Community interactions and density dependence in the southeast United States coastal shark complex

SEDAR65- RD05

Cassidy D. Peterson, Kristene T. Parsons, Dana M. Bethea, William B. Driggers III, Robert J. Latour

10/30/19

Vol. 579: 81–96, 2017
https://doi.org/10.3354/meps12288

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 14

Community interactions and density dependence in the southeast United States coastal shark complex

Cassidy D. Peterson[1,*], Kristene T. Parsons[1], Dana M. Bethea[2], William B. Driggers III[3], Robert J. Latour[1]

[1]Virginia Institute of Marine Science, College of William & Mary, PO Box 1346, Gloucester Point, VA 23062, USA
[2]NOAA Fisheries, Southeast Regional Office, Protected Resources Division, 263 13th Avenue South, St. Petersburg, FL 33701, USA
[3]National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories, PO Drawer 1207, Pascagoula, MS 39567, USA

ABSTRACT: Studies aiming to assess intra- and interspecies community relationships in marine habitats are typically limited to accessible, nearshore areas of restricted temporal and spatial scale, within which only segments of the populations of interest are available. Using multivariate first-order autoregressive state-space (MARSS-1) models, we estimated measures of interspecies interactions and density dependence of 7 Atlantic coastal shark species (4 large and 3 small coastal sharks) at 2 spatial scales. Localized analyses were based on data from 4 relatively spatially limited, fishery-independent surveys conducted along the southeast US Atlantic coast and within the Gulf of Mexico. We then compared these localized results to those generated using broad-scale indices of relative abundance estimated as common trends across the collection of 6 spatially restricted surveys. The MARSS-1 framework was also used to estimate relative community stability. Localized MARSS-1 analyses identified density-dependent compensation in all populations in addition to 9 interspecies interactions, while results of broad-scale MARSS-1 analyses revealed density dependence in 5 species and 9 interspecies interactions. More specifically, our results support the manifestation of density-dependent compensation of neonate and juvenile shark life stages within nursery areas. Overall, interactions within smaller spatial areas differed from those identified using the broad-scale relative abundance trends, indicating that small-scale interactions cannot be extrapolated to shark population growth rates of an entire stock.

KEY WORDS: Atlantic coastal sharks · Nursery areas · Multivariate first-order autoregressive state-space model · MARSS-1 · Early life history · Generalized linear models · GLMs

INTRODUCTION

Sharks occupy mid to upper trophic positions within their food webs and have the capacity to regulate ecosystems via top-down processes (van der Elst 1979, Stevens et al. 2000, Scheffer et al. 2005, Heupel et al. 2014). Despite limited research on the dynamic stability of shark communities, it has been shown that sharks and other top predators fulfill the crucial role of facilitating stability of the food web (Britten et al. 2014). Sharks exhibit K-selected life history strategies typified by late age at maturity, long reproductive cycle, low fecundity, and extended longevity (Cortés 1998, Musick et al. 2000, Stevens et al. 2000, Au et al. 2015). Life cycles of sharks are typically multifaceted, undergoing ontogenetic changes in habitat use (Heupel & Hueter 2002, McElroy et al. 2006, Grubbs 2010), diet (Lowe et al. 1996, Bethea et al. 2004, McElroy et al. 2006, Ellis & Musick 2007, Grubbs 2010), migration patterns (McCandless et al. 2005, Parsons & Hoffmayer 2005, Conrath & Musick 2008, Grubbs 2010), and consequently, intra- and

---

[*] Corresponding author: cpeterson@vims.edu

interspecies interactions (Papastamatiou et al. 2006, Grubbs 2010). Because sharks occupy wide spatial ranges and several discrete niches over the course of ontogeny, complete characterizations of population dynamics are difficult to define. Similarly, many species school by age, size, and sexual maturity status, as exemplified by differential habitat use between neonates, juveniles, and adults as well as between males and females (Springer 1967, Heupel & Hueter 2002, Parsons & Hoffmayer 2005, DeAngelis et al. 2008). Inevitably, predatory and competitive interactions of sharks must also change over their lifecycle (Grubbs 2010).

Understanding community interactions is necessary to adequately manage any species, particularly at the ecosystem level (Morin 2012). However, there is still much to be understood concerning intra- and interspecies interactions among elasmobranchs (Papastamatiou et al. 2006). Interactions among sharks via predator–prey relationships have been observed from diet studies (e.g. Hoffmayer & Parsons 2003, McElroy et al. 2006, Ellis & Musick 2007, Gurshin 2007, McElroy 2009). However, due to the challenge of identifying prey material down to species level, diet analyses often group prey species into broad taxonomic categories (e.g. 'elasmobranch,' Lowe et al. 1996, Simpfendorfer et al. 2001; 'unidentified teleosts,' Bethea et al. 2004), such that inferring specific predator–prey interactions is challenging (Grubbs et al. 2016). Furthermore, diet composition does not directly reflect the population-level importance of interactions between predator and prey species (Heithaus et al. 2010).

Several studies have proposed that resource partitioning is occurring within shark communities (Bethea et al. 2004, White & Potter 2004, Papastamatiou et al. 2006, Kinney et al. 2011, Shaw et al. 2016), reducing direct competition between species and promoting coexistence (Platell et al. 1998). Alternatively, species may be out-competed for their ideal habitat, such that they sacrifice conditions promoting optimal population growth in exchange for escaping competitive exclusion (Morin 2012). Studies of species interactions have traditionally been limited to easily accessible, shallow-water habitats in which shark congregations are known to occur (White & Potter 2004, DeAngelis et al. 2008; e.g. nursery areas, Heupel et al. 2007), such that interactions occurring on a broader scale or outside the local range of these studies remain unexplored.

It is common for several sympatric shark species to share nursery areas (Castro 1993, Bethea et al. 2004, Parsons & Hoffmayer 2007, Ulrich et al. 2007), which increases the potential for interspecies competition (Heupel et al. 2007, DeAngelis et al. 2008, Kinney et al. 2011). Neonatal and juvenile stages of several coastal shark species with relatively small birth sizes and slow initial growth rates seasonally inhabit nurseries for several years after birth (Heupel et al. 2007, Grubbs 2010). Predator avoidance has been shown to shape neonate and juvenile shark behavior within nursery areas (Heupel & Hueter 2002, Heithaus et al. 2007, DeAngelis et al. 2008), indicating that antipredatory behaviors (risk effects) play an important, but unmeasurable, role in juvenile and small prey species' population growth rates (Heithaus et al. 2008, 2010).

While rarely demonstrated in elasmobranchs, density-dependent regulation is a phenomenon in which the growth rate of a population is influenced by population size (Gedamke et al. 2007, 2009, Cortés et al. 2012). Several studies have proposed density dependence in elasmobranch populations based on observations including increased survival of neonatal and early juvenile individuals (Hoenig & Gruber 1990, Gruber et al. 2001, Gedamke et al. 2007, Kinney & Simpfendorfer 2009), increased growth rates and earlier age at maturity (Sminkey & Musick 1995, Carlson & Baremore 2003, Cassoff et al. 2007, Taylor & Gallucci 2009), smaller size at maturity (Carlson & Baremore 2003, Sosebee 2005, Taylor & Gallucci 2009, Coutré et al. 2013), and changes in fecundity (Taylor & Gallucci 2009). However, changes with respect to growth rate and age and size at maturity can also be confounded by other factors, such as selective fishing pressure (Márquez-Farias & Castillo-Geniz 1998, Stevens et al. 2000, Carlson & Baremore 2003, Sosebee 2005). Nevertheless, density dependence is commonly assumed in various elasmobranch population (Au & Smith 1997, Gedamke et al. 2009, De Oliveira et al. 2013) and stock assessment models (SEDAR 2013). Currently, the most commonly accepted compensatory response mechanism is thought to be neonate and juvenile survival (Cortés et al. 2012).

The large ranges and migratory patterns of many shark species make conducting generalized, broad-scale analyses challenging. Thus, studies concerning shark interactions have been limited to confined, small-scale analyses. In the present study, we sought to quantitatively examine species interactions (including density dependence) using multivariate first-order autoregressive state-space (MARSS-1) models within and between large and small coastal shark species complexes along the southeast US coast and within the Gulf of Mexico at both localized and broad spatial scales. As afforded by the MARSS-1 model structure, a secondary goal was to examine relative community stability of each species complex (see Supplement 1 at www.int-res.com/articles/suppl/m579p081_supp.pdf).

METHODS

Data sources

Catch and effort data from 6 fishery-independent surveys ranging from 1974–2014 along the southeast US Atlantic coast and Gulf of Mexico (for a list, see Table S1, and Figs. S1–S3 in Supplement 2 at www.int-res.com/articles/suppl/m579p081_supp.pdf) were examined to estimate time-series of relative abundance at localized and broad spatial scales, and infer species interactions and community stability. Analyses focused on 7 Atlantic coastal shark species, representing 2 management categories: 4 large coastal shark (LCS) species (sandbar shark *Carcharhinus plumbeus*, blacktip shark *C. limbatus*, spinner shark *C. brevipinna*, and tiger shark *Galeocerdo cuvier*) and 3 small coastal shark (SCS) species (Atlantic sharpnose shark *Rhizoprionodon terraenovae*, blacknose shark *C. acronotus*, and bonnethead shark *Sphyrna tiburo*; Table S2).

