DR. ALEXANDER C HANSELL (Orcid ID : 0000-0001-7827-1749)

Article type : Article

Corresponding Author Email ID: **Alexander.Hansell@Mass.gov**

Stock Assessment of the Lemon Shark off the Southeast United States

Alexander C. Hansell[1], Tobey H. Curtis[2], John Carlson[3], Enric Cortés[3], Gavin Fay[1], Steven X. Cadrin[1]

1. Department of Fisheries Oceanography, School for Marine Science and Technology, University of Massachusetts Dartmouth, New Bedford, MA, USA.
2. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Atlantic Highly Migratory Species Management Division, Gloucester, MA, USA.
3. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City, FL, USA.

Abstract

The Lemon Shark *Negaprion brevirostris* is a large coastal shark that commonly occurs in the shallow nearshore waters of the tropical western Atlantic Ocean. There are conservation concerns for this species due to fisheries exploitation, low productivity, anthropogenic disturbance at nursery sites, and the depleted status of other large coastal sharks, but no quantitative assessment of stock status is available. We synthesized available data to develop a stock assessment of the Lemon Shark in the western North Atlantic. All information on stock identity was considered to define a fishery management unit off the southeastern United States. Stock abundance and trends in fishing mortality were estimated from 1981 to 2017 using a

Bayesian state-space surplus production model. The model incorporated prior knowledge of Lemon Shark demography, catches, and a combination of 11 indices of abundance. Seven model configurations that fit the data well and produced plausible estimates were used to evaluate the sensitivity of posterior estimates to assumed priors and data decisions. Results suggest Lemon Shark stock abundance has been relatively stable since the mid-1990s, with some estimates of prior depletion. Estimates of relative fishing mortality indicate earlier periods of overfishing with a decrease in fishing mortality since the early 2000s. These estimates of population trends provide information for future fisheries management and conservation.

Introduction

The sustainability of elasmobranch fisheries is a global concern, with overfishing being a primary threat to many populations (Dulvy et al. 2014; 2017; Simpfendorfer and Dulvy, 2017). Sharks are targeted for their fins, livers, meat and skin, and also commonly caught as bycatch in non-target fisheries (Mandelman et al. 2008; Dent and Clarke, 2015). A combination of fisheries susceptibility and life history characteristics (i.e., slow growth, late sexual maturity, and few offspring) have led to high vulnerability for many shark species (Cortés, 2002; Dulvy and Forrest, 2010). Dulvy et al. (2014) estimated that 16% of global shark species are threatened from fishing pressure, with large-bodied shallow water species facing the highest level of threat, and another 20% of species lack sufficient information to determine a conservation listing according to International Union for Conservation of Nature (IUCN) criteria. Limited data has prevented analytical assessments for most elasmobranch species and resulted in disagreement over the population status of several shark species in the western North Atlantic (Baum et al. 2003; Burgess et al. 2005).

The United States of America (USA), has the seventh largest commercial shark fishery and one of the largest recreational shark fisheries in the world (Shiffman and Hammerschlag, 2014; Dent and Clarke, 2015). Other than the commercial fisheries for Spiny Dogfish *Squalus acanthias* and Smooth Dogfish *Mustelus canis*, the primary commercial shark fishery in the USA is for large coastal sharks. These sharks are targeted primarily using bottom longline gear in a fishery that operates from Virginia to Florida and throughout the Gulf of Mexico. Most large coastal sharks are in the families Carcharhinidae and Sphyrnidae. A typical bottom longline set has 500–1500 hooks, ranges in length from 8–24 km, and is left overnight to soak (Morgan et al. 2009; Hale et al. 2011). Large coastal sharks are also targeted in recreational fisheries, because anglers enjoy the thrill of catching large fish and the recreational fishery rapidly developed after the movie "Jaws" was released in 1975 (SEDAR, 2006). Recreational shark fishing occurs in state and federal waters along the entire Atlantic and Gulf of Mexico coastline (SEDAR, 2006; ASMFC, 2019). In general, the proportions of large coastal sharks caught in recreational and commercial fisheries are similar (SEDAR, 2006).

In the USA, the fishery for large coastal sharks historically harvested over a dozen species, including several that are now prohibited (Morgan et al. 2009). In 2006, stock assessment of the large coastal shark complex (11 species at the time) was discontinued because of varying life history parameters between species and insufficient data (Casey, 2006; SEDAR, 2006). Managing multiple species as a complex is not ideal because an increasing or decreasing biomass trend for one species can alter biomass estimates for the entire complex, and the decline of one species could be masked by increases in others giving a false perception of stability (Dulvy et al. 2000; Hayes et al. 2009; Hogan et al. 2013). Furthermore, the reproductive isolation of species in the complex and different vital rates among species violate common stock assessment and fishery management assumptions (Cadrin, 2020). Developing stock assessments for each species in the complex is considered a high priority, and management has continually made progress toward more species-specific measures (SEDAR, 2006; NMFS 2008; 2017; ASMFC, 2019). To date, the Blacktip *Carcharhinus limbatus* (Gulf of Mexico stock), Scalloped Hammerhead *Sphyrna lewini*, Dusky *Carcharhinus obscurus*, and Sandbar Shark *Carcharhinus plumbeu*s have had accepted stock assessments (Hayes et al. 2009; SEDAR, 2016; 2017; 2018), while other large coastal and prohibited species do not yet have accepted stock assessments.

Among these previously unassessed species is the Lemon Shark *Negaprion brevirostris*. On a global scale, population trends are unknown and the IUCN lists the Lemon Shark as Near Threatened (Sundström, 2015). In the USA, Lemon Sharks are managed as part of the large coastal shark complex, representing approximately 6% of recent commercial landings in that group (NMFS, 2019). Life history characteristics suggest the Lemon Shark is vulnerable to exploitation (Cortés, 1998). In recent years, there is some evidence that Lemon Shark catch rates have declined and nursery sites have been negatively impacted by anthropogenic pressures off the southeastern USA (Jennings et al. 2008; Ajemian et al. 2016; Plumlee et al. 2018). These factors have increased conservation concerns and led to changes in fisheries management. For example, the Florida Fish and Wildlife Conservation Commission added Lemon Sharks to the prohibited species list in 2010, preventing their harvest in Florida state waters (FWC, 2019). Increasing conservation concerns and management actions to protect Lemon Sharks highlight the need for improved understanding of status and trends in the Lemon Shark population and fishery.

