used generalized linear models to obtain trends in relative abundance of  
each species from 1970 onwards, analyzing every survey in which it was caught in at least three  
years. For each elasmobranch species, we used generalized linear models to obtain trends in  
relative abundance from each survey in which it was caught in at least three years (Table S3).  
110 Trend estimates for invertebrates were obtained from landings data using regressions with  
autoregressive errors and from one survey (16).

Our assessment of fisheries data for the great sharks revealed consistent patterns of  
precipitous decline over the past two decades. Analyses of logbook reports demonstrated  
115 decreases between 1986 and 2000 ranging from 40 to 89% for the elasmobranch-consuming  
species (14). Here we confirm those conclusions through comparisons with observer data  
collected between 1992 and 2005. Only for tiger sharks (*Galeocerdo cuvier*) do the estimates of  
temporal change differ between the two types of data, probably because of their differing temporal  
coverage: a significant decline in the 1980s and 1990s has apparently stabilized in the last four  
120 years. Rates of decline for the other eight species abundant enough to analyze in observer data  
were concordant with the logbook analysis: mako sharks (predominantly *Isurus oxyrinchus*) have  
declined moderately, while hammerhead (scalloped (*Sphyrna lewini*), great (*S. mokarran*), smooth

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Comment [J1]: I think we need a sentence here that clearly explains the time period we examined, and that 1970 was chosen as a baseline year, and why.

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(*S. zygaena*) and large coastal (genus *Carcharhinus*, including dusky (*C. obscurus*), sandbar (*C. plumbeus*), blacktip (*C. limbatus*), bull (*C. leucas*)) sharks have plummeted [in abundance](#) (Fig. 1A).

Multi-decadal dynamics of large sharks exhibited in the longest shark-targeted research survey (UNC) revealed declines similar to, or even greater than, the fisheries-dependent estimates (Table S4), implying the likely functional elimination of these apex predators. The UNC survey showed significant declines in six elasmobranch-consuming large shark species since the early 1970s, from **93% for sandbar sharks and 95% for blacktip sharks to over 99%** for bull, dusky, scalloped hammerhead, and tiger sharks (Fig. 2, 1<sup>st</sup> row). Because this survey is situated geographically where it intercepts sharks on their seasonal migrations, the observed trends in abundance for these species may be indicative of population changes along the eastern seaboard of the U.S..

The UNC survey also showed the loss of the largest individuals, with significant declines in mean length of blacktip, bull, dusky and sandbar sharks of 17 to 35% (Fig. S3), suggesting that overexploitation has left few remaining mature individuals in these populations. The remaining five of the eleven elasmobranch-consuming great sharks were so rare as to prevent detection of trends from this survey. Two of those, great white and sand tiger sharks, were each caught only once and early in the UNC survey (in 1974 and 1978 respectively). The only research survey that has caught the sand tiger shark in sufficient numbers for analysis is conducted in Chesapeake Bay and suggests a decline of over 99% [between 19\\*\\* and 20\\*\\*](#) (16, 17).

When the UNC survey is combined with all other research surveys, a consistent meta-analytic pattern of marked reductions is evident in great shark populations (Fig. 1A) that has occurred over the past 35 years. The only significantly increasing trend for any of these species was for scalloped hammerheads from a survey that exclusively sampled the juveniles which may reflect recently increased survival following the loss of their only predators, larger apex predatory sharks. Every other significant research survey estimate (n=11) for great sharks indicated decreasing trends in their abundance (Table S4).

Concurrent with the removal of large sharks, populations of elasmobranch mesopredators have increased enormously across the entire US Atlantic coast. This group of thirteen rays, skates, and small sharks is taxonomically diverse (six families), and includes species that inhabit benthic and pelagic waters from estuaries and the inshore coast to the continental shelf and slope, each of which is preyed upon almost exclusively by large sharks. Meta-analyses of research survey data revealed a common pattern of significant, high rates of increase over the past 16 to 35 years for all but one of these species (Fig. 1B, Table S4). We estimate that during this time the little skate (*Leucoraja erinacea*) population quadrupled in size, and populations of Atlantic sharpnose shark (*Rhizoprionodon terraenovae*), chain catshark (*Scyliorhinus retifer*), and smooth butterfly ray (*Gymnura altavela*) increased by approximately an order of magnitude (Fig 2, 2<sup>nd</sup> row).

Most conspicuous among the increasing mesopredators is the cownose ray (*Rhinoptera bonasus*). Six of seven research surveys covering the U.S. Atlantic cownose ray population's range (southeast Florida – to Long Island (18)) showed significant increases (e.g., Fig. 2, 2<sup>nd</sup> row, Table S4). Together, these rates of change (mean = 0.087, 95%CI: 0.021-0.127) indicate an order of magnitude increase in coast-wide abundance of cownose rays since the mid-1970s and, when combined with earlier population estimates from aerial surveys (19), imply that over 40 million cownose rays may now inhabit Chesapeake Bay during the summer and contribute to the massive fall migration southward to Florida. Based on life history contrasts with other fishes, a population rate of increase this high for a species with the late age at maturity and low fecundity of the cownose ray is only reasonable if its natural mortality rate were significantly depressed, as would occur with a decrease in predation (16). Thus, although reductions in cownose ray bycatch may have contributed partially to the increase since the 1990s, the ascendancy of cownose rays also requires that its natural predators, the great sharks have declined.

