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Supporting Online Material for

Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean

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Materials and Methods

Species

Great sharks

Large shark species in the northwest Atlantic were considered for inclusion in this category based on their size and occurrence of elasmobranchs in their diet. Eleven species met these criteria (Table S1). These sharks are among the largest (notable exclusions being basking and whale sharks, which feed at much lower trophic levels), reaching maximum lengths ranging from ~2.0m in blacktip and sandbar sharks up to 5-6m in great hammerhead and great white sharks (*S1*-*S3*). Bull, blacktip, sandbar, and scalloped hammerhead reach sexual maturity below or close to 2m, but all others mature at a greater length (*S1*-*S3*). These large fishes are all tertiary consumers (trophic level ≥4) with catholic diets. Five species (bull, great hammerhead, tiger, sand tiger, and great white sharks) are true apex predators, while the remaining six species feed at and near the top of the food web.

Smaller elasmobranchs form a key component of the diet of large sharks (*S1*, S2, *S4*, *S5*), and conversely, sharks are the most common predators of other elasmobranchs (*S6*, *S7*). Among the large sharks, however, there is considerable variation in the proportion of elasmobranchs consumed in their diet. Bull, great hammerhead, sand tiger, and great white sharks are each considered to be important predators on other elasmobranchs, with about 30-40% of their diet comprised of these fishes (*S5*). For the other species, the proportion of elasmobranchs in their diet has ranged in different studies between approximately 1 and 15% (see Table S1 references; *S5*). We compiled data on elasmobranch consumption by each of the large sharks, with particular consideration of the species included in the elasmobranch mesopredator category (see below). At the species level there is evidence that large sharks are predators of seven of the elasmobranch mesopredator species, little and clearnose skates, bullnose eagle ray, spotted eagle ray, cownose ray, bonnethead and Atlantic sharpnose sharks (Table S1). Notably, two species, blacktip and sandbar sharks, are known to eat the cownose ray, and four of the other great sharks species are known to consume species within the cownose ray genus (*Rhinoptera*). In general, there is a dearth of species-specific prey information for most sharks (most information in the literature is reported at higher taxonomic levels (usually family or genus)), and a lack of biological information in general for several of the little known mesopredator species. For example, there is no information in the literature (that we are aware of) on predators of five of the mesopredators (rosette skate, spiny and smooth butterfly ray, lesser devil ray, and chain catshark). However, there is evidence that large sharks consume species in ten out of the 11 mesopredator genera, and on the family (Scyliorhinidae) of the only other genus, that of the chain catshark (Table S1).

We assessed trends in relative abundance for ten of these 11 great shark species, based on the criterion that for each species there had to be at least one source of longline data (the most effective gear type for sampling these species) available for analysis. Evidence from a shark-targeted longline research survey in Chesapeake Bay (not available for analysis) suggests that the eleventh species, sand tiger shark (*Carcharias taurus*), has experienced declines similar to those of the other great sharks (*S8*). The sand tiger shark has been considered for proposed listing under the U.S. Endangered Species Act, and is currently listed as a Species of Special Concern and a prohibited species (to land) by the U.S. National Marine Fisheries Service (*S9*).

Mesopredatory elasmobranchs

We initially considered all small shark, and all skate and ray species from within the geographic range of our study that are preyed upon by larger shark species, and for which there were sufficient data available to assess their trends in relative abundance. However, because both low intrinsic rates of population increase and heavy fishing pressure limit the potential responses of elasmobranch mesopredator populations following a loss of their predators, we restricted our analyses to a subset of these species based on the following criteria: (i) of the mesopredators subject to fishing pressure (whether as direct targets or as bycatch), we included only those species with female age at maturity <4 years and thus relatively high potential rates of population increase. These criteria were relevant to all mesopredatory shark species, and excluded species like spiny dogfish (*Squalus acanthias*) and smooth dogfish (*Mustelus canis*), which mature late, and Atlantic angel shark (*Squatina dumeril*), which is presumed to mature late based on its size and the age at maturity of other species in its genus. For skates, this meant that three northern species (thorny (*Amblyraja radiata*), winter (*Leucoraja ocellata*), and barndoor (*Dipturus laevis*) skate) were excluded because of both late age at maturity and high rate of exploitation; (ii) for those mesopredators not subject to high exploitation rates we included species with female age at maturity up to 7 years; (iii) finally, we excluded stingrays from our analysis because they are subject to high rates of post-discard mortality (*S10*), presumably as a consequence of their thin body type relative to thicker bodied skates and their mistreatment by fishermen fearing their venomous spines.

Fourteen elasmobranch mesopredator species met our criteria (Table S1). They comprise 11 different genera from 7 families, and range from fairly well known species (e.g. Atlantic sharpnose, blacknose, and finetooth sharks, cownose rays) to very poorly known species (bullnose eagle ray, lesser devil ray, chain catshark, smooth and spiny butterfly ray).

Bivalves

We examined all northwest Atlantic bivalve species that are components of the cownose ray diet (*S11, S12*), for which sufficient data were available. These included only commercially fished species: the eastern oyster (*Crassostrea virginica*), hard clam (*Mercenaria mercenaria*), soft-shell clam (*Mya arenaria*), and bay scallop (*Argopecten irradians*). We suspect that cownose ray predation also now influences surf clam (*Spisula solidissima*) populations of the New Jersey and Delmarva Peninsula coasts but were unable to locate sufficient information to include this interaction in our analysis.

Data sources

Research survey data

We analyzed 17 scientific research surveys (Tables S2, S3) from U.S. coastal waters (Fig. S1) that recorded elasmobranch species, began prior to 1990, and were conducted using a consistent methodology over at least 12 years. Two of the surveys used longlines and were carried out specifically to sample sharks, the UNC survey (detailed below) and the SC survey (see *S13*, *S14* for details). Fifteen other surveys used either bottom trawls or seines, and were designed to sample a variety of finfish and invertebrate species. In total, all 17 surveys caught elasmobranch mesopredator species; 12 caught large sharks (Table S3). Survey start years ranged from 1959 to 1989, with a median start year of 1976 (Table S3).

The long-term UNC-IMS research survey of sharks has been conducted each year since 1972 by Dr. F.J. Schwartz of the University of North Carolina at Chapel Hill Institute of Marine Sciences in Onslow Bay off the central coast of North Carolina near Cape Lookout. The UNC-IMS data set that we analyzed comprised a total of 760 longline sets from 1972-2003. Survey methods (*S15*) have remained identical over this 32-year period. Unanchored longlines have been set biweekly from about April 15 to November 1 each year using a design employing the same gear at two fixed stations. Prior to setting out the longline, fresh fish were collected by trawling and used as whole fish to bait the hooks. Two successive sets of baited hooks constituted the sampling for every date (except less than one quarter of days when bad weather prevented establishment of the second set). Sampling was carried out during the day between the hours of 0800 and 1500hr. The East-West set was established first, near shore and approximately parallel to the beach of Shackleford Banks in 13 m depth, running up to 4.8 km eastward from 34º 38.029' N, 76º 37.835' W. Sets employed between 27 and 483 hooks (mean = 151), with one plastic foam international orange buoy of 1.3-m diameter attached for every 10 hooks and hooks spaced every 4.5 m. Case-hardened steel 9/0 Mustad tuna hooks were attached to 1.8-m drop lines of No. 2 (95 kg) porch swing chain, which were snapped onto the 7.6-cm braided nylon main line. Soak time after setting was 1 hr. During the ≈45 min required to pull in the line, the species, sex, and fork length of each hooked shark was recorded and all live sharks were tagged and returned to the sea. After 35-40 minutes travel time, the North-South set was established further offshore in Onslow Bay in 22 m depth, running southwards from 34º 33.071' N, 76º 37.422' W. The procedures followed were identical to those of the East-West set. Trawling for additional bait was occasionally required between sets.