The Lemon Shark occurs in coral reefs, mangroves and enclosed bays. In the western Atlantic they range from New Jersey to Brazil (Feldheim et al. 2001). Genetic analyses suggest there are two populations in the western Atlantic, a Northern Hemisphere and a Southern Hemisphere stock (Ashe et al. 2015). Adult sharks are mobile and move between the Gulf of Mexico and Atlantic (Kohler and Turner, 2019). They also make seasonal migrations along the east coast of the USA, between the Carolinas and Florida (Kessel et al. 2014). In the Northern Hemisphere, this species is philopatric and follows a biennial reproductive cycle. Every two years, mature female Lemon Sharks give birth to 4–17 sharks of ~ 50 cm total length (Gruber and Stout, 1983; Feldheim et al. 2002). Juvenile Lemon Sharks are highly site attached and can be found in nurseries in the southeast USA and Bahamas (Wetherbee et al. 2007; Reyier et al. 2008; Chapman et al. 2009). Male Lemon Sharks reach maturity at 12 years (225 cm), while females mature at 13 years (235 cm). The maximum observed age from ageing is 20 years; however, genetic inference estimates a theoretical maximum age of 37 years (Brown and Gruber, 1988; Brooks et al. 2016). Lemon Sharks mate in the spring and summer, with gestation lasting 10–12 months (Feldheim et al. 2002).

Here, we synthesize available data to conduct the first species-specific stock assessment for the Lemon Shark off the southeast USA. Lemon shark population dynamics are estimated using a Bayesian state-space surplus production model, which has performed well in similar data-limited situations, can use all the information available by accounting for prior knowledge of Lemon Shark demographics as well as uncertainty associated with data limitations. Results are expected to provide valuable information that can help improve Lemon Shark management off the southeast USA.

Methods

<u>Data-series</u>

Recreational catches of Lemon Sharks (in numbers) were obtained from three sources: the Marine Recreational Information Program (1981–2017; NAS 2017;

https://www.st.nmfs.noaa.gov/recreational-fisheries/data-and-documentation/queries/index), the Southeast Region Head Boat Survey (1986–2017), and the Texas Parks and Wildlife Department (1985–2017). The majority of recreational catches were from the Marine Recreational Information Program, with captures from the Southeast Region Head Boat Survey and the Texas Parks and Wildlife Department accounting for < 1%. Within the Marine Recreational Information Program dataset, fish were classified as "deceased" or "released alive". Of the fish released alive, a post release mortality rate of 12.5% was assumed, based on an estimate derived from physiological disturbance, reflex impairment, and post-release behavior (Danylchuck et al. 2014).

Commercial landings (live weight in pounds) were obtained from the Atlantic Coastal Cooperative Statistics Program (https://www.accsp.org), Gulf of Mexico Fisheries Information Network (https://www.gsmfc.org/fin.php), and Electronic Dealer records. Gulf of Mexico Fisheries Information Network and Atlantic Coastal Cooperative Statistics Program data were available from 1991 onwards, while Electronic Dealer data were available since 2013. Lemon Shark catch data from other countries in the region were not available. To obtain estimates of commercial Lemon Shark catch from 1981–1990 it was assumed that the percentage of Lemon Sharks in the catch was the same as the average proportion (< 1%) of Lemon Sharks in total large coastal shark catch from 1991–1995, when fishing practices should be most similar to those of 1981-1990.

Commercial catch was converted from weight to numbers so it could be directly compared to recreational catch. To convert commercial catch, annual mean fork lengths were obtained from the bottom longline observer program and converted to precaudal length estimates using a linear equation ($y = 0.92x - 0.7$; $R^2 = 0.99$). Annual average precaudal lengths were then converted to body weight in kg ($\text{Weight} = 8.11 \times 10^{-6} * \text{PCL}^{3.08}$; Gruber and Stout, 1983). For each year, commercial catch was divided by average weight to obtain an estimate of the number of commercial Lemon Shark captures.

Dead discards were included from the shark research fishery (100% observer coverage). For vessels in the shark bottom longline fishery which are not part of the shark research fishery, observer-reported Lemon Shark discard rates from 2010–2016, along with self-reported commercial fishing effort data were used to estimate Lemon Shark dead discards. Fishing effort data were available from the coastal logbook program for 1993–2017. Total dead discards were calculated as the product of observer reported yearly mean dead discard rates by hook and the yearly total fishing effort (bottom longline sets) reported to the coastal logbook program (Figure 1). Observer-reported discards do not include post-release (delayed) mortality for Lemon Sharks discarded alive.

Fishery-independent indices of abundance were available from several sources (Figure 2): the Bimini Biological Field Station longline survey (1992–2017); the Florida State University longline survey in the Florida Keys, USA (2011–2017) and in Andros, Bahamas (2014–2017); the South Carolina Department of Natural Resources trammel net survey (1995–2017), longline survey (2007–2017), and drumline survey (2013–2017); and the Texas Parks and Wildlife Department gill net survey (1982–2017). Fishery-dependent indices of abundance were available from the Shark Bottom Longline Observer Program Non-Research Fishery (1994–2007); the Shark Bottom Longline Observer Program Research Fishery (2008–2017); and from the Marine Recreational Information Program (1981–2017). To account for changes in catchability and other factors unrelated to abundance, all indices were standardized using generalized models (Maunder and Punt, 2004; Table A1–A10; Figure A1–A19). For the majority of indices, standardization did not alter observed nominal trends in relative abundance. However, standardization reduced annual fluctuations in catch rates for the Texas Parks and Wildlife Department gill net survey (Figure A1), both Shark Bottom Longline Observer Program time series (Figure A3), the Florida State University longline survey in Andros, Bahamas (Figure A9), and the Bimini Biological Field Station longline survey (Figure A11).

<u>Assessment model</u>

Surplus production models are a common stock assessment method used to assess sharks and require information on catch and relative abundance (Hilborn and Walters, 1992). Fitting surplus production models in a Bayesian state-space framework allows for the incorporation of prior knowledge and can help to account for uncertainty (Chaloupka and Balazs, 2007; Pedersen and Berg, 2017). State-space models describe temporal dynamics in the form of two linked processes: 1) a state model that describes unobserved population dynamics; and 2) an observation model based on relative abundance data that is a function of the unobserved state process. Error can come from either observations or the assumed production process (Chaloupka and Balazs, 2007). Error in the state model (process error) is attributed to demographic variability, and error in the observation model (observation error) can be the result of sampling error or temporal variability (Punt, 2003).

Here, we fit a Bayesian state-space surplus production model to data from Lemon Shark fisheries off the southeast USA, including prior knowledge about Lemon Shark demography. The Bayesian state-space surplus production model is comprised of the following probability density functions:

$g(N_{y+1} \mid N_y, \Theta)$ The state model for y = 1981…, 2017

$f(I_{i,y} \mid N_y, \Theta)$ The observation model

where N_y is the unobserved annual number of Lemon Sharks off the southeast USA for a given year y, $I_{i,y}$ is the annual observation of Lemon Sharks for a given index i and year y and Θ is the vector of model parameters.