Time-series of relative abundance

Catch per unit effort data from each survey were used to estimate annual indices of relative abundance using delta-lognormal generalized linear models (GLMs; McCullagh & Nelder 1989, Lo et al. 1992) for each species (see Peterson et al. 2017). Indices of abundance from the 4 temporally longest-ranging surveys represented the localized analyses. Indices of abundance for each species from all surveys were analyzed using a time-series reduction model (dynamic factor analysis, DFA) to produce a single trend over time. DFA is a multivariate modeling technique designed to extract latent common trends from a collection of short, non-stationary time series (Holmes et al. 2014; see Peterson et al. 2017 for complete details). These reduced trends represented the broad-scale analysis and were estimated on a standardized (*Z*-scored) scale. Consequently, broad-scale trends were rescaled to the maximum survey-based index value generated by delta-lognormal GLMs (DFA inputs) to retain a measure of relative scale necessary for log-transformation in the MARSS-1 analysis.

MARSS-1

Time-series of species relative abundance were analyzed using MARSS-1 models, which are derived from the Gompertz population growth equation (Ives et al. 2003). The MARSS-1 models are of the form:

$$\begin{aligned} \boldsymbol{x}_t &= \boldsymbol{B}\boldsymbol{x}_{(t-1)} + \boldsymbol{w}_t, \text{ where } \boldsymbol{w}_t \sim \text{MVN}(0, \boldsymbol{Q}) \\ \boldsymbol{y}_t &= \mathbf{I}\boldsymbol{x}_t + \boldsymbol{v}_t, \text{ where } \boldsymbol{v}_t \sim \text{MVN}(0, \boldsymbol{R}) \end{aligned} \tag{1}$$

where $\boldsymbol{x}$ is the vector of log-transformed true species relative abundance at time t, $\boldsymbol{B}$ is the species interaction matrix in which each element, b_{ji}, represents the effect of species i on the population growth rate of species j, $\boldsymbol{y}$ is the measured log-transformed species relative abundance, $\mathbf{I}$ is the identity matrix, and $\boldsymbol{w}$ and $\boldsymbol{v}$ represent the multivariate normally (MVN) distributed process and observation errors at time t with associated means of 0 and covariance matrices $\boldsymbol{Q}$ and $\boldsymbol{R}$ (Holmes et al. 2014).

The focus of this study was estimation of the $\boldsymbol{B}$ matrix, because elements of the species interaction matrix contain information on density-dependent compensation of each species and how species' interactions impact the overall population growth rates of other members of the complex. Specifically, diagonal values near 0 are indicative of density-dependent compensation as derived from the Gompertz population growth equation; diagonal elements with magnitudes near 1 suggest that the corresponding species does not experience density dependence. Off-diagonal elements, b_{ji}, measure the influence of species i on the population growth rate of species j (Ives et al. 2003). Values with 90% confidence intervals that did not overlap 0 or 1 were interpreted as representing significant interspecies interactions or density-dependent regulation, respectively. Interaction and density dependence coefficient values with 85% CIs that did not overlap 0 or 1, respectively, were interpreted as approaching significance.

MARSS-1 model fitting

Localized species interactions were investigated by fitting models to delta-lognormally generated indices of abundance from each survey with sufficient longevity (Virginia Institute of Marine Science Longline Survey, VIMS LL; Gulf of Mexico Shark Pupping and Nursery Gillnet Survey, GULFSPAN GN; SouthEast Area Monitoring and Assessment Program–South Atlantic Trawl Survey, SEAMAP-SA Trawl; and Southeast Fishery Science Center Longline Survey, SEFSC LL), and broad-scale interactions were identified by fitting models to the broad-scale, reduced common trends, which were representative of larger-scale trends in relative abundance for each species. To reduce the number of estimated parameters for assurance of appropriate model convergence, known yearly variances from the relative abundance indices were averaged to produce a single estimate of index variability for each species, which was specified in the observation error covariance matrix, $\boldsymbol{R}$. We also assumed that no covariance between species indices existed within the observation error matrix. The process error covariance matrix, which measures the degree to which each species is affected by environmental or other external perturbations, was estimated from 3 different structures: (1) a diagonal and equal structure in which all variances were assumed to be equal and covariance was set to 0, (2) a diagonal and unequal structure in which each variance was assumed to be unique and covariance was set to 0, and (3) an unconstrained matrix in which all variances and covariances were independently estimated.

Convergence problems arose when fitting MARSS-1 models, and were indicative of too many parameters being estimated without sufficient available degrees of freedom or that the model framework being applied was not appropriate for the data (Holmes et al. 2014). Hence, every element of the $\boldsymbol{B}$ matrix could not be estimated within a single model, and relevant species interactions were chosen *a priori* based on biological and ecological inferences derived from previous research (e.g. Bethea et al. 2004, Thorpe et al. 2004, Papastamatiou et al. 2006, Carlson 2007, Parsons & Hoffmayer 2007, Ulrich et al. 2007, Castro 2011, Shaw et al. 2016). The interactions were necessarily 1-sided (i.e. we estimated the effect of species X on species Y, but not the effect of species Y on species X in the same model), enabling the MARSS-1 models to converge. Models were fitted in several steps (see Supplement 3 at www.int-res.com/articles/suppl/m579p081_supp.pdf). Exploratory analyses were conducted by estimating 'base' $\boldsymbol{B}$ matrices to determine the directionality of the interactions to be included in the final $\boldsymbol{B}$ matrix. The successful interactions from the previous step were combined into a single $\boldsymbol{B}$ matrix, and between 16 and 32 unique combinations of the given interactions were fitted. Optimal models were ranked by corrected Akaike's information criterion (AICc; Hampton et al. 2013, Holmes et al. 2014). Up to 10 models within 5 ΔAICc units were analyzed, and models that resulted in the lowest uncertainty in parameter estimates that still displayed acceptable graphical model fits were chosen for final analysis. All models were fitted using the 'MARSS' package (Holmes et al. 2013) in R (version 3.1.1; R Core Team 2014).

Within the broad-scale analyses, before fitting a model to all species combined, MARSS-1 models were fitted to both the LCS and SCS complex independently. The resulting elements of each $\boldsymbol{B}$ matrix were manually specified within the final $\boldsymbol{B}$ matrix when all shark species were included. This effectively allowed us to model interactions between species complexes which would not have been otherwise possible due to the large number of parameters to be estimated. When all species were included in the MARSS-1 model, we assumed that the process error covariance matrix contained equal variances for all LCS species and a separate measure of equal variances for all SCS species due to divergence of life history strategies. Stability analyses were conducted comparing the relative community stability of the SCS, LCS, and aggregated complex (see Supplement 1).

RESULTS

Localized MARSS-1 modeling

A diagonal and equal process error covariance matrix structure was supported for each survey-specific MARSS-1 model, likely due to a reduced number of estimated parameters. A diagonal covariance matrix $\boldsymbol{Q}$ assumes that the environmental factors driving variation in the relative abundance of one species is uncorrelated to environmental factors driving the relative abundances of all other species (Holmes et al. 2014). We identified 16 instances of density dependence in the localized analyses, along with 9 significant species interactions (i.e. effects on population growth rate; Table 1, Figs. 1–4).

Broad-scale MARSS-1 modeling

Broad-scale time-series of relative abundance included single trends for sandbar, blacktip, spinner, and tiger shark populations, which were considered representative of individuals in both the southeast US Atlantic coast and Gulf of Mexico. Two broad-scale time-series were required to adequately describe the patterns of abundance for Atlantic sharpnose and blacknose sharks, each trend uniquely representative of southeast US Atlantic Ocean or Gulf of Mexico individuals, in general. Lastly, bonnetheads produced a single explanatory time-series

Table 1. Species interaction (***B***) matrix results from multivariate first-order autoregressive state-space (MARSS-1) models conducted on the Virginia Institute of Marine Science Longline Survey (VIMS LL), Southeast Fishery Science Center Longline Survey (SEFSC LL), SouthEast Area Monitoring and Assessment Program–South Atlantic Trawl Survey (SEAMAP Trawl), and Gulf of Mexico Shark Pupping and Nursery Gillnet Survey (GULFSPAN GN). Interpretation of the off-diagonal elements in the matrix is the effect that the column heading species has on the population growth rate of the species noted by the row heading, and diagonal elements are indicative of density dependence. SB: sandbar, BT: blacktip, SPN: spinner, TIG: tiger, SN: Atlantic sharpnose, BN: blacknose, and BH: bonnethead sharks. **Bolded**, *italicized*, and underlined values have 95, 90, and 85 % confidence intervals (CIs) that exclude 0 or 1 for community interactions and density dependence, respectively. Values highlighted in green represent significant positive interactions, grey represent negative interactions, and yellow represent density dependence. Strength of color corresponds to the α level (darkest corresponds to α = 0.05 and lightest corresponds to α = 0.15). Dashes indicate species that were not captured in sufficient numbers within the given survey to generate an index of relative abundance, such that an interation with other species could not be observed

Species	SB	BT	SPN	TIG	SN	BN	BH
VIMS LL							
SB	**0.5483**	0	*–0.2975*	**0.2641**	0	–	–
BT	0	***–0.3969***	0	0	0	–	–
SPN	0	**–0.5910**	**0.3698**	0	0	–	–
TIG	0	0	0	**0.5303**	0	–	–
SN	0	0	0	0	**0.6225**	–	–
SEFSC LL							
SB	0.8615	0	0	0	0	0	–
BT	0	**–0.0262**	0	0	–0.3494	**1.3009**	–
SPN	0	–0.3598	0.5890	0	0	0	–
TIG	**0.4788**	0	0	**–0.0799**	0	0	–
SN	–0.5562	0	0	0	0.8158	0	–
BN	0	0	0	**–0.4903**	0.0607	0.4452	–
SEAMAP-SA Trawl							
BT	–	**0.3027**	–	–	**1.4873**	0	0
SN	–	0	–	–	0.7648	0	0
BN	–	0	–	–	*0.7104*	**0.2126**	*0.4955*
BH	–	0	–	–	0	0	**0.5160**
GULFSPAN GN							
BT	–	**0.0488**	0	–	0	0	0
SPN	–	0	**0.1737**	–	0	0	0
SN	–	0	0	–	0.8245	0	0
BN	–	0	0	–	0	**0.5112**	0
BH	–	0	0	–	0.1278	0	*–0.3545*

that described abundance patterns within the southeast US Atlantic Ocean only (Fig. 5; for complete results and interpretations, refer to Peterson et al. 2017).