Fisheries data

For the large sharks, we also examined logbook (1986-2000) and observer (1992-2005) data from the U.S. pelagic longline fishery. Fisheries-dependent data are the only type that covers a substantial proportion of the geographic range of these shark populations, and pelagic longline gear is particularly suitable for catching these species. The U.S. pelagic longline fleet fishes offshore of the Grand Banks (50ºN), along the U.S. eastern coast and within the Gulf of Mexico, and as far south as the equator. The broad geographic coverage of these data therefore serves to complement the long temporal coverage of the research surveys. These data also include two species, shortfin mako and the great white shark, that consume elasmobranchs but were almost never caught in the research surveys (for great white n=1 in the UNC survey and n=0 for all other surveys; n=0 for shortfin mako in all surveys). In the fisheries data analyses, species within the same genera that could not reliably be distinguished from one another were grouped. This includes a grouping of hammerhead sharks, genus *Sphyrna* (scalloped, smooth, and great hammerheads), mako sharks, genus *Isurus* (primarily shortfin mako), and large coastal sharks of the genus *Carcharhinus* (blacktip, bull, dusky, sandbar, bignose, night, silky, spinner; the first four of which consume elasmobranchs).

Commercial landings data

Data on U.S. landings were obtained from the NMFS commercial landings database, while those for Canada came from the United Nations Food and Agriculture Organization (FAO). Data on eastern U.S. landings were available by state from Maine to Texas and are an aggregate of both fishery and aquaculture production. For the purposes of testing for effects of the increasing east coast population of cownose rays on bivalves, only shellfish landings from states where these cownose rays would be expected to interact with bivalves were included in the meta-analysis (New Jersey, south to eastern Florida). Landings from outside the region inhabited by this cownose ray population (e.g. Canada, Rhode Island, and Texas) are presented in Figure S2 for comparison. For one species, the hard clam, aquaculture makes up a large portion of production (up to 82%) since the mid-1980s (based on comparison of FAO aquaculture production data and NMFS commercial landings data for the U.S. east coast). Without a reasonable method of partitioning these two production sources by state, we were required to obtain fishery landings data for hard clams in U.S. states from other sources. Data were available only for Virginia and Rhode Island, from the Virginia public fishery hard clam production database (1973-1999) and the Rhode Island shellfish management plan (*S16*) respectively.

Trends in relative abundance models

Research survey data

Trends in relative abundance of each species, from each fishery-independent survey, were analyzed using generalized linear models (GLMs) with a negative binomial error structure and a log link. The negative binomial is an appropriate probability distribution for discrete, overdispersed data like the survey data, which contain a large number of zero (no catch) observations and are more variable than expected in a Poisson distribution. According to the negative binomial distribution, the probability of catching C_i individuals of a given species in survey tow i has mean μ_i,

$$p(C_i;k;\mu_i) = \frac{\Gamma\left(C_i + \frac{1}{k}\right)}{\Gamma(C_i+1)\Gamma\left(\frac{1}{k}\right)} \frac{(k\mu_i)^k}{(1+k\mu_i)^{C_i+\left(\frac{1}{k}\right)}} \text{, for } C_i = 0, 1, 2, \ldots,$$

where Γ is the gamma function and k is the negative binomial dispersion parameter. Using a log link in the GLMs means that the log of the mean catch is assumed to be a linear combination of predictor variables. The expected mean catch of a given species is then,

$$\log(\mu_i) = \boldsymbol{x}_i'\boldsymbol{\beta} + \log(\mathit{offset})$$

where $\boldsymbol{x}_i'$ is a vector of explanatory covariates for observation i, $\boldsymbol{\beta}$ is a vector of unknown coefficients for the explanatory variables and offset is the offset term. All analyses were conducted using SAS v9.1 (*S17*).

The breadth of ancillary data which could be used as explanatory covariates in estimating trends in relative abundance varied among surveys. For all surveys and species, we employed the general strategy of using the following covariates in the generalized linear models as the vector of explanatory variables ($\boldsymbol{x}_i'$): year, the second order polynomial of depth, the second order polynomial of bottom temperature and q (the seasonal cycle) (Table S4). The seasonal cycle, q, was characterized by a series of sine and cosine terms, with periods, j, of ½ and 1 year as,

$$q(d_i) = \sum_{j=1}^{2}\left[\varsigma_j \cos\left(\frac{2\pi j d_i}{365.25}\right) + \sigma_j \sin\left(\frac{2\pi j d_i}{365.25}\right)\right]$$

where d_i is the sequential day of the year that observation i occurred in, and ς_i and σ_i are estimated parameters. Modeling the seasonal cycle, q, also allowed us to generate common estimates for surveys conducted during multiple, distinct time-periods each year (NMFS offshore, NMFS inshore and SEAMAP surveys).

The NMFS surveys and the SEAMAP surveys covered relatively large latitudinal ranges (Fig.

S1) and there was some inter-annual variation in the timing of these surveys. For species that do not undertake seasonal migrations out of each survey area, this was not a concern. However, changes in the timing of the survey could have significant effects on estimates for those species that do migrate out of the area surveyed. To account for this effect, we used the additional term of latitude when modeling the NMFS and SEAMAP survey data. Furthermore, for these surveys we allowed the seasonal cycle, q, to vary by latitude by including the interaction term between latitude and q.

There were exceptions to our general strategy of parameter selection and error structure used for the generalized linear models (Table S4). Data from the CTDEP and GSO trawl surveys were available only in the form of mean annual estimates so only year could be included in the model. For these two surveys, the negative binomial error structure was not appropriate since it is used for discrete data only, and instead we used a gamma error structure and a log link for the generalized linear models. The probability of a mean catch C_i of a given species in year i was assumed to follow a gamma distribution with the mean μ_i,

$$p(C_i;\nu;\mu_i) = \frac{1}{\Gamma(\nu) C_i} \left(\frac{C_i \nu}{\mu_i} \right)^{\nu} \exp\left(-\frac{C_i \nu}{\mu_i} \right), \text{ for } 0 < C_i < \infty,$$

where Γ is the gamma function and v is the gamma distribution scale parameter. The expected mean catch is then, $\log(\mu_i) = x_i'\beta$

where x_i' is the year in which observation i occurred, and β is the coefficient for year.

When surveys followed a fixed station design (DNREC trawl survey, UNC longline survey, GSO trawl survey), we included a unique station identifier as a model factor. In some cases, covariates other than those in our standard list were available, including river basin for the VIMS seine survey, and the second order polynomial of salinity for the Maryland seine survey (MDNR).

Fisheries data

Methods of the logbook data analysis are reported in *S18* and its Supplementary Material, Trends in relative abundance for large shark species were estimated from the observer data using generalized linear mixed models with a negative binomial error structure and log link in the

GLIMMIX procedure of SAS v.9.1 (*S17, S19*). In these models, to account for non-independence of longline fishing sets made by the same vessel and on the same trip, we specified vessel as a G-side random effect and fishing trip as an R-side random effect with an autoregressive one (AR1) correlation structure. Additional details of the logbook and observer data analyses are found in Table S4.

Calculating change in abundance

Changes in abundance reported in the main text for individual species were computed by applying the estimated rate of change over the time period from the species' first appearance in the data set until the end of the data set. Thus, for example, in the UNC data set the rate of change for most species was calculated for the entire time period (1972-2003), but for sandbar sharks was calculated only from 1976 to 2003.

Meta-analysis of trends in relative abundance

We summarized trend estimates from multiple surveys for each species using meta-analytic techniques. The instantaneous rate of change of species s from survey i is estimated as $\hat{\theta}_{s,i}$. The units of the instantaneous rate of change will have the same units for all surveys (estimated using generalized linear models with a log link as described in the previous section) and can be thought of as slopes on a log scale. The estimate of $\theta_{s,i}$ will be approximately normal, that is, we assume

$$\hat{\theta}_{s,i} \sim N(\theta_{s,i}, v_{s,i}^2) .$$

We plotted the log-likelihood profile to check the normality assumption. As sample sizes were large for most surveys, this assumption was reasonable in most cases.

For the random effects meta-analysis of the instantaneous rate of change for a given species, we assumed that the true rates of change came from a normal distribution, i.e.

$$\theta_{s,i} \sim N(\theta_s, \sigma_s^2) .$$

Maximum likelihood estimation of the random effects meta-analysis was carried out in SAS using Proc Mixed (*S17*). Testing for heterogeneity is equivalent to testing H_0: $\sigma^2 = 0$ against H_1: $\sigma^2 > 0$. The standard likelihood ratio must be modified in this case because the null hypothesis is on the boundary of the parameter space (i.e. the variance cannot be less than zero), which in this case means the p-value of the naive likelihood ratio test must be divided by two (*S20*).

It is common in meta-analysis to use a fixed effect meta-analysis if there is not statistically significant heterogeneity among studies; however, the power of this test is low for small numbers of studies and a fixed effect meta-analysis will underestimate the standard errors of the estimate if heterogeneity is present. We thus used the random-effects meta-analysis in all cases. In the results section of the supplement, we examine cases where there may be differences among surveys and over different time periods.