State model

For the state model, the Pella-Tomlinson production function was chosen because it allows for alternative production functions (Pedersen and Berg, 2017). The expectation for the state equation is:

$$N_{y+1} = N_y + rN_y\left(1 - \left[\frac{N_y}{K}\right]^{m-1}\right) - C_y$$

where N is population abundance in year y, r is population growth rate, K is carrying capacity, m (> 1) is a unit-less shape parameter that determines the stock size where maximum production occurs, and C is total catch in year y. If the shape parameter equals one the model reduces to a Schaefer surplus production model. In this study, the Pella-Tomlinson model was reparametrized in terms of relative abundance ($P_y = N_y/K$) to reduce parameter confounding and to increase mixing speed (Meyer and Millar, 1999):

$$P_{y+1} = P_y + rP_y\left(1 - P_y^{m-1}\right) - \frac{C_y}{K}$$

Process error (σ^2) is accounted for in the state model by assuming multiplicative lognormal error:

$$P_y \sim \text{lognormal}\ (P_y, \sigma^2)$$

<u>Observation model</u>

The observation model connects the state model to each index of abundance i and year y, assuming each index is directly proportional to relative abundance (P_y). The observation model is:

$$I_{i,y} = q_i K P_y$$

where I_i is an index of abundance at year y, q is the catchability coefficient for that index i, and P is the relative abundance at year y. Observation error (τ^2) is estimated for each year y and index i by assuming multiplicative lognormal error:

$$I_{i,y} \sim \text{lognormal}\ (I_{i,y}, \tau_i^2)$$

<u>Priors</u>

Prior distributions specified for assessment model parameters are summarized in Table 1. A uniform prior was used for carrying capacity (K) in which the lower bound of the distribution was set at the maximum catch and the upper bound was set at the estimated carrying capacity for the entire large coastal shark complex (SEDAR, 2006). A lognormal prior was used for population growth rate (r), which was based on a distribution calculated from five independent estimates (Cortés, 2016). Population growth rate variance was set to cover a wide range of shark species with similar life histories (Cortés, 2016). The shape parameter (m) was derived from a linear equation that for a wide variety of species estimated the relationship between inflection point of maximum population growth and the rate of increase per generation (Fowler, 1988). This method was used because it has been applied to other shark species (Cortés, 2008) and there is typically not enough information to reliably estimate the shape parameter within the assessment model (Prager et al. 2002; Maunder 2003; Geng et al. 2020). In this study, preliminary exploration highlighted there was not enough information to reliably estimate the shape parameter. A uniform prior was assumed for initial population size (P_{1981}) from 70% to 100% (carrying capacity) because sharks were considered an underutilized resource in the 1980s and fishermen were encouraged to target them (ASMFC, 2019). Uniform priors that allowed for a wide range of realistic outcomes were assumed for catchability, process error variance and observation error variance (Gelman, 2006; Table 1).

<u>Estimation</u>

In summary, the Bayesian state-space surplus production model consists of the Pella-Tomlinson state model, the observation model, the estimated parameters $\Theta = \{r, K, P_{1981}, q_i, \sigma^2, \tau_i^2\}$, and their priors. The model was fit in R Studio using the package 'rjags' (Plummer, 2019). Four chains were run for a total of 5,006,000 iterations with a burn-in period of 500 samples, the chains were thinned every 10th step, and 500,000 samples were collected. Model parameters and their associated uncertainties were obtained from a Markov chain Monte Carlo (MCMC) algorithm, which drew from the marginal conditional posterior distributions of model parameters and latent states. The model was evaluated by examining routine diagnostics (i.e., posterior predictive check, Bayesian p-values, inspection of observed and estimated distributions, prior and posterior overlaps, Gelman-Rubin scores, split-$\hat{R}$, and trace plots of the samples from the posterior distribution for model parameters; Garret and Zeger 2000; Conn et al. 2018).

<u>Sensitivity analysis</u>

To investigate how alternative model configurations influenced results, seven plausible model configurations were considered: 1) Saturated run, using all available data; 2) Survey run, using only fishery-independent indices of abundance, because surveys are typically considered more reliable than fisheries-dependent catch rates; 3) USA run, using only indices of abundance from the USA, because catch data were only available from the USA; 4) Truncated run, indices of abundance earlier than the 1990s were not used, because before this only two indices are available and have conflicting trends; 5) Hierarchical run, a hierarchical model was used to create a single most probable index of relative abundance, because many of the indices are localized and have conflicting trends (Conn, 2009; Supplemental Material B); 6) High Catch, +1 proportional standard error (SE expressed as a percentage of the estimate) of recreational harvest was used as recreational catch estimates; 7) Low Catch, -1 proportional standard error of recreational harvest was used as recreational catch estimates (Figure 1).

Reference points

From the different model runs, useful reference points can be estimated, such as: the stock size that maximizes the production function, $N_{MSY} = K/(m+1)^{1/m}$; the fishing rate at maximum sustainable yield, $F_{MSY} = r*(1/(1+m))$; the maximum sustainable yield, $MSY = N_{MSY} * F_{MSY}$; and the minimum stock size threshold, $MSST = (1-M)*N_{MSY}$ (when M, the instantaneous natural mortality rate, <0.5; SEDAR, 2016). For MSST, a value of M = 0.083 yr-1 was used, which was derived from life history invariant estimators obtained from Cortés (2016). Reference points MSST and F_{MSY} are used to determine stock status for highly migratory species, in that the stock is considered overfished if the stock size is estimated to be less than MSST, and overfishing is occurring if F is estimated to be greater than F_{MSY} (SEDAR, 2006; SEDAR, 2016). To analyze the sensitivity of stock status to model results, three different scenarios were explored: 1) terminal year (2017), 2) average of final three years (2015–2017), and 3) terminal year (2017) for selected model results.

Results

Overall, the seven variants of the Bayesian state-space surplus production model showed little evidence for lack of convergence because Gelman-Rubin and split-$\hat{R}$ statistics were close to one for all parameters (Supplemental Material C). Trace plots indicate mixing for the majority of life history, variance, catchability, and stock abundance parameters (Figure D1–D7). However, for the USA model run, trace plots indicate less than ideal mixing and multimodality in stock abundance estimates (Figure D5). Comparison of prior and posterior overlaps indicate that data were not very informative about stock abundance in 1981, population growth rate and observation error estimates for the South Carolina Department of Natural Resources longline survey (Supplemental Material C). Posterior predictive checks and Bayesian p-values indicate that model runs had similar goodness of fits to most indices of abundance (Table A11). Models did not fit as well the Texas Parks and Wildlife Department gillnet survey and observation error estimates hit upper parameter bounds for this index (Figure 3; Figure D1–D7). The year effect estimates from the relative abundance indices were within the posterior 95% credible intervals for stock abundance for most years and model runs. In general, all model runs except for the Survey run had difficulty fitting the Texas Parks and Wildlife Department gillnet survey because of the large interannual variability of that index in the 1980s (Figure 3).

