# PATTERNS OF ABUNDANCE AND COMMUNITY DYNAMICS IN ATLANTIC COASTAL SHARKS

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# Preface

Chapter 1 will be submitted for publication in *Fish and Fisheries*, and Chapter 2 will be submitted for publication in *Marine Ecology Progress Series*. Both chapters are formatted under the respective guidelines of each journal.

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# Abstract

Broad scale analyses of shark population and community dynamics are particularly challenging given the complex life history strategies employed and their vast migratory patterns. Consequently, studies are generally limited to analyzing small-scale, localized dynamics that can be examined from easily accessible, nearshore environments. In particular, fishery-independent shark surveys are frequently limited by spatial political boundaries, such that they only sample a discrete portion of a migratory coastal shark's distribution. Given the age- and sex-structured movements of these species, a localized survey is likely unable to represent stock-wide changes in abundance, such that several small ranging surveys are treated as independent measures of abundance. Survey-based trends in abundance frequently display data conflict, likely due to high levels of uncertainty and variable timing in migrations. Similarly, sharks within communities interact, with the capacity of one species to alter the population size and growth rate of another species. However, these interactions have never been assessed at a wide geographic scale. In the current thesis, I used generalized linear models (GLMs) to estimate annual indices of abundance from eight species of Atlantic coastal sharks from six fishery-independent surveys along the U.S. east coast and within the Gulf of Mexico. These conflicting indices of abundance were input into a dynamic factor analysis (DFA) model with large-scale climatic indices and anthropogenic forces as covariates to produce simplified species-specific trends of abundance for each species throughout the sampled distribution. These common trends were then input into a multivariate, first-order autoregressive, state-space (MARSS-1) model to estimate interspecies interactions and density dependence. These broad-scale interactions were compared to localized interactions generated from conducting MARSS-1 analyses on GLM-based indices of abundance calculated from individual surveys. Resulting DFA common trends suggested that large coastal species followed similar patterns of abundance since 1975, where abundance was high at the beginning of the time series, declined into the early 1990s, was depressed for a length of time corresponding to age at maturity, and then showed initial signs of rebounding. The small coastal species showed more regional variability in abundance, likely due to separate Atlantic and Gulf of Mexico stocks for several of these species. Broad-scale community analysis results showed that seven out of ten coastal shark populations exhibited density dependence, and an additional seven interspecies interactions were identified that significantly influence the population growth rate of affected species. The localized, survey-specific MARSS-1 modeling results produced different results, suggesting that small scale results cannot be extrapolated across the entire stock. Nevertheless, results from these survey-specific models greatly assisted interpretation of the large scale results. Overall, by analyzing coastal shark population and community dynamics from a broader perspective, we can interpret broad trends in abundance and account for interactions that were previously unknown. These results may assist in assessment efforts by reducing conflicting information input into stock assessment models, and accounting for community relationships that may affect population growth rate of various species.

# Patterns and Drivers of Abundance in Atlantic Coastal Sharks

# General Introduction

## Shark biology

Sharks are members of the class Chondrichthyes, comprised of all cartilaginous fishes, which appeared during the early Paleozoic (>400 mya). Chondrichthyes are divided into two subclasses: Holocephali (chimaeras) and Elasmobranchii (sharks, skates and rays; Helfman et al. 2009). Modern sharks (Division: Neoselachii) arose 250 mya (Grogan et al. 2012), and displayed calcified vertebral centra, smaller and more flexible fin supports (ceratotrichia), a protrusible upper jaw, a tooth replacement mechanism, and a subterminal mouth, among other morphological traits. The Neoselachians are comprised of two subdivisions, Selachii (sharks) and Batoidea (skates and rays). The Selachians represent a diverse subdivision, comprised of two superorders, nine orders, and 34 families (Helfman et al. 2009).

Sharks have evolved to be apex predators, such that they have few (if any) natural predators. Hence, sharks have a slow metabolism relative to teleost (bony fish) species, grow slowly, have extended longevities, and generally reach large sizes. Consequently, sharks attain sexual maturity at late ages (Helfman et al. 2009). Because of their trophic status, sharks have evolved a life history strategy that is dependent on the absence of predators. For example, sharks allocate substantial maternal investment towards forming relatively large, survivable offspring in exchange for low fecundity.

All Chondrichthyans reproduce internally, and elasmobranchs employ three main reproductive strategies: 1) oviparity involves laying eggs within which embryos develop, 2) ovoviviparity (aplacental viviparity) involves females carrying self-contained, developing embryos within one or each of their two uteruses without any other nutritional assistance, and 3) viviparity is where females carry embryos and give further nutritional assistance to the growing embryos through placental attachment. Although, these broad classifications are complicated by additional reproductive strategies involving additional forms of maternal nourishment, including secretion of intra-uterine milk (histotroph) and supplementary ovulated fertilized or unfertilized follicles (yolk-filled eggs; oophagy). In exchange for the relatively extreme maternal investment, fecundities are low (2-50 pups/litter), and reproductive cycles are long. Within species that give live birth, gestation periods range from 9-24 months, and some species require a one to two year resting period to undergo vitellogenesis (production of yolk) before they can mate and undergo ovulation (Castro 2009; Conrath and Musick 2012). Hence, lifetime reproductive capacity is extremely low for elasmobranchs.

Following parturition, adult females immediately leave pupping grounds to avoid cannibalizing their young, and neonates receive no further maternal investment. Some species with larger birth sizes or fast initial growth rates use broad coastal areas to pup, other species use discrete nursery areas (typically productive estuarine environments) to avoid predation until they reach a sufficient size, after which the risk of predation decreases (Grubbs 2010). Within nursery areas, first year mortality has been predicted to be as high as 90% in a carcharhinid species (Heupel and Simpfendorfer 2002), although it has been proposed that first-year survival changes as a mechanism for density-dependent compensation (Gruber et al. 2001; Cortés et al. 2012).

Sharks are known to make large north-south and inshore-offshore migration in response to temperature changes for the main purposes of prey abundance and reproduction (Grubbs 2010; Castro 2011). Ontogenetic changes in migratory patterns emerge as sharks tend to aggregate based on sex, size, and maturity, such that migrations tend to become larger with increasing size (Grubbs 2010). Some coastal and pelagic species have been known to make trans-oceanic migrations (Kohler et al. 1998).

All elasmobranchs are carnivorous (Helfman et al. 2009), and shark diets have been shown to undergo ontogenetic changes. Furthermore, as diet is dependent on the prey field available, diets generally change over space. Consequently, sharks have the capacity to change trophic level over time and space. Changing diet coupled with the migratory nature of sharks suggests that the role of a shark within a given community is temporary, with the capacity to fluctuate over time and with changing conditions (i.e. prey abundance; Grubbs 2010).

### Shark fisheries

Sharks were considered underutilized until the 1930s, before which few, small artisanal shark fisheries existed within the U.S. In 1938, a shark fishery was prompted by demand for vitamin A found within shark liver (NMFS 1993), located within the Caribbean Sea, off the Florida coast, within the Gulf of Mexico, and off the Pacific coast (Wagner 1966). Synthetic vitamin A production in 1950 coupled with little use for other shark products and overfishing resulted in a largely abandoned fishery (Wagner 1966; NMFS 1993). The subsequent increase in shark populations in the absence of fishing led to complaints that sharks were damaging commercial fishing gear and target fishes, particularly within the trawl fishery, tuna purse seine fishery, Spanish mackerel fishery in Florida, and the shrimp trawl fishery. It was proposed that targeting sharks for harvest would rectify this problem (Wagner 1966).

Again, in the mid-1970s, sharks were deemed an underutilized natural resource as other commercially important stocks were declining, and commercial fishermen were encouraged to target sharks (Musick et al. 1993; ASMFC 2012; SEDAR 2012; McCandless et al. 2014). Increased demand for shark meat, cartilage, and fins drove the expansion of the fishery (NMFS 1993; ASMFC 2008). Notably, foreign demand for shark fins led to the practice of 'finning,' in which fins are removed from the shark after capture, and the carcass is discarded (NMFS 1993). Commercial landings of sharks peaked in 1989 (ASMFC 2008), which led to the development of the first shark fishery management plan (FMP; SEDAR 2012). Sharks are primarily commercially targeted using bottom longlines and gillnets (ASMFC 2012). Furthermore, sharks are frequently captured as bycatch within several other commercial fisheries (i.e. pelagic longlines, Berkeley and Campos 1988; shrimp trawl, SEDAR 2013, etc.).

Recreational shark fishing has historically existed along the US east coast, within the Gulf of Mexico, and Caribbean Sea, when sharks were considered "the poor man's marlin" (ASMFC 2008). After the release of the movie "Jaws" in 1975, public excitement stimulated the development of a directed recreational fishery (Musick et al. 1993; Cortés et al. 2006). Because of the ubiquitous nature of sharks, easy accessibility within nearshore environments facilitated the expansion of the recreational fishery. Currently, shark recreational fishing is dominated by charter vessels (ASMFC 2008).

## Shark population decline

The slow life history strategy employed by sharks results in extremely low intrinsic rates of population increase (Au et al. 2015), which when coupled with the increase of directed commercial and recreational fishing pressure led to drastic population declines into the 1990s. The magnitude of this decline has been contentiously debated within the scientific literature over the last several years. Initially, Musick et al. (1993) noted declines in abundance of 60-80% for four species (sandbar, dusky, sand tiger, and tiger) of sharks caught within the Virginia Institute of Marine Science (VIMS) longline survey since 1974. Within 15 years of the onset of industrial exploitation, Myers and Worm (2003) proposed that all exploited fishes had decreased by 80% before scientific monitoring began. In the northwest Atlantic Ocean, purported declines from 60% (grouped coastal species) up to 90% (hammerhead sharks) from 1986 abundances were estimated from pelagic longline data for several coastal and pelagic shark species (Baum et al. 2003). Furthermore, accounting for the existence of baseline shifts, Baum and Myers (2004) infamously proposed declines of up to 99% of pelagic species from pelagic longline data, despite low sample sizes and statistical insignificance. Consequently, these studies were rebutted by Burgess et al. (2005a), who stated that the conclusions drawn in Baum et al. (2003) and Baum and Myers (2004) were sensationalized, and not founded on accurate or sufficient information. Additional responses followed (Baum et al. 2005; Burgess et al. 2005b).

Results from the University of North Carolina's shark longline survey showed declines of 87% for sandbar sharks, 93% for blacktip sharks, 97% for tiger sharks, 98% for scalloped hammerhead sharks, and 99% or more for dusky, bull, and smooth hammerhead sharks (Myers et al. 2007), despite the limited spatial coverage of the survey (i.e. two fixed stations sampled bi-weekly from April to November; Schwartz et al. 2010). Within the VIMS longline survey, substantial population declines (sandbar shark 82% decline, dusky shark 96% decline, sand tiger shark 99.8% decline, tiger shark 97.5% decline relative to 1974 values) were inferred from declining catch-per-unit-effort (CPUE) data, despite changes in operational procedures (i.e. soak time, bait type, etc.; Ha 2005). Baum and Blanchard (2010) suggested declines of 76% in hammerhead and large coastal species from pelagic longline commercial fishery data. Contrarily, by 2009, the abundance of four coastal shark species (spinner, bull, lemon, tiger) showed signs of increase (14%, 12%, 6%, 3%, respectively) within the commercial bottom longline fishery, indicating stability or preliminary recovery (Carlson et al. 2012).

The 2002 LCS stock assessment suggested that while the Gulf of Mexico blacktip shark stocks experienced low levels of depletion from virgin abundance (8-23% decline), the sandbar sharks experienced a much larger decline (64-71% from virgin level; SEDAR 2006). The Atlantic blacktip shark stock likely faced greater declines than the Gulf of Mexico stock, considering the directed shark fishery along the U.S. east coast primarily targeted sandbar and blacktip sharks (SEDAR 2012). By 2009, the sandbar shark was estimated to be at 35% of virgin biomass and depletions had begun approaching zero (SEDAR 2011), while the Gulf of Mexico blacktip shark stock was estimated to be at 85-90% of virgin biomass in 2010 (SEDAR 2012).

While SCS species underwent declines of generally smaller magnitudes, due to their life history strategy, they have a higher capacity to recover (Au et al. 2015). In 2006, the SCS complex was estimated to have declined by 15% of virgin abundance (finetooth declined by 10%, blacknose declined by 17%, Atlantic sharpnose declined by 35-40%, and bonnethead declined by 35% with respect to virgin levels; SEDAR 2007). However, in 2009, when assessed as separate populations, the blacknose declines were shown to be much greater (Atlantic blacknose stock declined by 80%, and Gulf of Mexico blacknose stock declined by 85% relative to virgin levels; SEDAR 2011). Similarly, the bonnethead abundance was ~30-40% of virgin levels in 2012, while the Atlantic sharpnose abundance increased to 50-55% of virgin abundance (SEDAR 2013).

## Ecological impacts of sharks

The ecological effects of these depletions in apex predator abundance have also been debated contentiously. Several studies postulate that sharks control their food web via top-down regulation, and after shark populations are fished to low levels, mesopredatory release and subsequent trophic cascades result (Myers et al. 2007; Baum and Worm 2009; Ferretti et al. 2010; Burkholder et al. 2013). However, claims that sharks regulate community structure have also been refuted in the scientific literature due to the complexity, duplicity, and diversity of marine food webs (Grubbs et al. 2016).

Contrarily, Heithaus et al. (2008; 2010) stress that trophic cascades are not necessarily manifested in a vertical manner. Risk effects, or indirect effects of sharks (i.e.

antipredator behaviors in which prey species inhabit suboptimal environments to avoid predation; Heupel and Heuter 2002), can have larger impacts on community structure than predatory effects, especially considering the density-dependent compensation experienced by many marine species. These indirect effects can also result in trophic cascades. Impacts of changing predator abundance are likely to result in unexpected or unintuitive consequences due to the complex nature of marine communities. Hence, effects of sharks may not directly impact population growth rates of mesopredators (Heithaus et al. 2008; 2010). In particular, changes in shark abundance are most likely to cause ecosystem effects when: the shark species is preying upon or inducing antipredatory behavior in longer-lived species, the shark species of concern is the primary predator for a limited number of prey species, the shark species preys upon a keystone or high trophic-level species, the shark species alters community structure, the shark species preys on a species during a life history stage where density dependence occurs, or there are no other predators of the same trophic level present in the ecosystem (Heithaus et al. 2010). It has also been proposed that sharks (and other apex predatory species) have a stabilizing effect on their ecosystem (Britten et al. 2014; Heithaus et al. 2010).

## Shark management history

The first U.S. shark (FMP) was established in 1993 by the U.S. Secretary of Commerce as a result of overexploitation leading to declining abundances. Because sufficient information was not available to present species-specific management measures, 39 species of sharks were grouped into three categories for management: large coastal species (LCS), small coastal species (SCS), and pelagic species. The LCS group included sandbar (*Carcharhinus plumbeus*), blacktip (*C. limbatus*), dusky (*C. obscurus*), spinner (*C. brevipinna*), silky (*C. falciformis*), bull (*C. leucas*), bignose (*C. altimus*), tiger (*Galeocerdo cuvier*), sand tiger (*Carcharias taurus*), lemon (*Negaprion brevirostris*), night (*C. signatus*), nurse (*Ginglymostoma cirratum*), great hammerhead (*Sphyrna mokarran*), and scalloped hammerhead (*S. lewini*) sharks. The SCS group consisted of Atlantic sharpnose (*Rhizoprionodon terraenovae*), Caribbean sharpnose (*R. porosus*), bonnethead (*S. tiburo*), blacknose (*C. acronotus*), smalltail (*C. porosus*), finetooth (*C. isodon*), and Atlantic angel (*Squatina dumerili*) sharks. Lastly, the pelagic species group was comprised of shortfin mako (*Isurus oxyrinchus*), longfin mako (*I. paucus*), thresher (*Alopias vulpinus*), bigeye thresher (*A. superciliosus*), oceanic whitetip (*C. longimanus*), porbeagle (*Lamna nasus*), and blue (*Prionace glauca*) sharks. The shark FMP assumed the goals of halting commercial fishery growth, creating recreational bag limits, eliminating finning, and establishing a data collection program within the shark fishery. Evidence of overfishing was noted within the LCS group between 1986 and 1992, as the LCS group is the target of the shark fishery (NMFS 1993), likely due to their large body (and fin) sizes and close proximity to land (Dulvy et al. 2014).

Consequently, a LCS rebuilding plan was initiated that reduced catch by 34% per year in an effort to rebuild the stock by 5% each year to MSY levels, which was projected to be achieved by 1995-1999. These semi-annual quotas closed the fishery once reached. While the SCS and pelagic species groups were not overfished, the pelagic group experienced significant exploitation. A quota, similar to that established for LCS, was implemented for the pelagic species group, and SCS fishing continued unrestricted. Additional management measures included recreational bag limits, a ban on finning, implementation of a data collection and data reporting system (i.e. mandatory logbooks, dock interviews, observer coverage), and permit requirements, among others (NMFS 1993).

Unfortunately, the semi-annual quotas were quickly exceeded, promoting a derby-style fishery. Additional management measures were implemented in 1994 to help alleviate this reaction. A 1994 stock assessment found that recovery of the LCS group would take up to 30 years, and any increase in quota would not allow the group to recover. The SCS and pelagic species groups were also found to have low productivities (NMFS 2003). In 1996, the Magnuson-Stevens Act was reauthorized by congress, which called for all exploited fisheries to be rebuilt and maintained at levels that will produce optimal yield of the fishery, conservation and management measures to be based on the 'best scientific information available,' mandating consideration of socioeconomic impacts, minimization of bycatch and/or bycatch mortality, and identification and protection of essential fish habitat (EFH), among others (NMFS 2003, NMFS 2015). A subsequent assessment in 1996 found that LCS stocks were not rebuilding under the current management scheme, and called for a 50% cut in commercial quota and recreational bag limits, and an additional cut to the SCS quota, effective in 1997. Five shark species were also listed as prohibited. In response to these drastic reductions in quota, the Southern Offshore Fishing Association (SOFA), along with other commercial fishermen and shark dealers, filed a lawsuit against the Secretary of Commerce. In 1998, the court ruled that NOAA fisheries was responsible for conducting a thorough analysis on the economic effects of limiting catch, which was not completed. Nevertheless, 1997 landings quotas were maintained following an economic impact assessment. In 1998, an LCS stock assessment found that the LSC complex would not recover under the 1997 quotas. Consequently and in response to the reauthorization of the Magnuson-Stevens Act, a new FMP was established in 1999 that encompassed all Atlantic highly migratory species (HMS; Atlantic tunas, swordfish, and sharks; NMFS 2003).

The 1999 FMP continued management measures concerning sharks, including increased observer coverage, and continued limited access and reporting, while reducing commercial quotas and recreational bag limits, implementing minimum size requirement for recreational fishers, counted dead discards against the federal quota, implemented ridgeback/non-ridgeback categories within the LCS group (based on the presence/absence of a ridge along the dorsal surface of the body), and created a new deep water/other sharks management unit, which was later eliminated. Species-specific quotas were implemented for porbeagle and blue sharks, and the following sharks became prohibited: whale (*Rhincodon typus*), basking (*Cetorhinus maximus*), sand tiger, bigeye sand tiger (*O. ferox*), white (*Carcharodon carcharias*), dusky, night, bignose, Galapagos (*C. galapagensis*), Caribbean reef (*C. perezii*), narrowtooth (*C. brachyurus*), longfin mako, bigeye thresher, sevengill (*Notorynchus cepedianus*), sixgill (*Hexanchus griseus*), bigeye sixgill (*H. nakamurai*), Caribbean sharpnose, smalltail, and Atlantic angel sharks (NMFS 1999). In response to the 1999 FMP, SOFA, Bluewater Fisherman's Association, and the Recreational Fishing Alliance sued NOAA fisheries over Atlantic coastal shark management, pelagic shark management, and recreational measures, respectively. While the latter two lawsuits were dismissed as the court affirmed NOAA fisheries was acting in accordance with the Magnuson-Stevens Act, SOFA and NOAA fisheries did not reach a settlement until the year 2000, which required peer-review of stock assessments. As the 1998 assessment failed peer-review, 1997 quotas were maintained until an emergency rule was established for the 2002 fishing year. Consequently, in 2002, SCS and LCS shark stock assessments were conducted, which indicated that finetooth sharks were experiencing overfishing, the LCS complex was overfished and overfishing was occurring, and sandbar sharks were experiencing overfishing. This assessment passed peer review, initiating the implementation of Amendment 1 to the 1999 FMP, which set regional quotas, established trimester fishing seasons, adjusted quotas and time/area closures, and updated EFH (NMFS 2003).

In 2006, a new Atlantic HMS FMP was enacted that namely established mandatory workshops for shark fishermen and HMS dealers, considered action to rebuild and eliminate overfishing of finetooth sharks, and contemplated alterations to the previously established time/area closures (NMFS 2006). A series of amendments were added to this 2006 FMP that updated EFH (NMFS 2009), implemented a shark research program, required sharks to be landed with fins naturally attached (NMFS 2007), updated species-specific and group management as new assessments provided the best available data, and developed rebuilding programs as needed (NMFS 2007; 2010; 2013; 2015). Particular management actions with relevance to the current study include introduction of a shark research fishery in 2007, within which special permits are required. Sandbar sharks became prohibited outside of the research fishery (NMFS 2007). Finally, blacknose sharks were removed from the SCS quota such that a rebuilding plan could be implemented (NMFS 2010).

## Current shark status

The 2006 LCS stock assessment determined that species-specific assessments should be conducted, because the various life history and productivity differences of each stock result in nonsensical results when all species are pooled (SEDAR 2006). The most recent finetooth shark assessment, determined that finetooth sharks were not overfished and no overfishing was occurring (SEDAR 2007). Current shark assessments utilize state-space, age-structured production models (SSASPMs; SEDAR 2011; 2012; 2013). The current status of Atlantic blacktip sharks and Gulf of Mexico blacknose sharks are unknown due model fitting problems (SEDAR 2006; 2011; 2012). Most recent assessments indicate that the sandbar shark was overfished but was not experiencing overfishing (SEDAR 2011), the Atlantic blacknose stock was overfished and overfishing was occurring (SEDAR 2011), and the Gulf of Mexico blacktip stock, Atlantic sharpnose, and bonnethead sharks were not overfished or experiencing overfishing (SEDAR 2012; 2013). However, it is worthwhile to note that although the Atlantic blacktip stock status is unknown, blacktip sharks has been one of the two main targets of commercial exploitation along the U.S. east coast (along with sandbar sharks), and has likely undergone more extensive exploitation than in the Gulf of Mexico (SEDAR 2012). Furthermore, the bonnethead shark comprises two genetically distinct stocks in the Atlantic and the Gulf of Mexico, but was most recently assessed as a single stock. The resulting stock status will likely change when assessed as two separate stocks, especially considering the several years of overexploitation noted in the last assessment (SEDAR 2013).

**Study objectives**

Given the complex life history strategy of sharks (i.e. long lifespan, migratory nature, ontogenetic changes in habitat use and species interactions), comprehensive analyses of population-wide analyses are particularly challenging. Thus far, studies have relied on independent and fragmented information. For example, because sharks cross several political borders (i.e. state waters), several directed (state-funded) fishery-independent surveys are spatially limited relative to shark distributions. Consequently, indices of relative abundance from each survey spanning the range of the species of interest are treated as independent measures of shark abundance within stock assessments (SEDAR 2013). Likely due to high levels of uncertainty and the timing of each survey relative to environmentally driven shark migrations (e.g. Grubbs 2010), indices of abundance from disparate surveys frequently result in conflicting information. The state-space, age-structured production model used in shark stock assessments cannot reconcile antagonistic information, such that different combinations of like indices are alternatively tested within the model framework as sensitivity runs. Consequently, the 2013 shark stock assessment recommended additional research on the integration of local abundance indices into a global index (SEDAR 2013). Furthermore, the Atlantic States Marine Fisheries Commission recommended additional research should be conducted on identifying indices that contribute the most information to stock-wide trends (ASMFC 2013). Hence, in Chapter 1, I used a multivariate, dimension-reduction technique, dynamic factor analysis (DFA), to reconcile conflicting trends in abundance, which simultaneously represents a framework to assess which indices are contributing the most to the resulting trends.