Trends in large shark length

Trends in large shark length were analyzed using the UNC longline survey data with generalized linear models with a gamma error structure and a log link, after removing any biologically implausible length values (e.g, five lengths for dusky sharks were smaller than the minimum size of neonates). Month of catch was included as a covariate for each species length model. Results are shown in Fig. S3 and discussed in the main text.

Cownose ray absolute abundance & invertebrate consumption estimates

To estimate the number of cownose rays that currently pass through Chesapeake Bay during their fall migration, we combined our survey-based meta-analytic estimated rate of increase with Blaylock's population estimate of 9.3 million (s.e. = 1.8 million) for Chesapeake Bay, which was based on aerial surveys between 1986 and 1989 (*S11*). Then, to estimate the total food demand for benthic bivalve mollusks by cownose rays in the Chesapeake Bay area annually, we combined our cownose ray abundance estimate with its annual occupancy time in Chesapeake Bay of 100 days (*S11*) and its individual consumption rate. Blaylock (*S11*) estimated an individual daily consumption rate of 210g for the cownose ray. Schwartz (*S21*) estimated that individual cownose rays consume up to 1.5L of bivalve mollusks per day. This equates to 250g/day based on the conversion of 1.5L to 1kg bivalve mollusk, with about 25% meat, which is comparable to Blaylock's estimate. To be conservative, we used the lower estimate of 210g, yielding a total estimate of 840,000 metric tons (wet flesh) per annum.

Quantifying cownose ray impacts on bay scallops

Trends in bay scallop commercial landings data

To illustrate changes over time in the magnitude of North Carolina bay scallop landings (Fig. 1), we fitted these data with a generalized additive model (GAM) in R v2.2.1 (*S22*), using a gamma error structure and log link, with a loess curve of span 1, degree 2. The gamma is an appropriate probability distribution for these data, which are continuous, positive, and have non-constant variance.

Bay scallop density

To evaluate the population-level impacts of fall migrating rays across the full geographic range of traditional scalloping grounds in North Carolina, scallop densities were measured bi-weekly at six seagrass beds located within Core (Cedar Island, Yellow Shoal), Back (Oscar Shoal, Straights) and Bogue (Marker 34 and 40) Sounds from August through October in 2002, 2003, and 2004. Bay scallop density was measured within each seagrass bed in early August and again in mid-October because this period brackets the fall migration of the cownose rays. At each site 5 replicate 1-m^2 quadrats were haphazardly thrown near the edge and at the center of each seagrass bed (10 quadrats total per bed). All bay scallops within each quadrat were counted, measured and returned to their original location. Physical parameters (% cover of seagrass, salinity, temperature, sediment type) were also recorded during sampling. In the Back Sound portion of our study area, the North Carolina Division of Marine Fisheries (NCDMF) allowed a limited hand harvest of scallops coincident with the expected timing of fall immigration by cownose rays. Six harvest days were permitted between mid August and early September with a daily harvest rate of 10 bushels/fisherman. Few fishermen participated and fishing impacts were trivial compared to estimated losses from ray predation. Nevertheless, to prevent our density estimates from being confounded by this additional treatment and to quantify the relative impact of this harvest, the NCDMF established and we conducted our sampling in two 25 m^2 shellfish sanctuary areas within all seagrass beds. A substantially longer data base exists for one of the sites, Oscar Shoals. Although some small differences exist among years in methodologies, adult bay scallop density was measured in late July or early-mid August and again in September or October in 1992, 1993, 1994, 1996, 1998, 1999 and 2000 (detailed methods are reported in *S23*). For all years, bay scallop survival was calculated by dividing densities measured on the last sampling date by the density measured on the initial sampling date.

Experimental assessment of cownose ray predation

To determine to what extent any decrease in scallop density is attributable to ray predation, we established four 2-m^2 exclosures at the center and four at the edge of the 6 seagrass beds where NCDMF shellfish sanctuary areas were established. The exclosures, short (50 cm) PVC poles arranged as a stockade, exclude cownose rays while allowing other predators (crabs and whelks) into the matrix of poles (*S23, S24*). The number of scallops surviving within the stockade is compared to areas of free ray access (controls). The experiment was performed during the fall of 2002, 2003, and 2004. The stockades were constructed *in situ* and bay scallops allowed to move freely into and out of the exclosure. Exclosures were erected in mid August of each year and bay scallop density measured within the exclosure and in the controls at that time and again in late September. A similar set of experiments had been performed at the Oscar Shoal site in 1996 and 1998 (*S23*). As in the later experiments, naturally occurring bay scallops were allowed free access to the exclosure, but in addition ten marked and tethered bay scallops were placed within and outside the stockades. Mortality within the stockade should be substantially less than in the control areas if large mobile consumers are the chief predator on bay scallops during this time period. Bay scallop mortality within the stockades was calculated as 1 minus survival, computed by dividing densities measured on the last sampling date within the stockade by the density measured on the initial sampling date prior to construction of the enclosure. The difference between scallop survival inside and survival outside the stockades greatly underestimates the proportion of natural mortality attributable to large mobile consumers (of which cownose rays were the only ones observed) because bay scallops initially inside stockades emigrate throughout this period of time and thereby become susceptible to consumption by rays. Earlier tethering experiments (*S23*) indicate that emigration explains a large majority of the apparent mortality of bay scallops inside the stockades.

Supporting Text: Results and Discussion

Trends in relative abundance

Overall, the trend estimates from the 17 research surveys and the 2 fisheries data sets give broadly consistent estimates of population declines of great sharks and population increases in elasmobranch mesopredators (Table S5). Earlier trend estimates for great sharks from logbook reports (*S18*) have been criticized for using fisheries-dependent data reported by fishers and for relying on only one data source (*S25*, but see *S26*). Here, we have analyzed the complementary scientific observer data set from the same fishery, and shown similar results for each species (group) except tiger sharks (discussed below). We have also analyzed all available, long-term scientific research surveys (n=12) for great sharks. Importantly, the longline research surveys designed to catch sharks (UNC, SC) suggest declines for every great shark species, and show large, statistically significant declines for each great shark that was caught in sufficient numbers to estimate trends.

In a few cases, there are qualitative differences (i.e. increasing vs. decreasing trends) amongst elasmobranch species' trend estimates from different data sets. Such differences could arise for several reasons, including differences in the years (early vs. recent) or areas (e.g. north vs. south, inshore vs. offshore) sampled (Fig. S1, Table S5). Here we discuss the details of each of these cases.

Only 2 of the 30 trend estimates for great sharks are statistically significant increases. The first is for juvenile hammerhead sharks caught in the recent (1989-2005) SEAMAP survey. We also note that juvenile blacktip sharks in the SEAMAP survey and juvenile sandbar shark in the NMFS surveys show nonsignificant changes (Table S5). These data suggest that declines in the juveniles may have ceased for these species, and that juvenile survival could have increased because of declines of larger sharks. The second increasing trend occurs in the observer data set for the tiger shark: its abundance has apparently begun to increase in the past couple of years. This fishery catches mainly juvenile tiger sharks, and of all the shark species caught, tiger shark has the highest survival rate (*S27*). Thus, this change from a declining to an increasing trend also may represent an increase in juvenile survival associated with a decline in predation by large sharks.

For elasmobranch mesopredators, most differences in trend estimates within species appear to be caused by small sample size and/or high sampling variability at the edge of the species range. For example, there were 7 surveys for cownose ray, and 6 of these have estimates of instantaneous rates of increase between 0.044 and 0.17 per year (Table S5). Cownose rays in the NMFS-Offshore survey data have a non-significant trend estimate of -0.26 (95%CI: -0.54 – 0.01). NMFS-Offshore surveys caught cownose rays in only 3 years because of the survey location at the edge of the geographic region consistently inhabited by this species, and we thus do not regard this estimate as being indicative of temporal change in the population. A similar problem probably exists for the trend estimate derived from the NMFS-Inshore data for Atlantic sharpnose shark. This is the only non-significant estimate for this species, and these surveys occur at the extreme northern limit of this species' range.

For some of the smaller skates, differences in trend estimates may represent real differences among populations. For example, little skate shows statistically significant increases in three surveys, but does not appear to be increasing in Long Island Sound (CTDEP survey, Table S5). We suspect that this may represent a real pattern because there is an intense fishery for lobster bait in this region that catches little skate (*S28*).