Posterior estimates were similar for many of the parameters (Figure 4; Supplemental Material C). Except for the Hierarchical model run, the prior distribution of population growth rate was similar to the posterior distributions for all model runs. The posterior estimates of carrying capacity were at the lower end of the prior distribution (Figure 4). Posterior median estimates of carrying capacity were greater for the Survey and Hierarchical model runs (775,000 and 2,317, 000 animals respectively), but lower for the Low Catch run (159, 000 animals; Figure 4).

Relative fishing mortality was similar for all model runs and was highest in the early 1990s and early 2000s, but relatively stable at a low level from 2007 onward (Figure 5). Posterior stock abundance for years prior to 1992 varied among model configurations; two models estimated declines during this period (Survey, Truncated,), but the other five models displayed stable trends (Saturated, USA, High Catch, Low Catch, and Hierarchical). All model configurations estimated that abundance was relatively stable after 1992 (Figure 5). Three model runs (i.e., Saturated, High Catch, Low Catch) had similar estimates of stock abundance in 2017. In 2017, the USA model run had the highest estimate of stock abundance, while the model run using only survey data had the lowest estimate (Figure 5). For all model runs, from 1981 to 2017 the average median estimate of population depletion was 26% (range = 58-11%).

Median posterior MSY estimates were similar for all model configurations, except for the Saturated (3300 sharks) and Low Catch scenarios (1500 sharks; Figure 4). Median estimates of MSST ranged from 89,000 (Low Catch model) to 1,291,000 (Hierarchical model; Table 2). F_{MSY} estimates were similar for all model runs except for the Hierarchical model (Table 2; Figure 4).

There is a large degree of uncertainty in Lemon Shark stock status regardless of the terminal year(s) used, especially in the overfishing status of the two most pessimistic model runs. When using 2017 only as the terminal year, most models and scenarios estimate that the stock is not overfished and overfishing is not occurring (64%; Figure 6). However, when using the average of 2015-2017, a higher proportion of the simulations estimated the stock is overfished and overfishing is occurring (33%; Figure 6). Some model runs are viewed as less realistic (i.e., Survey and Hierarchical; see discussion), removing these model runs suggests that in 2017 the stock is not overfished and overfishing is not occurring (80%; Figure 6).

Discussion

The Bayesian state-space surplus production model provides the first indication of population trends for Lemon Sharks off the southeast USA. Results suggest Lemon Shark stock abundance has been relatively stable since the mid-1990s, and that fishing mortality has decreased since the early 2000s (Figure 5); however, stock status remains uncertain (Figure 6). Prior to this stock assessment, the only estimate of population status for Lemon Sharks was from the IUCN, which estimated the Lemon shark was Near Threatened (Sundström, 2015). The Near Threatened listing was based on expert opinion and the criterion for the listing was that the population must have declined over the last three generations by 20–25% (IUCN, 2019). Our assessment spans roughly two generations (36 years), and the average median estimate of population decline was 26% (Figure 5), lending support to the Near Threatened listing by the IUCN for Lemon Sharks off the southeast USA. However, this modest level of decline may not have been enough to reduce the population below its MSST (i.e., overfished condition), according to most model runs as of 2017 (Figure 6).

In the Atlantic Ocean, Lemon Shark stock structure is not well defined, but there is evidence that there is a Northern Hemisphere stock and a Southern Hemisphere stock (Ashe et al. 2015). In this study, the spatial extent of the assessment was determined by data availability. Catch data were only available from the USA, while relative abundance information was only available from the USA and the Bahamas. Incorporating relative abundance indices from both the USA and the Bahamas assumes Lemon Shark trends from these areas are reflective of the same population. The assessment presented here does not reflect the entire Northern Hemisphere stock but should adequately characterize the status of the USA Atlantic Lemon Shark management unit.

Historically, little attention was given to population dynamics or fisheries management of sharks (McAllister et al. 2004). In the USA, the first federal management plan for sharks was implemented in 1993 in response to perceived declines in abundance. The federal management plan highlighted the need for information to conduct species-specific stock assessments. Because of this plan, state and federal agencies began compiling more catch data and conducting studies on shark life history and relative abundance (NMFS, 1993). Because little attention was given to shark population dynamics prior to the 1990s, it is not surprising that a major source of uncertainty in our model runs is stock abundance estimates prior to this period. For most of the 1980s, five model runs estimated stable abundance (Saturated, USA, High Catch, Low Catch and Hierarchical), while two model runs indicated declines in stock abundance (Survey and Truncated; Figure 5). Given the documented declines of other large coastal sharks in this region (e.g., Sandbar, Dusky, and Scalloped Hammerhead Sharks) due to overfishing during this period (Hayes et al. 2009; SEDAR, 2016; 2017), some level of decline in Lemon Shark abundance would not be unexpected.

In general, surplus production models are being used less frequently in favor of age- or size-structured models, and they offer the flexibility to advance data-limited stock assessments when data collection systems are developed (Punt et al. 2020). However, for most shark species including the Lemon Shark, age-class specific data are not available, and data are insufficient to even estimate size composition reliably, which is why surplus production models are still routinely used (Hayes et al. 2009; Winker et al. 2017) , and Bayesian state-space production models offer a more formal approach to quantifying uncertainty (Chaloupka and Balazs, 2007; Pedersen and Berg, 2017). Continuing investments to provide age- or size-specific data would help to inform the Lemon Shark stock assessment, and age-structured models should be explored when those data are available.

Like every model, surplus production models have limitations. These models do not distinguish between mature and immature individuals and the proportions of both that are removed by fishing, yet variations between these groups can affect population growth rates and stock abundance. In this study, the model assumes total catch is known, but estimates of Lemon Shark catches are relatively uncertain (Figure 1) as is common for most shark populations worldwide (Cortés and Brooks, 2018). Catches largely determine the magnitude of population estimates, such that if catch is underestimated the model will underestimate the total population size. Like most stock assessments, surplus production models assume indices of abundance are proportional to population size throughout time. However, this assumption can be violated as catchability can change due to gear, introduction of management measures, and environment variability (Maunder and Punt, 2004; Maunder et al. 2006).

In this study, all indices of abundance were standardized to try to account for changes in catchability so each index could be assumed proportional to abundance (Supplemental Material A; Maunder and Punt 2004). For all indices, catchability was assumed to be constant, which is a common assumption in stock assessment. However, it is probable catchability varies throughout time and thus, future work should explore estimating time-varying catchability for Lemon Shark indices (Wilberg et al. 2009). Ideally, an index of abundance for Lemon Sharks would be available from a fishery-independent survey that samples the population throughout its range. However, many of the indices are spatially limited or only sample a segment of the population and may not reflect abundance trends throughout the area of inference or the entire population (Peterson et al. 2017). Additionally, the temporal coverage of many surveys (e.g., Florida State longline surveys and South Carolina drumline survey) is limited and thus, more years of sampling are needed for these indices to be informative. Conflicting trends among indices can lead to poor MCMC mixing and multimodality, which is a potential cause for the multimodality observed in the USA model run.