The same life history characteristics make shark community dynamics difficult to investigate. Studies investigating interspecies relationships have thus far been constrained to easily accessible, localized areas (such as shark nursery areas; e.g., Bethea et al. 2004; White and Potter 2004; DeAngelis et al. 2008). However, sharks spend a large portion of their lifecycles away from such environments. Consequently, in Chapter 2, I sought to quantitatively examine shark intra- and interspecies interactions via multivariate, first-order autoregressive, state-space (MARSS-1) models. Localized results based on indices of abundance derived from a single fishery-independent survey were compared to broad-scale results based on the common trends of abundance calculated in Chapter 1. By using quantitative tools, we can analyze shark population dynamics at a broad-scale, which cannot be done directly using conventional methods.

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# Chapter 1

# Reconciling conflicting indices to estimate relative coastal shark abundance

# Abstract

Relative abundance of many shark species in the Atlantic is assessed by compiling data from several independently conducted, but somewhat spatially limited surveys. Although these localized surveys sample the same populations, resulting trends in annual indices often conflict with one another, thereby hindering interpretation of abundance patterns at broad spatial scales. We used generalized linear models (GLMs) to generate indices of abundance for eight Atlantic coastal shark species from six fishery-independent surveys along the U.S. east coast and Gulf of Mexico from 1975 to 2014. These indices were further analyzed using dynamic factor analysis (DFA) to produce simplified, broad-scale common trends in relative abundance over the entire sampled distribution. Covariates included in the DFA were the North Atlantic Oscillation index, the Atlantic Multidecadal Oscillation index, annually averaged sea surface temperature, and species landings. However, none were statistically significant for seven out of the eight coastal shark species examined. Estimated common trends of relative abundance for all large coastal shark species showed similar decreasing patterns into the early 1990s, periods of sustained low index values thereafter, and recent indications of recovery. Small coastal shark species exhibited more regional variability in their estimated common trends, such that two common trends were required to adequately describe patterns in relative abundance or the single common trend identified was only representative of part of the species' distribution. Overall, all species concluded with an increasing trend, suggestive of initial recovery from past exploitation.

# Introduction

While it is generally agreed upon within the scientific community that shark stocks rapidly declined in abundance along the U.S. east coast beginning in the mid-1970s through to the early 1990s, the extent of that decline has been contentiously debated in the scientific literature with varyingly pessimistic outlooks (e.g. Musick *et al.* 1993; Musick *et al.* 2000; Cortés 2002; Baum *et al.* 2003; Myers and Worm 2003; Baum and Myers 2004; Baum *et al.* 2005; Burgess *et al.* 2005; Ha 2006; Baum and Blanchard 2010; Dulvy *et al.* 2014). Investigation into the declining trends of global shark landings revealed that decreasing catch was reflective of reduced shark abundance as opposed to the result of controls implemented through management (Davidson *et al.* 2015). These declines may hold economic and ecosystem-wide implications as effects of altered apex predator abundance propagate down the food web via trophic cascades, with sharks likely facilitating natural selection of their prey (Stevens *et al.* 2000; Scheffer *et al.* 2005; Baum and Worm 2009; Heupel *et al.* 2014).

Shark exploitation began in the mid-1970s coincident with declining stock abundances of other commercially important species, and since sharks were deemed an underutilized natural resource at that time, fishers were encouraged to focus on sharks for commercial harvest (Musick *et al.* 1993; McCandless *et al.* 2014). Simultaneously, directed recreational shark fisheries rapidly developed in response to public excitement stemming from the release of the movie “Jaws” in 1975 (Musick *et al.* 1993; Cortés *et al.* 2006). Yet, many sharks are inherently susceptible to fishing pressure due to their K-selected life history strategy (Musick *et al.* 2000; Stevens *et al.* 2000; Au *et al.* 2015). Large-bodied, coastal shark species were likely most affected by the development of targeted fisheries due to their high meat content, large fin sizes, and close proximity to land (Dulvy *et al.* 2014). Contrary to larger species, small coastal sharks in the northwest Atlantic, which generally are not considered apex predators, have experienced less dramatic declines in abundance (Dulvy *et al.* 2014). These smaller species generally have higher intrinsic population growth rates, and consequently are much less susceptible to fishing pressure (Au *et al.* 2015).

As a result of declines in large coastal shark populations, a shark Fishery Management Plan (FMP) was established by the National Marine Fishery Service (NMFS) in 1993, which initiated the implementation of several commercial and recreational regulations (SEDAR 2011). Prior to the enactment of management measures, shark population dynamics were not the focus of extensive scientific investigation. The FMP noted a lack of species-specific data (NMFS 1993), which stimulated numerous life history studies of northwest Atlantic shark populations and several state and federal agencies began collecting relative abundance information either through directed surveys or as bycatch of existing surveys. However, the expansive spatial distributions of Atlantic coastal sharks due to their sex- and size-specific migratory movements makes developing stock-wide characterizations of relative abundance challenging (Castro 2011; Kohler *et al.* 1998; Simpfendorfer and Heupel 2012). For example, sandbar sharks (*Carcharhinus plumbeus*, Carcharhinidae) mate within the coastal waters of Florida during June and July (Portnoy *et al.* 2007; Baremore and Hale 2012), and a year later, gravid females migrate northward along the Atlantic coast to pup in bays and estuaries during late spring and early summer, after which they migrate back offshore (Grubbs *et al.* 2005; McCandless *et al.* 2005, Baremore and Hale 2012). Neonates remain in these nurseries throughout the summer (McCandless *et al.* 2005; Conrath and Musick 2010), and overwinter off the coast of North Carolina (Grubbs *et al.* 2005; McCandless *et al.* 2005; Conrath and Musick 2008). These juveniles return to their natal nursery for the next five to 16 years (Merson and Pratt 2001; Grubbs *et al.* 2005; McCandless *et al.* 2005), before migrating offshore and into the Gulf of Mexico (Casey *et al.* 1985; Conrath and Musick 2008). Adult male sandbar sharks reside primarily offshore and only move inshore to mate (Casey *et al.* 1985; Portnoy *et al.* 2007; Conrath and Musick 2008).

At present, inferences about shark abundance in the Atlantic are largely based on catch-per-unit-effort (CPUE) data obtained from several spatially limited surveys. When multiple independent surveys each sample a small portion of a stock's migratory range, it is not uncommon for the resulting trends in CPUE to be in conflict, which creates uncertainty about true population trends (SEDAR 2013). Thus, developing a representative characterization of stock-wide dynamics and patterns in relative abundance for sharks in the Atlantic involves reconciling discrete, and often contradictory, fragments of information.

The objectives of the study were two-fold: i) develop simplified broad-scale trends of relative abundance for eight Atlantic shark species by integrating data from multiple spatially limited, fishery-independent survey programs, and ii) investigate the effects of hypothesized drivers (climatic, environmental, anthropogenic) on resultant stock-wide temporal patterns of relative abundance. We acquired raw data from six fishery-independent surveys for each species of interest and used those data to generate indices of relative abundance. Indices were then analyzed with a multivariate, time series, dimension reduction model (dynamic factor analysis; DFA) to extract the common underlying trends in relative abundance and determine which covariates were associated with temporal patterns in the species-specific relative abundances.

## Methods

### *Data sources*

Catch and effort data from six fishery independent shark surveys (Virginia Institute of Marine Science longline, VIMS LL; SouthEast Area Monitoring and Assessment Program trawl, SEAMAP Trawl; South Carolina red drum longline, SC LL; Georgia red drum longline, GA LL; Southeast Fisheries Science Center longline, SEFSC LL; Gulf of Mexico Shark Pupping and Nursery gillnet, GULFSPAN GN) were the basis for this study (Table 1; Figure 1). A minimum of three independent survey indices of abundance were required for a given species to be considered for analysis. Data from four large coastal sharks (LCS; sandbar; blacktip, *Carcharhinus limbatus*, Carcharhinidae; spinner, *C. brevipinna*, Carcharhinidae; tiger, *Galeocerdo cuvier*, Carcharhinidae), and four small coastal sharks (SCS; Atlantic sharpnose, *Rhizoprionodon terraenovae*, Carcharhinidae; blacknose, *C. acronotus*, Carcharhinidae; bonnethead, *Sphyrna tiburo*, Sphyrnidae; finetooth, *C. isodon*, Carcharhinidae) were analyzed (Tables 2 & 3).

### *Indices of abundance*

Generalized linear models (GLMs; McCullaugh and Nelder 1989) were used to standardize species-specific CPUE data from each survey program and provide estimated annual indices of relative abundance. Preliminary explorations of each survey dataset revealed high frequencies of zero observations, which were expected given the low overall abundance of the focal species. Consequently, three classes of GLMs were used to generate species-specific relative abundance indices from each survey: (1) delta-lognormal models in which the survey observations were defined as number of sharks captured per hook-hours (Lo *et al.* 1992; Maunder and Punt, 2004; Cortés *et al.* 2006), (2) hurdle (or zero-altered) models where survey observations were defined as discrete counts and effort was treated as an offset variable (Gurmu 1998; Cortés *et al.* 2006; Zuur *et al.* 2012), and (3) zero-inflated models where survey observations were again counts and effort was an offset (Minami *et al.* 2007; Zuur *et al.* 2012; Brodziak and Walsh 2013).

Delta-lognormal models contain two components: the binomial submodel fitted to presence/absence data (presence defined as at least one target species captured) and designed to estimate the probability of encountering the target species; and the lognormal submodel fitted to the log transformed nonzero observations and designed to estimate the mean CPUE. The general form of a delta-lognormal GLM is:

$$logit(\boldsymbol{\pi_B}) = \boldsymbol{X_B \beta_B} + \boldsymbol{\varepsilon_B}$$

$$\boldsymbol{\mu_{CPUE}} = \boldsymbol{X_{CPUE} \beta_{CPUE}} + \boldsymbol{\varepsilon_{CPUE}} \tag{1}$$

where $\boldsymbol{\pi_B}$ represents the probability that each observation (i.e. sampling event) is non-zero, $\boldsymbol{\mu_{CPUE}}$ is the log-transformed CPUE, and in both submodels $\boldsymbol{X}$ is the design matrix, $\boldsymbol{\beta}$ is the vector of estimated parameters, and $\boldsymbol{\varepsilon}$ is the associated error. The resulting predictions over years from both submodels are multiplied to generate a final annual index of relative abundance.

Hurdle models are essentially delta models in which the positive catch response variable assumes a zero-truncated discrete distribution. Evaluation of preliminary model fits and diagnostics were conducted to select a zero-truncated negative binomial or zero-truncated Poisson distribution. The general form of a hurdle GLM is:

$$logit(\boldsymbol{\pi_B}) = \boldsymbol{X_B \beta_B} + \boldsymbol{\varepsilon_B}$$

$$\log(\boldsymbol{\mu_{catch}}) = \boldsymbol{X_{catch} \beta_{catch}} + \log(\boldsymbol{effort}) + \boldsymbol{\varepsilon_{catch}} \tag{2}$$

where all matrices and vectors are as defined in eq. (1) and log($\boldsymbol{effort}$) is an offset to adjust for differing gear deployment duration.

Zero-inflated models are a mixture of two distributions, a degenerate component that is zero with certainty and a second component that includes zeros and positive values (Maunder and Punt 2004). In effect, the data are divided into two groups, where the first group contains only zeros (termed false zeros) and the second group contains the count data, which may include zeros (true zeros) along with positive counts (Zuur et al. 2009, 2012). Again, preliminary model fits and diagnostics were conducted to select a zero-truncated negative binomial or zero-truncated Poisson distribution. Zero-inflated models take the general form:

$$logit(\boldsymbol{\pi_{zero}}) = \boldsymbol{X_{zero}\beta_{zero}} + \boldsymbol{\varepsilon_{zero}}$$

$$\log(\boldsymbol{\mu_{true}}) = \boldsymbol{X_{true}\beta_{true}} + \log(\boldsymbol{effort}) + \boldsymbol{\varepsilon_{true}} \tag{3}$$

where the binomial component only includes sampling events with zero catch, $\boldsymbol{\pi_{zero}}$ represents the probability that an observed zero is a false zero, and count data including true zeros are modeled with the second component.

Predicted indices of relative abundance were generated using estimated marginal means (Searle *et al.* 1980), and for the delta-lognormal models, back transformed bias correction followed Lo *et al.* (1992). Uncertainty estimates for the annual indices were generated from 1000 nonparametric bootstrapped samples (Efron and Tibshirani 1993). Bootstrapped data sets were resampled by year with replacement. All analyses of survey data were performed with the software package R (version 3.1.1, R Core Development Team 2014) and the 'pscl' package (Jackman 2015) was used to fit hurdle and zero-inflated models.

Akaike's Information Criterion (AIC, Akaike 1973, Burnham and Anderson 2002) was used to discriminate among model parameterizations reflecting different combinations of covariates. Tested covariates varied by survey, while year was included in all models to ensure estimation of annual abundance indices (Table 4). Year, month/season, and station/location/area were treated as categorical variables, and levels of those categorical variables where the species of interest were not present during at least two sampling events were excluded from analyses. Latitude, longitude, and depth were treated as continuous variables. Scatter plot matrices (SPloMs) were used to assess correlation and collinearity of covariates and those that were correlated were not mutually included in any model. Graphical residual analysis was used to assess model fit. Resulting indices of abundance were standardized, or Z-scored, prior to implementation into the dynamic factor analysis model.

*Dynamic factor analysis*

Dynamic factor analysis (DFA) is a multivariate dimension reduction technique designed for short, non-stationary time series data. The approach involves fitting a specialized multivariate autoregressive state-space model to identify a set of underlying trends that explain temporal variation in a collection of time-series (Zuur *et al.* 2003a; b; Holmes *et al.* 2014). The general form of a DFA model can be written as:

$$\boldsymbol{y}_t = \boldsymbol{\Gamma}\boldsymbol{\alpha}_t + \boldsymbol{D}\boldsymbol{x}_t + \boldsymbol{\varepsilon}_t, \text{ where } \boldsymbol{\varepsilon_t} \sim MVN(0, \boldsymbol{H})$$

$$\boldsymbol{\alpha}_t = \boldsymbol{\alpha}_{t-1} + \boldsymbol{\eta}_t, \text{ where } \boldsymbol{\eta_t} \sim MVN(0, \boldsymbol{Q}) \tag{4}$$

where $\boldsymbol{y}_t$ is a vector ($n \times 1$) of abundance indices at time $t$, $\boldsymbol{\alpha}_t$ is the vector ($m \times 1$) of common trends ($m<n$) that are modeled as stochastic random walks, $\boldsymbol{\Gamma}$ is the matrix ($n \times m$) of estimated factor loadings on the common trends, $\boldsymbol{x}_t$ is the vector ($k \times 1$) of covariates, $\boldsymbol{D}$ holds the corresponding coefficients ($n \times k$), and $\boldsymbol{H}$ and $\boldsymbol{Q}$ denote the variance-covariance matrices associated with the observation error vector $\boldsymbol{\varepsilon}_t$ ($n \times 1$) and process error vector $\boldsymbol{\eta}_t$ ($m \times 1$), respectively (Zuur *et al.* 2003a; b; Holmes *et al.* 2014). The process component of DFA fits autocorrelated common trends to accommodate the time-series nature of the indices and resulting trends (Stachura *et al.* 2014). Factor loadings (elements of the $\boldsymbol{\Gamma}$ matrix) indicate the strength of the influence of each survey index on the resulting common trend. Values higher in magnitude ($\gtrsim 0.2$; Zuur *et al.* 2003b) denote a stronger effect of the given survey on the corresponding common trend. Since the indices were Z-scored, the resulting factor loadings, common trends, and fitted values were unitless (Zuur *et al.* 2003b).

To ensure that the model was identifiable, $\boldsymbol{Q}$ was set to the identity matrix ($\boldsymbol{I}$) and the matrix $\boldsymbol{H}$, which specifies the variance-covariance structure among the $n$ time-series was allowed to take on four forms: diagonal with equal variance and zero covariance, diagonal with unequal variance and zero covariance, nondiagonal with equal variance and equal covariance, and unconstrained with unique variances and covariances. Resulting common trends were varimax rotated to maximize the difference between factor loadings (Holmes *et al.* 2014). The underlying assumptions of a DFA model are equivalent to those of a linear regression, which are normality, independence, and homogeneity of residuals. As in the case of regression models, DFA is fairly robust to violations of normality, residuals can be homogenized via data transformations, but the assumption of independence is the most important (Zuur *et al.* 2003b). Model implementation occurred via the state-space multivariate autoregressive modeling package 'MARSS' (Holmes *et al.* 2013) in R (version 3.1.1).

Models were fitted in two-steps. First, all combinations of one, two, or three common trends and the four covariance matrix structures were explored without covariates and the most supported model was selected via corrected Akaike's Information Criterion (AICc) for low sample sizes (Holmes *et al.* 2014). An additional quantitative measure of model fit, which is calculated by the sum of the squared residuals of the fitted trend divided by the sum of the squared observations for each survey, was computed. Lower quantities (defined as $\lesssim 0.6$) were interpreted as indicative of better model fit, while higher values indicated that all or several years were poorly estimated by the resulting fitted trend (Zuur *et al.* 2003b). For comparative purposes, these values were averaged across all surveys within a given species. Second, the most supported model was then used to investigate the effects of several covariates.

Four covariates were examined: the North Atlantic Oscillation (NAO) index, the Atlantic Multidecadal Oscillation (AMO) index, annually averaged sea surface temperature (SST) between latitudes 24°N and 44°N (data provided by NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, http://www.esrl.noaa.gov/psd/data/climateindices/list/), and species landings (pers. comm., E. Cortés, NMFS, Panama City, FL). The NAO, which is a measure of pressure difference over the North Atlantic Ocean, and AMO, which encompasses basinwide sea surface temperature, circulation patterns, and sea level pressure, were selected as covariates because they directly impact climate patterns and have been shown to affect fish survival and ecosystem organization in the southeast U.S. Atlantic coast and Gulf of Mexico (Stenseth *et al.* 2002 and references therein; Nye *et al.* 2014; Karnauskas *et al.* 2015). Annually averaged SST was included because several studies have showed that shark movement is influenced by temperature patterns (e.g., Merson and Pratt 2001; McCandless *et al.* 2005; Castro 2011). Since AMO and SST were highly correlated, they were not mutually included in any DFA model. Lastly, species-specific landings were included to examine the effect of top-down pressure on species relative abundance. Because DFA requires complete covariate time-series, missing years in landings data were estimated by three-year moving averages, following procedures routinely applied in shark stock assessments (pers. comm., E. Cortés, NMFS, Panama City, FL). For two species (blacktip and tiger sharks), landings time-series did not encompass the temporal span of the index data, so hindcasting was based on the average of the first five years of landings data.

## Results

### *Indices of abundance*

In two species, there were not a sufficient number of observations in each dataset to generate hurdle and/or zero-inflated indices. Thus, tiger and spinner shark analyses were restricted to delta-lognormally generated indices of abundance. For the remaining species, interpretation of indices of abundance generally resulted in similar conclusions, regardless of GLM type (ex: blacktip shark Figure 2; Appendices 2-9). In particular, the hurdle and zero-inflated indices frequently showed overlapping trends. Nevertheless, superimposed indices of abundance for each species produce obvious data conflict (Figure 3).

*Dynamic factor analysis*

With the exception of one species (finetooth shark), a diagonal covariance structure was empirically supported suggesting that no covariance exists between survey indices (Table 5). In three of the six species in which delta-lognormal, hurdle, and zero-inflated GLMs were used to generate indices of abundance and subsequent DFA common trends, the most supported DFA common trends were generated by the delta-lognormal indices of abundance (Table 6). The resulting DFA common trends were generally similar regardless of index standardization method (ex: blacktip shark, Figure 4), with notable exceptions (Appendices 10-17). For the purposes of the current study, we will solely examine delta-lognormally generated results henceforth.

The DFA results for the large coastal sharks showed consistent trends in relative abundance across species (Figure 5). For the sandbar shark, two common trends best explained the collection of abundance indices. The primary common trend indicated that relative abundance peaked in the early 1980s, decreased until the early 1990s, remained low for several years, and exhibited a modest recovery in the late 2000s. This first common trend was well supported by the VIMS LL, SEFSC LL, and GA LL, with a negative loading by the SC LL. The secondary trend showed a similar pattern to the first and was primarily driven by the SEAMAP Trawl survey. As such, the secondary trend was largely uninformed until the year 1989. The gear specifications of the SEAMAP Trawl likely resulted in effective sampling of smaller size classes, such that the secondary trend was representative of the abundance of neonate and small juvenile sandbar sharks (Appendix 18). The presence of separate adult and small juvenile trends explains the mismatch between the peaks in each trend, one representing a peak in juvenile abundance and the other representing the peak of the same individuals after they had grown into large juveniles and adults. The blacktip shark showed a similar trend to sandbar shark, although there was a shorter delay in the initial recovery. The trend was strongly and positively driven by all surveys with the exception of the SEFSC LL, which suggests that the SEFSC LL index of abundance is following a trend that is opposite the estimated common trend during its operating timeframe.

The tiger shark trend also showed a decrease in abundance into the early 1990s, followed by a period of low relative abundance. However, in the early 2000s, the relative abundance of tiger shark increased much more rapidly than the other large coastal species. The tiger shark was the only species whose optimal DFA model incorporated any climatic indices as a covariate (NAO). The NAO index had a significantly negative effect on the SEFSC LL index and a significantly positive effect on the SC LL. Significant effects of tiger shark landings, also included in the optimal model, were a positive effect on the SEFSC LL and a negative effect on the SC LL tiger shark indices. Factor loadings indicated that the VIMS LL and SEFSC LL both significantly influenced the common trend, while the SC LL significantly and negatively influenced the common trend.

The spinner shark time series was much shorter, and raw indices of abundance showed little dichotomy in relative abundance across years, signified by low factor loadings. Nevertheless, the resulting trend was significantly driven by the SEAMAP Trawl and the landings covariate was included in the optimal spinner shark DFA model. The SEFSC LL index was significantly negatively affected by landings, while the SEAMAP Trawl index significantly increased with increasing landings.

The small coastal complex showed more diverse trends in relative abundance (Table 5; Figure 6), as both the Atlantic sharpnose shark and the blacknose shark exhibited two common trends. The first Atlantic sharpnose trend showed relative abundances that were relatively stable until the mid-1990s, where they showed a slight decline followed by a large increase starting in the mid-2000s. The first trend was primarily driven by the VIMS

LL and the GULFSPAN GN. The secondary trend was largely uninformed prior to the late 1980s, showed a large increase in abundance beginning in the late 1990s, and a moderate decline to the present. This second trend, which showed a similar, preceding pattern as the first trend, was significantly driven by the SEAMAP Trawl. The short longevity of the SC LL and the GA LL (2007 through 2013 or 2014) explain why both surveys positively drove the first trend and negatively drove the second trend, during which time the common trends showed relatively opposing tendencies. Additionally, none of the factor loadings relating the SC and GA LL indices on the two common trends were significantly different from zero, suggesting no strong relationship. Both blacknose shark common trends showed low abundances throughout 1990s and increasing abundances to present. The first common trend was primarily supported by the SEAMAP Trawl and negatively by the GULFSPAN GN, while the second trend was driven by the SEFSC LL. A similar situation seen in the Atlantic sharpnose shark results was observed regarding the relationship between the SC and GA LL indices and both common trends for the blacknose shark.