The only two exceptions to the general pattern of increasing abundance amongst the mesopredators are the blacknose shark, which has been decreasing according to the UNC survey, and the spotted eagle ray, which has been decreasing according to the recent SEAMAP survey (Table S5). Like the sharpnose shark, the blacknose shark is caught in several recreational and commercial fisheries (*S29*); however, its age at maturity is greater (3.8 years on average) than the Atlantic sharpnose shark (2.3 years) (*S30-S33*). Thus, it may be more susceptible to fishing than the Atlantic sharpnose, which is clearly increasing. Insufficient information about the fishing pressure on spotted eagle ray (which matures between the age of 4 and 6 years (*S34*)) limits our interpretation of abundance trends for this species.

Inferences from life history theory about the cownose ray rate of increase

Females in the U.S. Atlantic cownose ray population reach sexual maturity between age 7 and 8 (*S12*) and have one pup per year (*S35*). Like most other elasmobranch species, there are no direct estimates of natural mortality for the cownose ray. However, using the meta-analytic mean increase, 0.087 (95% CI: 0.034 – 0.14), as the rate of population increase (r), we can solve the Euler-Lotka equation to estimate the mortality that the cownose ray population must be subject to. The mortality rate was calculated as 0.076 (95% CI: 0.021-0.127), which is much lower than a species of fish with this population growth rate would be expected to have (compared to similarly sized species) under natural conditions. For example, using the observed growth rate and the asymptotic length (and an assumed temperature of 20ºC), Pauly's equation (*S36*) gives a natural mortality estimate of 0.26, while Hoenig's equation (*S37*), based on longevity, gives an estimate of 0.33. Thus, a natural mortality rate as low as that calculated in the Euler-Lotka equation implies that the cownose ray population has experienced substantially reduced natural mortality.

In addition, because the mortality rate of the cownose ray population also must include some bycatch mortality, the natural mortality must actually be somewhat less then the estimate of 0.076. We conclude that given the life-history of cownose rays and the observed rate of increase that the population must now have extraordinarily low natural mortality rate compared to what it would experience under normal levels of predation. We infer that the loss of naturally more intense predation by the great sharks explains why the cownose ray now deviates so greatly in mortality rate from what is expected on the basis of life history relationships (*S36*, *S37*).

Comparison of shrimp fishing effort between the southeast U.S. & northern Gulf of Mexico

Whereas the cownose ray population on the east coast of the U.S. has increased substantially, in the Gulf of Mexico, where shrimp trawl fishing effort is enormously greater, incidental catches have apparently reduced that cownose ray population (*S38*), and oyster landings have increased (Fig S2a). We compared shrimp fishing effort between the southeast U.S. (North Carolina to eastern Florida) and Gulf of Mexico within equivalent time periods for which data were available (1991-1993). Along the southeast U.S., the annual average number of shrimp fishing trips during that period was 55,878 (*S39*). This includes ocean waters, sound waters and some areas possibly unsuitable for cownose rays, such as rivers. We were not able to exclude unsuitable areas due to the resolution of the data. For the same time period, the Gulf of Mexico shrimp trawl fleet fished an annual average of 306,910 24-hour shrimping days or 7,365,829 fishing hours (*S40*). Typically, a southeast U.S. shrimp fishing trip in the early 1990s was approximately 5 hours long (*S39*). Thus the southeast U.S. shrimp fishing effort equaled 279,390 fishing hours (55,878 trips x 5 hours per trip), or 3.8% of the Gulf of Mexico effort.

As cownose rays migrate northward in the spring and southward in the late summer and fall along the coast of the southeast U.S., they will be exposed to local shrimp fisheries over restricted time periods. In North Carolina for example, the majority of the shrimp fishing occurs in July and August (*S41*) while cownose ray abundance does not peak in the region until September (*S23*), missing the time of most intense effort. In contrast, the northern Gulf of Mexico shrimp fishery maintains a very high intensity from May into December (NMFS commercial landings data), which includes the time at which cownose rays inhabit the area (*S38*). Thus, we conclude that the difference in shrimp fishing effort, and spatial and temporal overlap between cownose rays and fishing effort, could explain the different trends in abundance for these two cownose ray populations.

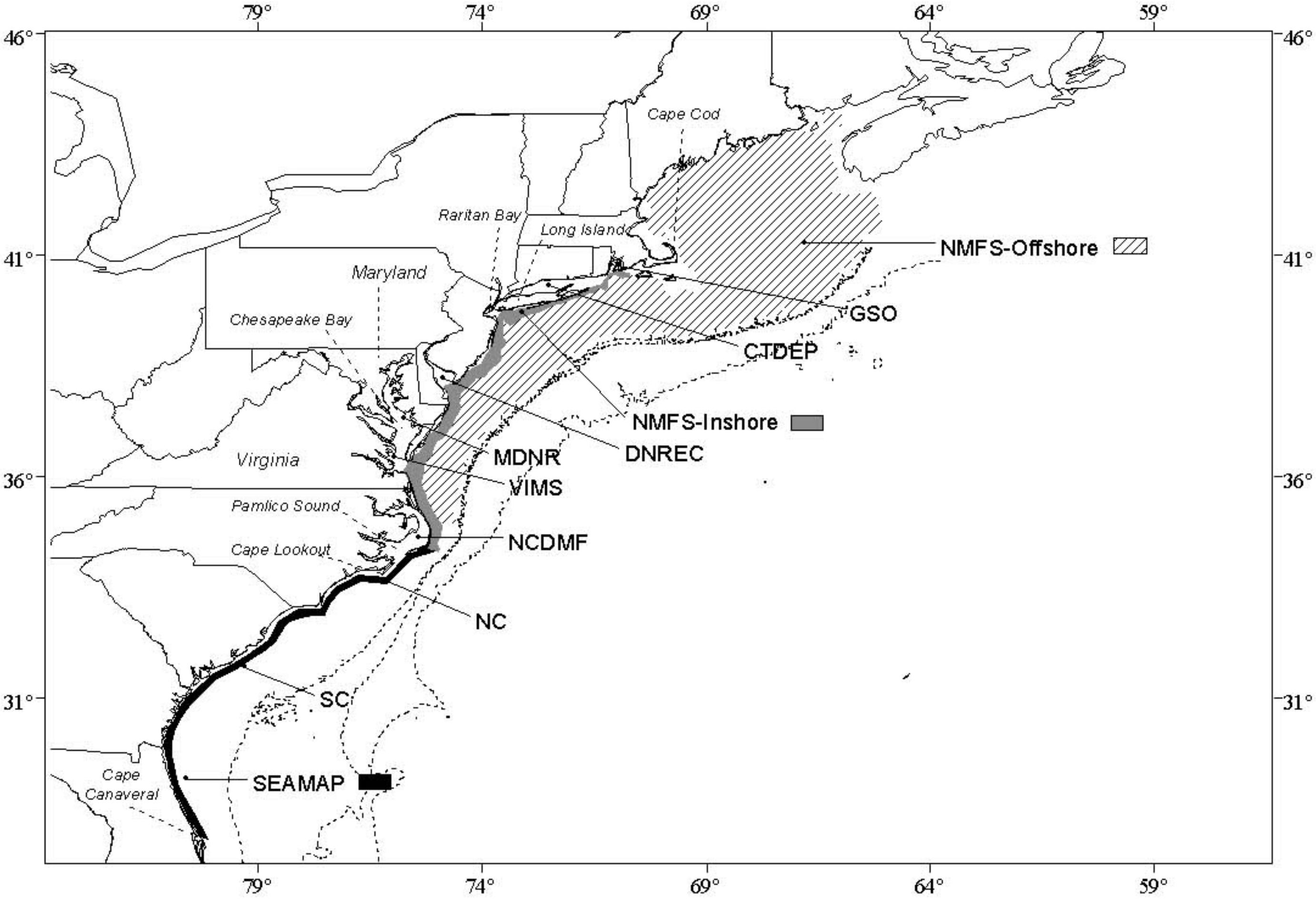

Figure S1. Map of the U.S. Atlantic coast showing the location of each of the 17 research surveys, with 200m, 500m, and 1000m isobaths (dotted lines) given for reference.