In the LCS and SCS MARSS-1 analyses of broad-scale indices of relative abundance, a diagonal and equal process error covariance matrix was most supported. The resulting ***B*** matrix from the LCS MARSS-1 model suggested density-dependent regulation in sandbar, blacktip, and tiger sharks, but not in spinner sharks (85 % CI: 0.818–1.036; Table 2, Fig. 6). In the Atlantic SCS complex, Atlantic sharpnose and blacknose sharks exhibited density-dependent compensation. Measures of density dependence were not statistically different from 1 for bonnetheads (85 % CI: 0.851–1.035). Within the Gulf of Mexico, density dependence was not observed in Atlantic sharpnose sharks (85 % CI: 0.745–1.094) or blacknose sharks (85 % CI: 0.5–1.119). Nine species interactions were identified within the broad-scale shark complex (Table 2, Fig. 6).

DISCUSSION

Density dependence

The results of the broad-scale analyses supported the existence of density dependence in 5 out of 9 coastal shark populations. Density dependence in elasmobranch populations has been postulated or assumed in the past (e.g. Sminkey & Musick 1995, Carlson & Baremore 2003, Gedamke et al. 2007, 2009, Coutré et al. 2013), and this study provides quantitative evidence that several stocks of southeast US Atlantic Ocean and Gulf of Mexico shark species experience density dependence. It is likely that the remaining 4 populations undergo density dependence at a stock-wide scale, but our underlying data did not permit precise estimation of these parameters. The absence of density dependence within elasmobranch species, which is generally not supported by the available scientific literature, would have substantial implications as population sizes decline. Unlike a species that exhibits density dependence, at small stock sizes, a decrease in abundance would not result in a compensatory increase in population growth rate, thus reducing the ability of depleted populations to recover.

Density dependence is thought to primarily manifest through survival of neonate and young juvenile sharks (Cortés et al. 2012). At the localized scale, sandbar sharks showed density dependence within Virginia coastal waters, likely due to the role of the Chesapeake Bay as an important primary nursery

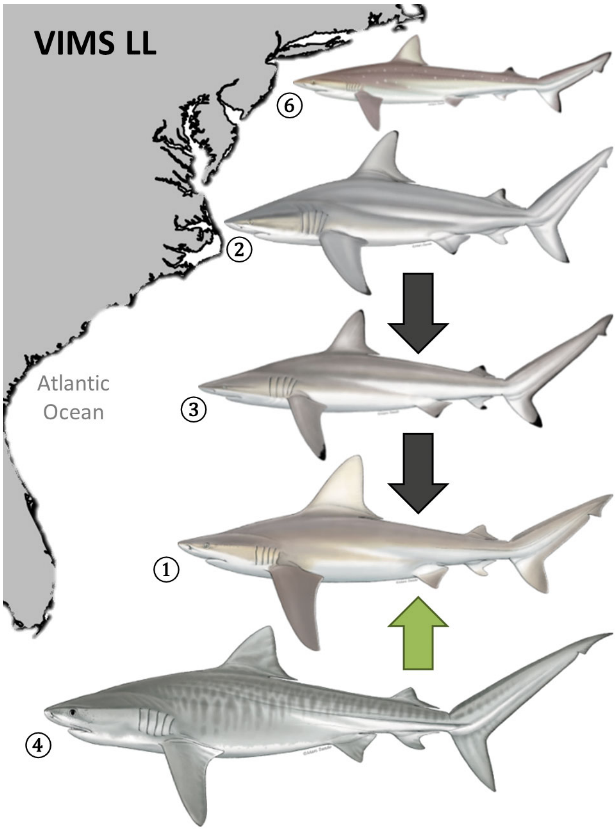

Fig. 1. Hypothesized interactions estimated by the Virginia Institute of Marine Science Longline Survey (VIMS LL) multivariate first-order autoregressive state-space (MARSS-1) modeling. Shark species are numbered as follows: (1) sandbar; (2) blacktip; (3) spinner; (4) tiger; (6) Atlantic sharpnose. All species presented experienced localized density dependence. Black arrows denote negative interactions in the direction of the arrow (i.e. arrows are pointing to the negatively affected species), and green arrow represents positive interactions in the direction of the arrow. Shark specimen illustrations were created and copyrighted by ©Marc Dando

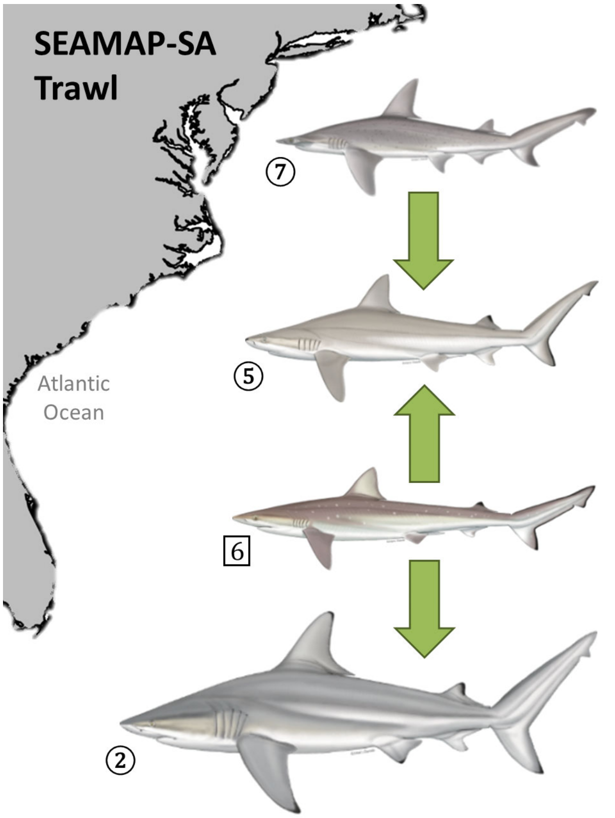

Fig. 2. Hypothesized interactions estimated by the South-East Area Monitoring and Assessment Program–South Atlantic Trawl Survey (SEAMAP-SA Trawl) MARSS-1 modeling. Shark species are numbered as follows: (2) blacktip; (5) blacknose; (6) Atlantic sharpnose; (7) bonnethead. Species represented by circled numbers experienced localized density dependence; boxed number did not. Green arrows represent positive interactions in the direction of the arrow (i.e. arrows are pointing to the positively affected species). Shark specimen illustrations were created and copyrighted by ©Marc Dando

area for this species (Grubbs et al. 2007). Hence, sandbar shark density dependence in this region may be linked to compensatory survival rates of early life stages within nursery habitats.

Juvenile blacktip sharks are known to stray into Virginia waters (Castro 2011). Density dependence was found for blacktip sharks in the VIMS LL survey, which primarily samples juvenile blacktip sharks (73% of blacktips sampled were immature based on median size at maturity from Branstetter 1987 and Carlson et al. 2006). The SEAMAP-SA Trawl samples waters adjacent to known, mixed-species nursery areas off the coast of North Carolina (Thorpe et al. 2004), South Carolina (Abel et al. 2007, Ulrich et al. 2007), and Georgia (Gurshin 2007). Although this survey does not precisely sample within primary nursery areas, predominantly located within protected bays and estuaries along the US Atlantic coast, immature individuals are sampled as they migrate between nurseries. Juvenile carcharhinid species are known to inhabit larger home ranges encompassing waters adjacent to designated nurseries with ontogeny (Heupel & Hueter 2002, McCandless et al. 2005). In the Gulf of Mexico, the GULFSPAN GN surveys a known nursery area (Bethea et al. 2004, 2015), primarily sampling juvenile blacktip sharks (96.2% immature), while the SEFSC LL also samples a high proportion of juvenile individuals (Ingram 2012).

