Cascading effects of the loss of top predators from the coastal ocean

Abstract

Impacts of chronic overfishing are evident worldwide in depressed populations, yet indirect ecosystem effects, mediated by the removal of predators, remain obscure. Here, we investigate the consequences of the functional elimination of an entire complex of marine predators, the great sharks. Overexploitation of these species has triggered the release of small sharks, skates, and rays across the continental shelf, slope, and coast of the warm temperate northwest Atlantic Ocean over the past 35 years. This rise in mesopredators is particularly consequential for the cownose ray. Absent top-down control by great sharks, the east coast population of cownose rays has exploded at 6-9% per annum, causing sufficient predation pressure on their molluscan prey to radically depress several bivalve fisheries and threaten the future of seagrass habitat with excavation. Our study provides the first documented example of a trophic cascade beginning with the apex predators of the sea, leading to a region-wide fundamental restructuring of a prey community, and terminating at the bottom of the food web with the extinction of a fishery (bay scallops).

One-sentence summary: (capturing the most important point)

Total word count (so far): ~2350

Reports (up to ~2500 words or ~3 journal pages) present important new research results of broad significance. Reports should include an abstract, an introductory paragraph, up to 4 figures or tables, and a maximum of 30 references. Materials and Methods should usually be included in supporting online material, which should also include information needed to support the paper's conclusions.

Text

Anthropogenic perturbations to ecological communities are often initiated with the removal of top predators (*1*, *2*). ~~–often has far-reaching consequences….~~

~~Because these species often exert considerable influence on their prey,~~ Modification of ~~apex~~ predator abundance can cascade throughout food webs with far-reaching impacts on ecosystem structure and function (*2-5*)~~, including mesopredator release, an increase in the abundance of intermediate consumers following a decline in predation by top predators (*6*, *7*), and trophic cascades, indirect effects occurring two or more trophic levels lower ( )~~. Such 'top-down' effects have been extensively studied, and are well documented in freshwater, terrestrial, and some coastal marine ecosystems ( ).

In the ocean, the most pervasive human activity, fishing, concentrates disproportionately on extraction of predators, particularly those at the top of the food web ( ). Consequently, the abundance of predators has been substantially reduced in marine ecosystems worldwide, and there is considerable concern about their conservation as well as the potential effects of eliminating top-down control from these systems ( ). Yet, the importance of top-down effects in the ocean remains unclear. Evidence of trophic cascades in marine ecosystems is equivocal (Estes, Dulvy, Micheli, Cox-Kitchell, Frank, Bascompte et al.) and it has been argued that top-down effects may be attenuated in complex marine food webs (Link, Bascompte et al.). Exploitation may have broad unintended consequences for marine ecosystems, but chronic undersampling of these vast three-dimensional ecosystems and limited capability of conducting controlled experimentation in the sea have limited the capacity of ecology to predict these indirect effects or (in most cases) even to recognize those that have occurred. This gap in understanding presents a critical challenge to mitigating human impacts and restoring marine ecosystems. Here we combine *(broad insights…)* powerful empirical evidence from multiple long-term research surveys, fisheries and landings data sets, with controlled ~~with the rigor of~~ predator exclusion experiments, demonstrating that a massive ecosystem transformation has occurred as a consequence of the loss of great sharks. We propose that in complex marine food webs top-down

effects, like the one we report, should be expected when entire functional groups are removed, as is commonly the case with industrial fisheries.