Fewer and potentially less informative indices of abundance were available for the bonnethead and finetooth sharks, which likely lead to the selection of a single common trend. Particularly, the bonnethead common trend, which showed an apparent increase in abundance, was solely influenced by the SEAMAP Trawl survey. Lastly, the finetooth shark abundance was uncertain prior to the early 2000s, after which it quickly increased and dipped slightly into the early 2010s. The finetooth common trend was strongly driven by both the SEAMAP Trawl and the SC LL surveys. Finetooth landings negatively influenced the SEAMAP Trawl index and positively influenced the SC LL index.

## Discussion

### *Index standardization method*

Indices of abundance provided acceptable fits as determined by graphical residual analysis, dispersion analysis, and estimated parameter values and standard errors. It was apparent that the resulting indices and DFA common trends were very similar regardless of the three GLM structures used to generate the indices of abundance, such that the overarching conclusions drawn from each common trend were essentially identical. Moreover, the fitted trends resulting from the delta-lognormally generated indices of abundance provided the optimal DFA fit, similar to findings reported in Carlson *et al.* (2012). While the majority of the optimal DFA fits included a diagonal covariance ($H$) matrix structure, altered $H$ structures generally did not greatly affect the resulting common trends.

*Climatic covariates*

None of the climatic indices tested in the DFA model were included in an optimal model, with the exception of the tiger shark. While this could be due to the information theoretic selection method used to elect the optimal model (by including a single covariate, the DFA model was required to estimate an extra parameter for each index included in the response vector), it could also be due to the adaptability and versatility of the species under consideration. Although several studies have linked small- and meso-scale shark distributions to climatic indices (Carlson 1999; Cotton *et al.* 2005; Brodziak and Walsh 2013; Hoffmayer *et al.* 2014; Mitchell *et al.* 2014; Báez 2015), studies have rarely examined whether broad-scale population abundance is affected by multidecadal oscillations. Although Perry *et al.* (2005) noted that slower growing species (like sharks) are more susceptible to changes in climate, it appears that when immediate environmental conditions are unfavorable for the species examined, they may stray to more suitable conditions. For instance, although blacknose sharks rarely migrate northward into Virginia waters and instead can be found off the coast of North Carolina during summer (Castro 2011), due to extremely warm water temperatures in the southeastern U.S. coast in the summer of 2015, the VIMS LL captured 16 blacknose sharks compared to only eight specimens previously recorded between 1973 and 2014 (unpublished data). Similar accounts of shark range expansion due to unfavorable environmental conditions have been documented (Wiley and Simpfendorfer 2007). Last *et al.* (2011) investigated the change in species composition along the coast of Tasmania, Australia, an area subjected to extreme temperature increases over the past 60 years, and found that five out of 10 elasmobranch species examined exhibited distributional changes. The overall abundance of the population does not seem to be affected by climatic indices, as similarly noted by Bigelow *et al.* (1999). Since the estimated DFA trends are predicting underlying relative abundance on an extremely broad geographic scale, it appears that local distributional changes driven by environmental forcings do not affect overall estimates of abundance generated by the DFA model.

On the other hand, the significant effect of NAO on the tiger shark would indicate that the tiger shark population is affected by climatic forcings. While the VIMS LL-generated index of abundance was not affected, both SEFSC LL and SC LL indices were influenced by the added covariates. Because the tiger shark range is so large and vast migrations are common (Kohler *et al.* 1998; Castro 2011), the data in this study likely still reflect local relative abundance even though they encompass the entire southeastern coastal Atlantic. Since representative data from the full tiger shark range do not exist, changes in distribution could be confounded with changes in relative abundance predicted with DFA.

### *Anthropogenic covariates*

While it is expected that any substantial top-down forcing would affect shark population abundance, the estimated harvest effects differed by survey or location. Species landings had both positive and negative effects on survey-specific indices of relative abundance. For example, increased spinner shark landings had a significantly negative effect on the SEFSC LL index and a positive effect on the SEAMAP Trawl index. While management measures restrict sizes available for retention, it would be expected that increased fishing would negatively affect large adults, like those captured in the SEFSC LL. On the other hand, fishing pressure may alleviate intra-species competition, and increase the abundance of smaller juveniles, which are more likely to be captured in the SEAMAP Trawl. Another potential explanation is that landings are predominantly occurring within the Gulf of Mexico, thereby negatively affecting SEFSC LL catches, but not catches along the east coast.

Within the context of the finetooth shark, a member of the small coastal complex which may not reach sizes large enough to escape trawl nets, increased landings result in lower abundances in the SEAMAP Trawl index. Conversely, finetooth shark abundance increased in the SC LL in response to increased landings. It is possible that there is less directed fishing on finetooth sharks off the coast of South Carolina, which represents a northern range boundary and is only seasonally inhabited by the species (Castro 2011).

Tiger shark landings negatively impacted the SC LL index and led to increases in the SEFSC LL. The distribution of directed tiger shark fishing likely shifted from the Gulf of Mexico and offshore Atlantic coast to the nearshore waters off South Carolina over the course of the 40-year span of the current study, explaining the effects of landings on tiger shark indices of abundance. Alternatively, the distribution of tiger sharks may have shifted over the course of the study, compounding the effect of landings. Overall, the significance of landings on shark relative abundance indicates that these species are susceptible to top-down regulation due to fishing.

### *Large coastal abundance*

The large coastal shark species all followed similar trends in relative abundance, with high levels at the beginning of the time series, followed by a decline until the early

1990s, and signs of recovery in the mid-2000s. The shark FMP was enacted in 1993 during the period of low overall shark abundance. Given the low intrinsic population growth rates of many shark species, it is reasonable to assume that efficacy of management regulations would not immediately translate into stock recovery. The results of this study support that reasoning since relative abundance trends of all large coastal species remained depressed following implementation of the FMP. The duration of low relative abundance varied by species however, and relative abundances of those with younger ages at maturity showed indications of recovery more quickly than those with older age at first reproduction (i.e. Table 2).

The sandbar shark period of extended low abundance may have also been assisted by state-wide fisheries targeting young and late juvenile animals, because state and federal management was not formally linked until 2009 (Grubbs 2010). The primary relative abundance trend for adult sandbar shark showed a rapid initial recovery that has since declined slightly. The recent dip in the sandbar shark trend is likely related to uncertainty in the estimated trend.

The recent increase in the blacktip shark trend was gradual and showed a great deal of variability, which could be attributed to various management measures, such as the mandatory implementation of bycatch reduction devices (BRDs) within the shrimp trawl fishery (SEDAR 2011; 2013; mandated in 1997 in the southeast Atlantic coast, 1998 in the western Gulf of Mexico, and 2004 in the eastern Gulf of Mexico; Scott-Denton *et al.* 2012). Despite surveys sampling two genetically distinct stocks of blacktip sharks, a single common trend was selected to encompass the trend in both the western Atlantic and the Gulf of Mexico, potentially indicating that sufficient data were not available within either or both stocks, or that both stocks followed a similar trend in abundance.

The tiger shark recovery was extremely large in magnitude, likely reflective of the high fecundity of these sharks, in which females produce an average of 41 pups every two years (Castro 2011). While the spinner shark common trend was shorter due to the limited length of each time series included, it does appear that this modest increase in relative abundance follows the trends of the other large coastal species, despite larger uncertainty in the resulting estimated trend.

### *Small coastal abundance*

While the large coastal species typically undergo extensive migrations between the Atlantic Ocean and the Gulf of Mexico, it is likely that gene flow around the Florida peninsula is restricted in small coastal species due to more localized movements (Kohler *et al.* 1998). Both the Gulf of Mexico populations of blacknose and bonnethead sharks are considered separate stocks due to differences in life history parameters and genetics (Carlson *et al.* 1999; Driggers *et al.* 2004; SEDAR 2011; 2013). Furthermore, bonnethead sharks have been shown to exhibit variation in life history parameters on a much smaller spatial scale along the Atlantic coast (Frazier *et al.* 2013) and within the Gulf of Mexico (Lombardi-Carlson *et al.* 2003). While less studied, differences have been reported in the life history characteristics of the finetooth shark between Atlantic coast specimens and congeners from the Gulf of Mexico (Carlson *et al.* 2003; Drymon *et al.* 2006). Ultimately, while life history parameters have not been shown to vary based on location, it has been suggested that migrations between the Atlantic Ocean and Gulf of Mexico of Atlantic sharpnose sharks are rare (Kohler *et al.* 1998).

Consequently, it is not surprising to note that there appears to be more local variability in small coastal shark abundance as demonstrated by the increased number of common trends estimated for the Atlantic sharpnose and the blacknose sharks. Regional increases in the Atlantic sharpnose, blacknose, and finetooth common trends also correspond with regional management implementation such as the BRDs (Scott-Denton *et al.* 2012). Additional survey data within the Gulf of Mexico will greatly aid interpretations of coast-wide patterns of relative abundance in blacknose and finetooth species, as estimated common trends for these species are only representative of Atlantic coast dynamics.

## Conclusion

Resulting broad-scale trends in relative abundance were successfully generated in the species examined, as indicated by model diagnostics and the alignment between the common trends, species' life history parameters, and historical management measures. Compared with other statistical dimension reduction approaches, DFA is advantageous for time series data due to its built-in autocorrelation and ability to accommodate missing years and shortened time series. We also consider the potential purposes that DFA can fulfill in the future. Azevedo *et al.* (2008) used common trends derived from DFA on Iberian anglerfish (*Lophius piscatorius*, Lophiidae; *L. budegassa*, Lophiidae) in place of conflicting indices of abundance as inputs into a biomass dynamic stock assessment model and reported less biased and more realistic results. It was also proposed that the complexity of the assessment model could be expanded to an age-structured production model. In the future, it would be worthwhile to see if these concise trends could be applied in Atlantic coastal shark assessments, eliminating the problematic practice of including conflicting indices into a single model (Hoyle *et al.* 2014).

Ultimately, the shark populations examined appear to be increasing in abundance. Following the drastic decrease in abundance that several (namely, large coastal) species underwent in the 1980s and 1990s (Musick *et al.* 1993), it is clear that after a one to two decade-long lag, Atlantic coastal sharks are positively responding to the series of management measures implemented starting in 1993. While these trends do not allow for estimation of the magnitude of shark declines, the common trends produced in this study demonstrate a recovery of Atlantic coastal shark abundances.

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Table 1. Summary of surveys included in the analysis: Virginia Institute of Marine Science longline (VIMS LL), South Carolina red drum longline (SC LL), Georgia red drum longline (GA LL), SouthEast Area Monitoring and Assessment Program Trawl (SEAMPA Trawl), SouthEast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN).

| **Survey** | **Sampling Gear** | **Sampling Years** | **Sampling Frequency** | **Sampling Area** | **Sampling Design** | **Target Species** | **Citation** |
|---|---|---|---|---|---|---|---|
| VIMS LL | Bottom longline | 1975-2014 | Once per month during the months June - September | Coastal Virginia | Fixed stations; approximately 4 hour soak time; 100 hooks per set; Atlantic menhaden used as bait | Large adult and juvenile coastal sharks | |
| SC LL | Bottom longline | 2007-2014 | August - December | Coastal South Carolina | Stratified random sampling; 30 min soak time; 40 hooks per set; Atlantic mackerel or striped mullet used as bait | Adult red drum | http://www.seamap.org/documents/Red%20Drum%20Longline%20Survey%20-%20South%20Carolina.pdf |
| GA LL | Bottom longline | 2007-2013 | April – December | Coastal south Georgia and north Florida | Stratified random sampling (April - August); sample artificial reefs (fall); 30 min soak time; 60 hooks per set; Pacific squid used as bait | Adult red drum | http://www.seamap.org/documents/Red%20Drum%20Longline%20Survey%20-%20Georgia.pdf |
| SEAMAP Trawl | Bottom trawl | 1989-2014 | One multi-leg cruise in the spring, summer, and fall | South Atlantic Bight; Cape Hatteras, NC and Cape Canaveral, FL | Stratified random sampling | Resident and transient fishes, crustaceans, sea turtles, and cephalopods | http://www.seamap.org/documents/CoastalSurveyinfo.pdf |
| SEFSC LL | Bottom longline | 2001-2014 | Late July - September | Gulf of Mexico; Atlantic below 37° N latitude (alternate years) | Stratified random sampling | Adult shark/ snapper/ grouper | Ingram *et al.* 2005;<br>WB. Driggers, III, personal communication |
| GULFSPAN GN | 6 panel multi-mesh gillnet | 1996-2014 | Monthly sampling from April - October; occasionally March, May, and November | Northwest, Gulf of Mexico coast of Florida; | Stratified random sampling; nets checked or pulled every 1 - 2 hr; From 1994 through 2005, stretched mesh sizes ranged from 8.9 cm to 14.0 cm, increasing by 1.3-cm (0.5-in) intervals, with an additional panel of 20.3 cm. In 2006, the 20.3-cm panel was removed and a 7.6-cm panel was added *ad hoc.* | Juvenile coastal sharks | Carlson *et al.* 2013;<br>JK. Carlson, personal communication |

Table 2. Life history characteristics of the six species included in the study, including age at median maturity ($A_{50\%}$), longevity ($A_{MAX}$), length of the reproductive cycle, fecundity per reproductive event, and von Bertalanffy asymptotic maximum length ($L_\infty$) and growth rate coefficient (K).

| | | | | | von Bertalanffy | |
|---|---|---|---|---|---|---|
| **Species** | **$A_{50\%}$** | **$A_{MAX}$** | **Repro. Cycle** | **Fecundity** | **$L_\infty$** | **K** |
| LARGE COASTAL SHARKS | | | | | | |
| Sandbar | 14 yrs[1] | 27 yrs[2] | 2.5 yrs[1] | 8 pups[1] | 165 cm PCL[3] | 0.086 / yr[3] |
| Blacktip: Atl. | 7 yrs[4] | 22 yrs[4] | 2 yrs[5] | 4 pups[5] | 159 cm FL[4] | 0.16 / yr[4] |
| Blacktip: GOM | 6 yrs[4] | 17 yrs[4] | 2 yrs[5] | 4 pups[5] | 142 cm FL[4] | 0.24 / yr[4] |
| Spinner | 7-8 yrs[6] | 20 yrs[6] | 2 yrs[7*] | 6-8 pups[8] | 226 cm FL[9] | 0.08 / yr[9] |
| Tiger | 10 yrs[10] | 29 yrs[10] | 2 yrs[8] | 41 pups[8] | 347 cm FL[10] | 0.12 / yr[10] |
| SMALL COASTAL SHARKS | | | | | | |
| Finetooth | 6.3 yrs[11†] | 18.2 yrs[11†] | 2 yrs[12] | 4 pups[10] | 131.3 cm FL[11†] | 0.19 / yr[11†] |
| Blacknose: Atl. | 4.5 yrs[13] | 17-19yrs[13,16] | 2 yrs[13] | 5 pups[8] | 113.6 cm FL[14] | 0.18 / yr[14] |
| Blacknose: GOM | NA | 16 yrs[15] | 1 yr[16] | 3 pups[16] | 113.7–124.1 cm FL[15] | 0.24–0.35 / yr[15] |
| Bonnethead: Atl. | 6.7 yrs[17] | 19 yrs[17] | 1 yr[18] | 9 pups[18] | 103.6 cm FL[17] | 0.18 / yr[17] |
| Bonnethead: GOM | 3-4 yrs[19] | 12 yrs[20] | 1 yr[19] | 10 pups[21] | 122.6 cm TL[20] | 0.25 / yr[20] |
| Atlantic Sharpnose | 3 yrs[22] | 23 yrs[23] | 1 yr[22] | 4-5 pups[22] | 94 cm TL[24] | 0.73 / yr[24] |

[1] Baremore and Hale 2012; [2] SEDAR 2011; [3] Sminkey and Musick 1995; [4] Carlson *et al.* 2006; [5] Castro 1996; [6] Branstetter 1987; [7] Joung *et al.* 2005; [8] Castro 2011; [9] Carlson and Baremore 2005; [10] Kneebone *et al.* 2008; [11] Drymon *et al.* 2006; [12] Castro 1993; [13] Driggers *et al.* 2004b; [14] Driggers *et al.* 2004a; [15] Carlson *et al.* 1999; [16] Sulikowski *et al.* 2007; [17] Frazier *et al.* 2014; [18] Frazier *et al.* 2013; [19] Manire *et al.* 1995; [20] Carlson and Parsons 1997; [21] Lombardi-Carlson *et al.* 2003; [22] Castro 2009; [23] Frazier *et al.* 2015; [24] Carlson and Baremore 2003

* Note that samples for this study were taken in waters off of Taiwan; study that estimated the reproductive cycle of spinner sharks within American waters.

† Finetooth life history parameters estimated from fish within the Gulf of Mexico indicate slightly smaller, faster maturing fish (Carlson *et al.* 2003).

Table 3. The below list denotes which indices of abundance were generated for each species from each survey: Virginia Institute of Marine Science longline (VIMS LL), South Carolina red drum longline (SC LL), Georgia red drum longline (GA LL), SouthEast Area Monitoring and Assessment Program Trawl (SEAMPA Trawl), SouthEast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN).

| | VIMS LL | SEAMAP Trawl | SC LL | GA LL | SEFSC LL | GULFSPAN GN |
|---|---|---|---|---|---|---|
| Sandbar | √ | √ | √ | √ | √ | |
| Blacktip | √ | √ | √ | √ | √ | √ |
| Spinner | √ | √ | √ | | √ | √ |
| Tiger | √ | | √ | | √ | |
| Finetooth | | √ | √ | | | √ |
| Blacknose | | √ | √ | √ | √ | √ |
| Bonnethead | | √ | √ | √ | | √ |
| Atlantic sharpnose | √ | √ | √ | √ | √ | √ |

Table 4. Potential covariates included in generalized linear models (GLMs) to estimate indices of abundance for each survey: Virginia Institute of Marine Science longline (VIMS LL), South Carolina red drum longline (SC LL), Georgia red drum longline (GA LL), SouthEast Area Monitoring and Assessment Program Trawl (SEAMPA Trawl), SouthEast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN).

| **Survey** | **Potential Covariates** |
|---|---|
| VIMS LL | Month, Station |
| SEAMAP Trawl | Month, Region, Latitude/Longitude |
| SC LL | Month, Location |
| GA LL | Month/Season, Region, Surface Salinity, Ending Latitude, Ending Longitude |
| SEFSC LL | Station, Starting Latitude, Starting Longitude, Starting Depth |
| GULFSPAN GN | Month, Area, Depth |

Table 5. The optimal dynamic factor analysis (DFA) models calculated from delta-lognormal indices of abundance for each species. The number of trends selected is denoted *m*. Covariance matrix structure refers to the ***H*** covariance matrix which specifies observation error. Mean fit is a relative measure of model fit calculated by summing the squared residuals of the fitted DFA common trends and dividing by the sum of the squared observations (delta-lognormal indices) for each survey, and averaging the values for each species. Larger values (≳0.6) indicate poor fit (Zuur et al. 2003b).

| | *m* (# trends) | covariance matrix structure | covariates | # surveys utilized | mean fit |
|---|---|---|---|---|---|
| Sandbar shark | 2 | diagonal and equal | none | 5 | 0.1905 |
| Blacktip shark | 1 | diagonal and equal | none | 6 | 0.4295 |
| Spinner shark | 1 | diagonal and equal | landings | 5 | 0.6792 |
| Tiger shark | 1 | diagonal and equal | NAO + landings | 3 | 0.1292 |
| Atlantic sharpnose shark | 2 | diagonal and unequal | none | 6 | 0.5051 |
| Blacknose shark | 2 | diagonal and unequal | none | 5 | 0.3683 |
| Bonnethead shark | 1 | diagonal and equal | none | 4 | 0.8127 |
| Finetooth shark | 1 | equalvarcov | landings | 3 | 0.5899 |

Table 6. Relative model fit of the dynamic factor analysis (DFA) common trends for each catch-per-unit-effort (CPUE) standardization method (delta-lognormal generalized linear model, GLM; hurdle Poisson or negative binomial GLM; zero-inflated Poisson or negative binomial GLM) for each species. Measures of relative model fit were calculated by summing the squared residuals of the fitted DFA common trends and dividing by the sum of the squared observations (delta-lognormal indices) for each survey, and averaging the values for each species. Larger values (≳0.6) indicate poor fit (Zuur et al. 2003b). The value in bold indicates the standardization GLM that produced the best fitting DFA common trend for each species.

| Species | Average Delta-lognormal Fit | Average Hurdle Fit | Average Zero-inflated Fit |
|---|---|---|---|
| Sandbar | **0.19** | 0.57 | 0.65 |
| Blacktip | **0.43** | 0.51 | 0.68 |
| Spinner | **0.68** | --- | --- |
| Tiger | **0.13** | --- | --- |
| Atlantic sharpnose | **0.45** | 0.55 | 0.56 |
| Blacknose | 0.37 | 0.81 | **0.25** |
| Bonnethead | 0.813 | **0.73** | 0.815 |
| Finetooth | 0.59 | **0.29** | --- |