Less is known about spinner shark movement patterns. Throughout the western North Atlantic Ocean, it is assumed that mature individuals remain offshore, with the exception of gravid females who

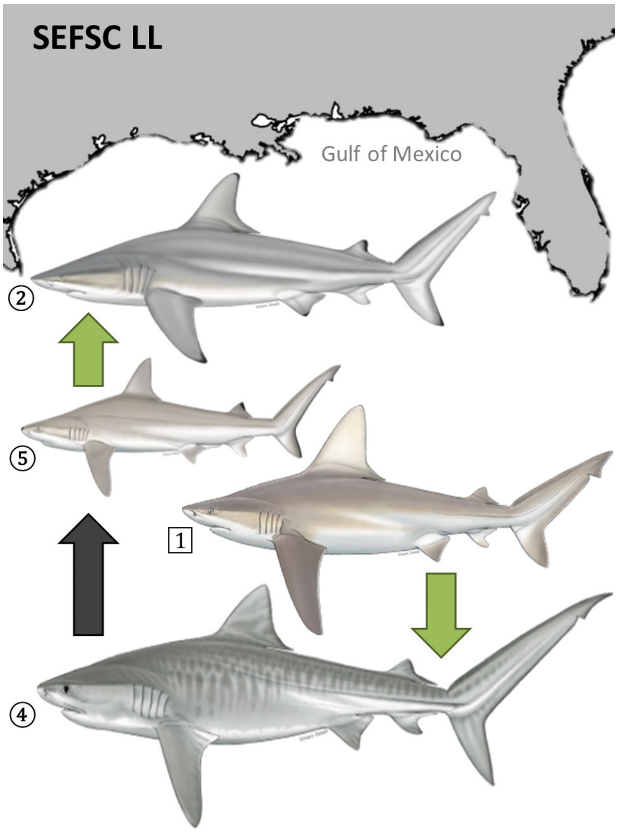

Fig. 3. Hypothesized interactions estimated by the Southeast Fishery Science Center Longline Survey (SEFSC LL) MARSS-1 modeling. Shark species are numbered as follows: (1) sandbar; (2) blacktip; (4) tiger; (5) blacknose. Species represented by circled numbers experienced localized density dependence; boxed number did not. Black arrow denotes negative interactions in the direction of the arrow (i.e. arrow is pointing to the negatively affected species), and green arrows represent positive interactions in the direction of the arrow. Shark specimen illustrations were created and copyrighted by ©Marc Dando

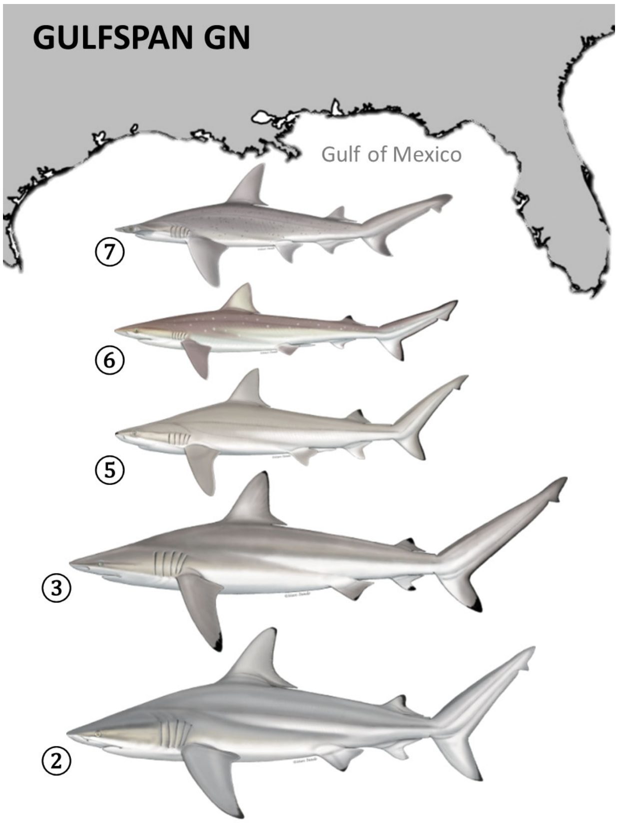

Fig. 4. Hypothesized interactions estimated by the Gulf of Mexico Shark Pupping and Nursery Gillnet Survey (GULFSPAN GN) MARSS-1 modeling. Shark species are numbered as follows: (2) blacktip; (3) spinner; (5) blacknose; (6) Atlantic sharpnose; (7) bonnethead. All species presented experienced localized density dependence. Shark specimen illustrations were created and copyrighted by ©Marc Dando

come inshore to pup (Castro 2011), while adults can be found nearshore in the western Gulf of Mexico (W. B. Driggers III unpubl. data). Based on size at maturity reported by Branstetter (1987), 93.6% of spinner sharks captured in the VIMS LL survey were immature. Similar to the case for blacktip sharks, the GULFSPAN GN survey has only captured 6 adults out of all spinner shark observations included in the present study (n = 903).

Tiger sharks do not use nursery areas (Driggers et al. 2008). Nevertheless, based on sex-specific lengths at maturity (Branstetter et al. 1987), almost all tiger sharks captured in the VIMS LL were immature (98.6%), while the SEFSC LL also samples juvenile tiger sharks (Driggers et al. 2008). Thus, our modeling results suggest that young-of-year and juvenile LCS species are driving localized and broad-scale density-dependent compensatory responses within the southeast US Atlantic coast and the Gulf of Mexico.

Within shallow coastal areas, Atlantic sharpnose sharks are ubiquitous in both the Atlantic (Thorpe et al. 2004, Abel et al. 2007, Gurshin 2007, Ulrich et al. 2007) and Gulf of Mexico (Hueter & Tyminski 2007, Neer et al. 2007, Parsons & Hoffmayer 2007). Although it has been hypothesized that Atlantic sharpnose sharks do not occupy discrete nursery areas (as defined by Heupel et al. 2007), but rather seasonally occupy shallow interconnected bays and inlets along a vast range of coastline (Heupel et al. 2007), they exhibited density dependence within coastal Virginia waters and in a nursery off the Gulf coast of Florida. While immature blacknose sharks are also known to use waters along the southeast US Atlantic coast (Ulrich et al. 2007) and within the Gulf of Mex-

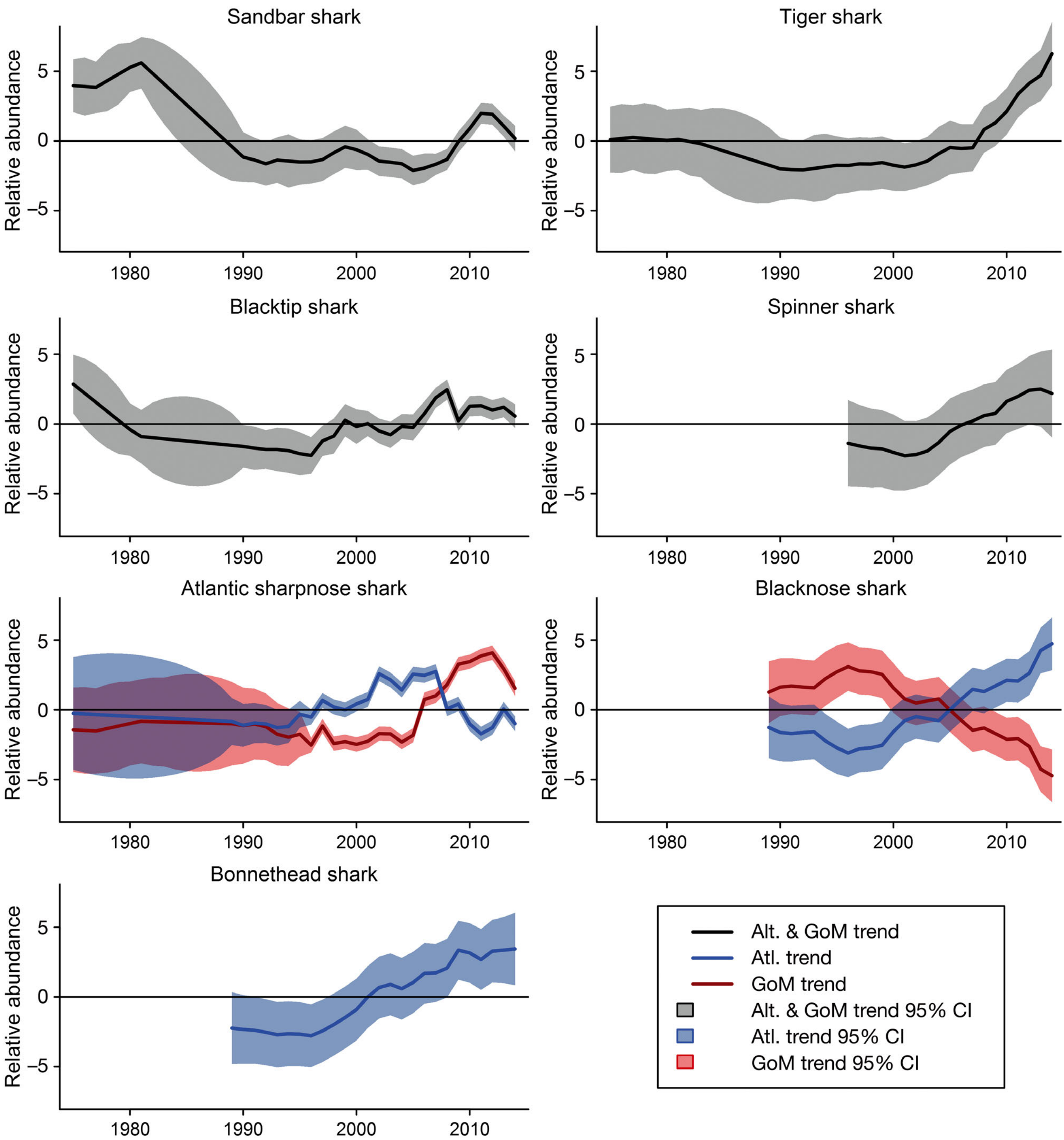

Fig. 5. Common trends produced from dynamic factor analysis (DFA) using delta-lognormally derived indices of relative abundance for the coastal shark complex that were input into the broad-scale MARSS-1 model. Trends (solid lines) are shown with corresponding 95% confidence intervals (shaded regions). Black trends are indicative of abundance throughout the southeast US Atlantic coast (Atl.) and the Gulf of Mexico (GoM), while blue and red trends uniquely represent abundance patterns in the Atl. and GoM, respectively (see Peterson et al. 2017)

ico (Hueter & Tyminski 2007, Bethea et al. 2015), mature individuals occupy similar shallow-water habitats (Ulrich et al. 2007). For example, although the SEFSC LL primarily captures mature blacknose sharks (W. B. Driggers III unpubl. data), density dependence was noted within this survey. Bonnetheads, another ubiquitous SCS species along the southeast US Atlantic coast (Ulrich et al. 2007) and within the Gulf of Mexico (Hueter & Tyminski 2007, Bethea et al. 2015), showed localized density de-

