

ARTICLE

Size Changes within a Southeastern United States Coastal Shark Assemblage: 1975–2018

Martin T. Benavides,*  F. Joel Fodrie, and Stephen R. Fegley

Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, North Carolina 28557, USA

Giada Bargione

National Research Council, Institute for Biological Resources and Marine Biotechnologies, Ancona 60125, Italy

Abstract

Harvest may have myriad effects on target species, including a change in population size structure. To assess whether size shifts have occurred among managed coastal species of shark (superorder Selachimorpha), we examined the population size structure of 12 species caught during a nearly five-decade-long fishery-independent survey conducted in Onslow Bay, North Carolina, using standardized longline gear. We evaluated trends in mean fork length (FL), median FL, and index of maximum FL ($L_{90\%}$) for each species separately across time using linear regression models. We also examined trends in size-classes (200-mm bins) and catch per unit effort for each species over time. For 10 of the 12 species (excluding sample-size-constrained Tiger Shark *Galeocerdo cuvier* and Bull Shark *Carcharhinus leucas*), size structure metrics indicated decreasing sizes over time, although statistical confidence for these patterns varied across species and metrics. Strongest statistical support for declining sizes was observed for Blacknose Shark *Carcharhinus acronotus* (mean FL, median FL, $L_{90\%}$), Dusky Shark *Carcharhinus obscurus* ($L_{90\%}$), Smooth Dogfish *Mustelus canis* ($L_{90\%}$), and Atlantic Sharpnose Shark *Rhizoprionodon terraenovae* ($L_{90\%}$). Magnitude of decreases in $L_{90\%}$ among these 10 species during the survey ranged from roughly 9% (Silky Shark *Carcharhinus falciformis*; 83-mm decrease) to 35% (Sandbar Shark *Carcharhinus plumbeus*; 541-mm decrease). Our findings indicate a potential for fishing pressure to exert directional selection on these coastal shark species, although further research is needed regarding the nature of size-dependent catchability and species-specific vital rates to adequately evaluate these dynamics. Furthermore, in addition to the removal of “great sharks,” decreasing sizes of small coastal sharks, such as Blacknose Shark, Smooth Dogfish, and Atlantic Sharpnose Shark (i.e., “mesopredators”), suggest that harvest may have pervasive effects on species throughout this assemblage.

Fishing causes substantial changes within exploited fish populations as a result of both selective removal of target species and bycatch of nontarget species. Size-selective harvesting of either targeted or bycatch fishes due to gear design (e.g., net mesh size) or management directive (e.g., minimum size limits) has been documented across diverse fishes, often leading to a reduction in mean or maximum

observed body size within a stock (Fenberg and Roy 2008). Truncation of size structure towards smaller individuals is ecologically and economically problematic. Growth overfishing is the harvesting of fish before they reach their growth potential and results in decreased yield per recruit. This was the first effect of overfishing to be conceptually defined and has been a concern throughout

*Corresponding author: benavides@unc.edu
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post World War II fisheries (Beverton and Holt 1957). Furthermore, some have suggested that maintaining “old-growth” age structure is as important as spawning biomass levels in determining the sustainability of fished stocks (Berkeley et al. 2004). In particular, big, old, fat, fecund female fish (BOFFFFs) are thought to disproportionately contribute to recruitment potential of a stock via both offspring quantity and quality. These BOFFFFs can also increase the diversity of larval source locations since fish can segregate spatially based on size or, in some cases, spawning routes can be learned from more experienced adults (Birkeland and Dayton 2005). Both factors help stabilize the population dynamics of harvested species (Hixon et al. 2014).

There are two classical, competing mechanistic hypotheses regarding the response of fished species to harvest pressure vis-à-vis population-level size structure, beyond the changes simply accountable to the disproportionate removal of larger fish by fisheries. Darwinian fisheries science has focused on the potential of harvest pressure to select for traits such as reduced growth or earlier size or age at maturity (Law 2007). In size-selective fisheries targeting large individuals, fish growing more quickly or reproducing at larger sizes and older ages may be captured before successfully contributing to the spawning population, greatly reducing their individual fitness relative to slower growers or earlier reproducers (Ratner and Lande 2001; Conover and Munch 2002). Over evolutionary scales, this truncates the size structure of an exploited population towards smaller fish. Alarming, these potential evolutionary consequences may be hard to reverse with the relaxation of fishing pressure due to hysteresis, a lag associated with relatively weak selection in the opposing direction (Allendorf and Hard 2009). While evolutionary dynamics may drive fished populations towards slower growers, alternatively, environmental drivers within exploited stocks could have the opposite effect on fish. The reduction of stock abundance can cause a release from intraspecific competition, resulting in greater per-capita availability of resources and increased growth as has also been documented in several marine fishes (Heino and Godo 2002). In a meta-analysis examining fish growth in relationship with exploitation rate, however, it was proposed that the size-selective removal of larger individuals had the more significant impact, rather than evolutionary changes in average growth rate (Hilborn and Minto 2008).

The response of a harvested stock’s life history vital rates and population-level size structure ultimately depends on the case-specific nature of density-dependent resource competition, genetic correlates or heritability of relevant traits, and the intensity (including temporal consistency) of size-selective harvest (Law 2007). However, there is a fundamental need to document patterns in size-

based indicators over appropriate timescales (i.e., decades) to guide us in understanding the dynamics and root mechanisms of size-structure shifts (Shin et al. 2005). Fisheries management would benefit from knowing if size-structure shifts are occurring or have occurred as this would allow for a more holistic assessment of the effects of fishing on harvested stocks. Sharks (superorder Selachimorpha) are an interesting and important test case for evaluating changes in size structure as there are a mix of factors that might buffer or exacerbate harvest-driven changes. Within this group, many species are defined by “survivor” life histories (i.e., slower growth, larger maximum size, longer maximum age, lower fecundity) and, as such, are vulnerable to overfishing (Stevens et al. 2000; Kindsvater et al. 2016). Sharks exhibit a variety of reproductive strategies; however, many of the species of interest to management are placental viviparous, with maximum offspring sizes showing a strong relationship to maximum maternal sizes (Parsons et al. 2008). The effects of maternal investment to offspring in sharks has received relatively limited attention and has yet to be fully explored; however, there is evidence suggesting that maternal shark size can affect both offspring quantity (litter size) and quality (fitness) (Carlson and Baremore 2003; Hussey et al. 2010; Baremore and Passerotti 2013; Bargione et al. 2019).