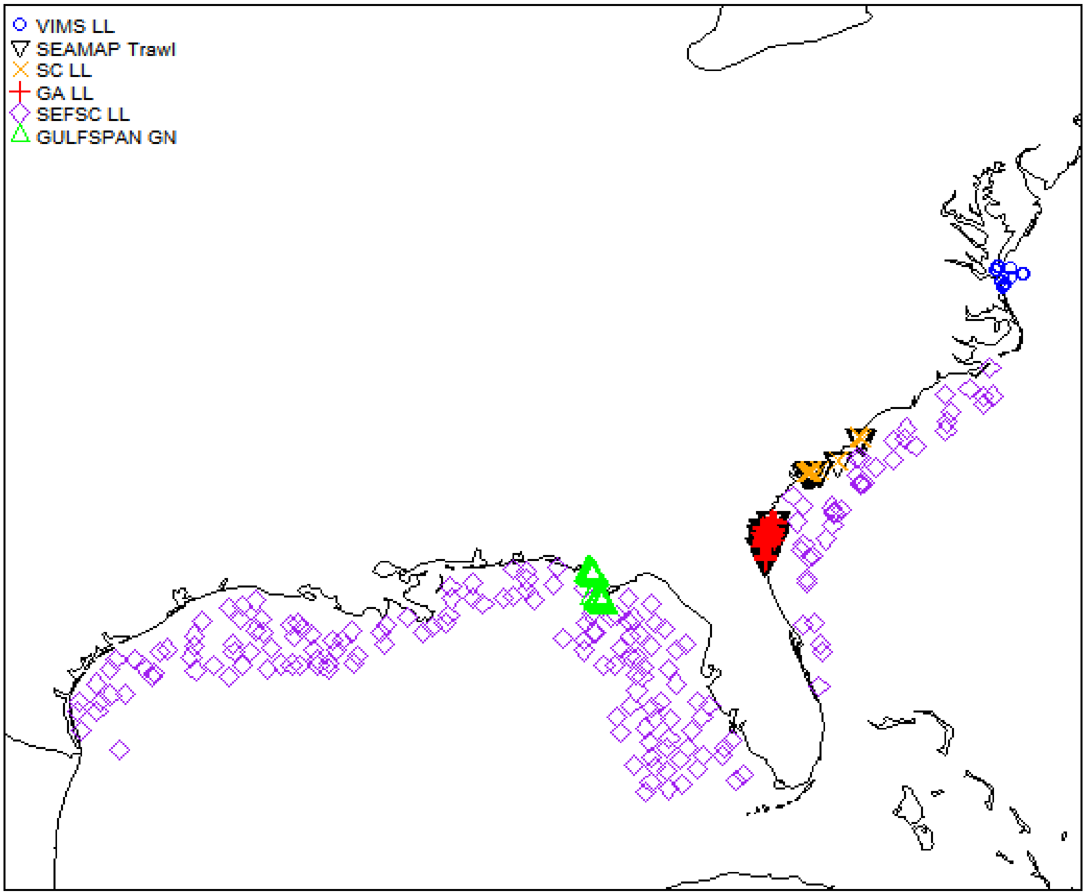
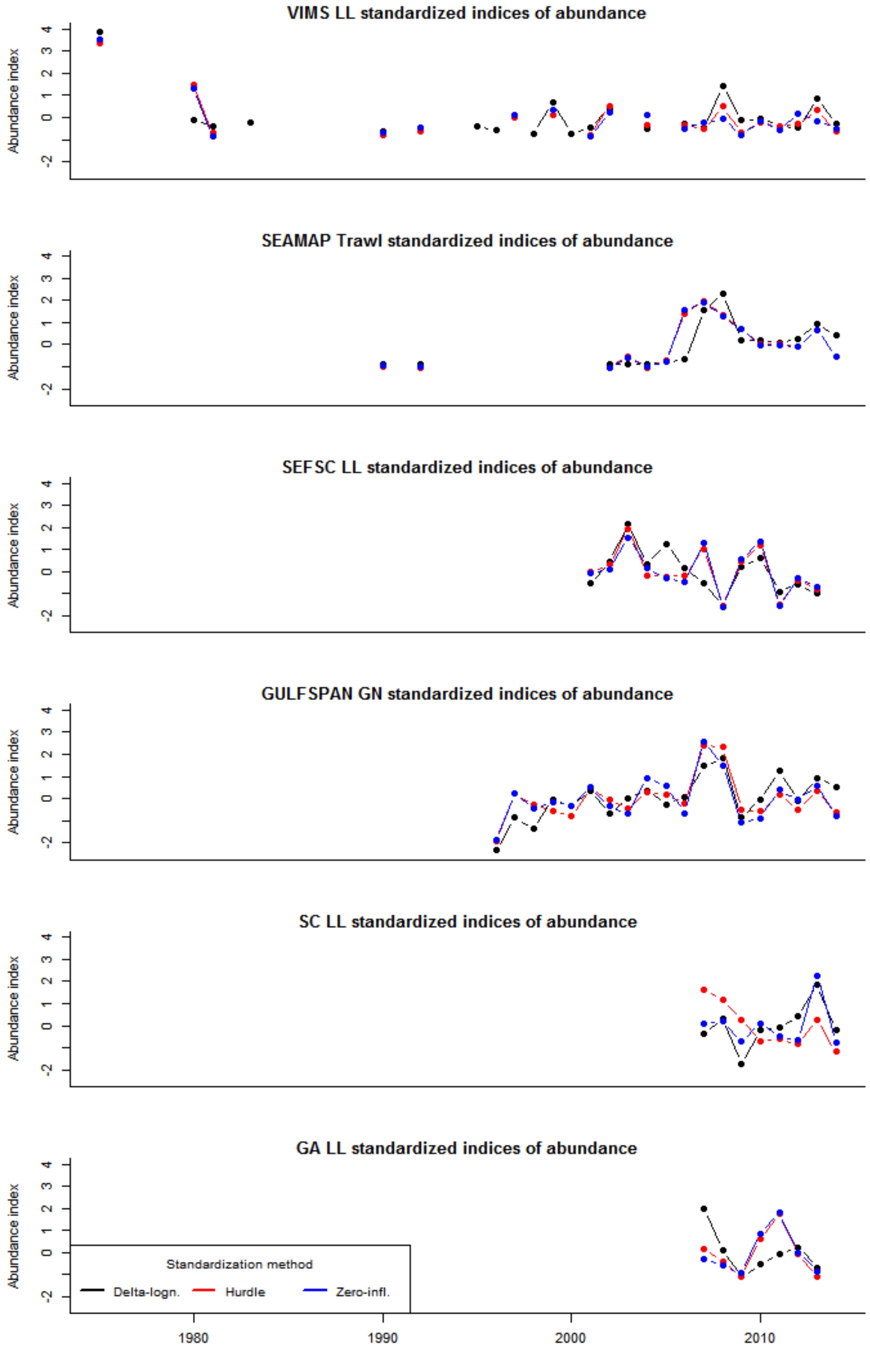


Figure 1. Map of representative stations/sites sampled (for the 2012 sampling year) within each survey: Virginia Institute of Marine Science longline (VIMS LL), South Carolina red drum longline (SC LL), Georgia red drum longline (GA LL), SouthEast Area Monitoring and Assessment Program Trawl (SEAMPA Trawl), SouthEast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN). Map generated using the rworldmap package in R (South 2011).


VIMS LL standardized indices of abundance

SEAMAP Trawl standardized indices of abundance

SEFSC LL standardized indices of abundance

GULFSPAN GN standardized indices of abundance

SC LL standardized indices of abundance

GA LL standardized indices of abundance

Figure 2. Standardized indices of abundance for the blacktip shark using each of the 3 catch-per-unit-effort (CPUE) standardization methods (delta-lognormal generalized linear model, GLM; hurdle Poisson or negative binomial GLM; zero-inflated Poisson or negative binomial GLM) for each survey: Virginia Institute of Marine Science longline (VIMS LL), SouthEast Area Monitoring and Assessment Program Trawl (SEAMPA Trawl), SouthEast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN), South Carolina red drum longline (SC LL), Georgia red drum longline (GA LL).

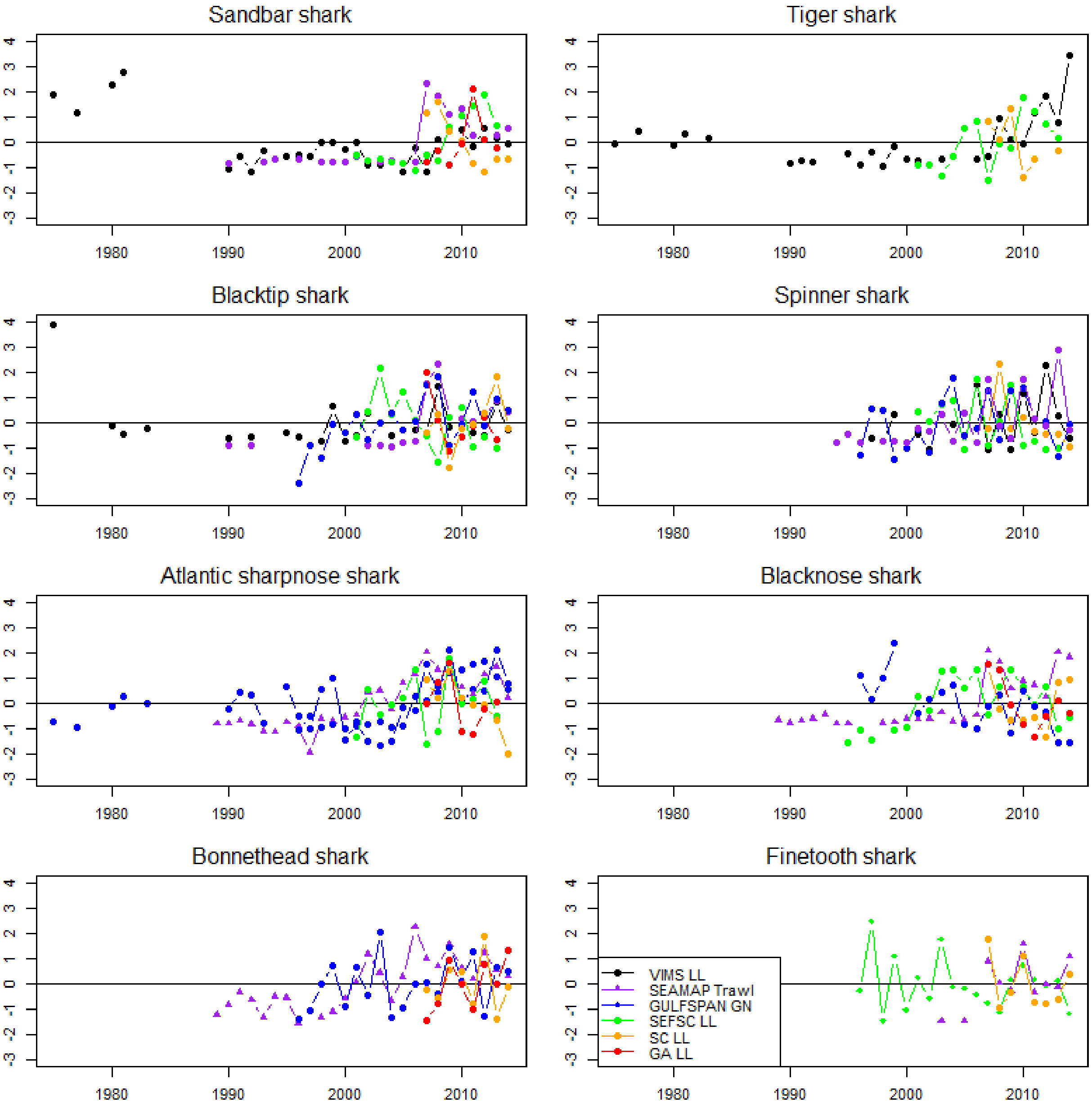


Figure 3. Standardized indices of abundance for each species generated by delta-lognormal generalized linear models (GLMs), representative of data conflict. Survey abbreviations are as follows: Virginia Institute of Marine Science longline (VIMS LL), SouthEast Area Monitoring and Assessment Program Trawl (SEAMPA Trawl), SouthEast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN), South Carolina red drum longline (SC LL), Georgia red drum longline (GA LL).

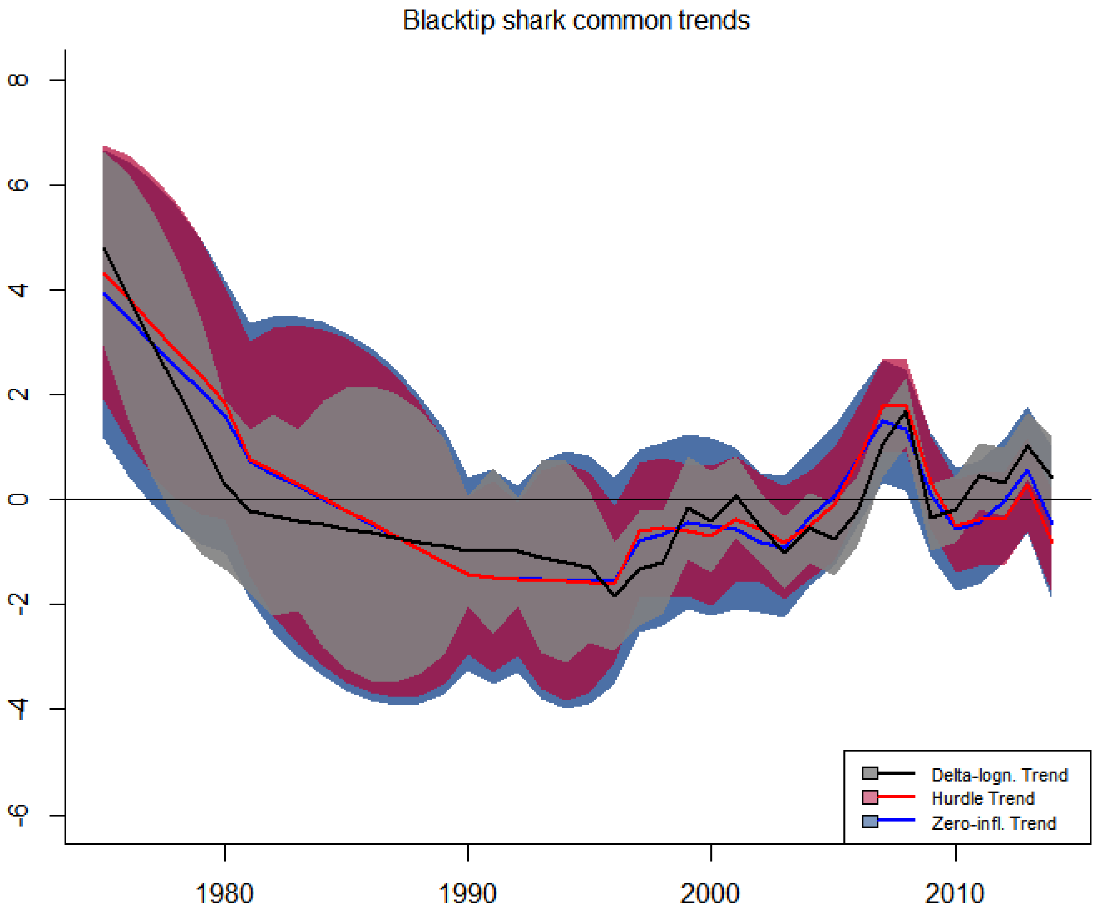


Figure 4. Resulting common trends produced from dynamic factor analysis (DFA) for the blacktip shark. Common trends (solid lines) and 95% confidence intervals (shaded regions) are presented from DFA results from each catch-per-unit-effort (CPUE) standardization method (delta-lognormal generalized linear model, GLM; hurdle Poisson or negative binomial GLM; zero-inflated Poisson or negative binomial GLM).

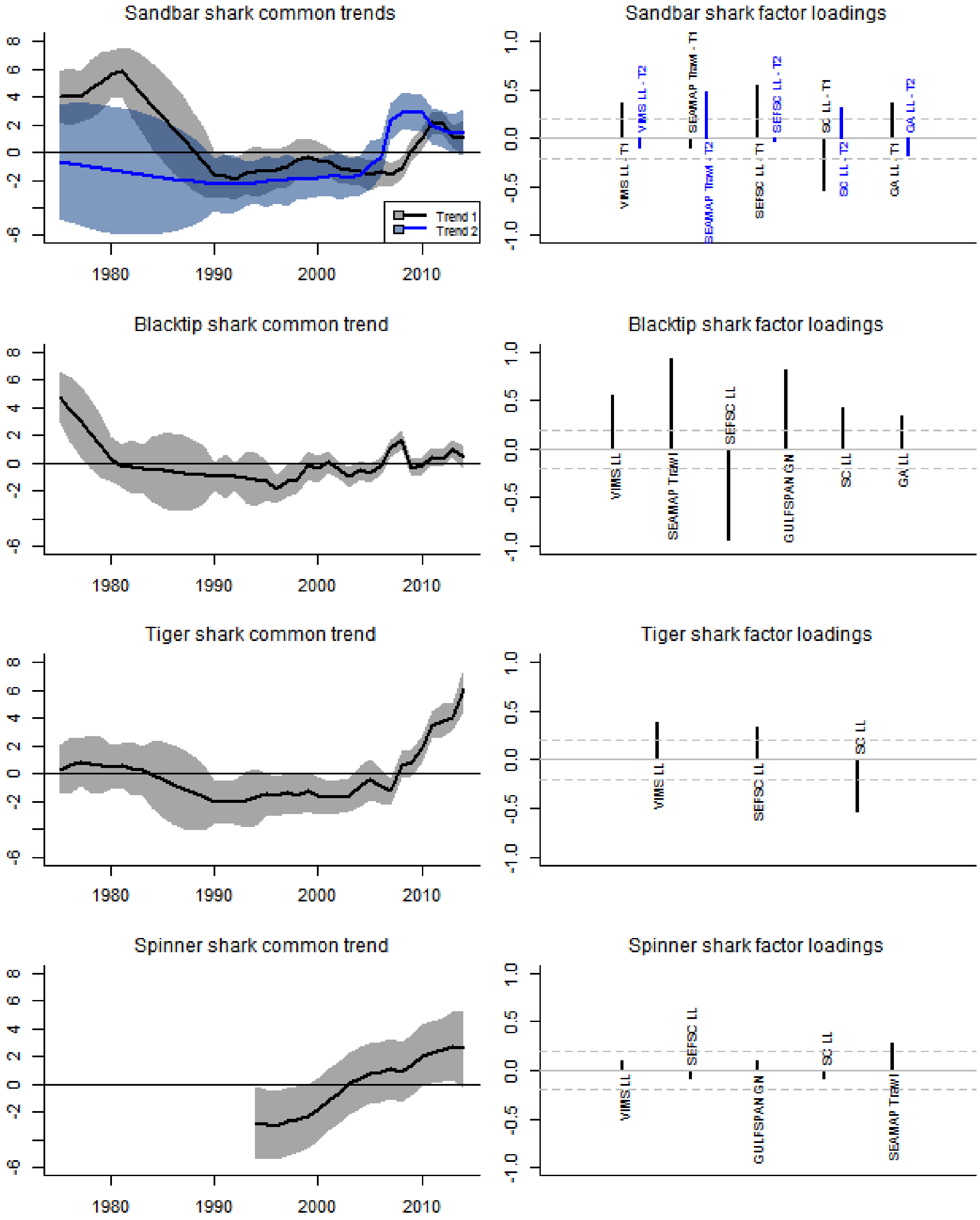
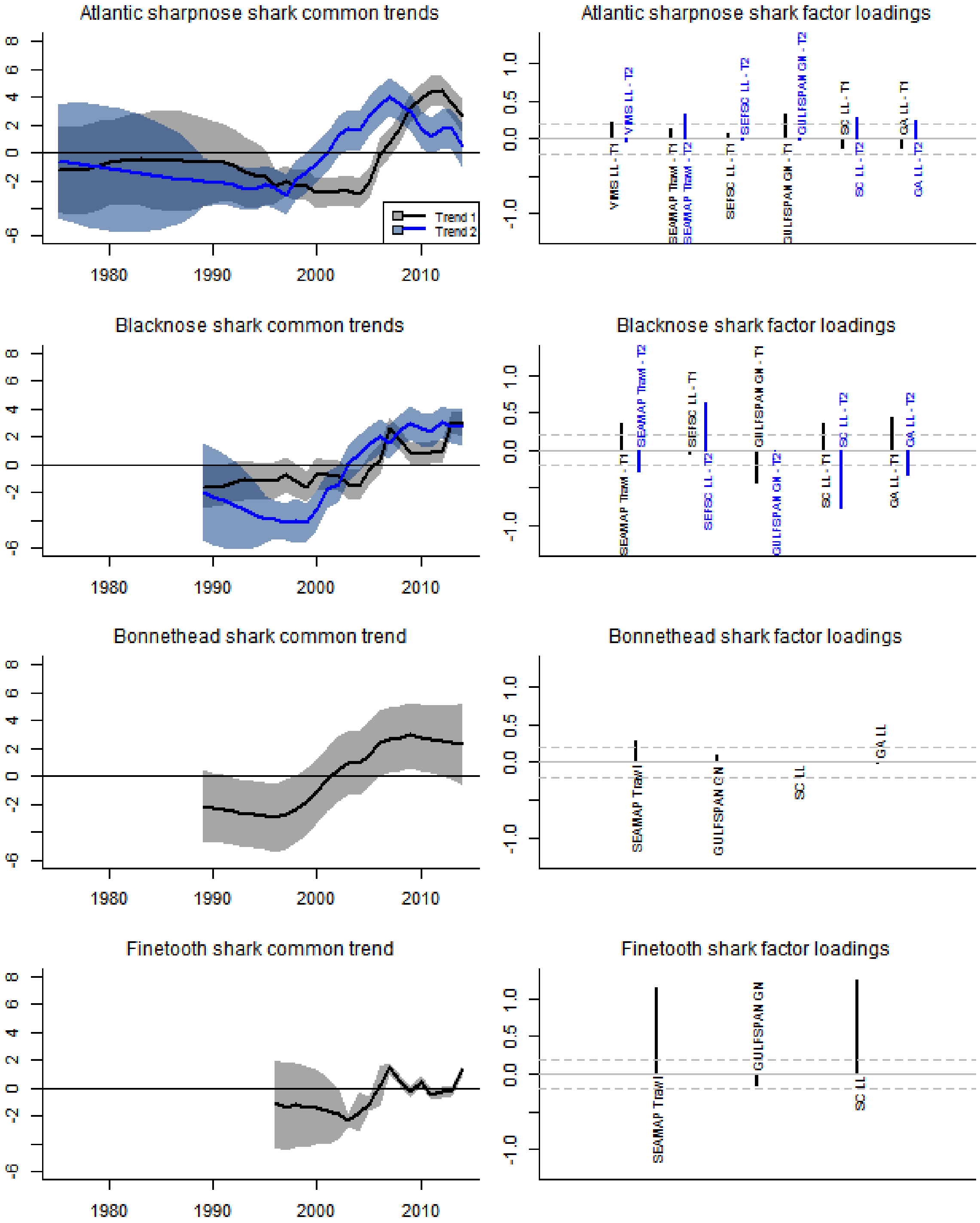


Figure 5. Common trends produced from dynamic factor analysis (DFA) using delta-lognormally derived indices of relative abundance for the large coastal shark (LCS) complex. Trends (solid lines) and 95% confidence intervals (shaded regions) are displayed on the left column, and factor loadings are displayed on the right column. Factor loadings greater than 0.2 represent corresponding indices that had a strong influence on the resulting common trend, and negative factor loadings indicate that the corresponding survey follows an opposite trend than the DFA common trend.



Atlantic sharpnose shark common trends

Atlantic sharpnose shark factor loadings

Blacknose shark common trends

Blacknose shark factor loadings

Bonnethead shark common trend

Bonnethead shark factor loadings

Finetooth shark common trend

Finetooth shark factor loadings

Figure 6. Common trends produced from dynamic factor analysis (DFA) using delta-lognormally derived indices of relative abundance for the small coastal shark (SCS) complex. Trends (solid lines) and 95% confidence intervals (shaded regions) are displayed on the left column, and factor loadings are displayed on the right column. Factor loadings greater than 0.2 represent corresponding indices that had a strong influence on the resulting common trend, and negative factor loadings indicate that the corresponding survey follows an opposite trend than the DFA common trend.

# Chapter 2

## Species interactions and density dependence of coastal shark communities

# Abstract

Studies aiming to assess intra- and interspecies community relationships 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 eight Atlantic coastal shark species, four Large Coastal Sharks (LCS) and four Small Coastal Sharks (SCS), using data from four relatively localized, fishery-independent surveys along the southeast U.S. coast and within the Gulf of Mexico. We then compared these small-scale results to those generated using broad-scale trends in relative abundance extracted as common trends derived from dynamic factor analysis (DFA) applied to indices estimated from six fishery-independent surveys. The MARSS-1 framework was also used to estimate relative community stability. Localized (survey-specific) MARSS-1 analyses identified density dependent compensation in five species and eight interspecies interactions, while results of broad-scale (DFA common trend) MARSS-1 analyses demonstrated density dependence in seven species and seven interspecies interactions. Furthermore, our results support the manifestation of density dependent compensation of neonate and juvenile shark life stages within nursery areas. Results of stability analyses were intuitive, supporting the interactions estimated within the MARSS-1 model. Overall, interactions within localized areas were different from those identified using the broad-scale DFA trends, indicating that small scale interactions cannot be extrapolated to population growth rates of the entire stock.

## Introduction

Sharks are typically considered apex predators that have the capacity to regulate ecosystems via top-down processes (Stevens et al. 2000, Scheffer et al. 2005, Baum & Worm 2009, 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). As top predators, sharks utilize 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). Shark life cycles are typically multifaceted, undergoing ontogenetic changes in habitat use (Heupel & Heuter 2002, McElroy et al. 2006, Grubbs 2010, Castro 2011), diet (Lowe et al. 1996, Bethea et al. 2004, McElroy et al. 2006, Ellis & Musick 2007, Grubbs 2010), migration patterns (Grubbs et al. 2005, McCandless et al. 2005, Parsons & Hoffmayer 2005, Conrath & Musick 2008, Grubbs 2010, Castro 2011), and consequently, intra- and interspecies interactions (Papastamatiou et al. 2006, Grubbs 2010). As a result, sharks occupy wide spatial ranges and several discrete niches over the course of ontogeny, making complete characterizations of population dynamics difficult to define. Similarly, many species school by age, size, and sexual maturity, as exemplified by differential habitat use between neonates, juveniles, and adults as well as between males and females (Heupel & Heuter 2002, Parsons & Hoffmayer 2005, DeAngelis et al. 2008, Drymon et al. 2010, Castro 2011). Inevitably, sharks' predatory and competitive interactions must also change over their lifecycle (Grubbs 2010).