Table 2. Species interaction (***B***) matrix results from multivariate first-order autoregressive state-space (MARSS-1) models conducted on the dynamic factor analysis (DFA) common trends for all species. Interpretation of the matrix, color coding, and species abbreviations follow those presented Table 1, with the addition of population designators, where Atl.: southeast US Atlantic coast, GOM: Gulf of Mexico

Species	SB	BT	SPN	TIG	GOM SN	Atl. SN	GOM BN	Atl. BN	Atl. BH
SB	**0.7847**	0	0	**0.1895**	0	0	0	0	0
BT	0	*0.6488*	0.2616	0	0	0	0	0	0
SPN	0	0	0.9273	0	0	0	0	0	0
TIG	0	0	*0.7468*	**0.4011**	0	0	0	0	0
GOM SN	0	*0.1388*	0	0	0.9194	0	0	0	0
Atl. SN	−0.1817	0	0	0	0	0.0824	0	0	0.0532
GOM BN	0	0	0	0	*−0.4346*	0	0.809	0	0
Atl. BN	0	*0.5921*	**−0.5450**	0	0	0	0	*0.2448*	*0.6360*
Atl. BH	*−0.1598*	0	0	0	0	0	0	0	0.9434

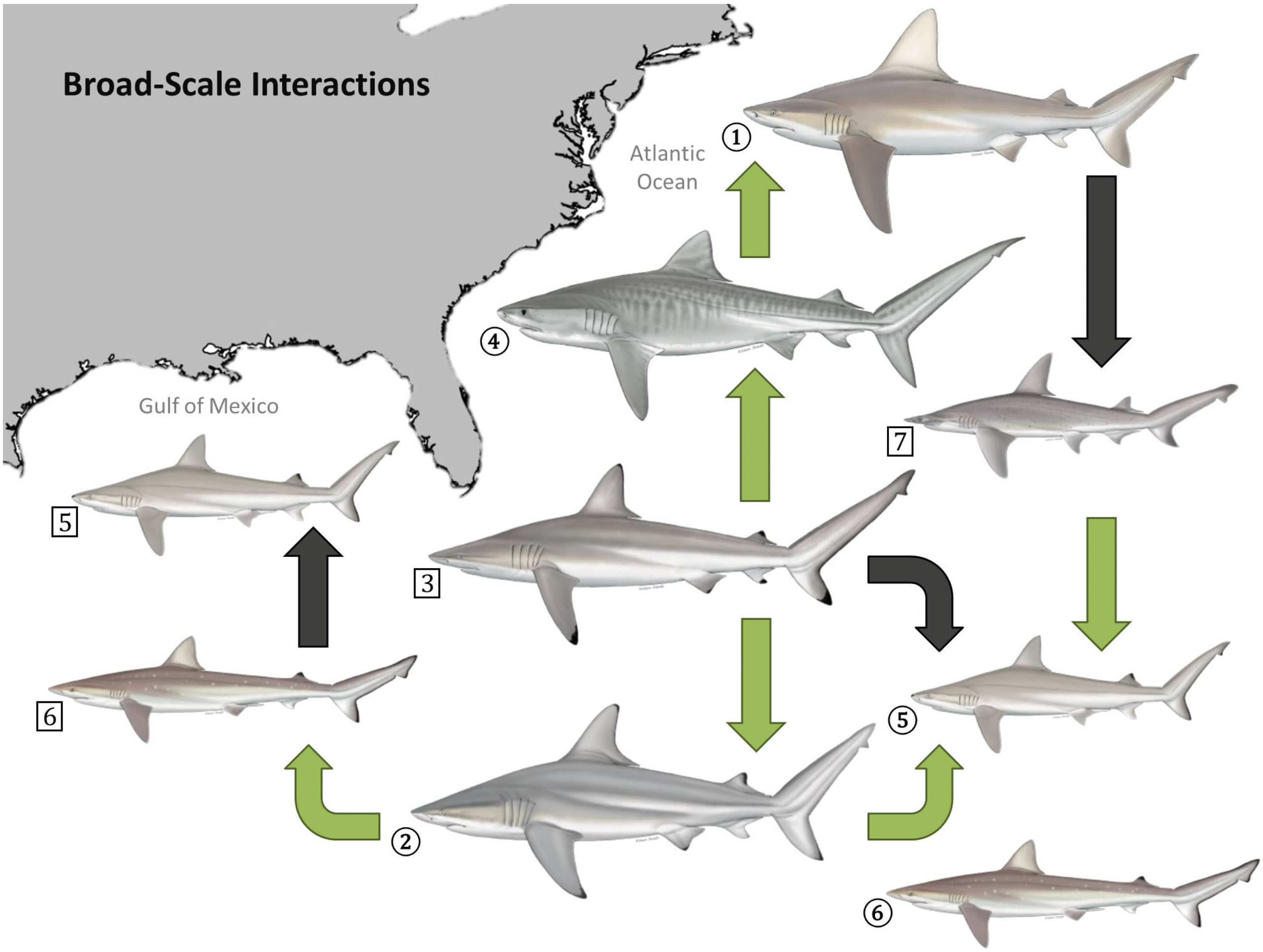

Fig. 6. Hypothesized interactions estimated by the broad-scale MARSS-1 modeling. Shark species are numbered as follows: (1) sandbar; (2) blacktip; (3) spinner; (4) tiger; (5) blacknose; (6) Atlantic sharpnose; (7) bonnethead. Black arrows denote negative interactions in the direction of the arrow (i.e. arrows are pointing to the negatively affected species), and green arrows represent positive interactions in the direction of the arrow. Species represented by circled numbers experienced broad-scale density dependence; boxed numbered species did not. Shark specimen illustrations were created and copyrighted by ©Marc Dando

pendence. While it is possible that immature individuals are driving these density-dependent trends for SCS species, an alternative life history strategy as compared to LCS species, in which juvenile and adult individuals of each species spend a substantial portion of time in nearshore areas (Hueter & Tyminski 2007, Ulrich et al. 2007, Bethea et al. 2015), may be driving density-dependent responses across distinct life stages.

Overall, these results support the prominent hypothesis that the primary mechanism of density dependence in these coastal shark species is through neonate and juvenile survival (Cortés et al. 2012), when these immature individuals reside within nursery grounds. This study highlights the importance of shark nursery areas in facilitating protected growth to maturity in coastal sharks (Heupel & Hueter 2002), particularly for LCS species. While Heithaus et al. (2007) suggested that areas where density-dependent selection occurs should be deemed critical habitat, Kinney & Simpfendorfer (2009) proposed that the importance of shark nursery areas has been overstated, citing several matrix-based demographic modeling studies (e.g. Brewster-Geisz & Miller 2000), which used sensitivity analyses to show that juvenile survival had much greater impacts on population size than first-year survival. However, basic Leslie matrix models that have been applied to shark species have not been structured to incorporate nonlinear functions for age- or stage-specific density dependence (Cortés 1998), thus precluding objective evaluation of this phenomenon. Additionally, several species exhibit natal homing, using nursery areas well into the juvenile life stage (e.g. Heupel et al. 2007, Hueter & Tyminski 2007, Castro 2011). If these areas are compromised through anthropogenic degradation, reduced resource availability could limit operative carrying capacity, effectively restricting the number of neonates that survive to maturity. We argue that it is important to continue to focus scientific attention on establishing shark nursery areas as essential fish habitat (NMFS 1999) to allow overexploited coastal shark populations to rebound, in conjunction with protecting other life stages (Kinney & Simpfendorfer 2009).

Broad-scale interspecies interactions

We considered interactions identified in the MARSS-1 analyses and the potential underlying mechanisms presented to be hypotheses that require empirical experimentation for validation. Broad-scale analyses revealed 9 statistically significant interactions that affect inter-specific population growth rates (Fig. 6). Juvenile diet and habitat overlap was observed between blacktip sharks and spinner sharks within a Gulf of Mexico nursery area (Bethea et al. 2004, 2015), while larger size classes (sub-adults and adults) have been known to co-school (Aubrey & Snelson 2007). Data from the VIMS LL indicated that when present, blacktip sharks and spinner sharks co-occurred in 35% of longline sets (C. D. Peterson unpubl. data), which suggests co-schooling behavior in the mid-Atlantic region. Our analyses demonstrated that the presence of spinner sharks had a positive effect on blacktip sharks, with values that approached statistical significance (85% CI did not overlap 0), indicating that co-schooling was beneficial for blacktip sharks.

Simultaneously, spinner sharks had a positive effect on the population growth rate of tiger sharks, which are known to feed on blacktip sharks and other medium-sized elasmobranchs (Bell & Nichols 1921, Lowe et al. 1996). This relationship may result from tiger shark predation on spinner sharks, or may represent an indirect effect in which spinner sharks increase the population growth rate of blacktip sharks, thereby increasing the number of blacktip sharks available as prey for tiger sharks. Similar indirect results have been observed using multivariate first-order autoregressive (MAR-1) modeling, in which secondary interactions were identified while primary interactions were repressed within the $\boldsymbol{B}$ matrix (Hampton et al. 2006). Additionally, effects of changing predator abundance may result in indirect effects on tertiary species, without displaying population level effects on mesoconsumers, particularly those that experience density dependence (Heithaus et al. 2010), like blacktip sharks in the present study. Furthermore, due to shared diagnostic characters and overlap in early taxonomic keys (Branstetter 1982), the potential for misidentification of spinner sharks and blacktip sharks suggests that interactions involving these species should be interpreted with care.