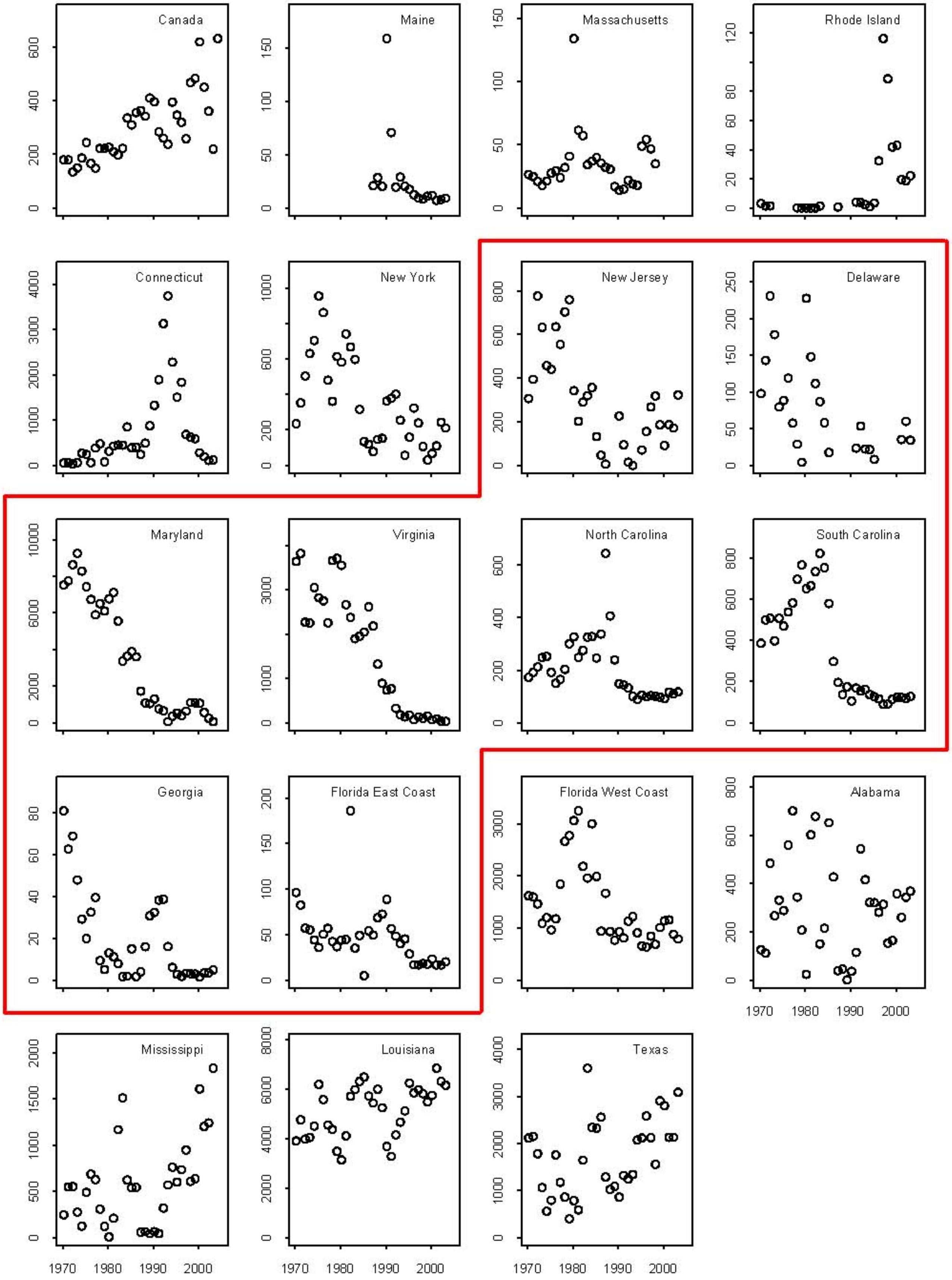

Figure S2a. Changes in landings (metric tons) by individual states of the U.S.A. plus east coast of Canada for oysters. Regions enclosed by red lines are those in which the east coast population of cownose rays is expected to interact with bivalves.

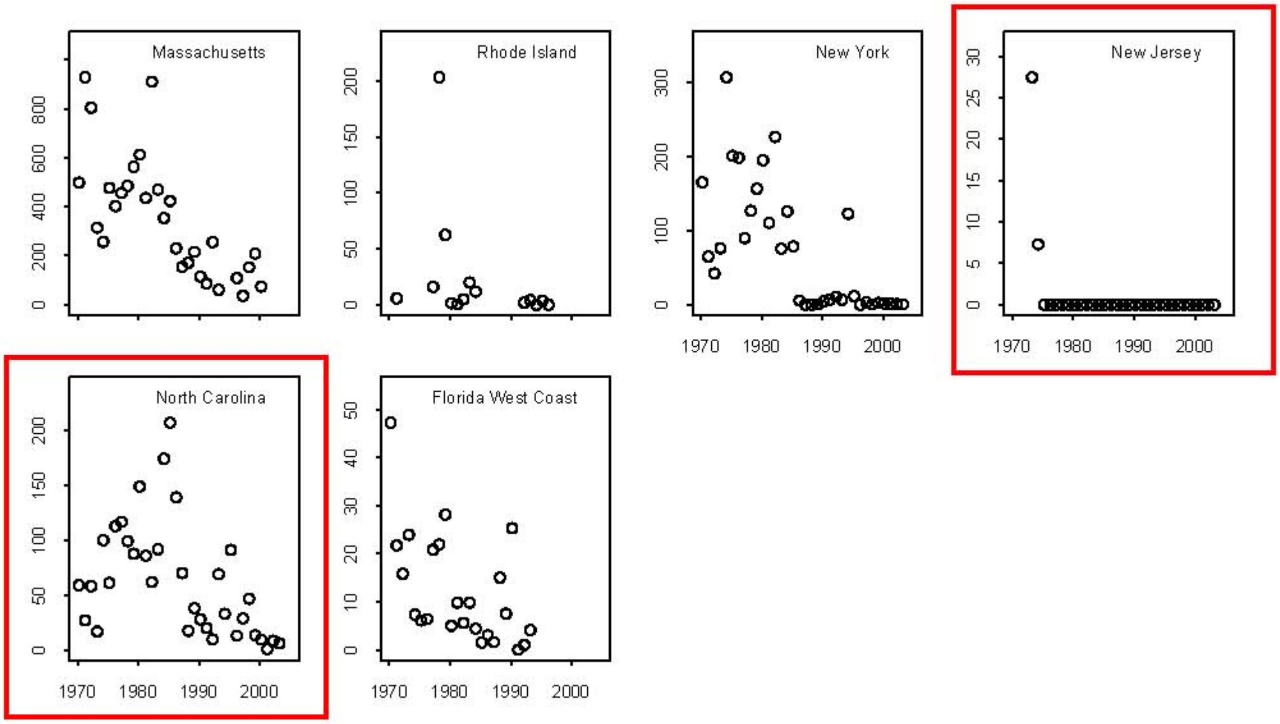

Figure S2b. Changes in landings (metric tons) by individual states of the U.S.A. for bay scallops. Regions enclosed by red lines are those in which the east coast population of cownose rays is expected to interact with bivalves.

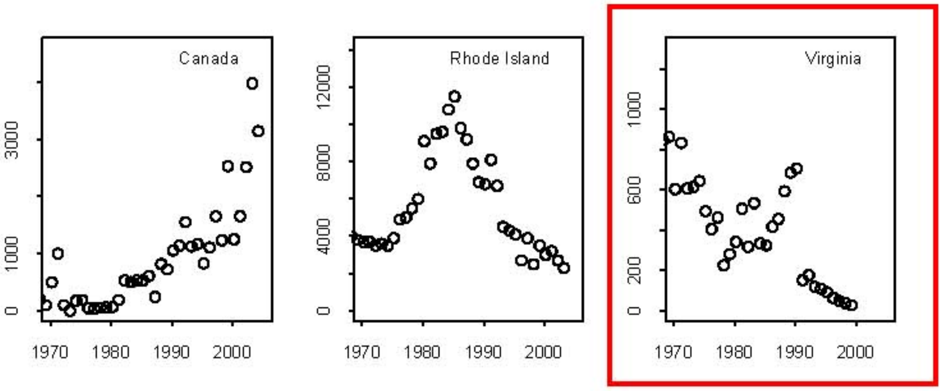

Figure S2c. Changes in landings (metric tons) by individual states of the U.S.A. plus east coast of Canada for hard clams. The region enclosed by red lines is that in which the east coast population of cownose rays is expected to interact with bivalves.