Gears used to harvest sharks include those that are likely to be size selective (i.e., gill nets), in addition to gears that are potentially less size selective (i.e., longlines) (Hovgård and Lassen 2000; Atlantic States Marine Fisheries Commission 2008). Because shark species can be grouped based on similar life history characteristics (see Cortés 2000), management has traditionally been conducted at multispecies levels along the U.S. Atlantic coast, using such groupings as the Large Coastal Shark (11 species), Small Coastal Shark (4 species), and Smoothhound (3 species) complexes (Final Consolidated Atlantic Highly Migratory Species Fishery Management Plan; NMFS 2006). At the same time, the population status of many species has been assessed individually, and as a result smaller complexes have been formed (e.g., Hammerhead complex [3 species]), species have been managed separately (e.g., Blacknose Shark *Carcharhinus acronotus*), or species have been added to the Prohibited Species list (19 species). These are jointly managed by the Atlantic States Marine Fisheries Commission in state waters (0–5 km from shore) and the National Oceanic and Atmospheric Administration (NOAA) Fisheries Highly Migratory Species Management Division in the Exclusive Economic Zone (5–322 km from shore) in the southeast (Atlantic States Marine Fisheries Commission 2008). These multispecies commercial fisheries operate without minimum size limits that often drive size-selective fisheries. Finally, pressure on “great sharks,” such as Bull Shark *Carcharhinus leucas* and Tiger Shark *Galeocerdo cuvier*, has been hypothesized

to have resulted in “mesopredator release” of smaller sharks and rays, which could further complicate the patterns of size structure within some fished species, such as Blacknose Shark (*sensu* Myers et al. 2007).

With the need to document size structure of coastal shark species in mind, we examined a decades-running survey of the coastal shark assemblage in Onslow Bay, North Carolina, to describe temporal patterns of population size structure among 12 commonly captured species. Our goal was to evaluate the null hypothesis that size-structure has not changed appreciably over time on a species-by-species basis.

METHODS

Long-term survey design.—To examine trends in size structure within coastal shark populations, we used species-specific time series size data generated during the course of a 1972–2018 fishery-independent shark survey in Onslow Bay, North Carolina. The survey has been conducted by the University of North Carolina at Chapel Hill’s Institute of Marine Science (UNC–IMS) since its inception and has employed standardized longline sampling gear at two fixed stations in Onslow Bay: 4 km (34.6338°N, 76.6306°W; 15-m depth) and 13 km (34.5512°N, 76.6237°W; 17-m depth) southeast of Beaufort Inlet. During each deployment at each station, a 7.6-mm braided nylon longline extends 1 km, with gangion lines attached to the mainline every 10 m (number = 100). Each gangion consists of a 1.8-m-long, #2-chain leader and a 9/0 Mustad tuna J hook. Polyball buoys are attached between every 10 gangions (100-m separation), allowing the longline gear to effectively fish the entire water column at each station.

In addition to standardized gears and stations, consistent deployment methods have been used since the first sets were made in 1972. Survey trips have been conducted biweekly, between April and November each year, on 10–15-m research vessels operated by UNC–IMS. A demersal trawl has been used at the start of each survey day to collect bait, overwhelmingly consisting of Spot *Leiostomus xanthurus* and Atlantic Croaker *Micropogonias undulatus*, which are attached through the operculum onto a hook (one fish per hook). Longline deployments occur between 0800 and 1300 hours, with the gear soaked for 1 h during each set. Weather permitting, gear is deployed at each station on each survey day and the inshore set (4 km) typically, but not always, is made first. Upon gear recovery, all captured sharks are identified to species, sexed, and measured for fork length (FL) and total length (TL) to the nearest millimeter. Live individuals are outfitted with an external dart tag and returned to the water (~90% of catch). To date, more than 1,000 longline sets have been made, resulting in the capture of >10,000 individuals

across 21 species. The survey is conducted under UNC–IMS Institutional Animal Care and Use Committee protocol 19-137.0.

Data analysis.—We selected 12 of the 21 shark species caught in the survey for analyses based on overall sample sizes, management context, and conservation interest: Atlantic Sharpnose Shark *Rhizoprionodon terraenovae* ($n = 3,685$), Blacknose Shark ($n = 1,456$), Dusky Shark *Carcharhinus obscurus* ($n = 1,033$), Blacktip Shark *Carcharhinus limbatus* ($n = 919$), Smooth Dogfish *Mustelus canis* ($n = 573$), Scalloped Hammerhead *Sphyrna lewini* ($n = 524$), Sandbar Shark *Carcharhinus plumbeus* ($n = 321$), Spinner Shark *Carcharhinus brevipinna* ($n = 273$), Silky Shark *Carcharhinus falciformis* ($n = 199$), Finetooth Shark *Carcharhinus isodon* ($n = 112$), Tiger Shark ($n = 45$), and Bull Shark ($n = 26$). While we generally excluded any species with a sample size lower than 100, Tiger Shark and Bull Shark were included as they are commonly caught members of the Large Coastal Shark complex and since both are species that have shown signs of maintaining or increasing biomass over the past several decades due to management actions (SEDAR 2006). For each of these species, separately, we binned data by year, combining individuals across all months and both stations to describe the entire surveyed population. We utilized FL data as this measurement was the most consistently collected across the entire survey, and we focused on data collected during 1975–2018 because data from the first three survey years did not consistently, clearly specify the length measurement. For each species \times year, we used three different size indices to obtain a more holistic and robust assessment of potential size changes over time: mean FL, median FL, and an index of maximum FL ($L_{90\%}$ or the 90th percentile of FL).