Increased population growth rate of sandbar sharks was observed in the presence of tiger sharks. Predatory interactions of tiger sharks on sandbar sharks have been previously reported off the Hawaiian Islands (Papastamatiou et al. 2006), and anecdotal observations of tiger sharks secondarily captured on hooks on which juvenile sandbar sharks were primarily captured have been reported on the VIMS LL and SEFSC LL surveys. A predatory release interaction is unlikely, due to the large sizes and generally high trophic position of sandbar sharks (Cortés 1999). However, if tiger sharks prey on juvenile and neonate sandbar sharks within their nursery grounds, this predatory interaction likely stimulated the population growth rate of density-dependent sandbar sharks (i.e. assuming all else remains constant, lower abundance of juvenile sandbar sharks results in a density-dependent compensatory response, likely facilitating increased population growth rate). Additional mechanisms underlying this interaction may be linked to annual environmental conditions, such as those driven by decadal oscillations that likely dictate regional organization (Peterson et al. 2017), resulting in correlated catches of tiger sharks and sandbar sharks.

A predatory interaction of sandbar sharks on bonnetheads within the southeast US Atlantic Ocean was identified, while spinner sharks had a negative effect on blacknose sharks. Sandbar sharks feed on various small and medium-sized elasmobranchs (Ellis & Musick 2007, Castro 2011) and follow shrimp trawlers to exploit bycatch within the Atlantic Ocean and the Gulf of Mexico (Carlson 1999, Castro 2011). Bonnetheads are commonly captured as bycatch within the shrimp fishery (SEDAR 2011, 2013, Scott-Denton et al. 2012), providing a mechanism facilitating this interaction. Furthermore, these species' distributions overlap within the Florida Keys (Heithaus et al. 2007), Gulf of Mexico (Hueter & Tyminski 2007, Parsons & Hoffmayer 2007, Bethea et al. 2015), and off the coast of South Carolina (Abel et al. 2007, Ulrich et al. 2007). Antipredatory behaviors of bonnetheads and blacknose sharks may occur in response to LCS species, in which prey species will forego optimal environmental conditions to avoid direct predation that may be playing an indirect role in the reduced population growth rate of bonnetheads and blacknose sharks (Heithaus et al. 2008, 2010). These antipredatory behaviors, typically displayed by long-lived species, have the ability to reduce effective carrying capacity of a species and are interrelated to direct predatory effects that magnify the negative effects of predators on prey species (Heithaus 2007, Heithaus et al. 2010).

The presence of blacktip sharks was found to have a positive effect on blacknose sharks within the southeast US Atlantic Ocean. Similarly, in the Gulf of Mexico, blacktip sharks had a positive effect on the population growth rate of the Atlantic sharpnose sharks. Blacknose, Atlantic sharpnose, and blacktip sharks consume small teleost species, such as clupeids (Hoffmayer & Parsons 2003, Bethea et al. 2004, Gurshin 2007, Barry et al. 2008, Castro 2011), and habitat overlap has been noted along the southeast US Atlantic coast (Ulrich et al. 2007), Florida Keys (Heithaus et al. 2007), and the Gulf of Mexico (Hoffmayer & Parsons 2003, Gurshin 2007, Hueter & Tyminski 2007, Parsons & Hoffmayer 2007, Bethea et al. 2015). It is likely that when local environmental conditions are favorable for population growth rate of one species, sympatric species may exhibit similar responses.

Within the Gulf of Mexico, the presence of Atlantic sharpnose sharks had a negative effect on blacknose sharks, suggestive of a competitive interaction. This hypothesis can be further demonstrated by considering that Atlantic sharpnose and blacknose sharks are known to feed on crustaceans as well as menhaden (*Brevoortia* spp.) and other small teleosts (Bethea et al. 2004, 2006, Castro 2011), inhabit similar ranges within the Gulf of Mexico (Bethea et al. 2004, 2015, Hueter & Tyminski 2007, Parsons & Hoffmayer 2007), and exhibit similar early life history characteristics (i.e. size at birth, growth rate, etc.). Niche overlap between these SCS species likely results in frequent interspecific competition for food and space resources.

Lastly, broad-scale MARSS-1 analyses identified a positive effect of bonnetheads on the population growth rate of blacknose sharks within the Atlantic Ocean. While this interaction could be the effect of both species benefiting from mutually favorable environmental conditions, it could also be due to an indirect predatory release mechanism. For example, within the Atlantic Ocean, bonnetheads almost exclusively feed on crabs and other benthic invertebrates (Gurshin 2007), while blacknose sharks consume several teleost species that feed on crabs (e.g. sciaenids; Ford 2012). When bonnetheads are abundant, they consume more crabs, such that other predators of the same crab species (e.g. sciaenids) are forced to spend more time foraging, making them susceptible to predation by predators, such as blacknose sharks (Preisser et al. 2005). Unfortunately, due to data limitations, we did not have a representative trend of bonnethead abundance from the Gulf of Mexico and as such were unable to assess species interactions of the Gulf of Mexico stock.

Localized interspecies interactions

While some interactions were preserved at the localized scale (e.g. positive effect of tiger sharks on sandbar sharks), not all broad-scale community interactions were maintained. However, some localized interactions may help to elucidate the mechanisms underlying the broad-scale results. For example, several positive interactions were identified from SEAMAP-SA Trawl survey data. As identified in the broad-scale analyses, bonnetheads showed a positive effect on blacknose sharks. Similarly, Atlantic sharpnose sharks had a positive effect on the population growth rate of both blacktip and blacknose sharks, while these interactions were reversed in the broad-scale $\boldsymbol{B}$ matrix. Although these interactions could derive from ecological origins, positive relationships noted within the SEAMAP-SA Trawl ***B*** matrix were likely exaggerated by anthropogenic factors. Mandatory commercial bycatch reduction device implementation was established off the southeast US Atlantic coast in 1997 (Scott-Denton et al. 2012), after which indices of relative abundance derived from the SEAMAP-SA Trawl denoted synchronous increases in abundance for blacktip, Atlantic sharpnose, and blacknose sharks. Consequently, management measures may have confounded any biological interactions that exist within the SEAMAP-SA Trawl survey area, so interspecific interactions should be interpreted with care. The broad-scale interactions that agree with the SEAMAP-SA Trawl-specific MARSS-1 results may likewise be misperceived.

The significantly negative effect of spinner sharks on sandbar sharks inferred from the VIMS LL ***B*** matrix may be indicative of a local competitive interaction. Although the diet of spinner sharks has not been extensively examined, evidence suggests the mutual consumption of clupeids (e.g. menhaden *Brevoortia* spp.) by juvenile spinner sharks in the Gulf of Mexico and sandbar sharks off the Atlantic coast (Bethea et al. 2004, McElroy 2009). Thus, interspecific interactions in the southeast US Atlantic Ocean may be facilitated by competition for overlapping prey resources among species (Abel et al. 2007). The negative effect of blacktip sharks on spinner sharks in coastal Virginia waters may indicate that, although blacktip shark populations benefit from co-schooling with spinner sharks (as noted in the broad-scale analysis), this co-schooling may be detrimental to the population growth rate of spinner sharks via resource competition.

Within the Gulf of Mexico, the positive effect of blacknose sharks on blacktip sharks reinforces the hypothesis that these 2 species share prey resources and annual catches are correlated due to annual patterns in distribution or availability to sampling gear. Additionally, the negative effect of tiger sharks on blacknose sharks suggests a predatory interaction following the preference of tiger sharks for consuming elasmobranch prey species, including blacknose sharks (Bell & Nichols 1921).

MARSS-1 modeling

Graphical analyses suggested that overall model fits were appropriate in the present study (see Figs. S4–S8 in Supplement 2), and models appeared to produce realistic characterizations of local and broad-scale shark community interactions. Similarly, the MAR-1 model framework matches empirical estimation of community interactions within planktonic freshwater lake communities (Hampton & Schindler 2006, Hampton et al. 2006), and provides simple approximations to complex, nonlinear processes (Ives et al. 2003). MAR-1 modeling results are robust to the foundational assumption of a Gompertz versus Ricker population growth structure (Mac Nally et al. 2010). Hence, several MAR-1 studies have been conducted on various freshwater and marine ecosystems (Hampton & Schindler 2006, Hampton et al. 2008, 2013, Grossman & Sabo 2010, Mac Nally et al. 2010, Francis et al. 2012, Britten et al. 2014).

Implementation of these models in a state-space framework (MARSS-1) provides additional flexibility in data structure and accounts for both observation and process error. While Ives et al. (2003) found that exclusion of observation error does not tremendously alter the interpretation of model results, particularly when it comes to relative stability, Hampton et al. (2013) noted that the state-space framework may be more essential in marine communities due to the open nature of these systems compared to enclosed freshwater lakes. The expectation-maximization fitting algorithm employed in our MARSS-1 analyses (Holmes et al. 2014) can accommodate missing data without prior linear interpolation or truncation. A downside to the state-space framework involves prespecifying the ***B*** matrix structure. Incorporating preexisting biological knowledge to specify the elements of the ***B*** matrix is vital, because a different configuration may result in different interpretation of results (Ives et al. 2003, Holmes et al. 2014).

The broad-scale time-series are representative of trends of relative abundance along the southeast US Atlantic coast and the Gulf of Mexico, including various size classes sampled by several gear types (see Peterson et al. 2017 for in-depth discussion concerning merging data from gears with variable selectivity functions). This is beneficial when considering how the whole population of a species will affect that of another species. For example, if species M affects species L only in their shared nursery areas and species N feeds on species L in adulthood, analysis of only 1 life stage of species L would result in incomplete characterizations of interactions impacting the population growth rate of species L. Secondarily, Ulrich et al. (2007) suggested that multiple gear types be used to adequately assess shark assemblages. Bonnetheads, for example, primarily feed on crabs, such that static gear baited with fish is unlikely to effectively sample these individuals (Ulrich et al. 2007). Consequently, by incorporating several sampling techniques, both inshore and offshore, and aggregating life history stages as in the broad-scale analyses, we have been able to describe the broadest and most complete estimates of whole-scale community dynamics possible.