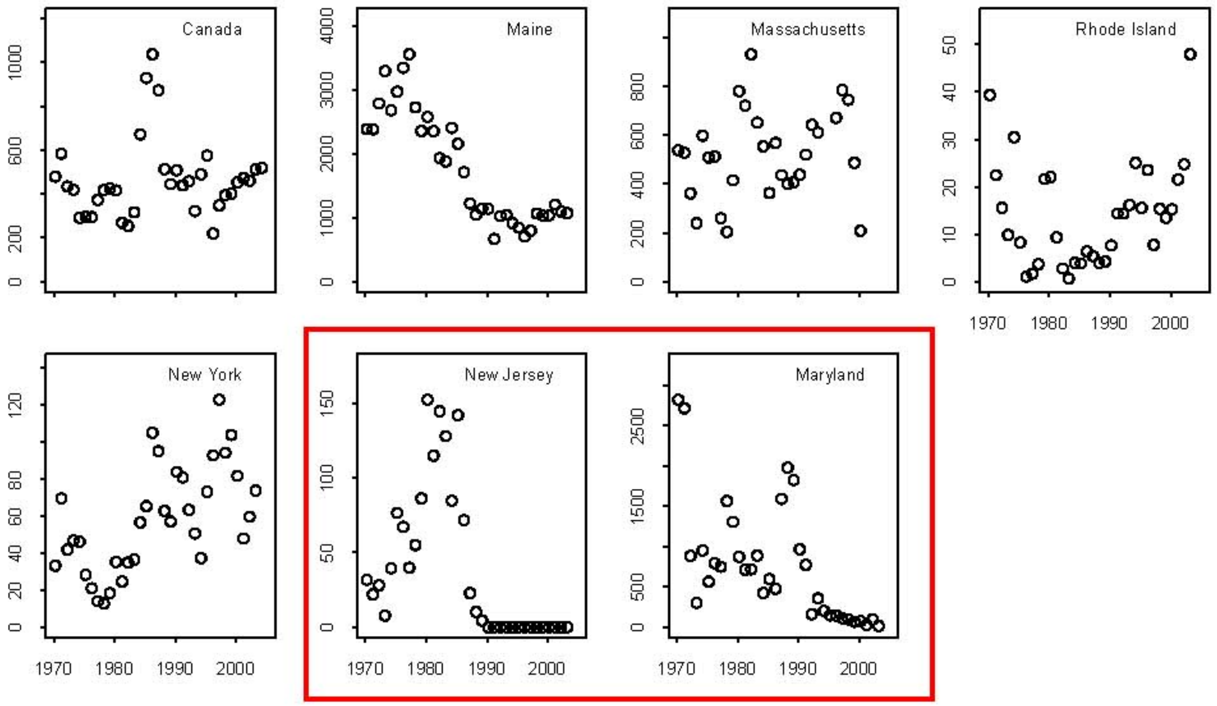

Figure S2d. Changes in landings (metric tons) by individual states of the U.S.A. plus east coast of Canada for soft-shell clams. Regions enclosed by red lines are those in which the east coast population of cownose rays is expected to interact with bivalves.

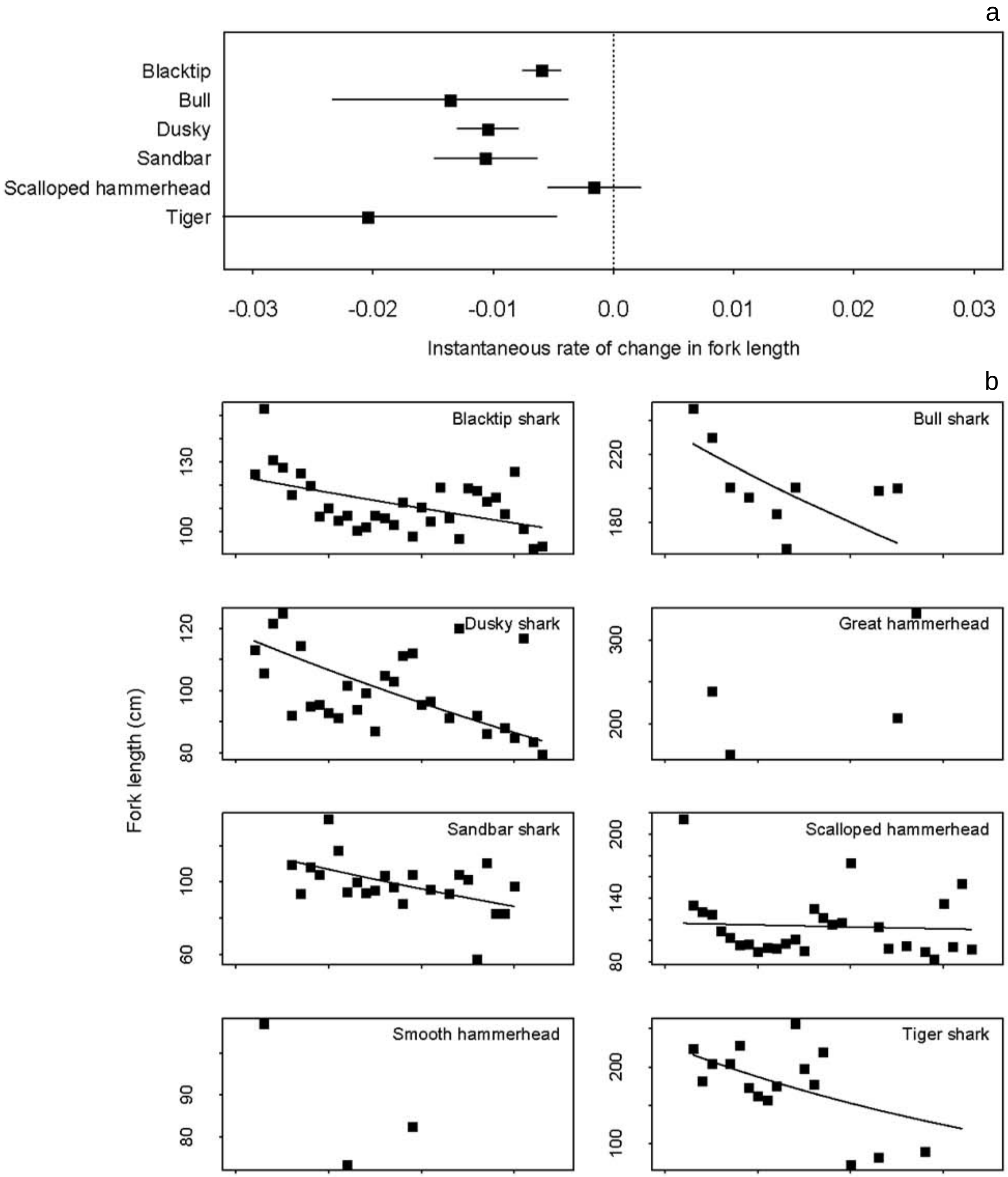

Figure S3. Change in length of great sharks between 1972 and 2003 from the University of North Carolina shark-targeted longline research survey (UNC): a) instantaneous rates of change (± 95% confidence intervals); b) overall trend (solid line) and individual year estimates (■). Species with length samples inmore than three years were modeled in a) and b); only raw data are shown for great and smooth hammerheads.

Table S1. Taxa of elasmobranchs (sharks, skates, rays) consumed by the apex (or nearly apex) shark species included in the large shark group. Prey are listed by species level and at the genus and/or family level because of the paucity of species-specific diet data available in the literature. Numbers correspond to references in the Table S1 reference list.