Among marine consumers, large sharks are top predators of global conservation concern. These sharks are circumglobal in distribution, and span the range from inshore coastal to oceanic habitats. Exploitation of these species is extreme. Direct exploitation has intensified worldwide over the past two decades, driven by an upsurge in demand for shark fins and meat (*10*, *11*), and large sharks suffer ongoing pervasive incidental take in many fisheries. Data to assess the impacts of exploitation on large sharks are sparse, but where available consistently indicate that these species have been driven to unprecedented low levels (*5*,). Whether functional elimination of these species also induces indirect effects on community structure, however, is an open question (*12*, *13*). We reasoned that weakened top-down control by these apex (and near apex) predators might have the greatest influence on other elasmobranchs, specifically species of smaller sharks, skates, and rays. Because of their substantial size, even as juveniles, such mesopredators are consumed almost exclusively by large sharks (SOM; Table S1). Moreover, interannual population variability in these species is minimal because of their very low reproductive rates, such that changes effected by predator removal should be detectable in time series data. We hypothesized that elimination of large sharks could trigger an elasmobranch mesopredator release, with possible cascading effects at lower trophic levels. We tested this hypothesis for the eastern seaboard of the United States, from Cape Cod (41.5ºN) to Cape Canaveral (28ºN), because this region encompasses the range of the ten main species of Northwest Atlantic great sharks (>2m) that consume elasmobranchs and can be characterized by its many fisheries, survey, and experimental data sets available for analysis and synthesis.

Large sharks have plummeted in the Northwest Atlantic over the past two decades, with the intensification of commercial and recreational exploitation. Analyses of the largest data set for the region, based on logbook reports from the U.S. pelagic longline fishery, indicate that declines ranging from 40 to 89% occurred for all seventeen species examined, over the 15-year period

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from 1986 to 2000 (*5*). Here we present results for th~~ose~~ ~~ten~~ species that consume other elasmobranchs (Fig. 1A; Table S1, S3). To complement these findings, we examined independent scientific observer data from the same fishery, collected by U.S. National Marine Fisheries Service (NMFS) between 1992 and 2005 (Fig. S1). We derived trends in relative abundance for the same shark ~~speciess along the east coast of the United States (Fig. S1)~~ using generalized estimating equations (*15*, *16*). These models allowed us to standardize catch rates for temporal, spatial, and operational differences among longline sets, while also accounting for covariance among sets made on the same trip.

~~For tiger sharks, results from the two data sources diverge because of their different temporal coverage: logbook data indicated significant declines between 1986 and 2000, while the observer data suggested an increasing trend driven by higher catches since 2002 (Fig. 1A; Table S3).~~ The ~~o~~Observer data showed instantaneous declines consistent with those in the logbook analysis: ~~for~~ groups of hammerhead sharks (scalloped (*Sphyrna lewini*), great (*S. mokarran*), smooth (*S. zygaena*)), large coastal species (genus *Carcharhinus*, including dusky (*C. obscurus*), sandbar (*C. plumbeus*), blacktip (*C. limbatus*), and bull (*C. leucus*) sharks), and mako sharks (predominantly shortfin makos (*Isurus oxyrinchus*)) have undergone substantial declines that appear not to have ceased (Table S3). Estimates for tiger sharks (*Galeocerdo cuvier*) from the two data sets differed because of their temporal coverage: following a significant decline in the 1980s and 1990s, this species has apparently begun to increase in the past four years (Table S3). For each of these species, results from the two analyses were combined using random effects meta-analysis (*SOM*), to illustrate the general pattern of decline that has occurred (Fig. 1A)~~, and indicate substantial declines that appear to be ongoing~~.

We extended temporal trends in abundance for large shark species back to ~~the~~ earlier decades~~ 1970s~~ by analyzing data from research surveys (Table S2). Research surveys are the only reliable source of data on sharks that includes this time period. Thus, ~~abundance trends~~ they provide critical long-term species-specific estimates of temporal change, al~~though~~beit each samples~~over~~ a ~~much~~ smaller geographic area than the fisheries data. We considered all available