Over their range on the eastern seaboard Cownose rays are responsible for consumption of substantial numbers of bivalve mollusks – predation Effects of the cownose ray increase have

180 | ~~cascaded down the food web to their bivalve molluscan prey, with demonstrable consequences for~~  
| ~~at least the bay scallop and the fishery it once provided.~~ Cownose rays migrate from their summer  
habitat in bays between Raritan Bay, New Jersey and Pamlico Sound, North Carolina to  
overwintering grounds on the central and southern Florida shelf (18). The rays migrate along the  
coastline, often entering and exiting bays and sounds en route. Their diet consists largely of  
benthic bivalve mollusks, including bay scallops (*Argopecten irradians*), soft-shell clams (*Mya*  
185 *arenaria*), hard clams (*Mercenaria mercenaria*), oysters (*Crassostrea virginica*), and several  
smaller, non-commercial molluscan bivalves (19, 20). Annual consumption of these species within  
the Chesapeake Bay, based on our abundance estimate, individual daily consumption rates of  
~210g shell-free wet weight (16) and occupancy times of 100 days each year, may now total  
840,000 metric tons (wet flesh). In comparison, the 2003 commercial harvest of these mollusks in  
190 Virginia and Maryland totaled only 300 metric tons, indicating that cownose ray consumption of  
bivalves in the Chesapeake Bay area is now likely over 2,500 times greater than the commercial  
harvests.

Quantitative field observations and predator-exclusion experiments demonstrate that the  
195 impact of cownose rays on bay scallop populations has intensified greatly over the past two  
decades (Fig. 3). Field sampling showed no evidence of ray-predation control on adult bay  
scallops during the southward fall migration (arrows in Fig. 3A) in 1983 and 1984 (four sites in Fig.  
3A; 22). In contrast, recent analogous sampling, confirmed by controlled ray-exclusion  
experiments [using stockades](#), revealed that since 1996 migrating cownose rays have caused  
200 almost total scallop mortality (Fig. 3A; 23) at every site with initial adult bay scallop densities  
above a threshold for intensive ray foraging of  $\sim 2\text{m}^{-2}$  (Fig. 3B,C). Abundance of bay scallops  
declined much less inside cownose ray exclosures than on unprotected grounds (Fig. 3A) and, in  
the absence of scallop emigration, numbers inside stockades would probably have remained  
nearly constant (23).

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**PETE TO FIX:** Cownose rays were abundant enough to reduce bay scallops in all of North Carolina's scallop beds to less than 1-2m<sup>-2</sup> by the end of their fall migration (October) in each of 2002 and 2003 (Fig. 3) and to terminate North Carolina's century-old scallop fishery by 2004. Because this predation precedes bay scallop spawning, cumulative effects of intense ray predation in previous years sufficed by 2004 to terminate North Carolina's century-old bay scallop fishery. ~~By~~Indeed, in fall 2004 densities of adult bay scallops on all traditional North Carolinian scalloping grounds were depressed below that necessary to establish a fishable cohort of new recruits (2m<sup>-2</sup>, Fig. 3; 24), apparently suffering jointly from direct ray predation as well as consequent Allee effects of density limitation on reproductive success (24). The fishery has remained closed for lack of fishable cohorts in the 2005-6 and 2006-7 winter scalloping seasons. Having depleted the more readily targeted epibiotic bay scallops, it is reasonable to expect future expansion of cownose ray foraging on infaunal bivalves buried in seagrass beds, with associated uprooting of vegetation and loss of nursery habitat (20, 25).

The vast increase in predation by cownose rays also may now be inhibiting recovery of, and restoration efforts for, oysters, soft-shell clams, and hard clams (16), compounding the effects of overexploitation, disease, habitat destruction, and water quality degradation, which are known separately and interactively to have acted historically to depress these species (21). Both research surveys and landings data for large inshore bivalves (soft-shell clams, hard clams, oysters and bay scallops) within the cownose ray's range of New York to Florida show them falling without substantial recovery as the rays increased (Fig. 2 3<sup>rd</sup> row) and failing to initiate recovery despite active shellfish restoration and enhancement programs. In contrast, areas beyond the northernmost limit of cownose rays (e.g. northeastern U.S.(Raritan Bay??-Pete to check -match with SOM on geography) and Atlantic Canada) demonstrate several examples of stable or increasing landings of inshore bivalves (Fig. S2; Table S5).