CONCLUSIONS

While some community interactions derived from the broad-scale MARSS-1 analysis are supported in the survey-specific MARSS-1 analyses, many interactions are distinct. This suggests that interactions that can be inferred from localized MARSS-1 analyses cannot be generalized across a broader distribution or entire shark stocks. Thus, whole shark population community analyses that functionally affect species population growth rates can only be obtained given inputs that encompass a broad area, providing merit to the procedure employed in the present study. Nevertheless, implementation of survey-specific analyses was useful for characterizing small-scale, localized interactions, and for assisting interpretation of broad-scale $\boldsymbol{B}$ matrix analyses.

These broad interactions have resulted in insights on a southeast US coastal shark complex that could not be directly observed, including density-dependent responses in all species examined. Interactions identified in the present study corroborate known relationships, while adding to our knowledge of interspecific shark interactions and formulating hypotheses regarding significant species interactions. With continued environmental changes and anthropogenic impacts, these interactions may change over time, necessitating further analyses. Likewise, the results of the present study provided analytically derived hypotheses about shark intra- and interspecies interactions that would greatly benefit from continued field and experimental research to uncover the true mechanisms underlying these responses. As anthropogenic forces continue to alter natural communities, understanding community dynamics and interrelationships can help us predict how these communities will change and how to manage them accordingly (Morin 2012).

Acknowledgements. We acknowledge Jeanne Boylan and Marcel Reichert (SCDNR) for providing the SEAMAP-SA Coastal Trawl Survey data and SEAMAP-SA (NOAA Fisheries, Charleston, SC) for providing the funding for this survey. We thank John Carlson (NOAA Fisheries, Panama City, FL) for starting the GULFSPAN GN survey, which is funded by the NOAA NMFS Highly Migratory Species Office. The GA LL data were provided by Carolyn Belcher and were funded through SEAMAP-SA. Bryan Frazier and Erin Levesque provided the SC LL data, which are funded by the Atlantic States Marine Fisheries Commission, SEAMAP-SA, South Carolina Saltwater Recreational Fishing License Funds, and the Federal Assistance for Interjurisdictional Fisheries Program. Recent funding for the VIMS LL was provided by NOAA Fisheries (Silver Spring, MD). We thank Christopher J. Sweetman, Bryan Frazier, and 3 anonymous reviewers for providing thoughtful comments on earlier drafts of this manuscript. Lastly, we acknowledge the many unnamed staff, students, researchers, and volunteers associated with the various surveys for their efforts collecting data and maintaining these valuable sampling programs. This is contribution 3662 of the Virginia Institute of Marine Science.

LITERATURE CITED

Abel DC, Young RF, Garwood JA, Travaline MJ, Yednock BK (2007) Survey of the shark fauna in two South Carolina estuaries and the impact of salinity structure. Am Fish Soc Symp 50:109–124

Au DW, Smith SE (1997) A demographic method with population density compensation for estimating productivity and yield per recruit of the leopard shark (*Triakis semifasciata*). Can J Fish Aquat Sci 54:415–420

Au DW, Smith SE, Show C (2015) New abbreviated calculation for measuring intrinsic rebound potential in exploited fish populations — example for sharks. Can J Fish Aquat Sci 72:767–773

Aubrey CW, Snelson FF Jr (2007) Early life history of the spinner shark in a Florida nursery. Am Fish Soc Symp 50: 175–189

Barry KP, Condrey RE, Driggers WB III, Jones CM (2008) Feeding ecology and growth of neonate and juvenile blacktip sharks *Carcharhinus limbatus* in the Timbalier-Terrebone Bay complex, LA, U.S.A. J Fish Biol 73:650–662

Bell JC, Nichols JT (1921) Notes on the food of Carolina sharks. Copeia 1921:17–20

Bethea DM, Buckel JA, Carlson JK (2004) Foraging ecology of the early life stages of four sympatric shark species. Mar Ecol Prog Ser 268:245–264

Bethea DM, Carlson JK, Buckel JA, Satterwhite M (2006) Ontogenetic and site-related trends in the diet of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* from the northeast Gulf of Mexico. Bull Mar Sci 78:287–307

Bethea DM, Ajemian MJ, Carlson JK, Hoffmayer ER and others (2015) Distribution and community structure of coastal sharks in the northeastern Gulf of Mexico. Environ Biol Fishes 98:1233–1254

Branstetter S (1982) Problems associated with the identification and separation of the spinner shark, *Carcharhinus brevipinna*, and the blacktip shark, *Carcharhinus limbatus*. Copeia 1982:461–465

Branstetter S (1987) Age and growth estimates for blacktip, *Carcharhinus limbatus*, and spinner, *C. brevipinna*, sharks from the northwestern Gulf of Mexico. Copeia 1987:964–974

Branstetter S, Musick JA, Colvocoresses JA (1987) A comparison of the age and growth of the tiger shark, *Galeocerdo cuvieri*, from off Virginia and from the northwestern Gulf of Mexico. Fish Bull 85:269–279

Brewster-Geisz KK, Miller TJ (2000) Management of the sandbar shark, *Carcharhinus plumbeus*: implications of a stage-based model. Fish Bull 98:236–249

Britten GL, Dowd M, Minto C, Ferretti F, Boero F, Lotze HK (2014) Predator decline leads to decreased stability in a coastal fish community. Ecol Lett 17:1518–1525

Carlson JK (1999) Occurrence of neonate and juvenile sandbar sharks, *Carcharhinus plumbeus*, in the northeastern Gulf of Mexico. Fish Bull 97:387–391

Carlson JK (2007) Modeling the role of sharks in the trophic dynamics of Apalachicola Bay, Florida. Am Fish Soc Symp 50:281–300

Carlson JK, Baremore IE (2003) Changes in biological parameters of Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the Gulf of Mexico: evidence for density-dependent growth and maturity? Mar Freshw Res 54: 227–234

Carlson JK, Sulikowski JR, Baremore IE (2006) Do differences in life history exist for blacktip sharks, *Carcharhinus limbatus*, from the United States South Atlantic Bight and Eastern Gulf of Mexico? Environ Biol Fish 77:279–292

Cassoff RM, Campana SE, Myklevoll S (2007) Changes in baseline growth and maturation parameters of Northwest Atlantic porbeagle, *Lamna nasus*, following heavy exploitation. Can J Fish Aquat Sci 64:19–29

Castro JI (1993) The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ Biol Fishes 38: 37–48

Castro JI (2011) The sharks of North America. Oxford University Press, New York, NY

Conrath CL, Musick JA (2008) Investigations into depth and temperature habitat utilization and overwintering grounds of juvenile sandbar sharks, *Carcharhinus plumbeus*: the importance of near shore North Carolina waters. Environ Biol Fishes 82:123–131

Cortés E (1998) Demographic analysis as an aid in shark stock assessment and management. Fish Res 39:199–208

Cortés E (1999) Standardized diet compositions and trophic levels of sharks. ICES J Mar Sci 56:707–717

Cortés E, Brooks EN, Gedamke T (2012) Population dynamics, demography, and stock assessment. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives, 2nd edn. CRC Press, Taylor & Francis Group, Boca Raton, FL, p 453–485

Coutré K, Gedamke T, Rudders DB, Driggers WB III, Koester DM, Sulikowski JA (2013) Indication of density-dependent changes in growth and maturity of the barndoor skate on Georges Bank. Mar Coast Fish 5:260–269

De Oliveira JAA, Ellis JR, Dobby H (2013) Incorporating density dependence in pup production in a stock assessment of NE Atlantic spurdog *Squalus acanthias.* ICES J Mar Sci 70:1341–1353

DeAngelis BM, McCandless CT, Kohler NE, Recksiek CW, Skomal GB (2008) First characterization of shark nursery habitat in the United States Virgin Islands: evidence of habitat partitioning by two shark species. Mar Ecol Prog Ser 358:257–271

Driggers WB III, Ingram GW Jr, Grace MA, Gledhill CT, Henwood TA, Horton CN, Jones CM (2008) Pupping areas and mortality rates of young tiger sharks *Galeocerdo cuvier* in the western North Atlantic Ocean. Aquat Biol 2:161–170

Ellis JK, Musick JA (2007) Ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in lower Chesapeake Bay and Virginia (USA) coastal waters. Environ Biol Fishes 80:51–67

Ford RM (2012) Diet and reproductive biology of the blacknose shark (*Carcharhinus acronotus*) from the southwestern Atlantic Ocean. MSc thesis, University of North Florida, Jacksonville, FL

Francis TB, Scheuerell MD, Brodeur RD, Levin PS, Ruzicka JJ, Tolimieri N, Peterson WT (2012) Climate shifts the interaction web of a marine plankton community. Glob Change Biol 18:2498–2508

Gedamke T, Hoenig JM, Musick JA, DuPaul WD (2007) Using demographic models to determine intrinsic rate of increase and sustainable fishing for elasmobranchs: pitfalls, advances, and applications. N Am J Fish Manag 27: 605–618

Gedamke T, Hoenig JM, DuPaul WD, Musick JA (2009) Stock-recruitment dynamics and the maximum population growth rate of the barndoor skate on Georges Bank. N Am J Fish Manag 29:512–526

Grossman GD, Sabo JL (2010) Incorporating environmental variation into models of community stability: examples from stream fish. Am Fish Soc Symp 73:1–20