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surveys from research institutes ~~or U.S. government agencies~~ that began prior to 1990, and were conducted using a consistent standardized methodology over at least 12 years (*14*). Twelve surveys met these criteria (Table S2). Together, they include data on all large sharks of interest (except the most oceanic species, shortfin mako) and cover the eastern coast of the U.S. (Fig. S1).~~For each of the twelve surveys that met these criteria, we used generalized linear models to derive an index of relative abundance for every species that had been recorded in at least three years~~ For each species, we used generalized linear models to obtain an index of relative abundance from each survey that had recorded it in at least three years. ~~and then combined the indices meta-analytically to determine an overall estimate of the rate of change (in relative abundance).~~ Two of the surveys were specifically designed to sample sharks, the longest of which ~~available shark-targeted survey, which until now has never been analysed,~~ was conducted over a thirty-two year period (1972-2003) using demersal~~pelagic~~ longlines off Cape Lookout, North Carolina, and until now has never been analysed. ~~This survey included data on all large sharks of interest, except shortfin mako, the most oceanic species. Data for sandbar, dusky, blacktip, and scalloped hammerhead sharks also were contained in at least one other available survey meeting our criteria for inclusion.~~

Rates of decline for large sharks, as estimated from this North Carolina shark survey, were consistent with or even greater than the fisheries estimates, implying the functional elimination of these species over the past thirty years. We found statistically significant declines for six species, that ranged from 93% (95% CI: 75 to 98%) in sandbar shark (Table S3) to over 99% for tiger (95% CI: 93.1 to 99.9%), bull (95% CI: 93.1~~2.8~~ to 99.9%), and scalloped hammerhead (95% CI: 98.7 to 99.8%) sharks (Fig. 2); estimated declines for the two other species of ~~the pattern of decline for two other species was similar to scalloped hammerheads~~ hammerheads also were substantial but were non-significant because of their small sample sizes (Table S3). ~~These r~~Results from this survey may well be indicative of trends in abundance for these species along the entire Atlantic coast: they match the overall pattern shown in the fisheries data for the

Comment [J3]: Rationale: a shark-targeted survey right on the range of where the effects are showing up at the lower trophic levels

Northwest Atlantic, and each species is thought to form but a single population within this region. ~~Moreover, overall declines are likely still greater, since exploitation of these species by industrial fishing began a decade before the data records began. White and sand tiger sharks were each caught only once during the entire North Carolina survey (in 1974 and 1978 respectively), a finding consistent with a strong decline in these species.~~ The survey also revealed the loss of large individuals of blacktip, bull, dusky and scalloped hammerhead sharks since the early 1970s, and several species that underwent significant declines in mean length (from * to 34%; Fig. S2), indicating that exploitation has disproportionately affected the largest sharks, leaving few remaining mature individuals. Two other apex predators, white and sand tiger sharks, were each caught only once during the entire North Carolina survey (in 1974 and 1978 respectively), a finding consistent with a strong decline in these species.

~~Overall, research surveys revealed a broadly consistent pattern of long-term decline in large sharks.~~ Almost all individual survey estimates for large shark species showed declines (Table S3). The few exceptions (only one of which is statistically significant) were from trawl surveys that exclusively sample juveniles of the large sharks. S~~The s~~tabilized or increased numbers of some species (blacktip, sandbar, and scalloped hammerheads) in recent years, as suggested by these surveys, may be attributed to increased juvenile survival following the sharp decline of their only natural predators, the apex predatory sharks (SOM). We combined individual survey indices (Table S3) meta-analytically (SOM) for each species to determine a mean estimate of their rate of change in relative abundance (Fig. S1).~~Estimates for individual species from different surveys were combined meta-analytically (*17*) as above (Fig. 1A).~~ Together, research surveys revealed a broadly consistent pattern of long-term decline in the large sharks (Fig. S1),

Comment [J4]: Implies v. strong d.d. mortality

Concurrent with the declines in large sharks, populations of elasmobranch mesopredators increased enormously. This group of shark, skate and rays comprised thirteen species (from six Families), each of which is preyed upon by the large sharks (Table S1). Using data from seventeen research surveys along the U.S. Atlantic coast (Table S2; Fig. S1), we derived trends