Nursery grounds are critically important to the early life stages of several shark species, where typically shallow, nearshore areas offer protection from significant predation risk (Heupel & Heuter 2002, Heupel et al. 2007). Generally, neonate and juvenile species with relatively small birth sizes and slow initial growth rates utilize nurseries for several years after birth (Heupel et al. 2007, Grubbs 2010). Nursery areas were originally thought to provide abundant, energy rich food resources, but current research suggests the predominant motivation for nursery utilization by sharks may be predator avoidance (Heupel & Heuter 2002, Heupel et al. 2007). It is common for several sympatric shark species to share nursery areas (Bethea et al. 2004, Parsons & Hoffmayer 2007, Ulrich et al. 2007, DeAngelis et al. 2008, Kinney et al. 2010), which increases the potential for interspecies competition (Heupel et al. 2007).

Understanding community interactions is necessary to adequately manage species, particularly at the ecosystem level (Morin 2011). 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 of tiger sharks (*Galeocerdo cuvier*; Lowe et al. 1996, Simpfendorfer et al. 2001), sandbar sharks (*Carcharhinus plumbeus*; McElroy et al. 2006, Ellis & Musick 2007, McElroy 2009), and several juvenile coastal species within nursery areas (Hoffmayer & Parsons 2003, Bethea et al. 2004). However, diet analyses often group prey species into broad taxonomic categories (i.e. 'elasmobranch'; Lowe et al. 1996, Simpfendorfer et al. 2001), such that inferring specific predator-prey interactions is challenging (Grubbs et al. 2016). Furthermore, diet composition does not directly reflect the importance of the interaction between the predator and prey species (Heithaus et al. 2010).

Resource partitioning studies that evaluate the extent of local interspecies competition have been conducted within several coastal shark nursery areas (Bethea et al. 2004, DeAngelis et al. 2008, Kinney et al. 2011, Ward-Paige et al. 2014), shallow seagrass beds in Australia (White & Potter 2004, Heithaus et al. 2013), and other easily accessible, nearshore environments (Platell et al. 1998, Papastamatiou et al. 2006). These studies have proposed that resource partitioning is occurring within shark communities, 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). Additionally, predator avoidance has been shown to dictate neonate and juvenile shark behavior within nursery areas (Heupel & Heuter 2002, Heithaus et al. 2007, DeAngelis et al. 2008), indicating that antipredator behaviors (risk effects) play an important, but unmeasurable, role in juvenile and small prey species' population growth rates (Heithaus et al. 2008, 2010). Studies of species interactions traditionally have been limited to easily accessible, shallow-water habitats in which shark congregations are known to occur (White & Potter 2004, DeAngelis et al. 2008), such that interactions occurring on a broader scale or outside the local range of these studies remain unexplored.

While rarely proven, several studies have proposed density dependent regulation of shark populations, where the growth of a population is a function of the density of the population (Gedamke et al. 2007, 2009, Cortés et al. 2012). Several mechanisms for density dependence have been offered, including increased survival of neonate 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 and Gallucci 2009). Currently, the most commonly accepted compensatory response mechanism of density dependence remains altered neonate and juvenile survival (Cortés et al. 2012). However, since proposed density dependence may be confounded by other factors, such as selective fishing pressure (Márquez-Farias & Castillo-Geniz 1998, Stevens et al. 2000, Carlson & Baremore 2003, Sosebee 2005), it has rarely been definitively demonstrated in elasmobranchs.

Nevertheless, density dependence has been assumed in various elasmobranch population (Au & Smith 1996, Gedamke et al. 2009, De Oliveira et al. 2013) and stock assessment models (SEDAR 2013).

The large ranges and migratory patterns of many shark species make any generalized, broad-scale analyses challenging. Thus, studies concerning shark interactions have been limited to localized, small-scale analyses. In the current study, we sought to quantitatively examine species interactions (including density dependence) within and between Large and Small Coastal Shark species complexes along the U.S. east coast. Secondarily, as afforded by the models employed, we examined relative community stability of each species complex.

## Methods

### *Data sources*

Catch data from six fishery-independent surveys along the U.S. east coast and the Gulf of Mexico (Virginia Institute of Marine Science longline, VIMS LL; Southeast Area Monitoring and Assessment Program trawl, SEAMAP Trawl; South Carolina Red Drum longline, SC LL; Georgia Red Drum longline, GA LL; Southeast Fishery Science Center longline, SEFSC LL; Gulf of Mexico Shark Pupping and Nursery gillnet, GULFSPAN GN; Figure 1) were examined to estimate trends in relative abundance, species interactions, and community stability of U.S. east coast shark complexes (Table 1).

### *Trends in 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 Chapter 1). At least three surveys could be used to generate indices of abundance for eight Atlantic coastal shark species, including four Large Coastal Shark (LCS) species (sandbar, blacktip *Carcharhinus limbatus*, spinner *C. brevipinna*, tiger) and four Small Coastal Shark (SCS) species (Atlantic sharpnose *Rhizoprionodon terraenovae*, blacknose *C. acronotus*, bonnethead *Sphyrna tiburo*, finetooth *C. isodon*; Table 2).

Indices of abundance for each species were input into dynamic factor analysis (DFA) models with environmental (North Atlantic Oscillation index) and anthropogenic (species landings) covariates to estimate underlying trends of abundance across the sampled distribution (see Chapter 1 for complete details). Resulting common trends were rescaled between the minimum and maximum values of the delta-lognormally generated indices of abundance to retain a measure of relative scale necessary for log-transformation.

*Multivariate, first-order autoregressive, state-space models (MARSS-1)*

Trends of species abundance were implemented into multivariate, first-order autoregressive, state-space models (MARSS-1), derived from the Gompertz population growth equation (Ives et al. 2003). The MARSS-1 models are of the form:

$$x_t = Bx_{t-1} + w_t, \text{ where } w_t \sim MVN(0, Q)$$

$$y_t = Ix_t + v_t, \text{ where } v_t \sim MVN(0, R) \tag{1}$$

where $x$ is the $n\times1$ vector of log-transformed measured species relative abundance at time $t$ for $n$ total species/populations, $B$ is the $n\times n$ species interaction matrix where the elements $b_{ji}$ represent the effect of species $i$ on the population growth rate of species $j$, $y$ is the $n\times1$ vector of true log-transformed species relative abundance, $I$ is the identity matrix, and $w$ and $v$ represent the multivariate normally distributed process and observation errors at time $t$ with associated covariance matrices $Q$ and $R$ (Holmes et al. 2014).

While the complexity of this model lies within the process component, which identifies the autoregressive community interactions within the system, the observation component serves to account for sources of observation or human-induced error. The focus of this study is estimation of the *B* matrix, because elements of the matrix contain information on density dependent compensation and how species interactions impact the overall population growth rates of other members included in the complex. Specifically, diagonal elements are a measure of density dependence such that values near one are indicative of density dependent compensation (i.e. abundance of species *i* at time *t* is measured as a function of element $b_{ii}$ multiplied by species abundance at time *t-1*). Off diagonal elements, $b_{ij}$, measure the influence of species *j* on the population growth rate of species *i*. Values that were statistically different from zero were interpreted as suggestive of density dependent regulation, or significant interspecies interactions.

This model structure also allows for the calculation of relative community stability via properties of the *B* matrix when the system is in equilibrium. Five equations were used to assess four measures of community stability: i) *resilience* is a measure of the time required for the mean of the stationary distribution to return to equilibrium following a perturbation, ii) *return rate* measures the length of time required for the variance of the community to return to equilibrium conditions following a perturbation (Ives et al. 2003, Hampton et al. 2013), iii) *variance of the stationary distribution* measures the extent to which environmental fluctuations are amplified by environmental perturbations (Ives et al. 2003, Grossman & Sabo 2010) or the 'volume' of the stationary distribution (Holmes et al. 2014), and iv) *reactivity* (and *worst-case reactivity*) measures the magnitude of the response of the community to a perturbation (Ives et al. 2003, Britten et al. 2014; Table 2). Worst-case reactivity was also calculated to alleviate uncertainty associated with the calculation of reactivity (via the *Q* matrix; Ives et al. 2003).

### *MARSS-1 model fitting*

Models were fitted in several steps. To ensure model convergence, known yearly variances from the DFA common trends were averaged to produce a single estimate of index variability for each species, which was specified along the diagonal of the observation error covariance matrix, *R*. Hence, we assumed that no covariance between species indices existed within the observation error (i.e., non-diagonal elements were set to zero). The process error covariance matrix, *Q*, which measures the degree to which each species is affected by environmental or other external perturbations, was estimated from three different structures: i) a diagonal and equal structure in which all variances are assumed to be equal and covariance is set to zero, ii) a diagonal and unequal structure in which each variance is assumed to be unique and covariance is set to zero, and iii) an unconstrained matrix in which all variances and covariances are independently estimated.

Convergence problems arose when trying to estimate every element of the *B* matrix. Hence, relevant species interactions were chosen *a priori* based on biological and ecological inferences derived from previous research (Bethea et al. 2004, Papastamatiou et al. 2006, Parsons & Hoffmayer 2007, Ulrich et al. 2007, Drymon et al. 2010, Castro 2011). The interactions were necessarily one sided (i.e., we estimated the effect of species X on species Y, and not the effect of species Y on species X), enabling the MARSS-1 models to converge. Thus, exploratory analyses were conducted by fitting 'base' *B* matrices to determine the directionality of the interactions to be included in the final *B* matrix. The successful interactions from the previous step were combined into a single *B* matrix, and between 16 and 32 unique combinations of the chosen interactions were fitted for each model run. Optimal models were selected by AICc (Hampton et al. 2013, Holmes et al. 2014). All models within two AICc units from the optimal model were analyzed, and models that resulted in the lowest uncertainty in parameter estimates were chosen for final analysis. Ninety-five and 90% confidence intervals (CIs) were used to assess significance of the elements of the final *B* matrix. All models were fitted using the 'MARSS' package (Holmes et al. 2013) in R (version 3.1.1).

The MARSS-1 models were fitted on two spatial scales: i) local (geographically limited) species interactions were investigated by fitting models to delta-lognormally generated indices of abundance from each survey with sufficient longevity (VIMS LL, GULFSPAN GN, SEAMAP Trawl, SEFSC LL), and ii) broad scale interactions were identified by fitting models to DFA common trends, which are representative of large scale trends in relative abundance for each species. 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 $B$ matrix were manually specified within the final $B$ matrix when all shark species were included. This effectively allowed us to model interactions between species complexes which would not have been otherwise possible because of the number of parameters to be estimated. When all species were included in the MARSS-1 model, the process error covariance matrix assumed equal variances for all LCS species and a separate measure of equal variances for all SCS species.

## Results

*Localized MARSS-1 modeling*

A diagonal and equal process error covariance matrix structure was used in each survey-specific MARSS-1 model. A diagonal covariance matrix $Q$ assumes that the environmental factors driving variation in one species relative abundance is uncorrelated to environmental factors driving all other species relative abundances (Holmes et al. 2014). Survey-based MARSS-1 modeling results suggested two significant interactions within coastal Virginia waters (Table 4). The sandbar shark showed density dependence within the VIMS LL sampling area (Figure 1), and the presence of tiger sharks had a significantly positive effect on the Atlantic sharpnose shark. Within the SEFSC LL sampling area (offshore Gulf of Mexico and southeast Atlantic coast), the sandbar shark showed local density dependence (Table 5). A positive effect of spinner sharks on the population growth rate of blacktip sharks was detected, while the sandbar shark had a negative effect on the spinner shark and the blacktip shark had a negative effect on the sandbar shark. The $B$ matrix derived from the SEAMAP Trawl MARSS-1 model suggests that blacktip, spinner, blacknose, and finetooth sharks within the coastal southeast Atlantic experience density dependence (Table 6). Three additional positive effects were identified: the blacktip shark had a positive effect on sandbar and spinner shark populations, and Atlantic sharpnose sharks had a positive effect on blacknose shark populations. Results of the GULFSPAN MARSS-1 $B$ matrix showed that the Atlantic sharpnose shark population exhibited density dependence in the northeastern Gulf of Mexico (Table 7). Additionally, the presence of Atlantic sharpnose sharks had a negative effect on the population growth rate of the blacknose shark along the northern Gulf coast of Florida (Figure 1).

### *Dynamic factor analysis*

For complete DFA results, refer to chapter 1. Common trends produced by DFA consisted of a single trend estimated for the blacktip, spinner, tiger, bonnethead, and finetooth sharks, and two common trends for the sandbar, Atlantic sharpnose, and blacknose sharks (Figures 2 & 3). Based on factor loadings, which relate the strength of the influence of each survey on the resulting common trends, the secondary sandbar trend was dominated by neonate and small juvenile individuals, so this trend was excluded from MARSS-1 analyses. The primary sandbar shark trend was representative of the Atlantic coast and Gulf of Mexico, similar to the blacktip and tiger sharks, and was therefore retained. The two common trends for the Atlantic sharpnose and blacknose sharks were each representative of the Atlantic or the Gulf of Mexico. However, the primary Atlantic sharpnose shark trend was strongly driven by both the Gulf of Mexico and the coast of Virginia. Additionally, the Gulf of Mexico GULFSPAN GN survey showed an opposite trend for Atlantic blacknose shark, demonstrated by a negative factor loading. Spinner, bonnethead, and finetooth shark common trends were only strongly influenced by the SEAMAP Trawl and the SC LL, indicating that species interactions can only be interpreted within the southeast Atlantic coast.

### *Broad-scale MARSS-1 modeling*

In the LCS and SCS MARSS-1 analyses using DFA common trends, a diagonal and equal process error covariance matrix was selected in the optimal model, likely due to the reduced number of estimated parameters. Resulting optimal $B$ matrices were compared using all three covariance structures, in addition to a compound symmetric structure to assess the effect of assuming independence between species. Relative values of the resulting $B$ matrix elements resulted in identical model interpretation.

The resulting $B$ matrix from the LCS MARSS-1 model suggested the existence of density dependent regulation in the sandbar, spinner, and tiger sharks, but not in the blacktip shark (Table 8). The presence of tiger sharks had a positive effect on the population growth rates of sandbar and spinner sharks. Moreover, spinner sharks had a positive effect on blacktip shark population growth rate.

Within the Atlantic SCS complex, bonnethead and finetooth sharks showed density dependence (Table 8). Measures of density dependence were not statistically different from zero for Atlantic sharpnose and blacknose sharks (95% CI: -0.85 – 1.36 and -0.50 – 1.28, respectively), such that no conclusion could be drawn. Within the Gulf of Mexico, density dependence was observed in the Atlantic sharpnose and blacknose sharks, and the blacknose shark had a negative influence on the population growth rate of the Atlantic sharpnose shark. The Atlantic sharpnose Gulf of Mexico trend (which also contains positive loadings from coastal Virginia) MARSS-1 results support the occurrence of density dependence within the Gulf of Mexico.

When LCS and SCS were modeled together, large species generally had a negative influence on small species (Table 8). For example, sandbar sharks had a negative effect on the population growth rate of the bonnethead shark in the Atlantic. In the Gulf of Mexico, tiger sharks had a negative influence on blacknose shark populations, while blacktip sharks had a positive effect on blacknose sharks. These significant species interactions were not detected among Atlantic populations.

### *Stability analysis*

Results from the stability analysis of the $B$ matrix suggested that the SCS complex was more resilient and had a faster return rate than the LCS complex and the aggregation of all shark species (Table 9), reaching the mean and variance of the stationary distribution more quickly than the other communities following a perturbation. The LCS community had a smaller variance of the stationary distribution, indicating that environmental fluctuations were not amplified by species interactions and the stationary distribution experienced a smaller inherent variability. The aggregated shark complex experienced the lowest reactivity, with perturbations resulting in a smaller displacement from equilibrium conditions than in the LCS or SCS coastal complexes.

## Discussion

### *Density dependence*

Within the localized, survey-specific MARSS-1 modeling framework, density dependence was noted in five species: sandbar (VIMS LL, SEFSC LL), Atlantic sharpnose (GULFSPAN GN), blacktip (SEAMAP Trawl), blacknose (SEAMAP Trawl), and finetooth (SEAMAP Trawl) sharks. Sandbar sharks showed density dependence within Virginia coastal waters, likely due to the role of the Chesapeake Bay as an important primary nursery area for this species (Grubbs et al. 2005). Density dependence is thought to primarily manifest via survival of neonate and young juvenile sharks (Cortés et al. 2012). Hence, sandbar shark density dependence in this region may therefore be linked to compensatory survival rates of early life stages within nursery habitats. Larger, adult sandbar sharks may compete for resources as well, or density dependent compensation found within the Gulf of Mexico noted by the SEFSC LL may also represent younger individuals.

The SEAMAP trawling occurs over a known nursery area off the coast of South Carolina (Ulrich et al. 2007), where density dependence was found within blacktip, spinner, and finetooth sharks. As all three of these species are known to inhabit nursery areas along the southeast Atlantic coast (Castro 1993a; Ulrich et al. 2007), immature sharks are likely driving density dependence. Similarly, the GULFSPAN GN survey samples a northwestern Florida shark nursery area (Bethea et al. 2004). Within shallow coastal areas, juvenile and adult Atlantic sharpnose sharks are ubiquitous (Parsons & Hoffmayer 2007, Ulrich et al. 2007, Drymon et al. 2010). Although it has been hypothesized that Atlantic sharpnose sharks do not occupy discrete nursery areas due to fast juvenile growth rates (Heupel et al. 2007), they exhibited density dependence within the northeastern Gulf of Mexico. Since over half of the Atlantic sharpnose sharks captured within the GULFSPAN GN were immature (59.7%; unpublished data), it is likely that neonate and juvenile individuals are driving the pattern of density dependence within this species, as suggested by Cortés et al. (2012).

The results of the broad scale study quantitatively supported the existence of density dependence in seven out of 10 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 lends quantitative support to the notion that at least some species experience density dependence. While it is likely that the remaining three populations exhibit density dependence and the underlying data did not permit precise estimation of these parameters, it is also possible that blacktip sharks, and Atlantic populations of Atlantic sharpnose and blacknose sharks do not exhibit broad-scale density dependence. No evidence suggests that density dependence does not occur within elasmobranch species. However, such a life history strategy would have substantial implications as population sizes decline, thus reducing the ability of depleted populations to recover.

*Interspecies interactions*

The significantly positive effect of the tiger shark on the Atlantic sharpnose shark inferred from the VIMS LL *B* matrix may be indicative of a competitive interaction. A predatory release mechanism, for example, in which the tiger shark preys on a species (e.g. sandbar shark, Papastamatiou et al. 2006, Castro 2011) that feeds on Atlantic sharpnose sharks, might have contributed to this interspecific interaction in the coastal mid-Atlantic region. Alternatively, if conditions are favorable for one species, they can be simultaneously favorable for sympatric species, such that positive correlations among species are formed. Such a correlation could occur between the Atlantic sharpnose shark and the tiger shark, driving this relationship despite their dissimilar life history characteristics (Castro 2011).

Additional competitive interactions between LCS (sandbar on spinner, blacktip on sandbar) were identified across the broad geographical areas surveyed by the SEFSC LL. Juvenile sandbar and blacktip sharks consume teleosts, primarily clupeids and sciaenids (Stillwell & Kohler 1993, Hoffmayer and Parsons 2003, McElroy et al. 2006, Ellis & Musick 2007, Barry et al. 2008, McElroy 2009). Although the diet of spinner sharks has not been extensively examined, evidence suggests the mutual consumption of clupeids (e.g., menhaden, *Brevoortia spp.*), by spinner sharks in the Gulf of Mexico and sandbar sharks in the Atlantic coast (Bethea et al. 2004, McElroy 2009). Thus, interspecific interactions in the southeast Atlantic may be facilitated by competition for overlapping prey resources among sandbar, blacktip, and spinner sharks (Bethea et al. 2004). Spinner sharks have a significantly positive effect on the blacktip shark, comparable in magnitude to the positive interaction observed in the broad-scale MARSS-1 model. In the GULFSPAN GN nursery area, Atlantic sharpnose and blacknose sharks show a competitive interaction, which is plausible based on observed overlap in habitat use (Drymon et al. 2010) and dietary breadth (Castro 2011).

Positive relationships noted within the SEAMAP Trawl *B* matrix could be exaggerated by anthropogenic factors. Mandatory bycatch reduction device (BRD) implementation was established off the southeast U.S. Atlantic coast in 1997 (Scott-Denton et al. 2012), after which catches of blacktip, Atlantic sharpnose, and blacknose sharks increased within the SEAMAP Trawl. Consequently, management measures may have confounded any biological interactions that exist within the SEAMAP Trawl survey area, so interspecific interactions should be interpreted with care.

Broad-scale analyses revealed seven additional statistically significant interactions that affect inter-specific population growth rates (Figure 4). Juvenile diet and habitat overlap was observed between blacktip and spinner sharks within a Gulf of Mexico nursery area (Bethea et al. 2004), while larger age classes (sub-adults and adults) have been known to co-school (D. Grubbs via Ha 2006). Data from the VIMS LL indicated that when present, blacktip and spinner sharks co-occurred in 35% of longline sets (unpublished data), which suggest co-schooling behavior in the Mid-Atlantic region, and this relationship has the potential to impact population growth rates of both species. In particular, our analyses demonstrated that the presence of spinner shark had a positive effect on the blacktip shark, indicating that co-schooling was beneficial for the blacktip shark. Simultaneously, the tiger shark, which is known to feed on blacktip sharks and other medium-sized elasmobranchs

(Castro 2011), had a positive effect on the population growth rate of the spinner shark. This relationship may result from tiger shark predation on density-dependent life stages (i.e. neonates) of spinner sharks, or from predation on blacktip sharks, thereby reducing competition for resources between blacktip and spinner sharks. Despite the model selection approach choosing a $B$ matrix that did not estimate the effect of tiger on blacktip sharks, it is possible that tiger sharks were feeding on blacktip sharks in areas outside the range of spinner sharks, such that blacktip sharks benefited from schooling with a species that is potentially less vulnerable to predation by tiger sharks. Similar 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 $B$ matrix by 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 (Heithaus et al. 2010). While spinner sharks may be more challenging for tiger sharks to capture due to larger maximum sizes relative to blacktip sharks (Castro 2011), improved knowledge of predator avoidance capabilities, migratory patterns, and seasonal co-occurrence of blacktip, spinner, and tiger sharks in the western North Atlantic is required before insightful conclusions can be drawn. Furthermore, blacktip and spinner sharks are easily confused due to similar morphologies (Castro 2011), and the potential for misidentification of these species suggests blacktip and spinner shark interactions should be interpreted with care.

Tiger sharks also demonstrated strong interactions with sandbar sharks along the U.S. east coast and within the Gulf of Mexico, where increased population growth of sandbar sharks was observed with 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). A predatory release interaction is unlikely, due to the large sizes and generally high trophic position of sandbar sharks. However, if tiger sharks preyed on juvenile and neonate sandbar sharks within their nursery grounds, this predatory interaction likely stimulated the population growth rate of density-dependent sandbar sharks. Our findings support that shark density dependent compensatory responses manifest in neonate and juvenile survival rates within nursery areas (Gruber et al. 2001). Additional mechanisms underlying the interactions between large and highly migratory tiger and sandbar shark populations are likely linked to trophic dynamics (e.g., resource partitioning resulting in a mutually beneficial relationship). These two species may also rely on similar environmental conditions such that a large abundance of tiger sharks is correlated to a similarly large abundance of sandbar sharks (apparent competition).