Both mean and median are commonly used to express the central tendency of a data set. Mean is more applicable for normal distributions, while median is a better descriptor for skewed distributions as it is relatively insensitive to outliers. Across our 12 focal species and 44-year survey, we observed both normal and skewed size distributions and therefore leveraged both descriptive statistics. Additionally, the 90th percentile is relatively sensitive to changes in maximum values, or presence/absence of large sharks in this instance (i.e., outliers). These three metrics complement each other as mean and median provide two measures of central tendency for the overall size distribution, one sensitive to outliers and the other insensitive, while $L_{90\%}$ quantifies the abundance of large individuals, relative to smaller individuals (Shin et al. 2005). We used R package Hmisc (F. E. Harrell, Vanderbilt University, personal communication; available at <https://cran.r-project.org/package=Hmisc>) to implement the Harrell–Davis quantile estimator for our calculation of $L_{90\%}$, which is more robust at lower sample sizes and extreme percentiles

than standard quantile calculations (Harrell and Davis 1982). Only species \times years with three or more specimens captured and measured were included in the $L_{90\%}$ calculations.

We used separate, linear regressions for each species and size metric over time (except for $L_{90\%}$ for Bull Shark and Tiger Shark, which lacked sufficient sample sizes) to assess the strength and ecological significance of relationships between year and shark size. Confidence intervals (CIs; 95% level) were computed for all linear regressions to better assess statistical certainty for each model (Nakagawa and Cuthill 2007). We used R package *estimatr* (G. Blair, J. Cooper, A. Coppock, M. Humphreys, L. Sonnet, N. Fultz, L. Medina, and R. Lenth, University of California Los Angeles, personal communication; available at <https://cran.r-project.org/package=estimatr>) to implement a heteroscedasticity-consistent standard error estimator (HC3) for computing confidence intervals and P -values for regression models. This estimator is relatively insensitive to data heteroscedasticity (Hayes and Cai 2007).

We estimated the magnitude of long-term size increases or decreases for each species and each FL index using linear regression models and associated confidence intervals. First, we determined the difference between the regression-model-estimated sizes for the first and last year in which each species was captured, both in absolute change as well as percent difference ("decline"). Second, as a conservative measure of size change ("conservative decline"), we estimated a minimum potential difference in sizes (mm and %) between the first and last year in which a species was recorded using the regression confidence intervals (i.e., using lower and upper CIs as appropriate to find the smallest potential difference between early and late records for apparent decreases in size). Finally, as an indicator of maximum potential changes ("extreme decline") in size (absolute and relative) over time and as a "worst-case scenario" in instances of apparent declines in size (no apparent increases in size were observed in this survey), we again compared regression confidence intervals between the first and last year in which each species was captured, but rather than selecting for the smallest potential change based on lower and upper CIs of early and late records, we identified the largest potential change through time based on CIs.

As a last measure of species-specific size-structure through time, we calculated the number of individuals for each species \times year in 200-mm size-class bins. The 200-mm bins appeared to provide valuable resolution for all species and were therefore used across all analyses. Due to the relative rarity of individuals over 2,000 mm, we collapsed all bins above this value into a single size-class. We also calculated mean catch per unit effort (CPUE) for each species across years to provide context regarding how population size or density and size structure may be related.

We computed CPUE for each species \times year based on the number of sharks caught per 100 hooks set.

The strength of our analytical approach relies on the availability of the 44-year data set on shark sizes across multiple species, despite some sample size limitations. Our inferences are drawn from a suite of information that includes effect sizes (i.e., mean differences over time), confidence intervals, and measures of statistical clarity (Nakagawa and Cuthill 2007). Importantly, given the multiple size metrics we considered, it would be conceptually problematic within a species to default to "statistically significant" changes for one size metric but "statistically insignificant" changes for another metric based solely on any arbitrary alpha (Amrhein et al. 2017; Hurlbert et al. 2019). All statistical analyses and plotting of data were conducted in R (R Foundation, Vienna).

RESULTS

Ten species were characterized by mean FLs that decreased over time to smaller average sizes (Figure 1). Exceptions included Tiger Shark and Bull Shark. Tiger Shark was almost absent in the survey from 1990 through 2010, with the exception of three small (<1,000 mm FL) individuals bracketed by the occurrence of relatively large individuals (1,500–2,500 mm FL) in the survey during the 1970s–1980s and 2010s (Figure 1). Except for one small (390 mm FL) Bull Shark captured in 2008, which had significant leverage in the regression analysis, individuals routinely measured ~2,000 mm FL throughout the survey. Examination of the other species revealed the largest relative decline in mean FL for Sandbar Shark (20%; 214 mm; $R^2 = 0.07$), while the declines across the remaining species ranged from 2% to 17% (Table 1). The strongest statistical support ($P = 0.001$) for a mean FL decline was found in Blacknose Shark, which declined by 11% (116 mm; $R^2 = 0.28$) (Table 1). Blacknose Shark was also the only species characterized by a potential decline (4%; 41 mm) in mean FL using the relatively conservative approach (Table 1). Using the "worst-case scenario," mean FL declined 12–55% across 10 species (largest decline for Sandbar Shark), with average sizes potentially shrinking by >32% in seven of those species (Table 1).