Elasmobranch community inversions, similar to that documented here, may be occurring in other mesopredator species / and in other coastal seas. Studies in the northeast Atlantic Ocean

**Comment [J2]:** RAM, do you want to insert what you wanted here about competitive release?

**Comment [CHP3R2]:** Please don't – it will cloud the issue, I fear.



235 | have noted that elasmobranch mesopredator species have increased in abundance despite  
substantial fishing pressure (e.g. 27, 28) – [competitive release or unknown reasons](#). We suggest  
that these changes were likely facilitated by the loss of predation from large sharks. Impacts of  
elasmobranch mesopredator release are expected to cascade to the base of the food web, at  
least for eagle and cownose rays, because of the strong interspecific interactions with their  
240 | invertebrate prey. ~~Pete(?)~~-[we have only followed cownose ray impacts, not the other 11  
mesopredators –for commercially targeted species we have much greater understanding of the  
pop. Dynamics of their prey](#) In Japan's Ariake Bay in the northwest Pacific Ocean, for example,  
wild-stock and cultured bivalve shellfish have been recently decimated by expanding numbers of  
eagle rays (*Aeobatus flagellum*) (29), where fishing exploitation on apex predator sharks is  
probably intense.

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Our study provides evidence for a previously unrecognized marine ecosystem transformation  
that is most likely explained by the functional elimination of apex predators, the great sharks.  
~~Other explanations, competitive release, may have played a role, but cannot account for the huge  
reductions in mortality estimated in the elasmobranch mesopredators, such as cownose rays. [We  
250 | show that, in~~ addition to directly threatening the long-term persistence of large sharks,  
overexploitation of these species appears to have led to a region-wide proliferation of  
mesopredatory elasmobranchs. Consequences of this fundamental community restructuring have  
cascaded down the food web from cownose rays to bay scallops, and possibly other bivalves, and  
have potential [for broader ecosystem effects by te-extending](#) to seagrass habitat exacerbating  
255 | stresses on already highly degraded coastal benthic ~~systemse~~[communities](#). Thus, like the classic  
killer whale - sea otter – urchin – kelp trophic cascade (8), the indirect ecosystem consequences  
of eliminating top-down control by great sharks carry risks of broader marine ecosystem  
degradation. ~~More broadly, w~~[We](#) propose that rather than attenuating in complex marine food  
webs, top-down effects must be widely if not universally expected when entire [functional groups\(a  
260 | new term introduced here\)](#) are removed, as is commonly the case with industrial fisheries.  
Illumination of the operation of indirect species interactions within marine and other environments

brightens the future for development of what is now so widely sought, ecosystem-based management to achieve sustainability of natural living resources.

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- 320 **Supporting Online Material**  
[www.sciencemag.org](http://www.sciencemag.org)  
Materials and Methods  
Supporting Results  
Tables S1 – S5  
325 Figs. S1 – S3

330 **Figure Captions**

**Fig. 1.** Instantaneous rates of change in relative abundance ( $\pm$  95% confidence intervals) for (A) large sharks and (B) elasmobranch mesopredators, as estimated by random-effects meta-analyses of fisheries (red) and research survey (black) data. Analyses are species-specific except for fisheries data for hammerhead sharks (scalloped, smooth, great hammerhead), large coastal sharks (blacktip, bull, dusky, sandbar, bignose, night, silky, spinner; the first four of which consume elasmobranchs), and mako sharks (primarily shortfin mako), each of which is grouped by genus.

**Fig. 2.** Change in relative abundance (overall trend (solid line) and individual year estimates (■)) of species at each trophic level as estimated from single data sources: large shark species (top row, estimated from the UNC shark research survey), elasmobranch mesopredator species (2<sup>nd</sup> row, estimated from each of several research surveys, data source acronyms as in Table S2), and bivalve mollusk species (bottom row, estimated from landings data from within the cownose ray's range). Proposed top-down effects linking trophic levels are denoted by arrows: functional elimination of large shark species linked leading to elasmobranch mesopredator increases release (thick solid arrow), experimentally tested relationship between cownose rays and bay scallops (thin solid arrow), and suggested relationship between cownose ray and inhibition of recovery of other bivalve mollusks (dashed arrow). Data source details and methods are in Supplementary Material.

**Fig. 3.** (A) Map of southeastern U.S. indicating the study location (dashed box), and detailed schematic of North Carolina's southern Outer Banks showing 7 sites where bay scallop densities were monitored in the years indicated. Total mortality (black bars) is calculated by comparing August surveys (pre- cownose ray migration) to late September/October surveys (post-migration). Low bay scallop densities prior to cownose ray migration are indicated by an asterisk ( $>1-2 \text{ m}^{-2}$ ) or 0 (indicates no bay scallops). Asterisks indicate bay scallop densities below  $1-2 \text{ m}^{-2}$ ; 0 indicates no bay scallops. Hatched bars represent mortality within experimental stockades

(performed in a subset of years) designed to exclude large rays. Scallops were free to move in and out of stockade areas; thus, mortality is greatly overestimated within the stockades (23).

360 Arrows denote the direction of cownose ray migration through the area based on gillnet collections and surveys of local fishermen. (B) Mean bay scallop density measured in midsummer (July to early August) and mortality measured over the period from early summer to early fall at Oscar Shoal during 10 years of surveys. (C) Trend lines, based on 12 weekly surveys in 1998 and 8 in 2002 and 2003, showing the density of bay scallops at Oscar Shoal.

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