A predatory interaction of tiger sharks on blacknose sharks within the Gulf of Mexico was identified in the present study. Tiger sharks have been known to feed on various small and medium-sized elasmobranchs (Lowe et al. 1996, Kohler et al. 1998, Simpfendorfer et al. 2001, Castro 2011). However, predator avoidance behaviors may also be playing an indirect role in the reduced population growth rate of blacknose sharks, in which the prey species will forego optimal environmental conditions to avoid direct predation (Heithaus et al. 2008, 2010). These anti-predatory behaviors, which are typically displayed by long-lived species, have the capacity to reduce effective carrying capacity of the environment for a species, and can act synergistically with direct predatory effects to magnify the negative effects of predators on prey species (Heithaus et al. 2010).

Within the Gulf of Mexico, presence of blacknose sharks had a positive effect on Atlantic sharpnose sharks. The DFA common trend for the Atlantic sharpnose shark is primarily driven by the VIMS LL and the GULFSPAN GN surveys, while the blacknose common trend was largely driven by the SEFSC LL survey. While both blacknose DFA common trends followed a similar pattern, it is worthwhile to note that the GULFSPAN GN negatively loaded onto the Atlantic trend. Thus, it is possible that the interaction between the two species was competitive, despite producing a positive value. This hypothesis can be further demonstrated by considering the competitive interaction between Atlantic sharpnose and blacknose sharks of similar magnitude found in the GULFSPAN GN $B$ matrix. Atlantic sharpnose and blacknose sharks are known to feed on menhaden and other small teleosts (Bethea et al. 2006, Castro 2011), and Drymon et al. (2010) suggested that these species inhabit similar habitat ranges within the Gulf of Mexico. Niche overlap between these small coastal sharks might result in frequent interspecific competition for food resources.

The presence of blacktip sharks was found to have a positive effect on blacknose sharks within the Gulf of Mexico. While the Gulf of Mexico blacknose shark common trend was primarily driven by the SEFSC LL (with smaller, negative loadings from the SEAMAP Trawl), the blacktip shark trend was positively influenced by the SEAMAP Trawl and negatively driven by the SEFSC LL. Hence, this positive interaction coefficient could be indicative of negative competitive interactions. Due to high uncertainty, this hypothesis could not be supported in corresponding SEFSC LL and SEAMAP Trawl $B$ matrix interactions. Blacknose and blacktip sharks consume small teleost species, like clupeids (Hoffmayer and Parsons 2003, Barry et al. 2008, Castro 2011), and habitat overlap has been noted within the Atlantic coast (Ulrich et al. 2007), Florida Keys (Heithaus et al. 2007), and the Gulf of Mexico (Drymon et al. 2010). Notwithstanding, it is likely that when local environmental conditions are favorable for population growth rate of one species, sympatric species may exhibit similar responses.

Lastly, MARSS-1 analyses identified a predatory interaction of sandbar on bonnethead sharks in the Atlantic Ocean. Sandbar sharks have been known to feed on bonnethead sharks and follow shrimp trawlers to exploit bycatch within the Atlantic Ocean

(Castro 2011) and the Gulf of Mexico (Carlson 1999). Bonnethead sharks are commonly captured as bycatch within the shrimp fishery (Scott-Denton et al. 2012, SEDAR 2013), providing a mechanism facilitating this interaction. Furthermore, these species' distributions have been shown to overlap within the Florida Keys (Heithaus et al. 2007) and off the coast of South Carolina (Ulrich et al. 2007). Antipredator behaviors of bonnethead sharks may occur in response to sandbar sharks that further reduces intraspecific population growth rate (Heithaus et al. 2008, 2010).

Finetooth sharks have widely been shown to compete (in habitat and diet) with spinner and blacktip sharks in the Gulf of Mexico (Hoffmayer & Parsons 2003, Bethea et al. 2004, Parsons & Hoffmayer 2007, Drymon et al. 2010). Unfortunately, we did not have a representative trend of finetooth shark abundance from the Gulf of Mexico and as such were unable to assess this interaction. Similarly, interactions between bonnethead sharks and other species from the Gulf of Mexico could not be assessed.

### *Community stability*

Despite likely violating the assumption of equilibrium conditions, the results of the stability analyses were intuitive, and lend further credibility to the accuracy of the $B$ matrix from which these conclusions were derived. The small coastal sharks analyzed have faster growth rates relative to LCS, enabling the SCS complex to recover more quickly from environmental or anthropogenic disturbances (i.e. faster resiliency and return rate). The LCS species examined are migratory and likely avoid unfavorable environmental conditions (Chapter 1), such that these environmental variables likely have a limited effect on equilibrium conditions. This environmental insensitivity of the LCS complex was reflected in the smaller variance of the stationary distribution. Lastly, despite controversy, it has been shown that community stability increases with the number of species (McCann 2000). In the current study, when all sharks were included in the analyses, the reactivity (and worst-case reactivity) was the smallest, indicating that perturbations had a smaller overall effect on the broader community.

*MARSS-1 modeling*

Graphical analysis suggested that overall model fits were appropriate in the current study, and models appeared to produce realistic characterizations of local and broad-scale shark community interactions. Similarly, the MAR-1 model framework has been shown to match empirical estimation of community interactions within planktonic freshwater lake communities (Hampton et al. 2006, Hampton & Schindler 2006), and provide simple approximations to complex, nonlinear processes (Ives et al. 2003). Further, MAR-1 results have been shown to be robust to the foundation of a Gompertz versus Ricker population growth model (MacNally et al. 2010). Hence, several MAR-1 studies have been conducted on various freshwater and marine ecosystems (Hampton & Schindler 2006, Hampton et al. 2008, Grossman & Sabo 2010, MacNally et al. 2010, Francis et al. 2012, Hampton et al. 2013, Britten et al. 2014).

Nevertheless, implementation of these models in a state-space framework (MARSS-1; i.e. including observation error) provides additional flexibility in data structure and accounts for both known sources of error (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 MARSS-1 analyses (Holmes et al. 2014) can accommodate missing data without prior linear interpolation or truncation. Consequently, in the current study, the entire 40-year time-series could be utilized for analyses, without truncating all common trends to the length of the shortest or eliminating species from analysis. A downside to the state-space framework involves pre-specifying the *B* matrix structure to ensure convergence. Incorporating preexisting biological knowledge to specify the elements of the *B* matrix to be estimated is vital, because a different configuration will result in different interpretations of results (Ives et al. 2003, Holmes et al. 2014).

### *Conclusions*

While some community interactions derived from the broad-scale (DFA common trend) MARSS-1 analysis are supported in the survey-specific MARSS-1 analyses (i.e. positive effect of spinner on blacktip shark), the majority of identified interactions are distinct. This suggests that localized interactions that can be inferred from survey-specific MARSS-1 analyses cannot be generalized across a broader distribution or the entire life-cycle of each stock. Thus, whole population community analyses that actually affect species population growth rates can only be obtained given inputs that encompass a broad area, providing merit to the procedure employed in the current analysis. Nevertheless, implementation of survey-specific analyses was useful for characterizing small-scale, localized interactions, and for assisting interpretation of broad-scale *B* matrix analyses.

The DFA common trends are representative of trends of relative abundance across the southeast Atlantic coast and the Gulf of Mexico, including various size classes sampled by several gear types. This is beneficial when considering how the whole population of a species will affect the entire stock of another species. For example, if species B affects species A only in their shared nursery areas and species C feeds on species A in adulthood, analysis of only one life stage of species A would result in incomplete characterizations of interactions potentially impacting the population growth rate of species A. Secondarily, Ulrich et al. (2007) suggested that multiple gear types be used to adequately assess shark assemblages. Bonnethead sharks, 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 and aggregating life history stages, we have been able to describe the broadest and most comprehensive estimates of whole-scale community dynamics possible.

These broad interactions have resulted in insights on a southeast U.S. coastal shark complex that could not be directly observed. Interactions identified in the current study corroborate known relationships, while adding to our knowledge of interspecific shark interactions. With continued environmental changes and anthropogenic impacts, these interactions may change over time, necessitating further analyses. Likewise, the results of the current 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 instigating 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 2011).

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Table 1. Summary of surveys included in the analysis: Virginia Institute of Marine Science longline (VIMS LL), South Carolina red drum longline (SC LL), Georgia red drum longline (GA LL), SouthEast Area Monitoring and Assessment Program Trawl (SEAMPA Trawl), SouthEast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN).

| **Survey** | **Sampling Gear** | **Sampling Years** | **Sampling Frequency** | **Sampling Area** | **Sampling Design** | **Target Species** | **Citation** |
|---|---|---|---|---|---|---|---|
| VIMS LL | Bottom longline | 1975-2014 | Once per month during the months June - September | Coastal Virginia | Fixed stations; approximately 4 hour soak time; 100 hooks per set; Atlantic menhaden used as bait | Large adult and juvenile coastal sharks | |
| SC LL | Bottom longline | 2007-2014 | August - December | Coastal South Carolina | Stratified random sampling; 30 min soak time; 40 hooks per set; Atlantic mackerel or striped mullet used as bait | Adult red drum | http://www.seamap.org/documents/Red%20Drum%20Longline%20Survey%20-%20South%20Carolina.pdf |
| GA LL | Bottom longline | 2007-2013 | April – December | Coastal south Georgia and north Florida | Stratified random sampling (April - August); sample artificial reefs (fall); 30 min soak time; 60 hooks per set; Pacific squid used as bait | Adult red drum | http://www.seamap.org/documents/Red%20Drum%20Longline%20Survey%20-%20Georgia.pdf |
| SEAMAP Trawl | Bottom trawl | 1989-2014 | One multi-leg cruise in the spring, summer, and fall | South Atlantic Bight; Cape Hatteras, NC and Cape Canaveral, FL | Stratified random sampling | Resident and transient fishes, crustaceans, sea turtles, and cephalopods | http://www.seamap.org/documents/CoastalSurveyinfo.pdf |
| SEFSC LL | Bottom longline | 2001-2014 | Late July - September | Gulf of Mexico; Atlantic below 37° N latitude (alternate years) | Stratified random sampling | Adult shark/ snapper/ grouper | Ingram *et al.* 2005;<br>WB. Driggers, III, personal communication |
| GULFSPAN GN | 6 panel multi-mesh gillnet | 1996-2014 | Monthly sampling from April - October; occasionally March, May, and November | Northwest, Gulf of Mexico coast of Florida; | Stratified random sampling; nets checked or pulled every 1 - 2 hr; From 1994 through 2005, stretched mesh sizes ranged from 8.9 cm to 14.0 cm, increasing by 1.3-cm (0.5-in) intervals, with an additional panel of 20.3 cm. In 2006, the 20.3-cm panel was removed and a 7.6-cm panel was added *ad hoc*. | Juvenile coastal sharks | Carlson *et al.* 2013;<br>JK. Carlson, personal communication |

Table 2. Life history characteristics of the six species included in the study, including age at median maturity ($A_{50\%}$), longevity ($A_{MAX}$), length of the reproductive cycle, fecundity per reproductive event, and von Bertalanffy asymptotic maximum length ($L_\infty$) and growth rate coefficient (K).

| | | | | | von Bertalanffy | |
|---|---|---|---|---|---|---|
| **Species** | **$A_{50\%}$** | **$A_{MAX}$** | **Repro. Cycle** | **Fecundity** | **$L_\infty$** | **K** |
| LARGE COASTAL SHARKS | | | | | | |
| Sandbar | 14 yrs[1] | 27 yrs[2] | 2.5 yrs[1] | 8 pups[1] | 165 cm PCL[3] | 0.086 / yr[3] |
| Blacktip: Atl. | 7 yrs[4] | 22 yrs[4] | 2 yrs[5] | 4 pups[5] | 159 cm FL[4] | 0.16 / yr[4] |
| Blacktip: GOM | 6 yrs[4] | 17 yrs[4] | 2 yrs[5] | 4 pups[5] | 142 cm FL[4] | 0.24 / yr[4] |
| Spinner | 7-8 yrs[6] | 20 yrs[6] | 2 yrs[7*] | 6-8 pups[8] | 226 cm FL[9] | 0.08 / yr[9] |
| Tiger | 10 yrs[10] | 29 yrs[10] | 2 yrs[8] | 41 pups[8] | 347 cm FL[10] | 0.12 / yr[10] |
| SMALL COASTAL SHARKS | | | | | | |
| Finetooth | 6.3 yrs[11†] | 18.2 yrs[11†] | 2 yrs[12] | 4 pups[10] | 131.3 cm FL[11†] | 0.19 / yr[11†] |
| Blacknose: Atl. | 4.5 yrs[13] | 17-19yrs[13,16] | 2 yrs[13] | 5 pups[8] | 113.6 cm FL[14] | 0.18 / yr[14] |
| Blacknose: GOM | NA | 16 yrs[15] | 1 yr[16] | 3 pups[16] | 113.7–124.1 cm FL[15] | 0.24–0.35 / yr[15] |
| Bonnethead: Atl. | 6.7 yrs[17] | 19 yrs[17] | 1 yr[18] | 9 pups[18] | 103.6 cm FL[17] | 0.18 / yr[17] |
| Bonnethead: GOM | 3-4 yrs[19] | 12 yrs[20] | 1 yr[19] | 10 pups[21] | 122.6 cm TL[20] | 0.25 / yr[20] |
| Atlantic Sharpnose | 3 yrs[22] | 23 yrs[23] | 1 yr[22] | 4-5 pups[22] | 94 cm TL[24] | 0.73 / yr[24] |

[1] Baremore & Hale 2012; [2] SEDAR 2011; [3] Sminkey & Musick 1995; [4] Carlson et al. 2006; [5] Castro 1996; [6] Branstetter 1987; [7] Joung et al. 2005; [8] Castro 2011; [9] Carlson & Baremore 2005; [10] Kneebone et al. 2008; [11] Drymon et al. 2006; [12] Castro 1993b; [13] Driggers et al. 2004b; [14] Driggers et al. 2004a; [15] Carlson et al. 1999; [16] Sulikowski et al. 2007; [17] Frazier et al. 2014; [18] Frazier et al. 2013; [19] Manire et al. 1995; [20] Carlson & Parsons 1997; [21] Lombardi-Carlson et al. 2003; [22] Castro 2009; [23] Frazier et al. 2015; [24] Carlson & Baremore 2003

* Note that samples for this study were taken in waters off of Taiwan; study that estimated the reproductive cycle of spinner sharks within American waters.

† Finetooth life history parameters estimated from fish within the Gulf of Mexico indicate slightly smaller, faster maturing fish (Carlson et al. 2003).

Table 3. Equations used to calculate stability measures. $B$ is community dynamics matrix; $p$ is number of species included; $Q$ is the covariance matrix that specifies the process error; $V_\infty$ is the covariance matrix for the stationary distribution.

| **Stability Measure** | **Calculation** |
|---|---|
| Variance of stationary distribution | $\det(B)^{2/p}$ |
| Resilience | $\max eig(B)$ |
| Return rate | $\max eig(B \otimes B)$ |
| Reactivity | $-\frac{tr(Q)}{tr(V_\infty)}$ |
| Worst case reactivity | $\max eig(B'B) - 1$ |

Table 4. Species interaction (*B*) matrix results from multivariate, first-order autoregressive, state-space (MARSS-1) models conducted on the Virginia Institute of Marine Science longline (VIMS LL) survey. Species abbreviations are as follows: sandbar (SB), blacktip (BT), spinner (SPN), tiger (TIG), Atlantic sharpnose (SN) sharks. Values in bold have 95% confidence intervals that exclude zero.

| VIMS LL | SB | BT | SPN | TIG | SN |
|---|---|---|---|---|---|
| SB | **0.7820** | 0 | 0 | 0.1061 | 0 |
| BT | 0 | 0 | -0.0682 | 0 | 0 |
| SPN | 0 | 0 | 0 | 0 | 0 |
| TIG | 0 | 0 | 0 | 0 | 0 |
| SN | 0.0153 | 0 | 0 | **0.2225** | 0 |

Table 5. Species interaction (*B*) matrix results from multivariate, first-order autoregressive, state-space (MARSS-1) models conducted on the SouthEast Fishery Science Center longline (SEFSC LL) survey. Species abbreviations are as follows: sandbar (SB), blacktip (BT), spinner (SPN), tiger (TIG), Atlantic sharpnose (SN), blacknose (BN) sharks. Values in bold have 95% confidence intervals that exclude zero, and italicized values have 90% confidence intervals that exclude zero.

| SEFSC LL | SB | BT | SPN | TIG | SN | BN |
|---:|:---:|:---:|:---:|:---:|:---:|:---:|
| SB | **0.7158** | *-0.4771* | 0 | 0 | 0 | 0 |
| BT | 0 | 0 | **0.5665** | 0 | 0 | 0.0507 |
| SPN | **-0.4054** | 0 | 0 | 0 | 0 | 0 |
| TIG | 0 | 0 | 0 | 0 | 0 | 0 |
| SN | 0 | 0 | 0 | 0 | 0 | 0 |
| BN | 0 | 0 | 0 | 0 | 0 | 0 |

Table 6. Species interaction (*B*) matrix results from multivariate, first-order autoregressive, state-space (MARSS-1) models conducted on the SouthEast Area Monitoring and Assessment Program trawl (SEAMAP Trawl) survey. Species abbreviations are as follows: sandbar (SB), blacktip (BT), spinner (SPN), Atlantic sharpnose (SN), blacknose (BN), bonnethead (BH), finetooth (FT) sharks. Values in bold have 95% confidence intervals that exclude zero.

| SEAMAP Trawl | SB | BT | SPN | SN | BN | BH | FT |
|---|---|---|---|---|---|---|---|
| SB | -0.06190 | **0.8733** | 0 | 0 | 0 | 0 | 0 |
| BT | 0 | **0.8584** | 0 | 0 | 0 | 0 | 0 |
| SPN | 0 | **0.2346** | 0 | 0 | 0 | 0 | 0 |
| SN | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BN | 0 | 0.1882 | 0 | **0.4886** | **0.4614** | 0 | 0 |
| BH | 0.06410 | 0 | 0 | 0.2825 | 0 | 0 | 0 |
| FT | 0 | 0 | 0 | 0 | 0 | 0 | **0.8344** |

Table 7. Species interaction (*B*) matrix results from multivariate, first-order autoregressive, state-space (MARSS-1) models conducted on the Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN) survey. Species abbreviations are as follows: blacktip (BT), spinner (SPN), Atlantic sharpnose (SN), blacknose (BN), bonnethead (BH), finetooth (FT) sharks. Values in bold have 95% confidence intervals that exclude zero.

| GULFSPAN GN | BT | SPN | SN | BN | BH | FT |
|---|---|---|---|---|---|---|
| BT | 0 | 0.0780 | 0 | 0 | 0 | 0 |
| SPN | 0 | 0 | 0 | 0 | 0 | 0 |
| SN | 0 | 0 | **0.8081** | 0 | 0 | 0 |
| BN | 0 | 0 | **-0.2117** | 0 | 0 | 0 |
| BH | 0 | 0 | 0 | 0 | 0 | 0 |
| FT | -0.8267 | 0.0408 | 0 | 0 | 0 | 0 |

Table 8. 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. Species abbreviations are as follows: sandbar (SB), blacktip (BT), spinner (SPN), tiger (TIG), Atlantic coast Atlantic sharpnose population (Atl. SN), Gulf of Mexico Atlantic sharpnose population (GOM SN), Atlantic blacknose population (Atl. BN), Gulf of Mexico blacknose population (GOM BN), Atlantic bonnethead population (Atl. BH), Atlantic finetooth population (Atl. FT). Values in bold have 95% confidence intervals that exclude zero, and italicized values have 90% confidence intervals that exclude zero.

| DFA Common Trends | SB | BT | SPN | TIG | GOM SN | Atl. SN | Atl. BN | GOM BN | Atl. BH | Atl. FT |
|---|---|---|---|---|---|---|---|---|---|---|
| SB | **0.6912** | 0 | 0 | *0.1925* | 0 | 0 | 0 | 0 | 0 | 0 |
| BT | 0 | -0.1122 | *0.5578* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SPN | -0.3444 | 0 | **0.6958** | **0.5378** | 0 | 0 | 0 | 0 | 0 | 0 |
| TIG | 0 | 0 | 0 | **0.9429** | 0 | 0 | 0 | 0 | 0 | 0 |
| GOM SN | 0 | 0 | 0 | 0 | **0.7306** | 0 | 0 | **0.2852** | 0 | 0 |
| Atl. SN | 0 | 0 | 0 | 0 | 0 | 0.2547 | 0 | 0 | 0.6596 | -0.1732 |
| Atl. BN | 0 | 0.0261 | 0 | 0.1115 | 0 | 0 | 0.3914 | 0 | 0 | 0 |
| GOM BN | 0 | **0.8311** | 0 | *-0.3835* | 0 | 0 | 0 | **0.9417** | 0 | 0 |
| Atl. BH | *-0.1313* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **0.9212** | 0 |
| Atl. FT | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **0.8277** |

Table 9. Results of broad-scale stability analysis for ALL species (Large and Small Coastal species combined), Small Coastal Sharks (SCS), and Large Coastal Sharks (LCS), including interpretation of results is as defined in Ives et al. (2003). Values in bold indicate the species group that exhibits the most stability for each stability measure.

| Stability measure | Calculation | ALL | SCS | LCS | Interpretation |
|---|---|---|---|---|---|
| resilience | $\max(\lambda_B)$ | 0.9429 | **0.9417** | 0.9429 | smaller means more stable |
| variance of stationary distribution | $\det(B)^{\frac{2}{p}}$ | 0.3055 | 0.3739 | **0.2255** | smaller means more stable |
| return rate | $\max(\lambda_{B\otimes B})$ | 0.8890 | **0.8868** | 0.8890 | smaller means more stable |
| worst case reactivity | $\max(\lambda_{B'B})-1$ | **0.6710** | 0.3296 | 0.4682 | larger means more stable |
| reactivity | $-\frac{tr(Q)}{tr(V_\infty)}$ | **-0.0520** | -0.1645 | -0.1261 | larger means more stable |

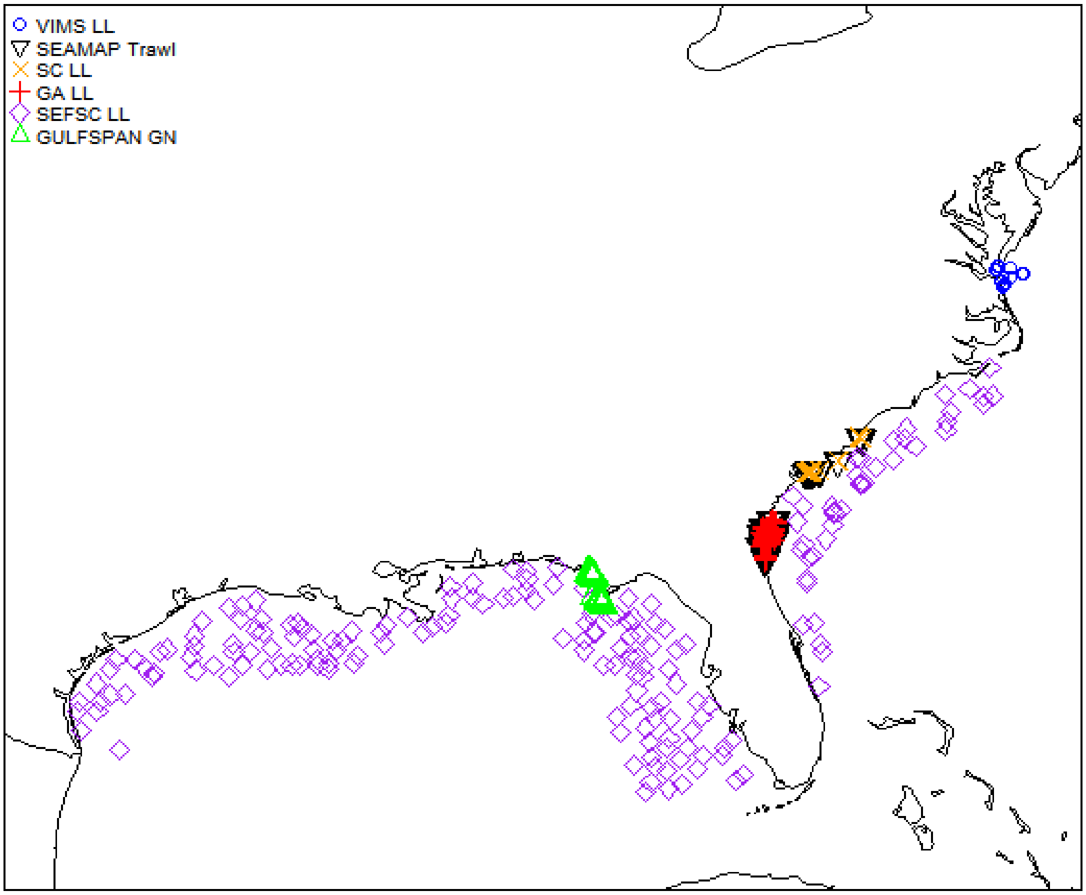


Figure 1. Map of representative stations/sites sampled (for the 2012 sampling year) within each survey: Virginia Institute of Marine Science longline (VIMS LL), South Carolina red drum longline (SC LL), Georgia red drum longline (GA LL), SouthEast Area Monitoring and Assessment Program Trawl (SEAMPA Trawl), SouthEast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN). Map generated using the rworldmap package in R (South 2011).