Grubbs RD (2010) Ontogenetic shifts in movements and habitat use. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives II: biodiversity, adaptive physiology, and conservation. CRC Press, Taylor & Francis Group, Boca Raton, FL, p 319–350

Grubbs RD, Musick JA, Conrath CL, Romine JG (2007) Long-term movements, migration, and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. Am Fish Soc Symp 50:87–107

Grubbs RD, Carlson JK, Romine JG, Curtis TH and others (2016) Critical assessment and ramifications of a purported marine trophic cascade. Sci Rep 6:20970

Gruber SH, de Marignac JRC, Hoenig JM (2001) Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark-depletion experiments. Trans Am Fish Soc 130: 376–384

Gurshin CWD (2007) Shark nursery grounds in Sapelo Island National Research Reserve, Georgia. Am Fish Soc Symp 50:141–151

Hampton SE, Schindler DE (2006) Empirical evaluation of observation scale effects in community time series. Oikos 113:424–439

Hampton SE, Scheuerell MD, Schindler DE (2006) Coalescence in the Lake Washington story: interaction strengths in a planktonic food web. Limnol Oceanogr 51: 2042–2051

Hampton SE, Izmest'eva LR, Moore MV, Katz SL, Dennis B, Silow EA (2008) Sixty years of environmental change in the world's largest freshwater lake — Lake Baikal, Siberia. Glob Change Biol 14:1947–1958

Hampton SE, Holmes EE, Scheef LP, Scheuerell MD, Katz SL, Pendleton DE, Ward EJ (2013) Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. Ecology 94: 2663–2669

Heithaus MR (2007) Nursery areas as essential shark habitats: a theoretical perspective. Am Fish Soc Symp 50:3–13

Heithaus MR, Burkholder D, Hueter RE, Heithaus LI, Pratt HL Jr, Carrier JC (2007) Spatial and temporal variation in shark communities of the lower Florida Keys and evidence for historical population declines. Can J Fish Aquat Sci 64:1302–1313

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23:202–210

Heithaus MR, Frid A, Vaudo JJ, Worm B, Wirsing AJ (2010) Unraveling the ecological importance of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives II: biodiversity, adaptive physiology, and conservation. CRC Press, Taylor & Francis Group, Boca Raton, FL, p 611–637

Heupel MR, Hueter RE (2002) Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. Mar Freshw Res 53:543–550

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287–297

Heupel MR, Knip DM, Simpfendorfer CA, Dulvy NK (2014) Sizing up the ecological role of sharks as predators. Mar Ecol Prog Ser 495:291–298

Hoenig JM, Gruber SH (1990) Life-history patterns in the elasmobranchs: implications for fisheries management. In: Pratt HL Jr, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. Tech Rep 90. NOAA, Honolulu, HI, p 1–16

Hoffmayer ER, Parsons GR (2003) Food habits of three shark species from the Mississippi Sound in the northern Gulf of Mexico. Southeast Nat 2:271–280

Holmes EE, Ward EJ, Willis K (2013) MARSS: multivariate autoregressive state-space modeling. R package version 3.9. https://cran.r-project.org/web/packages/MARSS/MARSS.pdf

Holmes EE, Ward EJ, Scheuerell MD (2014) Analysis of multivariate time-series using the MARSS package version 3.0. NOAA Fisheries, Northwest Fisheries Science Center, Seattle, WA

Hueter RE, Tyminski JP (2007) Species-specific distribution and habitat characteristics of shark nurseries in Gulf of Mexico waters off peninsular Florida and Texas. Am Fish Soc Symp 50:193–223

Ingram W (2012) Indices of blacktip shark based on NMFS bottom longline surveys (1995 2011). SEDAR29-WP-03. SEDAR, North Charleston, SC

Ives AR, Dennis B, Cottingham KL, Carpenter SR (2003) Estimating community stability and ecological interactions from time-series data. Ecol Monogr 73:301–330

Kinney MJ, Simpfendorfer CA (2009) Reassessing the value of nursery areas to shark conservation and management. Conserv Lett 2:53–60

Kinney MJ, Hussey NE, Fisk AT, Tobin AJ, Simpfendorfer CA (2011) Communal or competitive? Stable isotope analysis provides evidence of resource partitioning within a communal shark nursery. Mar Ecol Prog Ser 439:263–276

Lo NCH, Jacobson LD, Squire JL (1992) Indices of relative abundance from fish spotter data based on delta-lognormal models. Can J Fish Aquat Sci 49:2515–2526

Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environ Biol Fishes 47:203–211

Mac Nally R, Thompson JR, Kimmerer WJ, Feyrer F and others (2010) Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). Ecol Appl 20:1417–1430

Márquez-Farias JF, Castillo-Geniz JL (1998) Fishery biology and demography of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, in the southern Gulf of Mexico. Fish Res 39:183–198

McCandless CT, Pratt HL Jr, Kohler NE, Merson RR, Recksiek CW (2005) Distribution, localized abundance, movements, and migrations of juvenile sandbar sharks tagged in Delaware Bay. Am Fish Soc Symp 50:45–62

McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman & Hall, London

McElroy WD (2009) Diet, feeding ecology, trophic relationships, morphometric condition, and ontogeny for the sandbar shark, *Carcharhinus plumbeus*, and smooth dogfish *Mustelus canis*, within the Delaware Bay estuary. PhD dissertation, University of Rhode Island, Kingston, RI

McElroy WD, Wetherbee BM, Mostello CS, Lowe CG, Crow GL, Wass RC (2006) Food habits and ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in Hawaii. Environ Biol Fishes 76:81–92

Morin PJ (2012) Community ecology, 2nd edn. Wiley-Blackwell, Chichester

Musick JA, Burgess G, Cailliet G, Camhi M, Fordham S (2000) Management of sharks and their relatives (Elasmobranchii). Fisheries 25:9–13

National Marine Fisheries Service (1999) Final fishery management plan for Atlantic tuna, swordfish, and sharks. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Sustainable Fisheries, Highly Migratory Species Management Division, Silver Spring, MD

Neer JA, Blackburn JK, Thompson BA (2007) Shark nursery areas of central Louisiana's nearshore coastal waters. Am Fish Soc Symp 50:317–330

Papastamatiou YP, Wetherbee BM, Lowe CG, Crow GL (2006) Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. Mar Ecol Prog Ser 320:239–251

Parsons GR, Hoffmayer ER (2005) Changes in the distribution and relative abundance of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the north central Gulf of Mexico. Copeia 2005:914–920

Parsons GR, Hoffmayer ER (2007) Identification and characterization of shark nursery grounds along the Mississippi and Alabama gulf coasts. Am Fish Soc Symp 50:301–316

Peterson CP, Belcher CN, Bethea DM, Driggers WB III, Frazier BS, Latour RJ (2017) Preliminary recovery of coastal sharks in the south-east United States. Fish Fish 18: 845–859

Platell ME, Potter IC, Clarke KR (1998) Resource partitioning by four species of elasmobranchs (Batoidea: Urolophidae) in coastal waters of temperate Australia. Mar Biol 131:719–734

Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86:501–509

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Scheffer M, Carpenter S, de Young B (2005) Cascading effects of overfishing marine ecosystems. Trends Ecol Evol 20:579–581

Scott-Denton E, Cryer PF, Duffy MR, Gocke JP and others (2012) Characterization of the U.S. Gulf of Mexico and South Atlantic penaeid and rock shrimp fisheries based on observer data. Mar Fish Rev 74:1–27

SEDAR (2011) SEDAR 21 Highly migratory species: sandbar shark, dusky shark, and blacknose shark stock assessment report. SEDAR, North Charleston, SC. http://sedarweb.org/sedar-21

SEDAR (2013) SEDAR 34 Highly migratory species: Atlantic sharpnose shark and bonnethead shark. SEDAR, North Charleston, SC. http://sedarweb.org/sedar-34

Shaw AL, Frazier BS, Kucklick JR, Sancho G (2016) Trophic ecology of a predatory community in a shallow-water, high-salinity estuary assessed by stable isotope analysis. Mar Coast Fish 8:46–61

Simpfendorfer CA, Goodreid AB, McAuley RB (2001) Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. Environ Biol Fishes 61:37–46

Sminkey TR, Musick JA (1995) Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. Copeia 1995:871–883

Sosebee KA (2005) Are density-dependent effects on elasmobranch maturity possible? J Northwest Atl Fish Sci 35: 115–124

Springer S (1967) Social organization of shark populations. In: Gilbert PW, Mathewson RF, Rall DP (eds) Sharks, skates and rays. John Hopkins Press, Baltimore, MD, p 149–174

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci 57:476–494

Taylor IG, Gallucci VF (2009) Unconfounding the effects of climate and density dependence using 60 years of data on spiny dogfish (*Squalus acanthias*). Can J Fish Aquat Sci 66:351–366

Thorpe T, Jensen CF, Moser ML (2004) Relative abundance and reproductive characteristics of sharks in southeastern North Carolina coastal waters. Bull Mar Sci 74:3–20

Ulrich GF, Jones CM, Driggers WB III, Drymon JM, Oakley D, Riley C (2007) Habitat utilization, relative abundance, and seasonality of sharks in the estuarine and nearshore waters of South Carolina. Am Fish Soc Symp 50:125–139

van der Elst RP (1979) A proliferation of small sharks in the shore-based Natal sport fishery. Environ Biol Fishes 4: 349–362

White WT, Potter IC (2004) Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. Mar Biol 145:1023–1032

Editorial responsibility: Alistair Hobday,
Hobart, Tasmania, Australia

Submitted: February 27, 2017; Accepted: July 28, 2017
Proofs received from author(s): September 5, 2017