Likely, the most reliable indices of abundance are from the bottom longline observer program, because of their temporal (1994–2017) and spatial coverage (Figure 2). Similar to other shark assessments, data from the bottom longline observer program were split into two indices because observer coverage changed in 2008 (SEDAR, 2018). The longline index in Bimini is also dependable because Lemon Sharks comprise a high proportion of the catch and the survey samples important Lemon Shark habitat (Hansell et al. 2018). In contrast, the South Carolina Department of Natural Resources longline survey, the Marine Recreational Information Program index and the Texas Parks and Wildlife Department gillnet survey have issues that most likely prevent them from being directly proportional to abundance. The trend from the South Carolina Department of Natural Resources longline survey conflicts with the other two indices of abundance from South Carolina (i.e., trammel net and drumline). Further, the index shows a substantial decline from 2009–2011, which disagrees with all other indices during this time (Figure 2). The Marine Recreational Information Program time series has good spatial coverage and covers the entire assessment period; however, it is created from angler interviews and there are substantial uncertainties in year effect estimates (Figure A5). The Texas Parks and Wildlife

Department gillnet survey has high observation error estimates that hit upper parameter bounds, is localized, only catches juveniles and in recent years rarely catches Lemon Sharks. However, similar trends have been observed from recreational shark tournaments in the area (Ajemian et al. 2016). The hierarchical index was strongly influenced by the Texas Parks and Wildlife Department gillnet survey (Supplemental Material B).

Different model configurations were investigated to account for uncertainty in some of the common assumptions of surplus production models. Two model runs investigated the sensitivity of the assessment model to different catch scenarios, the High Catch scenario most likely provides an upper confidence limit of posterior parameter estimates, while the Low Catch scenario provides a lower confidence limit. These two model runs cover a wide range of removals and thus, help to account for uncertainty in post-release mortality estimates. The Survey model run used only fisheries-independent catch rates, which are typically considered a more reliable estimate of relative abundance than fisheries-dependent catch rates. A hierarchical index of abundance was created to help reconcile the conflicting trends of the multiple spatially limited surveys and produce a combined index of abundance for the stock (Figure 2; Conn, 2009; Supplemental Material). The Truncated model run did not use relative abundance data prior to 1992 and thus, allowed for the examination of the influence of the Marine Recreational Information Program and Texas Parks and Wildlife Department gillnet survey. Both the Hierarchical and Truncated model runs suggested that Lemon Sharks may have experienced a historical decline, but the population has been relatively stable since the mid-1990s (Figure 5). The Survey and Hierarchical model runs should be viewed with caution because both models have strong fits to the Texas Parks and Wildlife Department gillnet survey. Excluding these somewhat unrealistic model runs, leads to a clearer picture of stock status in 2017, which suggests the stock is not overfished and overfishing is not occurring (Figure 6).

Despite the limitations associated with surplus production models, in some cases they can out-perform more complex assessments and can reliably estimate important reference points (Geromont and Butterworth, 2015). Bayesian surplus production models are still routinely used to assess data-limited stocks (ICES, 2018). In general, Bayesian methods have been recommended to assess shark populations because data for these species are either limited or uncertain (McAllister et al. 2004). In this study, the assessment model was developed in a Bayesian framework, which allowed us to incorporate prior knowledge about Lemon Shark life history, which has been studied extensively, and portray uncertainty associated with key model parameters and reference points (Cortés, 1998; Gruber et al. 2001; Cortés, 2016). Additionally, fitting the model in a state-space framework allowed for the estimation of uncertainty in both the population process and observations. Models that account for both types of uncertainty generally out-perform models that only estimate process or measurement error (Punt 2003; Ono et al. 2012).

There is still a need for species-specific assessments as the population status of most large coastal shark species in the USA remains unknown. Before this assessment, four large coastal sharks—Blacktip, Scalloped Hammerhead, Dusky, and Sandbar—have had species or stock-specific assessments (Hayes et al. 2009; SEDAR, 2016; 2017; 2018). The Gulf of Mexico Blacktip Shark, one of the largest contributors to recent USA landings, is considered not overfished and not subject to overfishing (SEDAR, 2018), but both the Scalloped Hammerhead and Dusky Shark stocks are considered overfished and subject to overfishing (Hayes et al. 2009; SEDAR, 2016), while the Sandbar Shark is overfished, but rebuilding (SEDAR, 2017). The diversity of results from these assessments highlights the need for species-specific assessments. However, the breadth of federal and state shark fisheries management regulations implemented in the USA Atlantic over the last two decades (e.g., NMFS 1999; 2008; 2017) appear to be yielding benefits to the Lemon Shark population. As the majority of fishing mortality in recent years is derived from recreational post-release mortality (Figure 1), continued emphasis on the use of gears (e.g., circle hooks) and best practices for safe handling and release (e.g., NMFS 2017; FWC 2019) will further enhance the long-term sustainability of Lemon Sharks and other coastal shark stocks.

Conclusions

We synthesized available data to develop the first stock assessment model for the Lemon Shark off the southeast USA. Bayesian state-space surplus production models suggest Lemon Shark stock abundance has been relatively stable since the mid-1990s, and that fishing mortality has decreased since the early 2000s. Stock status is uncertain; however, removing less realistic model runs indicates it is likely the stock is not overfished and overfishing is not occurring. The results of this project improve our understanding of stock trends and provide information for fisheries managers that will hopefully provide a solid basis for future management advice.

However, the current USA shark fisheries management approach appears to be adequately preventing regional Lemon Shark population declines.

Acknowledgements:

We dedicate this manuscript to the memory of Samuel H. Gruber in recognition of his lifelong pursuit to advance scientific understanding of the lemon shark. We would like to thank: Dean Grubbs, Mark Fisher, Bryan Frazier and Cami McCandless for providing data. Also, thanks to Chang Liu, Tammy Silva, and Joe Iafrate for providing valuable feedback on early versions of the model. Lauran Brewster, Greg Skomal, Diego Bernal and Karyl Brewster-Geisz provided valuable feedback on early versions of the manuscript. We also thank the two anonymous reviewers and the Associate Editor who provided constructive and helpful feedback. Thank you to the Cadrin Lab at University of Massachusetts Dartmouth. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect those of their institutions.

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Table 1: Priors in Bayesian state-space surplus production models used to investigate the stock dynamics of Lemon Sharks *Negaprion brevirostris* off the southeast USA.

Parameters	**Distribution**	**Values**
Population growth rate (r)	Log-normal	0.07 (SD = 0.04)
Carrying capacity (K)	Uniform	47–35677 thousand fish
Shape parameter (m)	Derived	3.5
Initial stock abundance (P_{1981})	Uniform	0.7–1
Catchability (q)	Uniform	0.0001–3
Process error variance (σ^2)	Uniform	0.05–0.5
Observation error variance (τ^2)	Uniform	0.05–0.5

Table 2. Reference points from different Bayesian state-space surplus production models used to investigate the stock dynamics of Lemon Sharks *Negaprion brevirostris* off the southeast USA. See text for description of reference points and model runs.