Median sizes also trended toward smaller fish for 9 of 12 species (Figure 2). Among the nine sharks with declining trend lines, changes in median FL ranged from 2% to 18%. Again, Blacknose Shark exhibited the best statistical support for a decline in median FL ($P = 0.008$) of 10% (104 mm; $R^2 = 0.2$) (Table 1), and viewed conservatively, only Blacknose Shark showed a potential decline in median FL (2%; 21 mm) (Table 1). Potential declines in median FL ranged from 13% to 51% in a "worst-case scenario" among species other than Spinner Shark, Tiger Shark, or Bull Shark. As with mean FL, largest potential

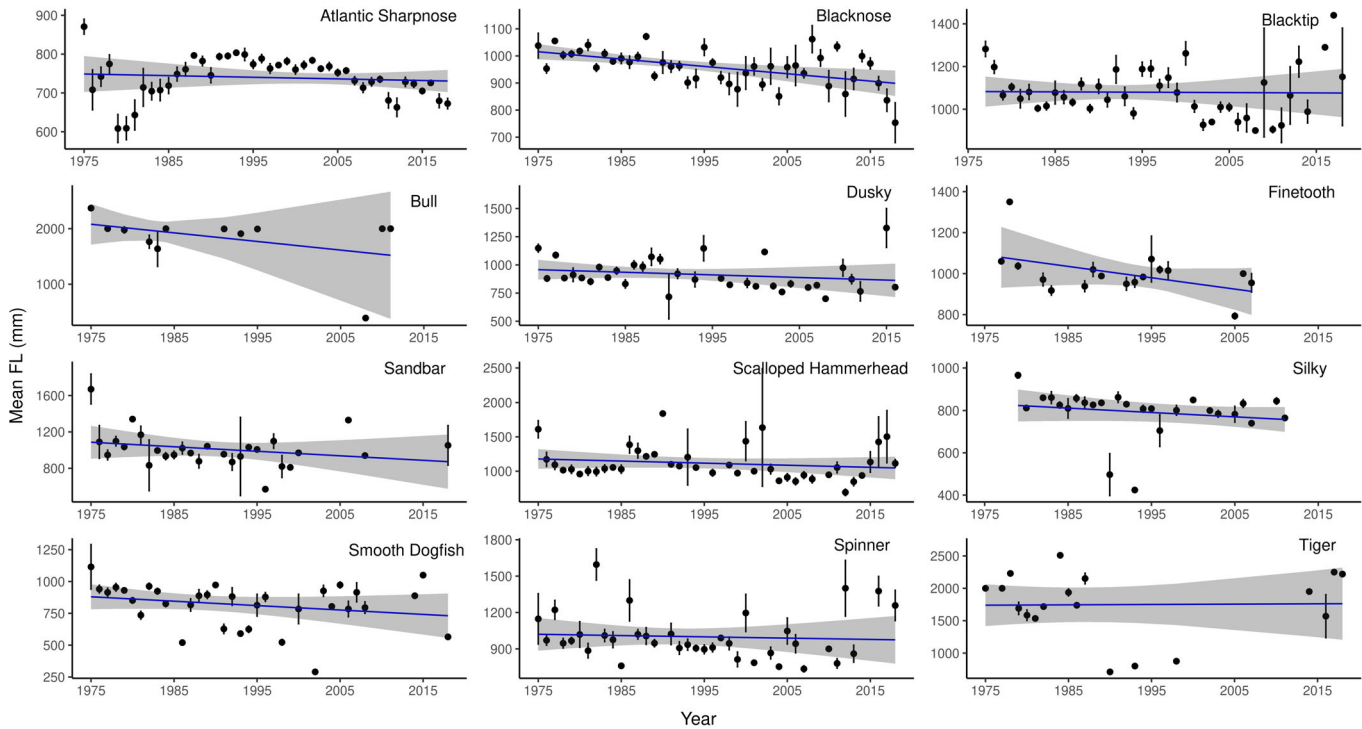


FIGURE 1. Mean FL (error bars show ± 1 standard error) with linear regression models (blue line) and 95% confidence intervals (shaded area) for each species.

declines in median FL were indicated for Sandbar Shark, with four species expressing $>31\%$ reductions in median FL over time (Table 1).

Survey results indicated $>9\%$ relative decreases in $L_{90\%}$ for all 10 species for which linear regression models were run (relative changes based on absolute trend lines; Figure 3). The largest relative declines were seen in Sandbar Shark (35%; 541 mm; $R^2 = 0.35$) and Spinner Shark (28%; 399 mm; $R^2 = 0.14$) (Table 1). We found the strongest statistical support ($P < 0.04$) for $L_{90\%}$ declines in four species: Blacknose Shark (10%; 115 mm; $R^2 = 0.19$), Dusky Shark (23%; 297 mm; $R^2 = 0.11$), Smooth Dogfish (17%; 178 mm; $R^2 = 0.23$), and Atlantic Sharpnose Shark (10%; 88 mm; $R^2 = 0.51$) (Table 1). Using our conservative approach to account for intra- and interannual variability in observations, we recorded small but distinct declines in $L_{90\%}$ for Blacknose Shark (3%; 32 mm), Smooth Dogfish (2%; 24 mm), and Atlantic Sharpnose Shark (5%; 45 mm) (Table 1). Using our “worst-case scenario” framework, relative declines in $L_{90\%}$ among species ranged between 15% and 63%, with five species potentially exhibiting $>45\%$ relative decreases in $L_{90\%}$ over time (Table 1).

Several sharks exhibited obvious reductions in catches of individuals within the largest size-class (i.e., 1,000-mm bin) of each species through time, including Blacknose Shark, Silky Shark, Blacktip Shark, Sandbar Shark, Smooth Dogfish, and Scalloped Hammerhead (Figure 4).

Across these species, the loss of the largest individuals was generally evident sometime during the 1990s, mirroring declines in overall CPUE for those species over the same period. Atlantic Sharpnose Shark was also characterized by a loss of the largest size-class (800–1,000 mm FL) by the end of the survey period. However, (1) catches of 800–1,000-mm-FL individuals were highest in the years between 1980 and 2005, while for other species highest catches of the largest size-class tended to occur between 1975 and 1995, and (2) Atlantic Sharpnose Shark was the only species that showed an increasing trend in annual mean CPUE (all size-classes combined), from one shark per 100 hooks in the 1970s to seven sharks per 100 hooks by the 2000s (Figure 4).