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in abundance for each mesopredator (Table S3; *14*). ~~We analysed the seventeen research surveys that met our selection criteria and included these species (Table S2). An index of relative abundance was derived for each mesopredator, from each of the surveys that had recorded it in at least three years (Table S3).~~ for all small shark, skate and ray species that have higher intrinsic rates of increase than the large sharks and do not experience significant fishing mortality (n=13 species; *14, 18,* Fig. S1). The surveys indicate substantial increases in these species over the past 16 to 35 years, including a quadrupling of little skate (*leucoraja erinacea*) and approximately order of magnitude increases in Atlantic sharpnose shark (*Rhizoprionodon terraenovae*), chain catshark (*Scyliorhinus rotifer*), and smooth butterfly ray (Fig 2, 2ⁿᵈ row). We show via meta-analysis that all but one of ~~the~~such elasmobranch mesopredators ~~for which data were available~~ ha~~s~~ve experienced significant rates of increase~~d dramatically over the past 16 to 35 years along the U.S. Atlantic coast~~ (with most between 0.04 and 0.08; Fig. 1B). ~~Most of the significant instantaneous rates of increase were between 0.04 and 0.08, indicating a quadrupling of mesopredators like little and rosette skate (*Leucoraja erinacea, L. garmani*) and increases of about an order of magnitude in Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) and chain catshark (*Scyliorhinus rotifer*) (Fig. 2E-H).~~ The consistent ~~and dramatic~~ region-wide proliferation~~expansion~~ of mesopredatory elasmobranchs, and the breadth of communities they inhabit, including benthic and pelagic waters from the inshore coast to the continental shelf and slope, imply a large-scale fundamental restructuring of marine ecosystems that has occurred as an indirect effect of overfishing top predators.

Most conspicuous (TEK ref) of the increasing mesopredators is the cownose ray (*Rhinoptera bonasus*). We analysed seven independent surveys that covered the range of the U.S. population (southern Florida (27ºN) – Long Island, New York (41ºN) (*19*)). A consistent pattern ~~of increase~~ emerged (6 – 9% growth annually) indicating a ten-fold increase in cownose rays since the mid-1970s (~~instantaneous rate of change: 0.087 ± 0.022 S.E.,~~ Fig. 2, row 3~~I~~-L). This rate of increase is close to the estimated maximum intrinsic rate of increase for this species (insert note), suggesting that total mortality for this species must have been low during this period~~.~~. We

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estimate that there may now be over 40 million cownose rays along the east coast of the U.S. (*20*, *21*). The most reasoned explanation for the ascendancy of cownose rays is release from predation, initiated by overexploitation of the great sharks, namely blacktip, bull, dusky, great hammerhead, sandbar, and shortfin mako sharks, which are its only ~~known~~ effective natural predators (Table S1).

Effects of the cownose ray explosion have cascaded down the food web to benthic invertebrates, with profound consequences for their bivalve prey and fisheries they provide. The east coast population of cownose rays undertakes annual migrations from overwintering grounds on the central and southern Florida shelf to summer habitat in various bays from Pamlico Sound in North Carolina to Raritan Bay in New Jersey (*19*). During the spring and fall migrations, the rays follow the coastline, either in the coastal ocean off the beach or entering and exiting bays and sounds en route. The cownose ray diet consists largely of benthic bivalve mollusks, including soft-shell (*Mya arenaria*), ~~and~~ hard ~~(quahogs~~ (*Mercenaria mercenaria*) and razor (*Tagelus plebeius*) clams, oysters (*Crassostrea virginica*), and bay scallops (*Argopecten irradians*) (*20*, *22*). Annual consumption of these and other bivalve species within the Chesapeake Bay, based on individual daily consumption rates of about 210g shell-free wet weight (*20, 23*) and occupancy times of 100 days each year, may now total 850,000 metric tons of wet flesh. In comparison, the 2003 commercial harvest of these mollusks in Virginia and Maryland totaled only 300 metric tons (wet flesh), indicating that cownose ray consumption in the Chesapeake Bay area is now likely over 2,500 times greater than the human commercial harvest of bivalve mollusks across all estuarine waters of these two ~~bay~~ states. Although overharvesting, disease, habitat destruction, and water quality degradation have been previously implicated as factors affecting populations of these shellfish, the ~~enormous~~ vast increase in consumption by cownose rays likely contributes both to the recent declines and failures in restoration of these bivalves. A ~~North Carolina~~ research survey in Pamlico Sound, North Carolina (the only one~~survey time series~~ known within the cownose ray range that records the large~~r~~ bivalves) shows mollusks plummeting since 1990 (Fig. 1C, 2bottom row~~M~~). Landings data indicate that inshore bivalve shellfish species (soft-shell