Reference Points	**Saturated**	**High Catch**	**Low Catch**	**Survey**	**USA**	**Truncated**	**Hierarchical**
MSY (Thousands)	3.3 (7, .75)	4.9 (8.3, 1.8)	1.5 (3.4, 0.4)	4.1 (8.5, .28)	3.8 (10, 0.5)	4 (6.6, 1.25)	5.7 (7,3 0.08)
F_{MSY}	0.013 (0.031, 0.002)	0. 013 (0.025, 0.002)	0.014 (0.034, 0.003)	0.008 (0.024, 0.002)	0.014 (0.38, 0.002)	0.01 (0.01, 0.001)	0.004 (0.015, 0.001)
MSST (Thousands)	207 (327,128)	313 (531, 188)	89 (141, 52)	432 (782, 202)	227 (390, 129)	307 (523, 171)	1291 (14679, 134)

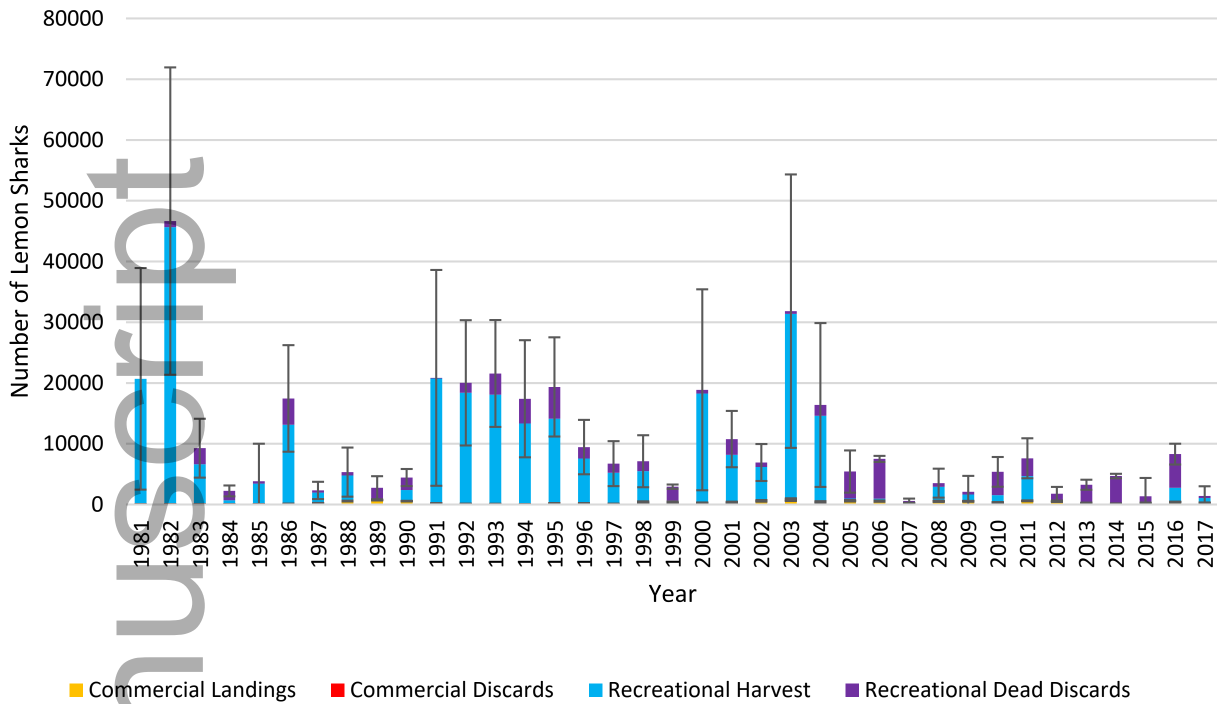

Figure 1: Harvest of Lemon Sharks *Negaprion brevirostris* in the USA. Error bars are the percent standard error estimates produced by the Marine Recreational Information Program. Commercial discards include dead discards only; recreational discards include dead discards and live post-release mortality.