DISCUSSION

Expanding on previous analyses that suggest the loss of “great sharks” from the coastal ocean over the last several decades (Myers et al. 2007; Powers et al. 2013), our analyses suggest that within-species size changes over time may be pervasive throughout the entire coastal shark assemblage visiting Onslow Bay (Table 1). Indeed, survey results indicated decreases in size structure among members of the Large Coastal Shark complex (Blacktip Shark, Silky Shark, Spinner Shark), Small Coastal Shark complex (Atlantic Sharpnose Shark, Finetooth Shark),

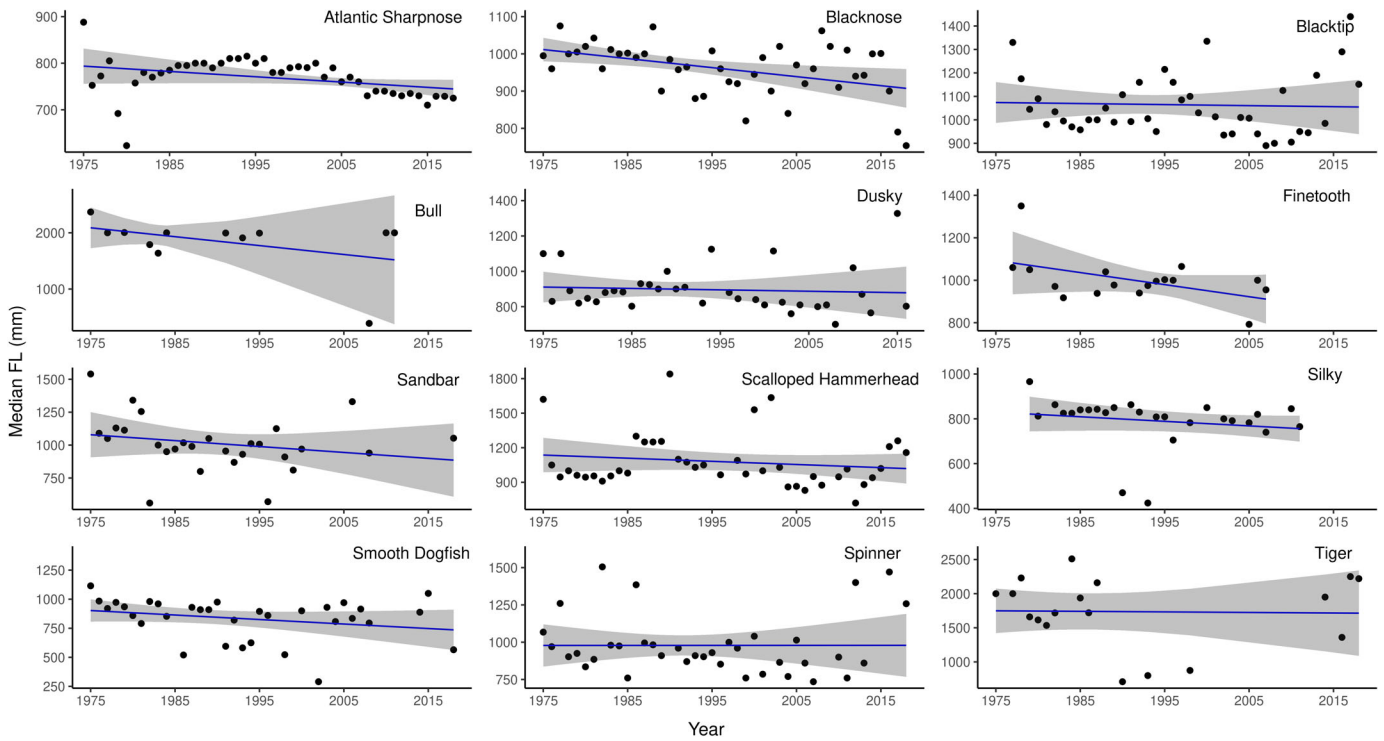


FIGURE 2. Median FL with linear regression models (blue line) and 95% confidence intervals (shaded area) for each species.

Hammerhead Shark complex (Scalloped Hammerhead), Smoothhound complex (Smooth Dogfish), Prohibited Species (Dusky Shark), Research-Only Species (Sandbar Shark), and single species (Blacknose Shark). Below, we consider how observed decreases in sizes across species fit in the context of management, genetic versus environmental drivers of size structure within fished populations, and purported “mesopredator release.”

We acknowledge that the nature of this long-term, two-station, observational data set presents some conceptual challenges for generalizing local results to regional changes in size structure among species. In attempts to present the data in a manner that is both straightforward and comparable across species, we have applied linear models to all of our data; however, it should be noted that not all assumptions are met by all species. Furthermore, we acknowledge that given some uncertainty about maximum sizes for some species in the early years, there are instances where outliers may have undue leverage, particularly for $L_{90\%}$ metrics. For example, we note that we have an individual Sandbar Shark from 1975 in excess of 2 m FL, which falls outside currently accepted size ranges for Sandbar Shark (Baremore and Hale 2012), although earlier accounts show maximum lengths of up to 2.3 m (Springer 1960). We note that even if these early outliers are removed from the analyses for affected species (e.g., Sandbar Shark and Sharpnose Shark), our qualitative

conclusions regarding the size stability and decreases are robust. We have also attempted to respect these constraints by evaluating multiple metrics of size structure for thoroughness as well as using a “totality of evidence” approach regarding size trends, confidence intervals, and statistical clarity to draw ecological inferences. We also conclude that there is important meaning at the assemblage level in the consistency of trends across species over decadal time scales. Across all 12 species for which we evaluated mean and median sizes (and all 10 species assessed using $L_{90\%}$), we recorded decreasing sizes through time based on the raw sign of fitted slopes. The binomial probability of recording consistently negative slopes across 12 species—presuming size-structure was actually stable—is less than 0.05% (<1 in 4,000). Therefore, we conclude that the interpretation of across-assemblage decreases in sizes is robust.