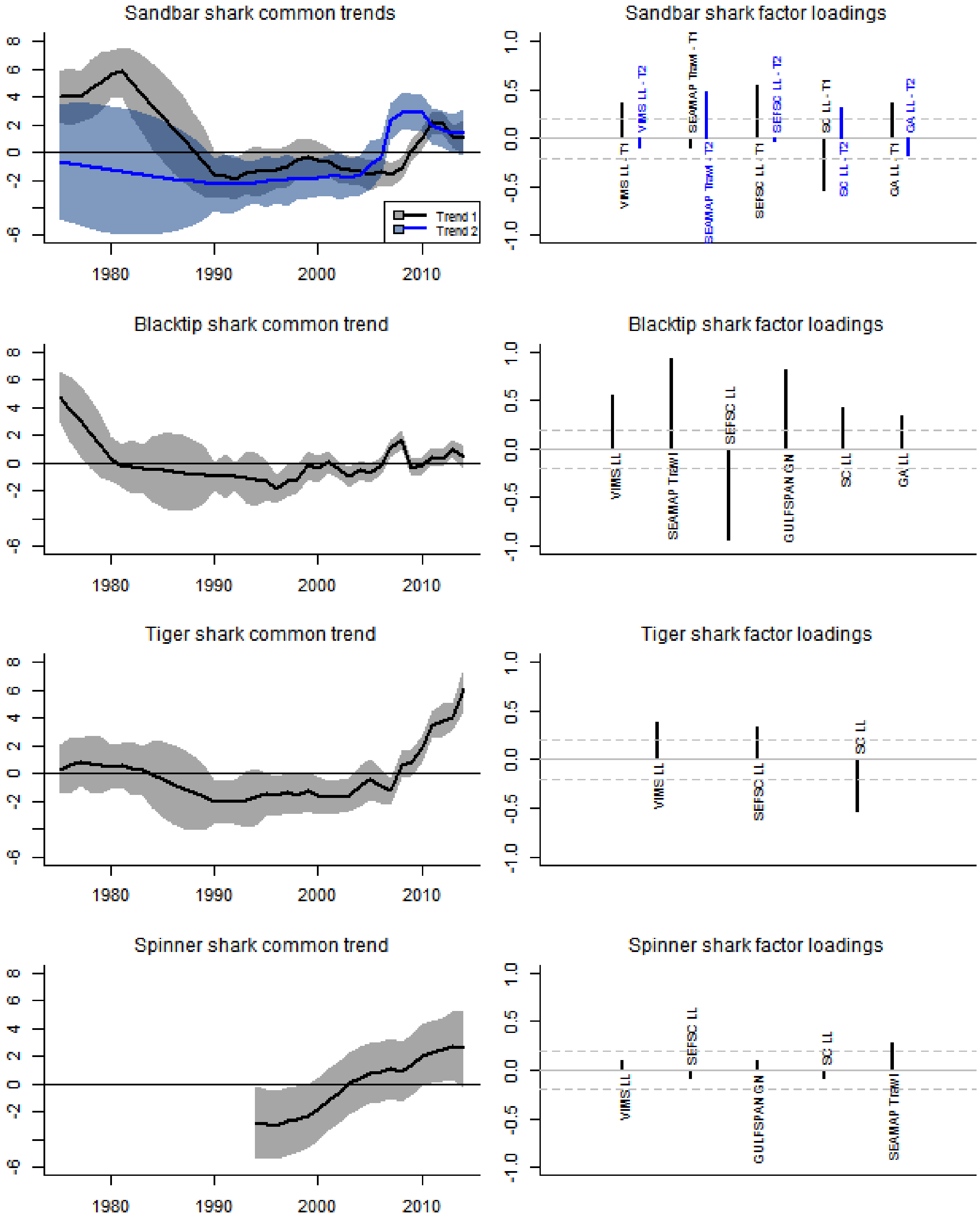


Figure 2. Common trends produced from dynamic factor analysis (DFA) using delta-lognormally derived indices of relative abundance for the large coastal shark (LCS) complex. Trends (solid lines) and 95% confidence intervals (shaded regions) are displayed on the left column, and factor loadings are displayed on the right column. Factor loadings greater than 0.2 represent corresponding indices that had a strong influence on the resulting common trend, and negative factor loadings indicate that the corresponding survey follows an opposite trend than the DFA common trend.

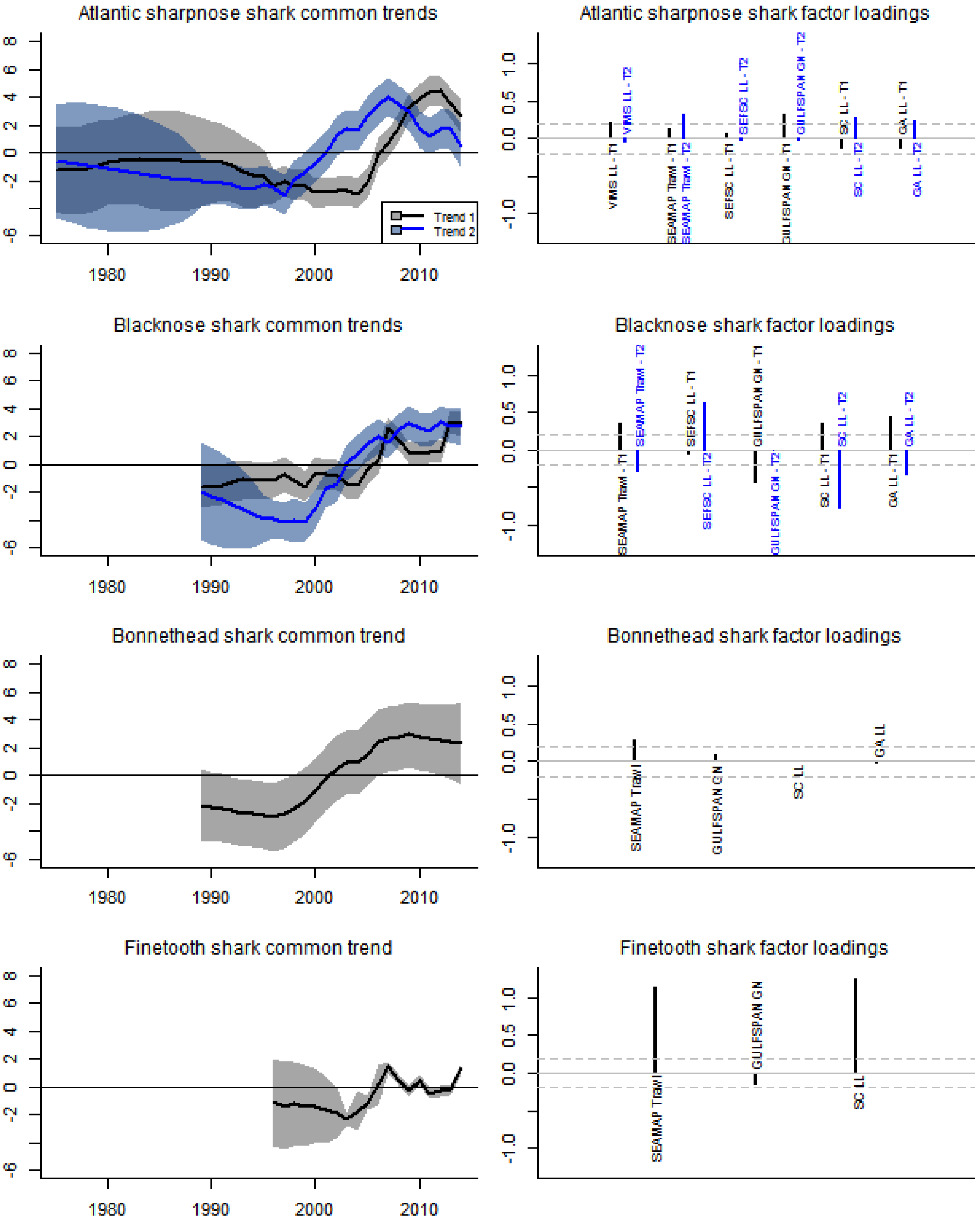


Figure 3. Common trends produced from dynamic factor analysis (DFA) using delta-lognormally derived indices of relative abundance for the small coastal shark (SCS) complex. Trends (solid lines) and 95% confidence intervals (shaded regions) are displayed on the left column, and factor loadings are displayed on the right column. Factor loadings greater than 0.2 represent corresponding indices that had a strong influence on the resulting common trend, and negative factor loadings indicate that the corresponding survey follows an opposite trend than the DFA common trend.

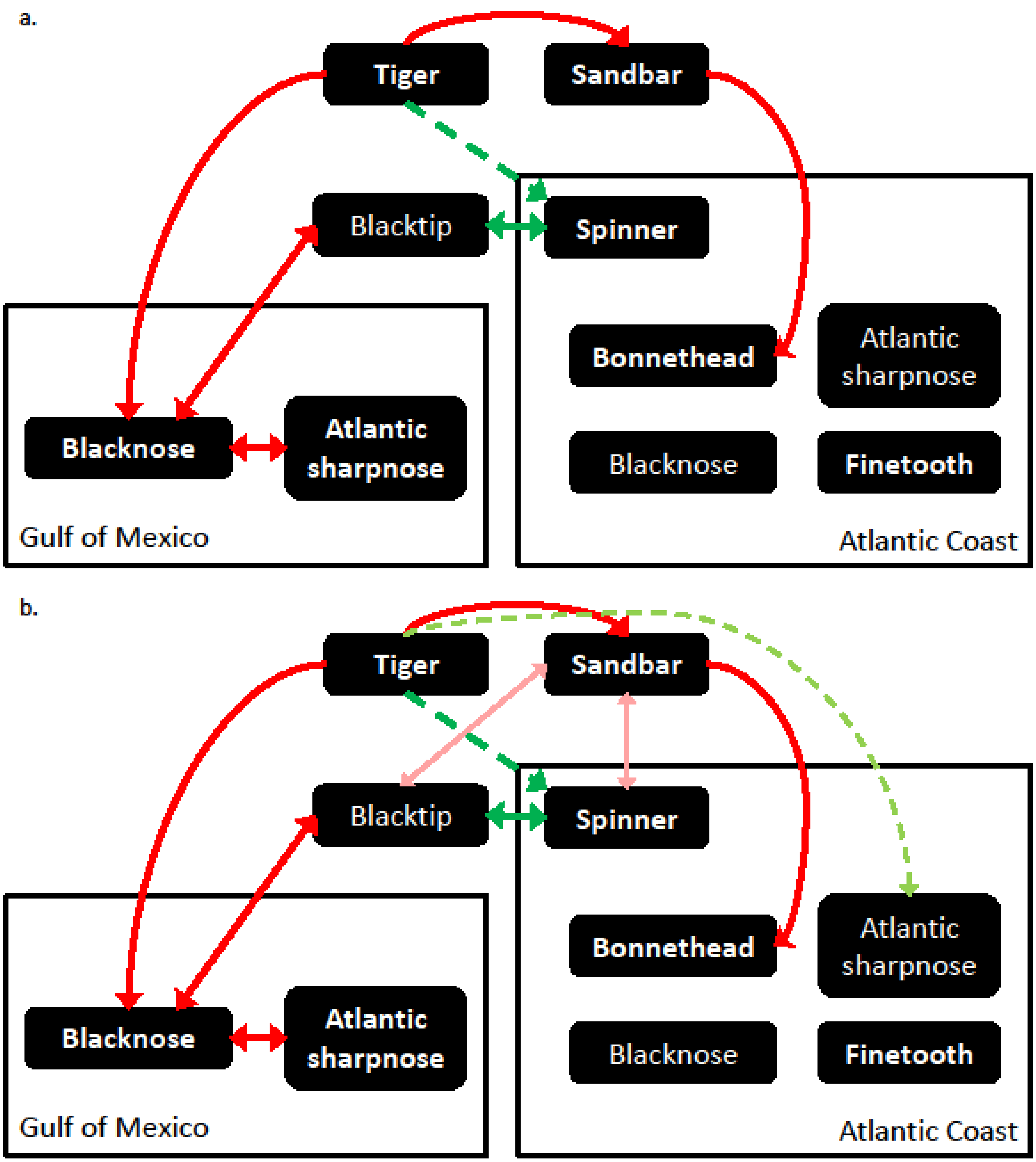


Figure 4. Flow diagrams of a) hypothesized interactions estimated by the broad-scale multivariate, first-order, autoregressive, state-space (MARSS-1) modeling, and b) broad-scale interactions with three additional localized interactions. Not all species-specific MARSS-1 interactions were included because of anthropogenic factors that likely influenced results from the SouthEast Area Monitoring and Assessment Program trawl (SEAMAP Trawl) survey results. Species in bold were found to experience broad-scale density dependence. Red arrows suggest negative interactions (competitive or predatory) in the direction of the arrow (i.e. arrows are pointing to the receiving species). Green arrows suggest beneficial interactions (commensal or mutual) in the direction of the arrow. Solid lines indicate direct interactions, while dashed arrows indicate indirect interactions. Lighter colored arrows represent localized interactions that cannot be generalized to the entire populations.

# Appendix

Appendix 1. Results of index of abundance fitting for each GLM type: delta-lognormal, hurdle, and zero inflated. Shortened covariates include latitude (lat), longitude (long), and salinity (sal). Survey abbreviations are as follows: Virginia Institute of Marine Science longline (VIMS LL), SouthEast Area Monitoring and Assessment Program trawl (SEAMAP Trawl), Southeast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN), South Carolina Red Drum longline (SC LL), and Georgia Red Drum longline (GA LL).

| Species | Survey | GLM Type | Covariates |
|---|---|---|---|
| Sandbar | VIMS | Delta-lognormal: lognormal component | year, month, station |
| | | Delta-lognormal: binomial component | year, month, station |
| | | Hurdle: negative binomial component | year, month, station |
| | | Hurdle: binomial component | year, month, station |
| | | Zero-inflated: negative binomial component | year, month |
| | | Zero-inflated: binomial component | year, station |
| | SEAMAP | Delta-lognormal: lognormal component | year, month |
| | | Delta-lognormal: binomial component | year, month, region |
| | | Hurdle: negative binomial component | year, month, region |
| | | Hurdle: binomial component | year, month, region |
| | | Zero-inflated: negative binomial component | year, month, lat |
| | | Zero-inflated: binomial component | year, region |
| | SEFSC | Delta-lognormal: lognormal component | year, lat, long, depth |
| | | Delta-lognormal: binomial component | year, long, depth |
| | | Hurdle: negative binomial component | year, lat, long, depth |
| | | Hurdle: binomial component | year, long, depth |
| | | Zero-inflated: Poisson component | year, lat, long, depth |
| | | Zero-inflated: binomial component | year, long, depth |
| | GA | Delta-lognormal: lognormal component | year, sal |
| | | Delta-lognormal: binomial component | year, sal |
| | | Hurdle: Poisson component | year, sal |
| | | Hurdle: binomial component | year, sal, season |

| | | | |
|---|---|---|---|
| | | Zero-inflated: Poisson component | year, sal |
| | | Zero-inflated: binomial component | year, season |
| | SC | Delta-lognormal: lognormal component | year, month, location |
| | | Delta-lognormal: binomial component | year, month, location |
| | | Hurdle: Poisson component | year, location |
| | | Hurdle: binomial component | year, month, location |
| | | Zero-inflated: negative binomial component | year, location |
| | | Zero-inflated: binomial component | year, month, location |
| Blacktip | VIMS | Delta-lognormal: lognormal component | year |
| | | Delta-lognormal: binomial component | year, month, station |
| | | Hurdle: negative binomial component | year |
| | | Hurdle: binomial component | year, month, station |
| | | Zero-inflated: Poisson component | year, month, station |
| | | Zero-inflated: binomial component | year |
| | SEAMAP | Delta-lognormal: lognormal component | year, month |
| | | Delta-lognormal: binomial component | year, month, region |
| | | Hurdle: negative binomial component | year |
| | | Hurdle: binomial component | year, month, region |
| | | Zero-inflated: negative binomial component | year |
| | | Zero-inflated: binomial component | year |
| | SEFSC | Delta-lognormal: lognormal component | year, lat, long, depth |
| | | Delta-lognormal: binomial component | year, lat, long, depth |
| | | Hurdle: negative binomial component | year, lat, long, depth |
| | | Hurdle: binomial component | year, lat, long, depth |
| | | Zero-inflated: Poisson component | year, lat, long, depth |
| | | Zero-inflated: binomial component | year, lat, long, depth |
| | GULFSPAN | Delta-lognormal: lognormal component | year, month, area |
| | | Delta-lognormal: binomial component | year, month, area |
| | | Hurdle: negative binomial component | year, month, area |
| | | Hurdle: binomial component | year, month, area |

| | | | |
|---|---|---|---|
| | | Zero-inflated: negative binomial component | year, month, area |
| | | Zero-inflated: binomial component | year, month, area |
| | GA | Delta-lognormal: lognormal component | year |
| | | Delta-lognormal: binomial component | year |
| | | Hurdle: Poisson component | year |
| | | Hurdle: binomial component | year |
| | | Zero-inflated: Poisson component | year, season |
| | | Zero-inflated: binomial component | year, season |
| | SC | Delta-lognormal: lognormal component | year, month, location |
| | | Delta-lognormal: binomial component | year, month |
| | | Hurdle: negative binomial component | year |
| | | Hurdle: binomial component | year, month, location |
| | | Zero-inflated: negative binomial component | year, month |
| | | Zero-inflated: binomial component | year, month, location |
| Spinner | VIMS | Delta-lognormal: lognormal component | year, station |
| | | Delta-lognormal: binomial component | year, month, station |
| | | Zero-inflated: negative binomial component | year, month, station |
| | | Zero-inflated: binomial component | none |
| | SEAMAP | Delta-lognormal: lognormal component | year |
| | | Delta-lognormal: binomial component | year, month, region |
| | SEFSC | Delta-lognormal: lognormal component | year |
| | | Delta-lognormal: binomial component | year, lat, long, depth |
| | | Hurdle: negative binomial component | year, long |
| | | Hurdle: binomial component | year |
| | | Zero-inflated: negative binomial component | year, long |
| | | Zero-inflated: binomial component | year, lat, long, depth |
| | GULFSPAN | Delta-lognormal: lognormal component | year, month, area |
| | | Delta-lognormal: binomial component | year, month, area |
| | | Hurdle: negative binomial | year, month |

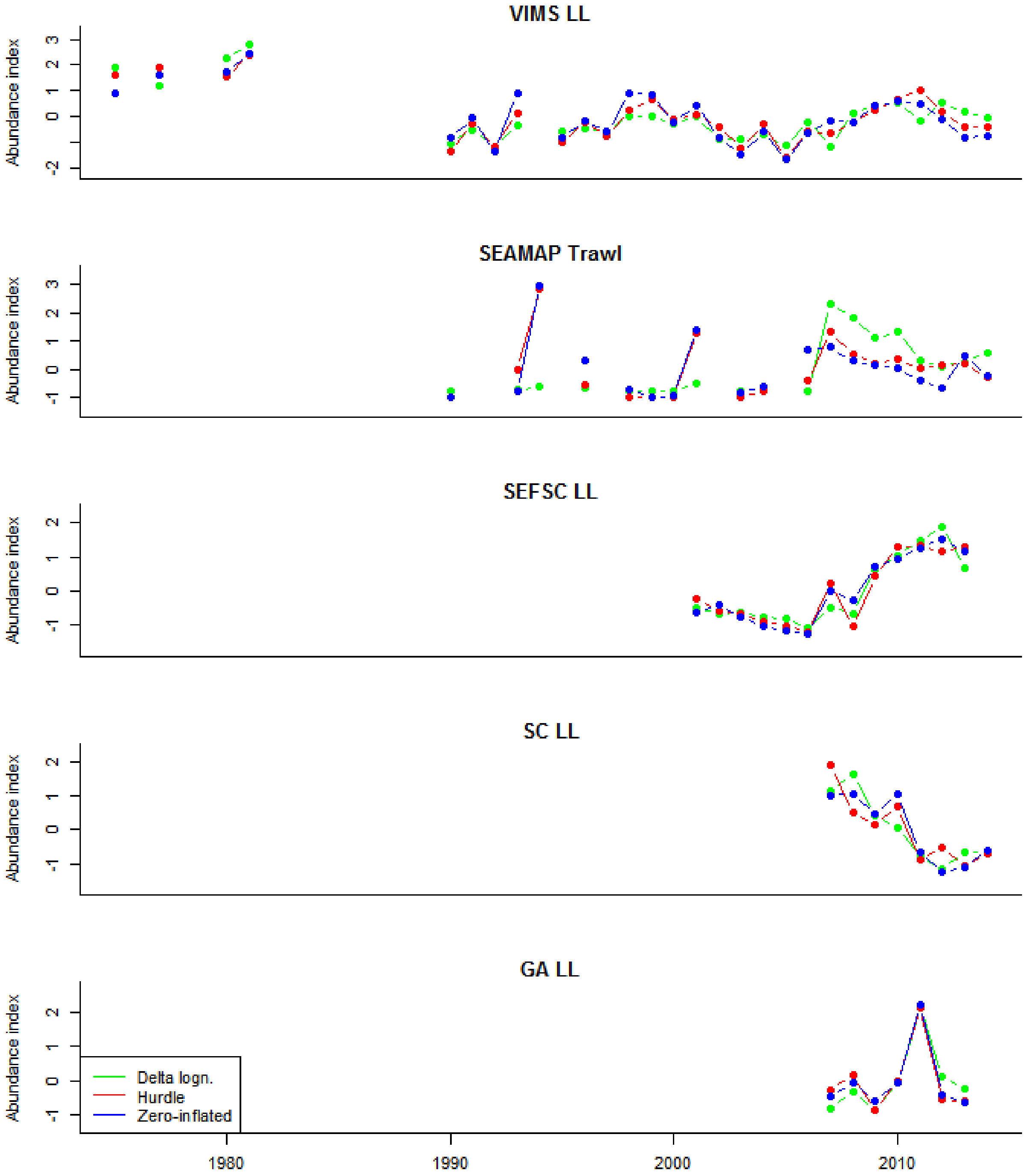
| | | | |
|---|---|---|---|
| | | component | |
| | | Hurdle: binomial component | year, month, area |
| | | Zero-inflated: negative binomial component | year, month |
| | | Zero-inflated: binomial component | year, month, area |
| | SC | Delta-lognormal: lognormal component | year, month, location |
| | | Delta-lognormal: binomial component | year, month, location |
| | | Hurdle: negative binomial component | year, location |
| | | Hurdle: binomial component | year, month, location |
| | | Zero-inflated: negative binomial component | year, location |
| | | Zero-inflated: binomial component | year, month, location |
| Tiger | VIMS | Delta-lognormal: lognormal component | year |
| | | Delta-lognormal: binomial component | year, month, station |
| | | Zero-inflated: Poisson component | year, station |
| | | Zero-inflated: binomial component | year |
| | SEFSC | Delta-lognormal: lognormal component | year, lat, depth |
| | | Delta-lognormal: binomial component | year, lat, long, depth |
| | | Zero-inflated: negative binomial component | year, lat, long, depth |
| | | Zero-inflated: binomial component | year, depth |
| | SC | Delta-lognormal: lognormal component | year |
| | | Delta-lognormal: binomial component | year, month |
| Atlantic sharpnose | VIMS | Delta-lognormal: lognormal component | year, month, station |
| | | Delta-lognormal: binomial component | year, month, station |
| | | Hurdle: negative binomial component | year, month, station |
| | | Hurdle: binomial component | year, month, station |
| | | Zero-inflated: negative binomial component | year, month |
| | | Zero-inflated: binomial component | year |
| | SEAMAP | Delta-lognormal: lognormal component | year, month, region, lat |
| | | Delta-lognormal: binomial component | year, month, region |
| | | Hurdle: negative binomial | year, month, long |

| | | | |
|---|---|---|---|
| | | component | |
| | | Hurdle: binomial component | year, month, long |
| | | Zero-inflated: negative binomial component | year, month, region, lat |
| | | Zero-inflated: binomial component | year, month, region |
| | SEFSC | Delta-lognormal: lognormal component | year, lat, long, depth |
| | | Delta-lognormal: binomial component | year, lat, long, depth |
| | | Hurdle: negative binomial component | year, lat, long, depth |
| | | Hurdle: binomial component | year, long, depth |
| | | Zero-inflated: negative binomial component | year, lat, long, depth |
| | | Zero-inflated: binomial component | year, lat, long, depth |
| | GULFSPAN | Delta-lognormal: lognormal component | year, month, area |
| | | Delta-lognormal: binomial component | year, month, area |
| | | Hurdle: negative binomial component | year, month, area |
| | | Hurdle: binomial component | year, month, area |
| | | Zero-inflated: negative binomial component | year, month, area |
| | | Zero-inflated: binomial component | year, month, area |
| | GA | Delta-lognormal: lognormal component | year, month, region |
| | | Delta-lognormal: binomial component | year, month, sal |
| | | Hurdle: negative binomial component | year, month, region |
| | | Hurdle: binomial component | year, month, region |
| | | Zero-inflated: negative binomial component | year, month |
| | | Zero-inflated: binomial component | year, month, region |
| | SC | Delta-lognormal: lognormal component | year, month, location |
| | | Delta-lognormal: binomial component | year, month, location |
| | | Hurdle: negative binomial component | year, month, location |
| | | Hurdle: binomial component | year, month, location |
| | | Zero-inflated: negative binomial component | year, location |
| | | Zero-inflated: binomial component | year |
| Blacknose | SEAMAP | Delta-lognormal: lognormal component | year, region, lat |