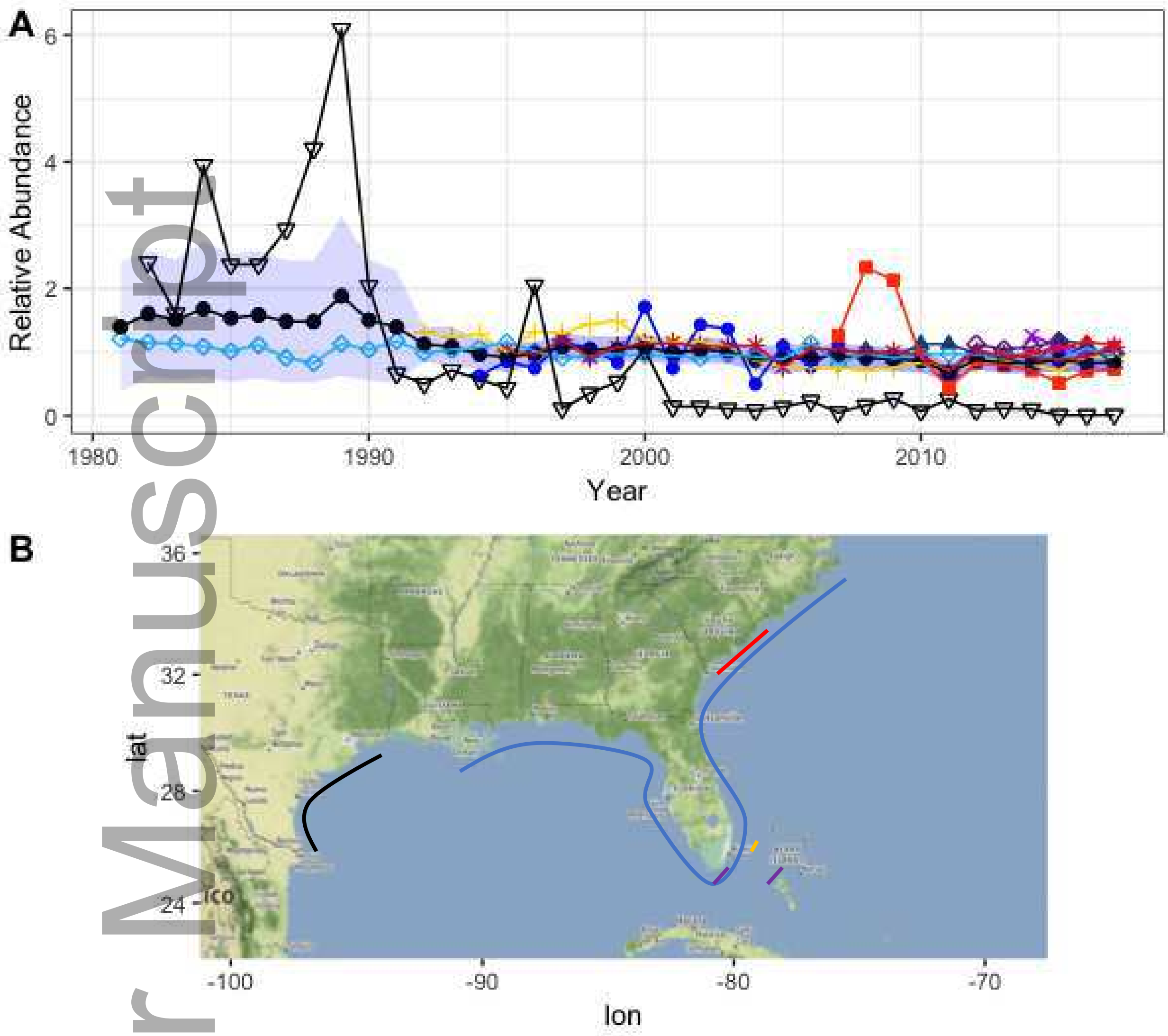

Figure 2: Lemon Shark *Negaprion brevirostris* statistically standardized indices of relative abundance (A) and their relative spatial extent (B). Abundance indices are the following: the Bimini Biological Field Station longline survey (yellow); Florida State University longline survey in the Florida Keys, USA (purple diamond) and in Andros, Bahamas (purple asterisk); the South Carolina Department of Natural Resources trammel net survey (red asterisk), longline survey (red square), and drumline survey (red circle); the Texas Parks and Wildlife Department gill net survey (inverted black triangle); Shark Bottom Longline Observer Program Non-research Fishery (blue circle); the Shark Bottom Longline Observer Program Research Fishery (blue triangle); the Marine Recreational Information Program (blue diamond); and the Hierarchical Index (black circle), with its standard error estimates (blue shaded area).

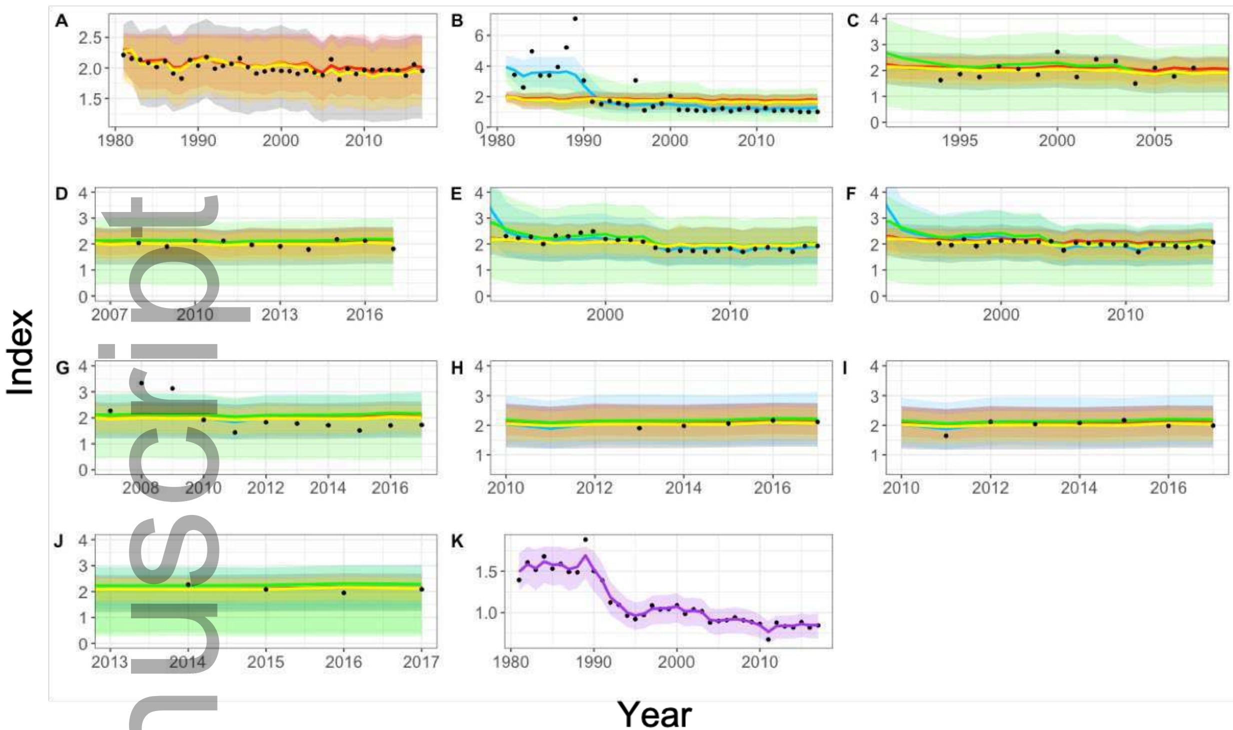

Figure 3: Bayesian state-space surplus production model fits to the eleven indices of relative abundance: A) Marine Recreational Information Program; B) Texas Parks and Wildlife gillnet survey; C) Bottom Longline Observer Program Non-research Fishery; D) Bottom Longline Observer Program Research Fishery; E) Bimini Biological Field Station longline survey; F) South Carolina Department of Natural Resources trammel net survey; G) South Carolina Department of Natural Resource longline survey; H) South Carolina Department of Natural Resource drumline survey; I) Florida State longline survey in the Florida Keys, USA; J) Florida State longline survey in the Andros, Bahamas; K) Hierarchical Index. Black circles are estimates of relative abundance, solid color lines are median posterior estimates of stock abundance, shaded areas are the posterior 95 % credible intervals. Colors correspond to the following model runs: Saturated – black; Survey– blue; USA– red; Truncated– green; Hierarchical– purple; High Catch – Orange; and Low Catch – yellow. See text for description of model runs.

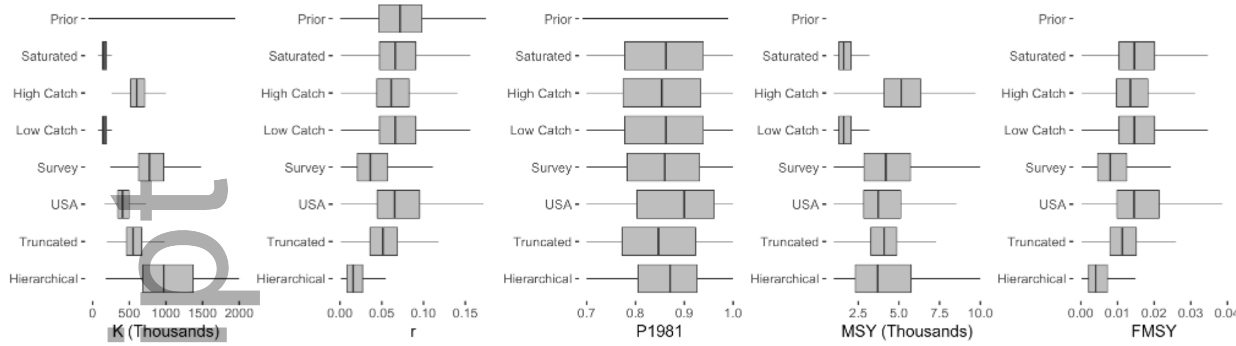

Figure 4: Standard boxplots for each model run, prior (when applicable) and posterior estimates for the parameters carrying capacity (K), population growth rate (r), initial stock abundance (P_{1981}), the maximum sustainable yield (MSY) and the fishing mortality that produces maximum sustainable yield (F_{MSY}). All model runs are Bayesian state-space surplus production models investigating Lemon Shark *Negaprion brevirostris* population dynamics off the southeast USA.