For nine species we evaluated, decreases in size over time co-occurred with long-term declines in catch rates in the UNC–IMS shark survey (Figure 4). Although shark-species-specific harvest records are patchy before the mid-1990s, we speculate that fishing pressure was a significant contributor to both the size and catch patterns we observed. At the assemblage level, commercial landings for sharks included in this study in the NOAA Fisheries South Atlantic region rose during the 1970s and 1980s to a peak of 4,324 metric tons in 1994 (NOAA

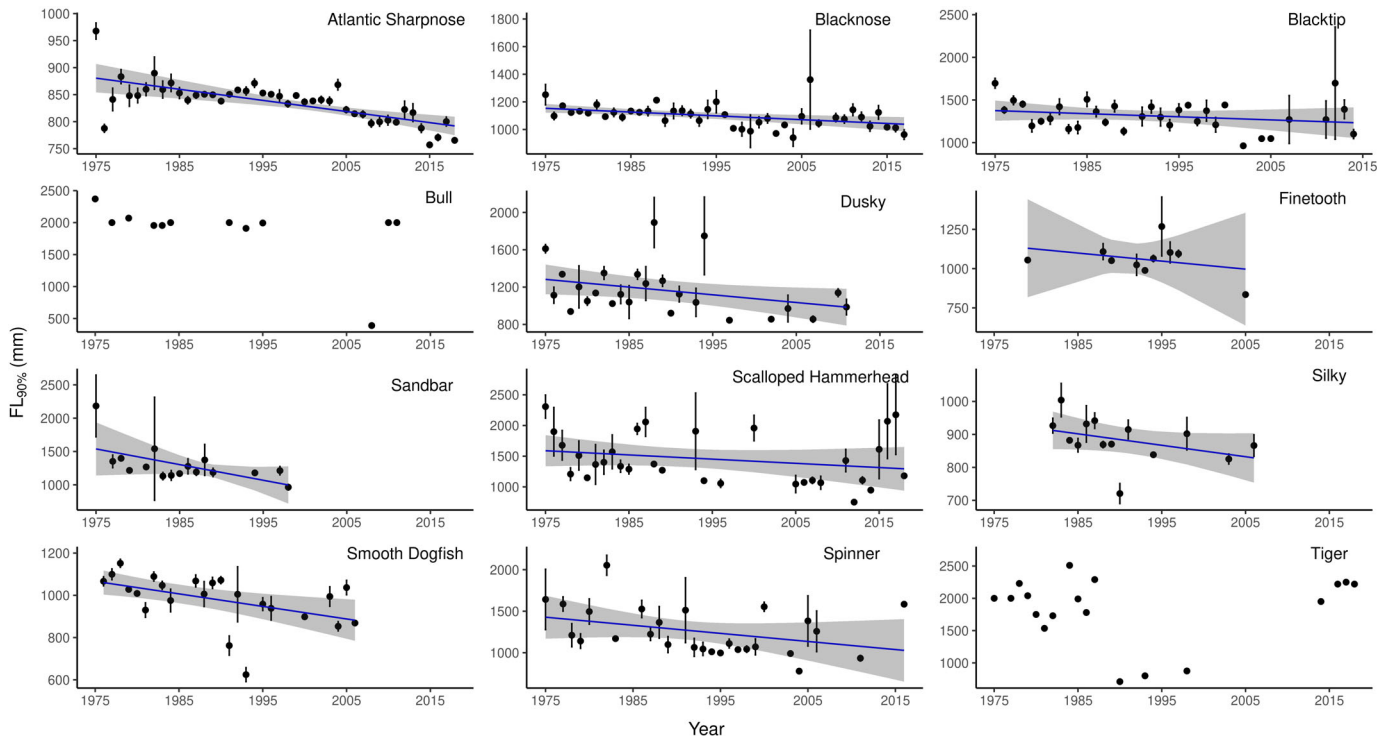


FIGURE 3. Index of maximum FL (error bars show ± 1 standard error) with linear regression models (blue line) and 95% confidence intervals (shaded area) for each species.

2019). Since that peak, landings have declined by 10-fold at the assemblage level, with similar declines in harvest for many species constituting the assemblage. Exceptions include Blacknose Shark and Blacktip Shark, which showed modest increases in landings over time, as well as Atlantic Sharpnose Shark, for which landings increased by 10-fold since NOAA landings records began. These recent, lower landings for most species are presumed to result from harvest-induced reductions in shark abundances, as well as reductions in allowable catches, although some gear changes (most notably circle hooks) were enacted since 2000 to prevent takes of protected or prohibited nontarget species (NMFS 2006). Notably, the mid-1990s peak in catches, and rapid decline in landings since, corresponds to the loss of the largest size-classes of Blacknose Shark, Silky Shark, Blacktip Shark, Sandbar Shark, Smooth Dogfish, and Scalloped Hammerhead (Figure 4).

An alternative hypothesis that cannot be completely ruled out with this spatially limited data set is that the changes in catch rates or size composition reflect the redistribution of animals in response to environmental conditions (range shifts) as has been documented across this region (Morley et al. 2017) and elsewhere (e.g., Perry et al. 2005; Mueter and Litzow 2008; Nye et al. 2009).