	Large Sharks										
Elasmobranch Mesopredators **Family** Genus Common name, *Scientific name*	Bull shark, *Carcharhinus leucas*	Blacktip shark, *C. limbatus*	Dusky shark, *C. obscurus*	Sandbar shark, *C. plumbeus*	Tiger shark, *Galeocerdo cuvier*	Great white shark, *Carcharodon carcharias*	Shortfin mako, *Isurus oxyrinchus*	Great hammerhead, *Sphyrna mokarran*	Scalloped hammerhead, *S. lewini*	Smooth hammerhead, *S. zygaena*	Sand tiger, *Carcharias taurus*
Rajidae (Skates)	8	8	8,11,14	12,2	8	7	7,19	8	9	8	7,14,18
Little skate, *Leucoraja erinacea*				12,2							
Rosette skate, *L. garmani*											
Clearnose skate, *Raja eglanteria*				12							
Gymnuridae (Butterfly rays)	8	8,10,1	8,11		8			6	9		
Gymnura species		10	11					6	9		
Smooth butterfly ray, *Gymnura altavela*											
Spiny butterfly ray, *G. micrura*											
Myliobatidae (Mantas and eagle rays)	5,8	8	11	12	8,17	3,7	4,7,19	2,6		13	7,14
Aetobatus species (eagle rays)					8		7,19	2		13	7,14
Spotted eagle ray, *A. narinari*					8		7	2		13	14
Mobula species (devil rays)	5,8		11								
Lesser devil ray, *M. hypostoma*											
Myliobatis species						7					7,14,18
Bullnose eagle ray, *M. freminvillii*											14
Rhinopteridae (Cownose rays)	15	1	11	8,12			7,19	8			
Rhinoptera species (cownose rays)	15	1	11	8,12			19	8			
Cownose ray, *R. bonasus*		1		12							
Scyliorhinidae (catsharks)	5	10	8,11			7	4	6	9		18
Chain catshark, *Scyliorhinus retifer*											
Sphyrnidae (hammerhead sharks)	5,8	1,10	11	8	8	3,7	4,7				
Sphyrna species		1		8		3,7	4,7				
Bonnethead shark, *S. tiburo*		1		8							
Carcharhinidae (requiem sharks)	5,8	8,10	8,11	12	8	3,7	4,7,19	6	8,9		7,14,18
Carcharhinus species	5,8	8,10	8,11	12	8	3,7	4,7	6	8		14,18
Blacknose shark, *C. acronotus*											
Finetooth shark, *C. isodon*											
Rhizoprionodon species	5,8	1,8,10	11,21	8,20	8	3,7	4,7	6	8,9		18
Atlantic sharpnose shark, *R. terraenovae*		1									

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Table S2. Data sources.

Data type	Data Acronym	Source	Reference or web access
Survey	CTDEP	Connecticut Department of Environmental Protection, Fisheries Division	http://dep.state.ct.us/burnatr/fishing/fdhome.htm
	DNREC	Delaware Department of Natural Resources and Environmental Control, Division of Fish & Wildlife	http://www.fw.delaware.gov/.
	GSO	University of Rhode Island, Graduate School of Oceanography	http://www.gso.uri.edu/
	MDNR	Maryland Department of Natural Resources, Fisheries Service	http://www.dnr.state.md.us/fisheries/
	NCDMF	North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries	http://www.ncfisheries.net/
	NMFS-Off & NMFS-In	National Oceanic & Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS), Northeast Fishery Science Center	http://www.nefsc.noaa.gov/
	SC	South Carolina Department of Natural Resources	S13, S14
	SEAMAP	Southeast Area Monitoring and Assessment Program, South Atlantic	http://www.dnr.sc.gov/marine/mrri/SEAMAP/seamap.html
	UNC	University of North Carolina - Institute of Marine Sciences, Longline shark monitoring survey	http://www.marine.unc.edu/Research
	VIMS	Virginia Institute of Marine Science	http://www.fisheries.vims.edu/trawlseine/sbmain.htm
Fisheries	Logbook	NOAA, NMFS, Southeast Fishery Science Center	http://www.sefsc.noaa.gov/fls.jsp
	Observer	NOAA, NMFS, Southeast Fishery Science Center	http://www.sefsc.noaa.gov/pop.jsp
Landings	Landings	NOAA, NMFS, Office of Science & Technology	http://www.st.nmfs.gov/st1/commercial
	Landings	UN Food and Agriculture Organization, Fisheries Department, Fishery Information, Data and Statistics Unit	http://www.fao.org/fi/statist/statist.asp

Table S3. Survey, fisheries and landings data set descriptions, including area, gear type, season and years sampled, and total sample size. Species sampled in each data set: great shark species (L), elasmobranch mesopredator species (M), bivalve species (S).

Data type	Acronym	Area	Gear	Season	Years	Samples	Species
Survey	CTDEP	Long Island Sound	Trawl	Fall/Spring	1984 – 2004	-	M
	DNREC	Delaware Bay	Trawl	Year round	1966 – 2004	1874	L,M
	GSO	Narragansett Bay, Rhode Island	Trawl	Year round	1959 – 2002	-	M
	MDNR	Chesapeake Bay	Seine	Summer	1960 – 2005	8022	M
	NCDMF	Pamlico Sound, North Carolina	Trawl	Summer/Fall	1987 – 2004	1889	M
	NMFS-Off	Northeast U.S. Offshore	Trawl	Spring	1968 – 2005	10185	L,M
	NMFS-Off	Northeast U.S. Offshore	Trawl	Fall	1963 – 2005	8829	L,M
	NMFS-Off	Northeast U.S. Offshore	Trawl	Summer	1963 - 1995	1758	L,M
	NMFS-In	Northeast U.S. Inshore	Trawl	Spring	1976 – 2005	2084	L,M
	NMFS-In	Northeast U.S. Inshore	Trawl	Fall	1974 – 2005	2228	L,M
	NMFS-In	Northeast U.S. Inshore	Trawl	Summer	1977 – 1981	351	L,M
	SC	Coastal South Carolina	Bottom longline	Year round	1983-84, 1993-95	131	L,M
	SEAMAP	Coastal Southeast U.S.	Trawl	Spring	1989 – 2005	1441	L,M
	SEAMAP	Coastal Southeast U.S.	Trawl	Fall	1989 – 2005	1389	L,M
	SEAMAP	Coastal Southeast U.S.	Trawl	Summer	1989 – 2005	1393	L,M
	UNC	Coastal North Carolina	Longline	April - November	1972 – 2003	760	L,M
	VIMS	Chesapeake Bay	Seine	Summer	1968 – 2003	3166	M
Fisheries	Logbook	Northwest Atlantic	Pelagic longline	Year round	1986 – 2000	214234	L
	Observer	Northwest Atlantic	Pelagic longline	Year round	1992 – 2005	6967	L
Landings	NMFS Landings	Coastal Eastern U.S.	Various	Year round	1950 – 2003	-	S
	FAO Landings	Atlantic Canada	Various	Year round	1950 – 2003	-	S

Table S4. Summary of generalized linear models used to estimate trends in abundance for large sharks and elasmobranch mesopredators. All data were modeled using generalized linear models, except for the observer data, which was modeled using generalized linear mixed models. All models included year as a covariate; *q* represents a seasonal term composed of a series of sine and cosine terms with periods of one year and one half year. Data source acronyms as in Table S3.

Data Source	Covariates	Error distribution	Link	Offset
CTDEP	no covariates available	Gamma	Log	None
DNREC	depth, depth^2, station, *q*	Negative binomial	Log	Swept area
GSO	no covariates available	Gamma	Log	None
NCDMF	no covariates available	Gamma	n.a.	n.a.
NMFS-Off	depth, depth^2, temperature, temperature^2, latitude, *q*, latitude**q* interaction	Negative binomial	Log	Swept area
NMFS-In	depth, depth^2, temperature, temperature^2, latitude, *q*, latitude**q* interaction	Negative binomial	Log	Swept area
SEAMAP	depth, depth^2, temperature, temperature^2, latitude, *q*, latitude**q* interaction	Negative binomial	Log	Swept area
SC	depth, depth^2, *q,* time of set, soak time,	Negative binomial	Log	Number of hooks
MDNR	month, temperature, temperature^2, salinity, salinity^2	Negative binomial	Log	None
UNC	station, *q*	Negative binomial	Log	Number of hooks
VIMS	river basin	Negative binomial	Log	None
Logbook	area, season, temperature, use of light sticks, area*season, area*light sticks	Truncated negative	Log	Number of hooks
Observer	area, *q*, depth, depth^2, temperature, time of set, number of light sticks, hook depth, hook type, soaktime, target species, bait, area**q* interaction, fishing trip, vessel	Negative binomial	Log	Number of hooks

Table S5. Model results for each species of great shark and elasmobranch mesopredator, from each of the research survey and fisheries data sources used in the meta-analysis shown in Figure 2, including the first and last year of capture in the data set, the number of years caught, the total number of the species caught, the model estimate (± 95% confidence intervals (CI)) of the instantaneous rate of change, for all years of data (All) and for only those years onwards from the baseline of 1970 (1970-). Statistical significance levels for model estimates are * = <0.05; **=<0.01; ***=<0.001; ****=<0.0001, otherwise non-significant.