clams, hard clams (quahogs), oysters and bay scallops) have declined between New York and Florida as cownose rays increased (Fig. 1C, 2bottom rowN-P, S3). In contrast, oyster, quahog, and soft-shell clam landings increased in areas beyond the northernmost limit of cownose rays (e.g. Connecticut, Nova Scotia), while in the Gulf of Mexico, where incidental catches in the intensive shrimp trawl fisheries have apparently prevented the cownose ray population from increasing (Shepherd & Myers 2005), oyster landings have also increased (Fig. S3).

Quantitative field observations separated by two decades, combined with recent predator-exclusion experiments, demonstrate that impacts of cownose ray predation on bay scallops have grown dramatically. Fisheries-independent field sampling in both 1983 and 1984 to test whether cownose rays substantially reduced bay scallop abundances during their fall migration through the prime scallop grounds of North Carolina sounds revealed little evidence of any ray predation-control of adult bay scallop abundances (*24*). As the cownose ray population skyrocketed multiplied over the following decades, however, their predation on bay scallops intensified. Indeed, analogous quantitative assessments, confirmed by implementation of experimental ray-exclusion stockades, revealed that by 2002 and 2003 cownose ray predation during fall migration had increased to the pointdegree that bay scallops in all scallop beds of the state were depleted to levels below 1-2 m^{-2} by October each year (Fig. 3, *25*). By 2004 ray predation was sufficiently intense to cause the terminationextinction of North Carolina's century-old bay scallop fishery, a commercial and recreational fishery closure that continues today. Because the densities to which bay scallops are now reduced in North Carolina during fall passage of cownose rays prior to scallop spawning are below what seems required to establish a fishable cohort of new scallop recruits (*26*, *27*), bay scallops now suffer jointly from direct predation by rays as well as consequent Allee effects of density limitation on spawning and fertilization success. Now that more readily targeted epibiotic bay scallops have been depleted by migrating cownose rays, it is reasonable to expect widespread future expansion of their foraging for infaunal bivalves in seagrass beds, with predictable uprooting and consequent destruction of submerged aquatic vegetation to an uncertain degree (*28*).

Although our study is novel in its clear demonstration that extinction of a fishery and suppression of recovery in others are best explained by the operation of a powerful trophic cascade, initiated by functional elimination of apex pelagic predators, evidence is accumulating that such ecosystem-based processes must be widely if not universally considered in conservation and sustainable management of living marine and aquatic resources. Evidence that changing abundances of smaller elasmobranchs can be attributed to declines in a larger competing skate (Dulvy ref) and that wild-stock and cultured bivalve shellfish have been recently decimated by expanding numbers of a predatory eagle ray in Ariake Bay, Japan (Yamaguchi ref), where fishing exploitation on apex predators is likely intense, suggests that some strong interspecific interactions, the functional backbone of trophic cascades and other indirect ecosystem impacts, are widespread among coastal elasmobranchs and between rays and their molluscan prey. Like the most well documented trophic cascade in the ocean, the role of sea otter predation on the west coast (Estes ref) and lobster predation on the east coast (Scheibling or Steneck ref) of North America in controlling sea urchin populations and their potential to convert emergent kelp habitat to crustose algal "urchin barrens", the indirect ecosystem consequences of functional elimination of the great sharks has the potential to destroy productive nursery habitat, in this case seagrass beds (Orth ref) as cownose rays turn to preying on buried mollusks in the absence of a bay scallop resource. Future impacts on seagrass-associated fisheries could be devastating. Strong cascades of indirect effects in aquatic ecosystems are clearly not limited to coastal systems with a seafloor member. The classic trophic cascade from predatory fish through zooplankton to phytoplankton in northern temperate lakes (Carpenter ref) and the apparent pelagic cascade linking cod to zooplankton off the Scotian Shelf (Frank ref) operate completely within the water column. Illumination of the operation of such indirect interactions within marine and aquatic environments brightens the future for development of what is now so widely sought, ecosystem-based management to achieve sustainability of natural living resources.