Temperature was the only environmental variable that was somewhat consistently reported across the time series utilized; however, given that the present study is focused on interannual trends and temperature is highly seasonal, we chose not to include this variable in our analyses as it would primarily indicate the effect of seasonality rather than differences between years. Presumably, all of the species in the present study exhibit ontogenetic changes in habitat use (Grubbs 2010), and thus range shifts could explain variation in size composition at a particular location. For example, Bangley et al. (2018) noted potential increased juvenile Bull Shark occurrence in North Carolina starting in the 2010s. We acknowledge this possibility but suggest it as an unlikely explanation for the declining trends seen across the species studied, most of which have been known to use North Carolina waters as pupping areas for several decades (Schwartz 2003). Moreover, as the catch rates of seven of our focal shark species in Onslow Bay increase as water temperatures exceed 25°C (Benavides 2020), regional warming over time should have increased opportunities to catch very large individuals—detectable in the $L_{90\%}$ metric. Alternatively, there is the possibility that sexual dimorphism could affect the results, where a change in the ratio of males to females could drive the size decreases. Accordingly, we examined the

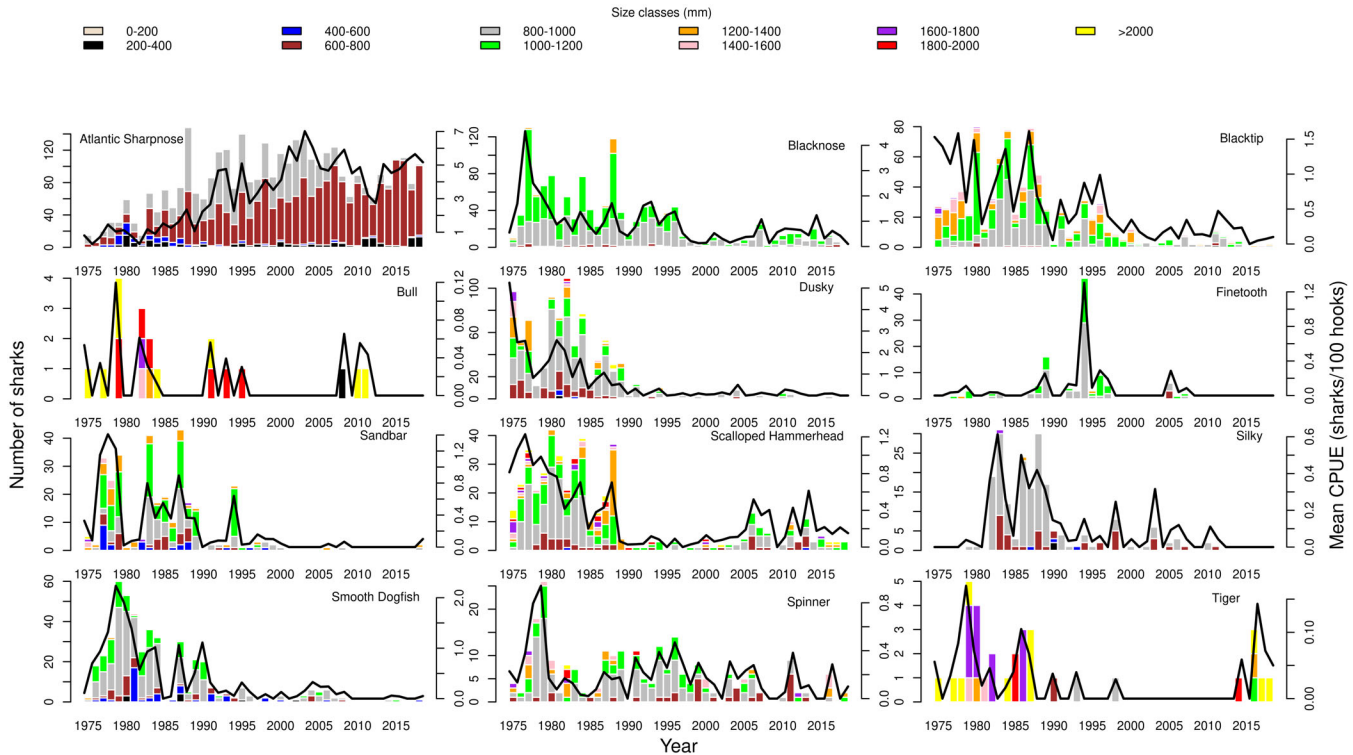


FIGURE 4. Stacked bar graphs displaying annual length-frequency distributions for each study species, with mean catch per unit effort shown as a line plot.

ratio of males to females, species by species, across years and found no clear patterns.

While there is compelling evidence that more restrictive harvest management over the last two decades has begun to reverse trends in shark abundance towards recovery (Peterson et al. 2017), the UNC–IMS survey data suggest that sizes in recent periods have not recovered to the sizes observed in earlier periods of the survey. However, we note that over the last 5 years the mean size of Spinner Shark, Blacktip Shark, Dusky Shark, Tiger Shark, and Scalloped Hammerhead suggest early signs of increase, which deserves continued monitoring and inspection (Figure 1). Dusky Shark has been prohibited from harvest since 2000 (SEDAR 2011b) and would be expected to be among the species to grow in mean size over time (sensu Fenberg and Roy 2008). Other species showing early signs of increase belong to the Large Coastal Shark or Hammerhead Shark complexes, perhaps indicating the effectiveness of these management units for a conservation framework, although given issues with assessing at the multispecies level it is likely that any signs of recovery would be driven by reductions in the allowable catch or quota for these complexes (SEDAR 2006; Peterson et al. 2017).

Across management units, the consistent patterns of size decreases among species over the last five decades

may also suggest something about mechanisms by which fishing impacts size structure. Shark management complexes generally operate without minimum size limits, thereby reducing the potential to drive size-selective fishing. Perhaps coastal shark population size shifts could be driven by the selectivity of fishing gear (Stevens et al. 2000), which often target larger individuals. Alternatively, perhaps fishing pressure is concentrated in areas where larger individuals are available to gear, leading to their selective removal. Furthermore, recreational fisheries for species in the Large Coastal Shark and Hammerhead Shark complexes operate with minimum size requirements, while commercial fisheries for “ridgeback” species within the Large Coastal Shark complex operated with a minimum size from 1999 to 2003 (NMFS 2006). If minimum size regulations were a primary driver of reductions in mean body size, it makes little sense that species within these management units would be showing the most notable signs of potential increase over the last few survey years. Finally, the lack of recovery in either catch rates or sizes of Sandbar Shark since the mid-1990s, despite its status as a research-only-harvest species, suggest several hypotheses: (1) the life history of this species does not allow recovery under current, presumably modest, rates of research harvest; (2) environmental conditions have shifted and do not support rapid recovery of this species; and (3)

the life history of this species does not allow recovery under current, poorly quantified rates of nontarget bycatch mortality (Crowder and Murawski 1998).