Species	Data	First	Last	*n*	*n*	Years	Instantaneous rate of change		
Common name	source	year	year	years	caught	in model	Estimate	upper CI	lower CI
					Great Sharks				
Blacktip	UNC	1972	2003	32	905	All	-0.084****	-0.065	-0.103
	SEAMAP	1990	2005	12	29	All	0.040	0.133	-0.053
Bull	UNC	1973	1995	10	23	All	-0.181****	-0.093	-0.270
Dusky	UNC	1972	2003	29	1036	All	-0.149****	-0.120	-0.179
	NMFS-Off	1967	1999	11	38	All	-0.075*	-0.005	-0.144
		1972	1999	8	26	1970 -	-0.068	0.004	-0.140
	NMFS-In	1974	2005	17	100	All	-0.092**	-0.035	-0.149
	SEAMAP	1990	2004	6	24	All	-0.199*	-0.032	-0.365
Great hammerhead	UNC	1975	1997	4	5	All	-0.080	0.037	-0.197
Sandbar	DNREC	1966	2004	26	242	All	-0.048****	-0.035	-0.062
		1970	2004	22	159	1970 -	-0.041****	-0.023	-0.060
	UNC	1976	2000	23	310	All	-0.077****	-0.039	-0.114
	NMFS-Off	1967	2002	22	73	All	0.014	0.057	-0.028
		1973	2002	20	68	1970 -	0.009	0.054	-0.036
	NMFS-In	1974	2005	27	107	All	0.019	0.048	-0.010
	SC	1983	1995	5	196	All	-0.281****	-0.225	-0.337
	SEAMAP	1990	2005	13	71	All	-0.029	0.070	-0.128
Scalloped hammerhead	UNC	1972	2003	29	495	All	-0.127****	-0.104	-0.149
	NMFS- In	1980	1995	3	4	All	-0.110	0.065	-0.285
	SEAMAP	1989	2005	17	126	All	0.094**	0.155	0.033
Smooth hammerhead	UNC	1973	1989	4	5	All	-0.172*	-0.010	-0.334
Hammerhead species	SC	1983	1994	3	11	All	-0.110	0.089	-0.308
	Logbook	1986	2000	15	60,402	All	-0.158****	-0.143	-0.172
	Observer	1992	2005	14	1,292	All	-0.110****	-0.062	-0.157
Large coastal species	Logbook	1986	2000	15	80,480	All	-0.118****	-0.103	-0.133
	Observer	1992	2005	14	8,186	All	-0.084****	-0.048	-0.121
Mako species	Logbook	1986	2000	15	65,795	All	-0.037****	-0.025	-0.050
	Observer	1992	2005	14	3,433	All	-0.032*	-0.001	-0.063
Tiger	UNC	1973	2002	18	39	All	-0.117****	-0.064	-0.169
	SC	1983	1995	5	142	All	-0.027	0.029	-0.083
	Logbook	1986	2000	15	16,030	All	-0.076****	-0.061	-0.091
	Observer	1992	2005	14	1,190	All	0.037*	0.071	0.002
Great white	Logbook	1986	2000	15	6,087	All	-0.117****	-0.074	-0.146
					Elasmobranch Mesopredators				
Atlantic sharpnose	UNC	1973	2003	31	2239	All	0.084****	0.098	0.071
	NMFS-Off	1974	2003	15	39	All	0.084**	0.138	0.031
		1974	2003	15	39	1970 -	0.084**	0.138	0.030
	NMFS-In	1974	2005	26	331	All	-0.025	0.002	-0.053
	SEAMAP	1989	2005	17	13187	All	0.065****	0.079	0.051
	SC	1983	1995	5	135	All	0.103***	0.159	0.047
Blacknose	SEAMAP	1989	2005	17	156	All	0.043	0.091	-0.004
	UNC	1972	2003	32	1304	All	-0.090****	-0.073	-0.107
Bonnethead shark	SEAMAP	1989	2005	17	4925	All	0.028**	0.045	0.010

Bullnose eagle ray	DNREC	1966	2004	28	3701	All	0.008*	0.015	0.001
		1970	2004	24	3153	1970 -	0.010*	0.019	0.001
	NMFS-Off	1967	2005	23	297	All	0.056*	0.104	0.009
		1973	2005	21	279	1970 -	0.053*	0.102	0.003
	NMFS-In	1974	2005	32	2230	All	-0.003	0.014	-0.020
	SEAMAP	1989	2005	17	5300	All	0.041***	0.065	0.018
Chain catshark	NMFS-Off	1963	2005	43	778	All	0.052****	0.065	0.038
		1970	2005	36	715	1970 -	0.070****	0.087	0.053
Clearnose skate	CTDEP	1984	2004	21	-	All	0.199****	0.281	0.118
	DNREC	1966	2004	28	5778	All	-0.049****	-0.042	-0.057
		1970	2004	24	3359	1970-	-0.008	0.001	-0.018
	NCDMF	1988	2004	7	9	All	0.053	0.206	-0.099
	NMFS-Off	1967	2005	39	1053	All	0.034****	0.047	0.022
		1970	2005	36	1029	1970-	0.029****	0.042	0.016
	NMFS-In	1974	2005	32	2678	All	0.047****	0.057	0.036
	SEAMAP	1989	2005	17	6991	All	0.014	0.034	-0.007
Cownose ray	DNREC	1979	2003	14	76	All	0.117****	0.168	0.065
		1979	2003	14	76	1970 -	0.111****	0.168	0.054
	MDNR	1976	2003	12	26	All	0.063**	0.102	0.024
	NCDMF	1987	2004	17	230	All	0.175****	0.219	0.132
	NMFS-Off	1972	1976	3	23	All	-0.265	0.011	-0.541
		1972	1976	3	23	1970 -	-0.432	0.063	-0.928
	NMFS-In	1974	2005	27	544	All	0.044*	0.081	0.006
	SEAMAP	1989	2005	17	4817	All	0.059**	0.105	0.014
	VIMS	1992	2003	7	11	All	0.104*	0.201	0.008
		1992	2003	7	11	1970 -	0.101*	0.200	0.002
Finetooth shark	UNC	1977	1997	14	93	All	0.039	0.114	-0.037
	SEAMAP	1990	2005	7	23	All	0.092	0.261	-0.078
Lesser devil ray	SEAMAP	1990	2005	15	347	All	0.105**	0.173	0.037
Little skate	CTDEP	1984	2004	21	-	All	-0.008	0.010	-0.025
	DNREC	1966	2004	25	2499	All	0.048****	0.058	0.039
		1970	2004	21	2378	1970 -	0.082****	0.096	0.068
	NMFS-Off	1963	2005	43	161330	All	0.018****	0.022	0.015
		1970	2005	36	151031	1970 -	0.015****	0.019	0.011
	NMFS-In	1974	2005	32	142760	All	0.076****	0.084	0.067
	GSO	1959	2002	44	-	All	0.054****	0.064	0.044
		1970	2002	33	-	1970-	0.056****	0.071	0.041
Rosette skate	NMFS- Off	1963	2005	43	1014	All	0.039****	0.052	0.025
		1970	2005	36	939	1970 -	0.037****	0.053	0.022
Smooth butterfly ray	DNREC	1967	1999	4	11	All	-0.108*	-0.025	-0.191
		1971	1999	2	3	1970 -	n.a.	n.a.	n.a.
	NCDMF	1989	2004	6	44	All	0.344****	0.474	0.215
	SEAMAP	1989	2005	17	5247	All	0.131****	0.148	0.114
Spiny butterfly ray	DNREC	1966	2002	22	55	All	-0.029*	-0.004	-0.053
		1970	2002	19	45	1970 -	-0.030	0.002	-0.062
	NMFS-Off	1973	2005	19	52	All	0.041	0.085	-0.003
		1973	2005	19	52	1970 -	0.030	0.073	-0.014
	NMFS- In	1974	2005	32	589	All	0.016	0.033	-0.001
	SEAMAP	1989	2005	17	317	All	0.102****	0.152	0.053
Spotted eagle ray	SEAMAP	1990	2005	16	159	All	-0.070**	-0.017	-0.122

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