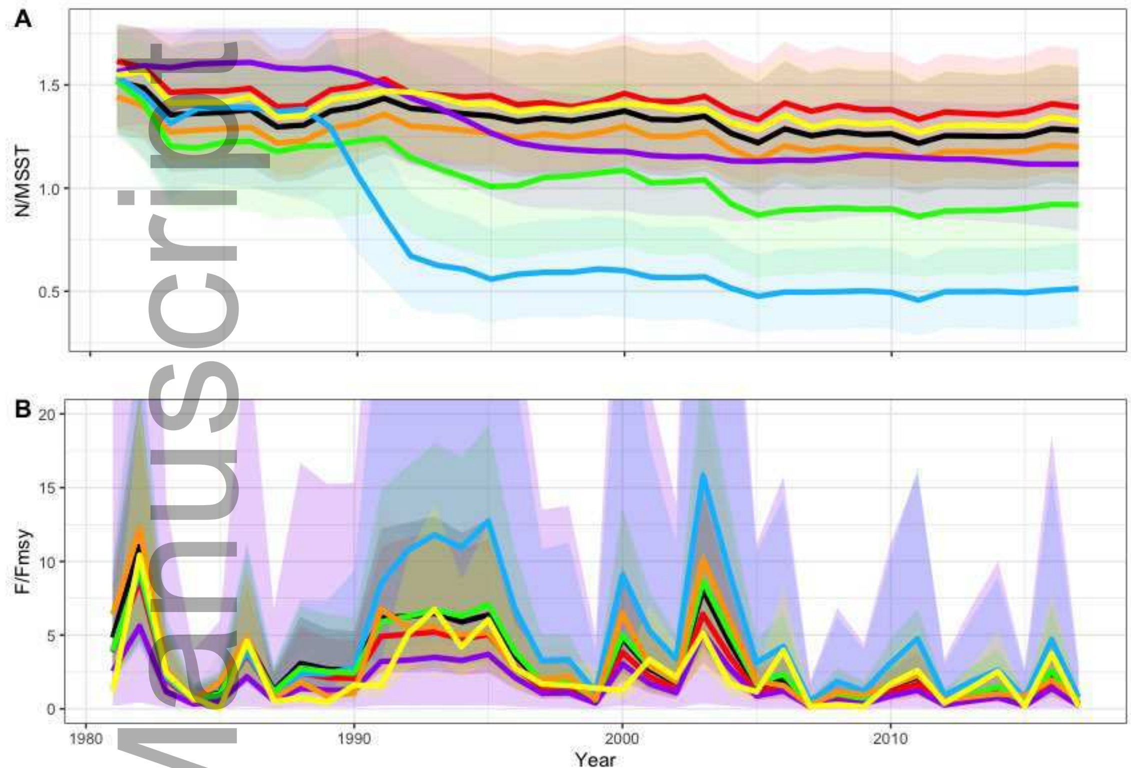

Figure 5: Posterior relative abundance (A) and fishing mortality (B) estimates produced from different Bayesian state-space surplus production models investigating Lemon Shark *Negaprion brevirostris* stock dynamics off the southeast USA. Solid lines represent median estimates for each model run, while shaded areas represent corresponding 95 % credible intervals. Colors correspond to the following model runs: Saturated – black; Survey – blue; USA – red; truncated – green; Hierarchical – purple; High Catch – Orange; and Low Catch – yellow. See text for description of model runs.

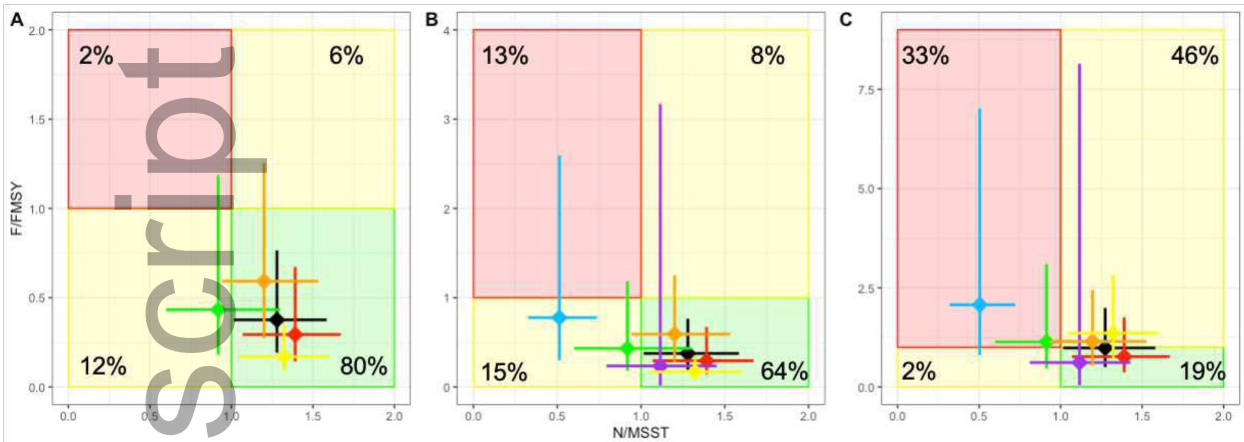

Figure 6: Phase plot of average population size and fishing mortality rate relative to reference points for selected models in 2017 (A), all models in 2017 (B), and all models from 2015 – 2017 (C). All estimates are from Bayesian state-space surplus production models investigating Lemon Shark *Negaprion brevirostris* stock dynamics off the southeast USA. The color square corresponds to different stock status: green = not overfished and not subject to overfishing; red = overfished and subject to overfishing; yellow (top right) = not overfished and subject to overfishing; and yellow (bottom left) = overfished and not subject to overfishing. Percentages are the probabilities for each stock status based on all model runs. Diamonds represent median posterior estimates; horizontal and vertical lines are the 95 % credible intervals. Colors correspond to the following model runs: Saturated – black; Survey – blue; USA – red; Truncated – green; Hierarchical – purple; High Catch – Orange; and Low Catch – yellow. See text for description of model runs.