At a minimum, our data indicate that compensatory processes within the life history of sharks do not appear broadly capable of completely counteracting the effects of fishing on population size structure, but rather size truncation is the norm as might be expected (Stevens et al. 2000). This, however, does not preclude the possibility that individual growth rates have increased for some species experiencing significant decreases in abundance over time (e.g., Blacknose Shark, Blacktip Shark, Dusky Shark). In this regard, simply reversed, Atlantic Sharpnose Shark was the lone species in our survey defined by increases in catch rates over time. Carlson and Baremore (2003) reported that Atlantic Sharpnose Shark exhibited increased juvenile growth rates in response to population declines, suggesting this may be a mechanism for density-dependent regulation. Thus, higher intraspecific competition for resources (i.e., lower growth rates), rather than just fishing pressure, could explain some of the decreases in sizes we observed for Atlantic Sharpnose Shark (*sensu* Cushing 1995).

While the assemblage-level decreases in size we observed may reflect the long-term press of continually removing the large(r) individuals from the stock, the opportunity for selective forces to impact shark populations is possible as well (Walker 1998). We cannot distinguish between these different, but potentially co-occurring, mechanisms with our analyses. Rather, the results presented here represent an important first step by documenting size-based indicators over population-appropriate timescales (i.e., years to decades), which should guide further exploration into the dynamics and root mechanisms of size-structure shifts. Despite the logistic challenges of examining sharks in the context of Darwinian fisheries (e.g., across generation times of sharks, handling sharks for controlled experiments), we suggest this is an important area of investigation given the particular life histories and management approaches within this guild.

The size decreases reported in this study represent possible changes in recruitment, given empirical evidence of size- and age-based maternal investment by sharks (Hussey et al. 2010). In teleost fishes, BOFFFFs are known to contribute disproportionately to offspring growth and survival. For instance, older or larger rockfish *Sebastes* spp. exhibit increased maternal provisioning in the form of enlarged oil globule volume for eggs (Sogard et al. 2008), resulting in increased larval growth rate and survival (Berkeley et al. 2004). Maternal provisioning in sharks can occur via enlarged livers of offspring, with neonatal sharks showing a short-term declining trend in liver mass following parturition (Gilmore et al. 1983; Francis and

Stevens 2000). Presumably, the excess liver reserves provide a maternal head start for offspring to use in the first weeks of life, and this provisioning can vary with size, as evidenced by reproductive output increasing at larger maternal sizes in two carcharhinid shark species (Hussey et al. 2010). Given the limited attention maternal investment in sharks has received and the potential for changes in size structure to affect reproductive output, this is an area of pressing need for further study.

There has been increasing interest in the “rise of the mesopredator,” in which the loss of apex predators is accompanied by the expansion in density or distribution of middle-rank predators (i.e., mesopredator release; Prugh et al. 2009). This has led to concerns of potential food-web-level trophic cascades (Polis 1994), defined as inverse patterns of abundance at successive trophic levels that are transmitted down the food web (Brashares et al. 2010). Myers et al. (2007) found sharp declines in abundance for species of “great sharks” (>2 m; e.g., Bull Shark, Dusky Shark, Sandbar Shark, Tiger Shark) using the UNC-IMS survey data, which they attributed to direct exploitation. Myers et al. (2007) linked the declines in great sharks to the abundance of smaller species, such as Atlantic Sharpnose Shark. While our findings do not conflict with the results of Myers et al. (2007), our results suggest that the direct effects of fishing may be more pervasive throughout the shark assemblage, rather than focused on just the largest species with subsequent cascading impacts.

In particular, Atlantic Sharpnose Shark (acknowledging potential density-dependent drivers of size shifts), Blacknose Shark, Finetooth Shark, and Smooth Dogfish are all relatively small-bodied and aptly described as mesopredators. For all four of these species, long-term trends suggest decreases in size, which runs counter to the notion of top-down “release.” Combined with the long-term declines in catch rates of Blacknose Shark and Smooth Dogfish, these size decreases suggest that mesopredators also experience population responses to (top-down) fishing pressure. Indeed, Blacknose Shark exhibited perhaps the clearest shift over time, with all of the indices examined showing declines of ~10% throughout the survey period with high statistical confidence (Table 1), as well as relatively lower proportions of larger size-classes in later years of the survey (Figure 4). Blacknose Shark was assessed as overfished with overfishing still occurring, whereas Atlantic Sharpnose Shark, Finetooth Shark, and Smooth Dogfish were all assessed as not being overfished and with overfishing not occurring, resulting in quotas for Blacknose Shark only being reduced, starting in 2010 (SEDAR 2007, 2011a, 2013, 2015). We suggest continued monitoring of Blacknose Shark size structure to determine if these reductions in catches could help to reverse some of the decreases reported in this study.

This study provides a baseline for future coastal shark size structure comparisons, while also providing insight into how shark populations may have responded to fishing via environmental versus genetic mechanisms. Over the next few decades, there is perhaps a unique opportunity to monitor size structure in populations of coastal sharks in the South Atlantic Fishery region as managers attempt to reverse past overharvesting practices (Peterson et al. 2017). As in other fishery stocks, size structure is a critical component of monitoring and an indicator of stock health and resilience in the context of harvest pressure (Berkeley et al. 2004) and other compounding perturbations, such as bottom disruption of resources (Duplisea et al. 2002) or climate change syndromes (Morley et al. 2017).

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ORCID

Martin T. Benavides  <https://orcid.org/0000-0002-0032-780X>

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