-Increase in elasmobranch mesopredators, catsharks – ; small skates (cuckoo and starry skate) attributed to competitive release from decline of large skates (Dulvy et al. 2000 Con. Biol.)
-Evidence of similar ray explosions and bivalve shellfish crashes in Japan indicate that this trophic cascade from great sharks to mesopredators to bivalves is a wide-spread feature of ocean ecosystem organization, critical to ecosystem-based mismanagement of marine fisheries;
–link between apex predators cascades all the way down to seagrasses – exacerbating stresses on already highly degraded coastal benthic communities – management implications.
-operation of a powerful trophic cascade initiated by over-fishing of the great sharks along the Atlantic coast (rays).
Thus, like the classic consequences of over-fishing sea otters on the west coast, the over-fishing of coastal pelagic sharks on the east coast carries huge risks of ecosystem transformation and degradation, with negative effects of many fisheries dependent on SAV habitat.

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Supporting Online Material
www.sciencemag.org
Materials and Methods
Supporting Results
Tables S1-S3
Figs. S1 – S3

Potential Reviewers:
Nick Dulvy, Enric Sala, James Estes, Daniel Pauly

Figure Captions

Fig. 1. Instantaneous rates of change in relative abundance (± 95% confidence intervals) for (A) large sharks, (B) elasmobranch mesopredators, and (C) molluskan bivalve species, as estimated in the random-effects meta-analysis from fisheries (orange), research survey (blue), or landings (green) data. Analyses are species-specific wherever possible; grouped species are as follows: hammerhead sharks (scalloped, smooth, great hammerhead), large coastal sharks (dusky, blacktip, night, sandbar, silky, bull, bignose, spinner-mention which ones consumed), mako sharks (composed primarily of shortfin mako with some longfin mako), mollusk species (oysters, hard clams, soft-shell clams).

Fig. 2. Change in relative abundance (overall trend (solid line) and individual year estimates (■)) as estimated from single research survey (A-M) and landings (N-P) data sets for large sharks: (A) sandbar, (B) dusky, (C) bull, (D) scalloped hammerhead; elasmobranch mesopredators: (E) rosette skate, (F) little skate, (G) chain catshark, (H) Atlantic sharpnose shark, and cownose rays in (I) Delaware Bay, (J) North Carolina Inner Bays, (K) Chesapeake Bay, Virginia, (L) Chesapeake Bay, Maryland; and bivalve mollusks: (M) mollusk species (oysters, hard clams, bay scallops), (N) bay scallop, (O) hard clams, and (P) soft-shell clams. y-axis scales?

Fig. 3. .pdf, .ps, .eps, .prn, .doc, .wpd Map of the mid Atlantic coast of the USA indicating the location of the southern portion of the North Carolina outer banks (dashed box). A detailed schematic is presented showing the locations of six sampling sites within the outer banks where bay scallop densities were monitored in the years denoted. Total mortality (black bars) is calculated based on initial surveys performed in August compared to surveys performed in late September or October. Hatched bars represent mortality within stockades of rebar poles designed to exclude large predatory rays and performed in a subset of years. Finally, arrows denote the direction of migration for cownose rays through out the study area based on gillnet collections and surveys of local commercial fishermen.

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