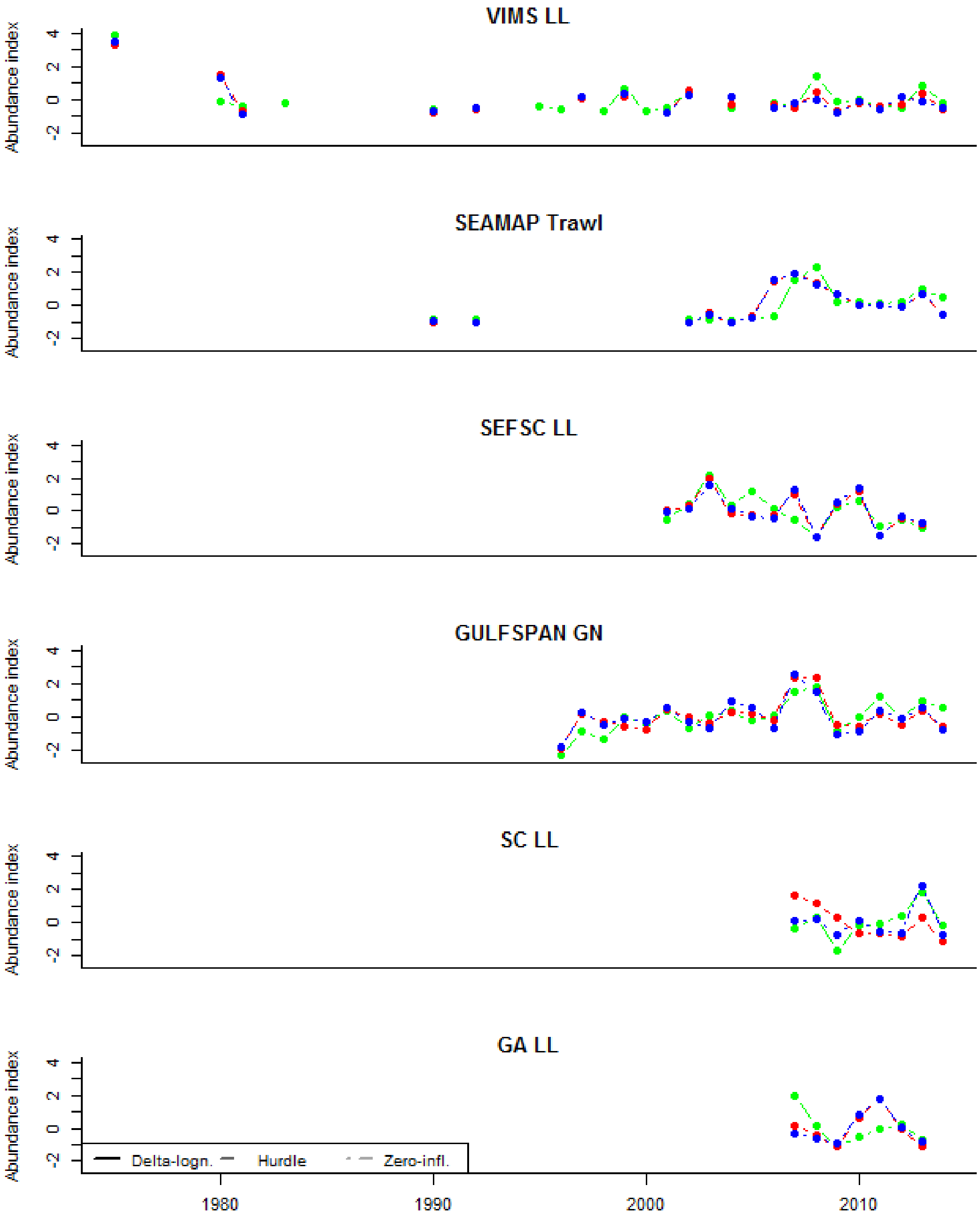
| | | | |
|---|---|---|---|
| | | Delta-lognormal: binomial component | year, month, region |
| | | Hurdle: negative binomial component | year, month, region, lat |
| | | Hurdle: binomial component | year, month, region |
| | | Zero-inflated: negative binomial component | year, month, region |
| | | Zero-inflated: binomial component | year, region |
| | SEFSC | Delta-lognormal: lognormal component | year, lat, long, depth |
| | | Delta-lognormal: binomial component | year, lat, long, depth |
| | | Hurdle: negative binomial component | year, lat, long, depth |
| | | Hurdle: binomial component | year, lat, long, depth |
| | | Zero-inflated: negative binomial component | year, lat, long, depth |
| | | Zero-inflated: binomial component | year, lat, long, depth |
| | GULFSPAN | Delta-lognormal: lognormal component | year, area |
| | | Delta-lognormal: binomial component | year, month |
| | | Hurdle: negative binomial component | year |
| | | Hurdle: binomial component | year, month |
| | | Zero-inflated: negative binomial component | year |
| | | Zero-inflated: binomial component | year, month |
| | GA | Delta-lognormal: lognormal component | year, season |
| | | Delta-lognormal: binomial component | year, month, sal |
| | | Hurdle: negative binomial component | year, season |
| | | Hurdle: binomial component | year, season |
| | | Zero-inflated: negative binomial component | year, season |
| | | Zero-inflated: binomial component | year, season |
| | SC | Delta-lognormal: lognormal component | year, month, location |
| | | Delta-lognormal: binomial component | year, month, location |
| | | Hurdle: negative binomial component | year, month, location |
| | | Hurdle: binomial component | year, month, location |
| | | Zero-inflated: negative binomial component | year, month |

|  |  |  |  |
|---|---|---|---|
|  |  | Zero-inflated: binomial component | year, location |
| Bonnethead | SEAMAP | Delta-lognormal: lognormal component | year, region |
|  |  | Delta-lognormal: binomial component | year, month, region |
|  |  | Hurdle: negative binomial component | year, region |
|  |  | Hurdle: binomial component | year, region |
|  |  | Zero-inflated: negative binomial component | year, month, region |
|  |  | Zero-inflated: binomial component | year, month, region |
|  | GULFSPAN | Delta-lognormal: lognormal component | year |
|  |  | Delta-lognormal: binomial component | year, month, area |
|  |  | Hurdle: negative binomial component | year |
|  |  | Hurdle: binomial component | year, month, area |
|  |  | Zero-inflated: negative binomial component | year |
|  |  | Zero-inflated: binomial component | year, area |
|  | GA | Delta-lognormal: lognormal component | year, month |
|  |  | Delta-lognormal: binomial component | year, month |
|  |  | Hurdle: negative binomial component | year, month |
|  |  | Hurdle: binomial component | year, month |
|  |  | Zero-inflated: negative binomial component | year, month |
|  |  | Zero-inflated: binomial component | year |
|  | SC | Delta-lognormal: lognormal component | year, month, location |
|  |  | Delta-lognormal: binomial component | year, month, location |
|  |  | Hurdle: negative binomial component | year |
|  |  | Hurdle: binomial component | year, month, location |
|  |  | Zero-inflated: negative binomial component | year |
|  |  | Zero-inflated: binomial component | year |
| Finetooth | SEAMAP | Delta-lognormal: lognormal component | year, region |
|  |  | Delta-lognormal: binomial component | year, month, region |
|  |  | Hurdle: negative binomial component | year, region |

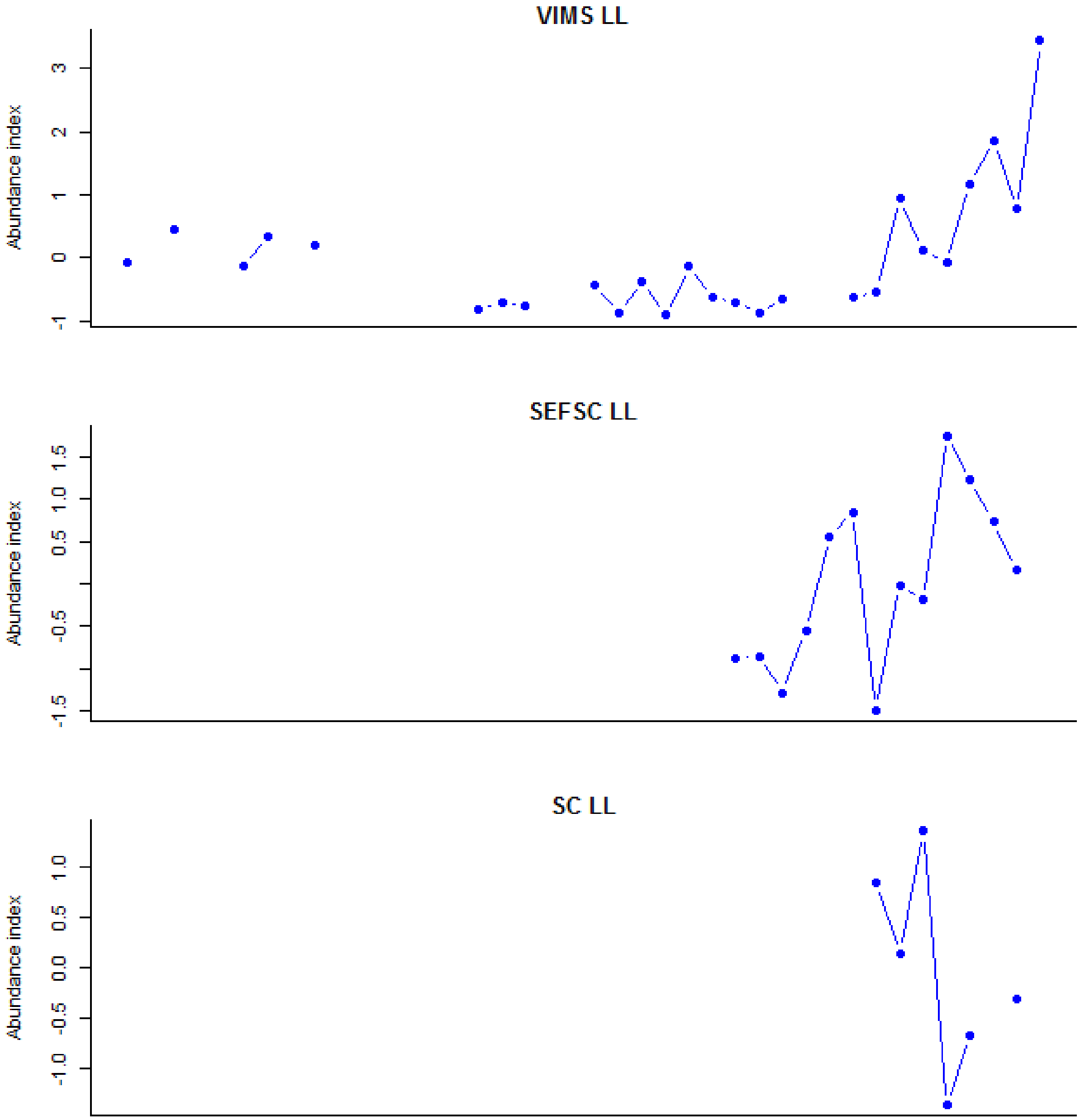
| | | | |
|---|---|---|---|
| | | Hurdle: binomial component | year, month, region |
| | | Zero-inflated: negative binomial component | year, region |
| | | Zero-inflated: binomial component | year |
| | GULFSPAN | Delta-lognormal: lognormal component | year, area |
| | | Delta-lognormal: binomial component | year, area |
| | | Hurdle: negative binomial component | year, month, area |
| | | Hurdle: binomial component | year, area |
| | | Zero-inflated: negative binomial component | year, month |
| | | Zero-inflated: binomial component | year, month, area |
| | SC | Delta-lognormal: lognormal component | year, month, location |
| | | Delta-lognormal: binomial component | year, month, location |
| | | Hurdle: negative binomial component | year, location |
| | | Hurdle: binomial component | year, month, location |
| | | Zero-inflated: negative binomial component | year, month, location |
| | | Zero-inflated: binomial component | year, location |



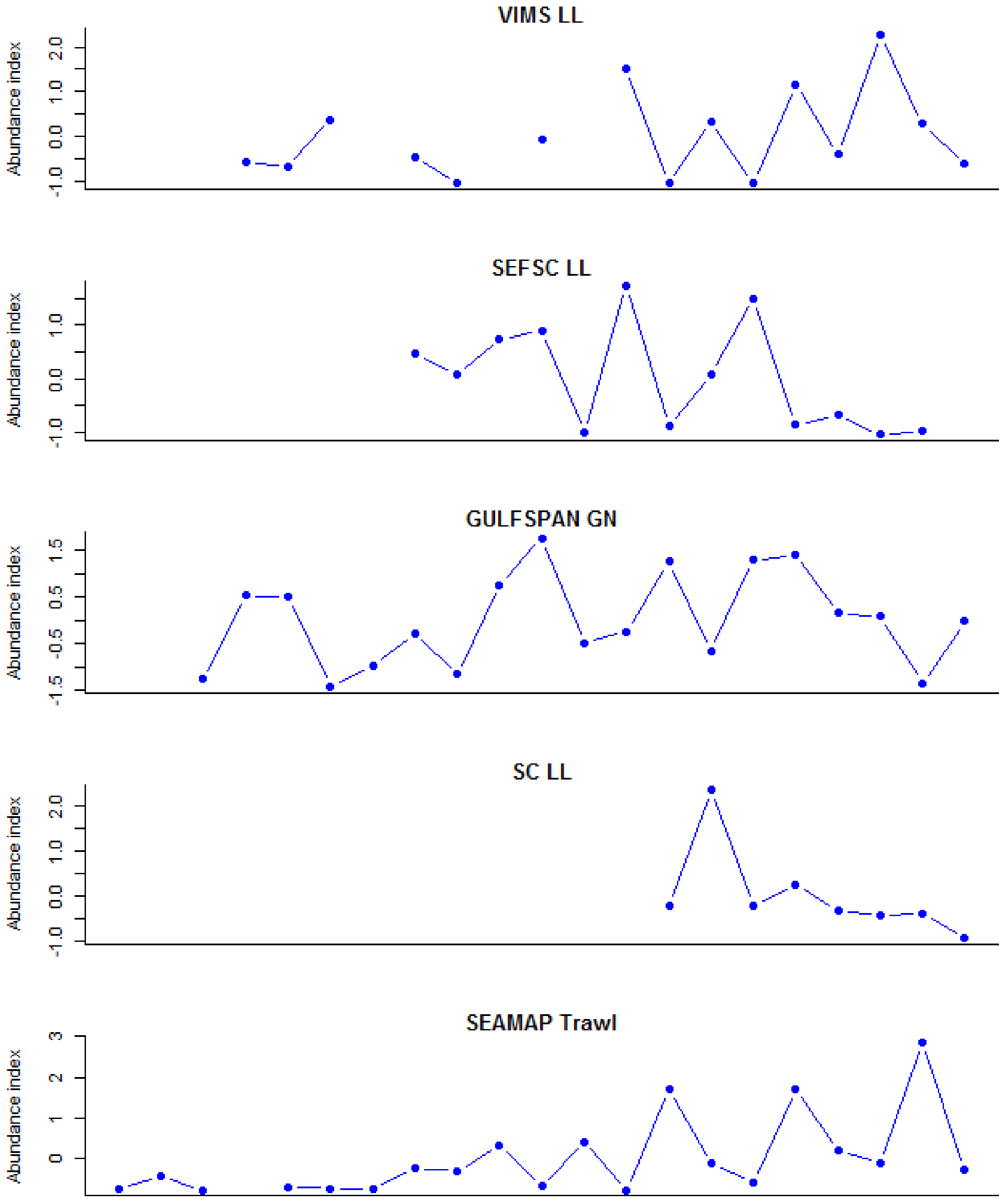
Appendix 2. Survey-based indices of abundance for the sandbar shark calculated by three catch-per-unit-effort (CPUE) standardization methods: 1) delta-lognormal generalized linear models (GLMs), 2) hurdle (or zero-altered) GLMs, and 3) zero-inflated GLMs. Survey abbreviations are as follows: Virginia Institute of Marine Science longline (VIMS LL), SouthEast Area Monitoring and Assessment Program trawl (SEAMAP Trawl), Southeast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN), South Carolina Red Drum longline (SC LL), and Georgia Red Drum longline (GA LL).



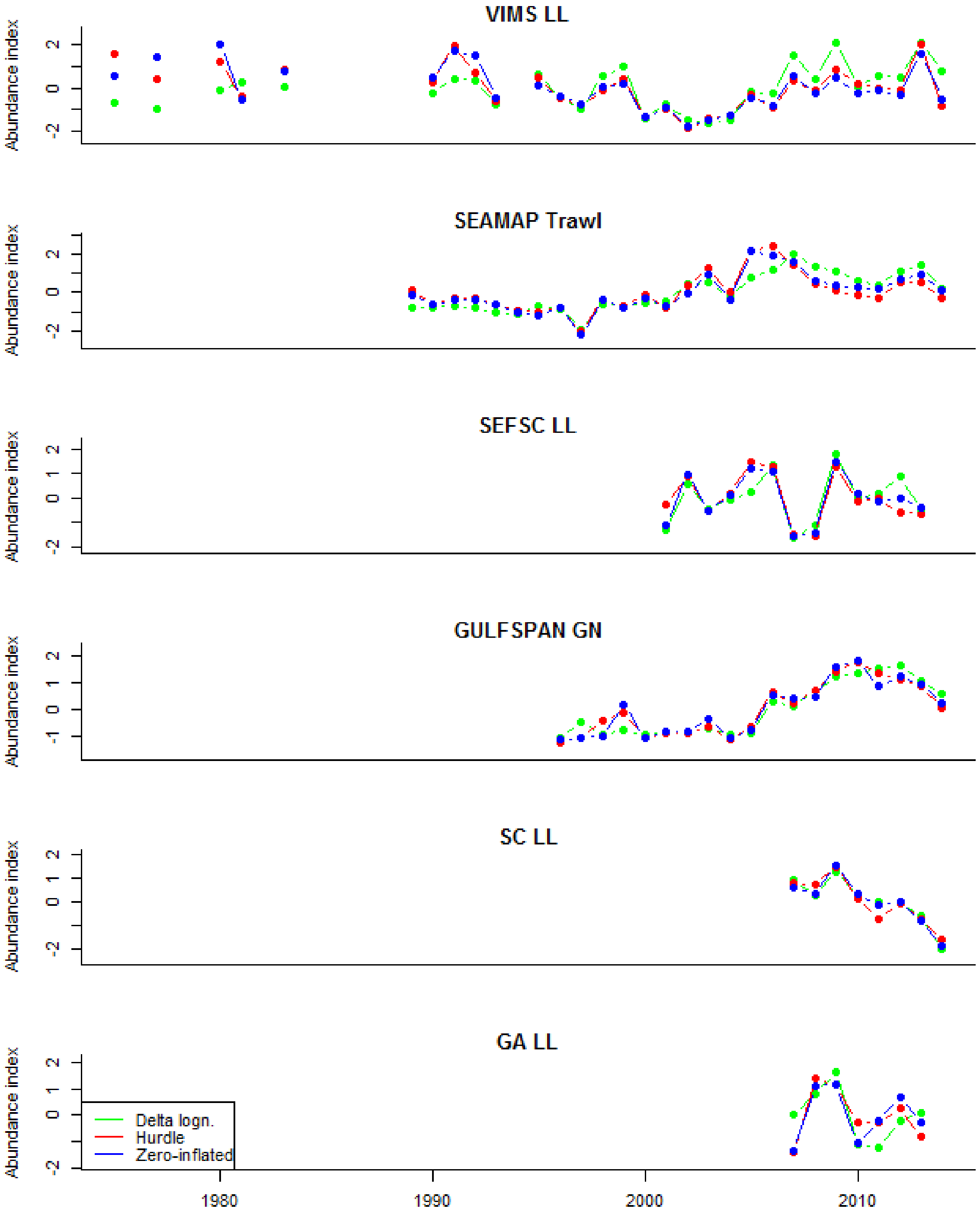
Appendix 3. Survey-based indices of abundance for the blacktip shark calculated by three catch-per-unit-effort (CPUE) standardization methods: 1) delta-lognormal generalized linear models (GLMs), 2) hurdle (or zero-altered) GLMs, and 3) zero-inflated GLMs. Survey abbreviations are as follows: Virginia Institute of Marine Science longline (VIMS LL), SouthEast Area Monitoring and Assessment Program trawl (SEAMAP Trawl), Southeast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN), South Carolina Red Drum longline (SC LL), and Georgia Red Drum longline (GA LL).



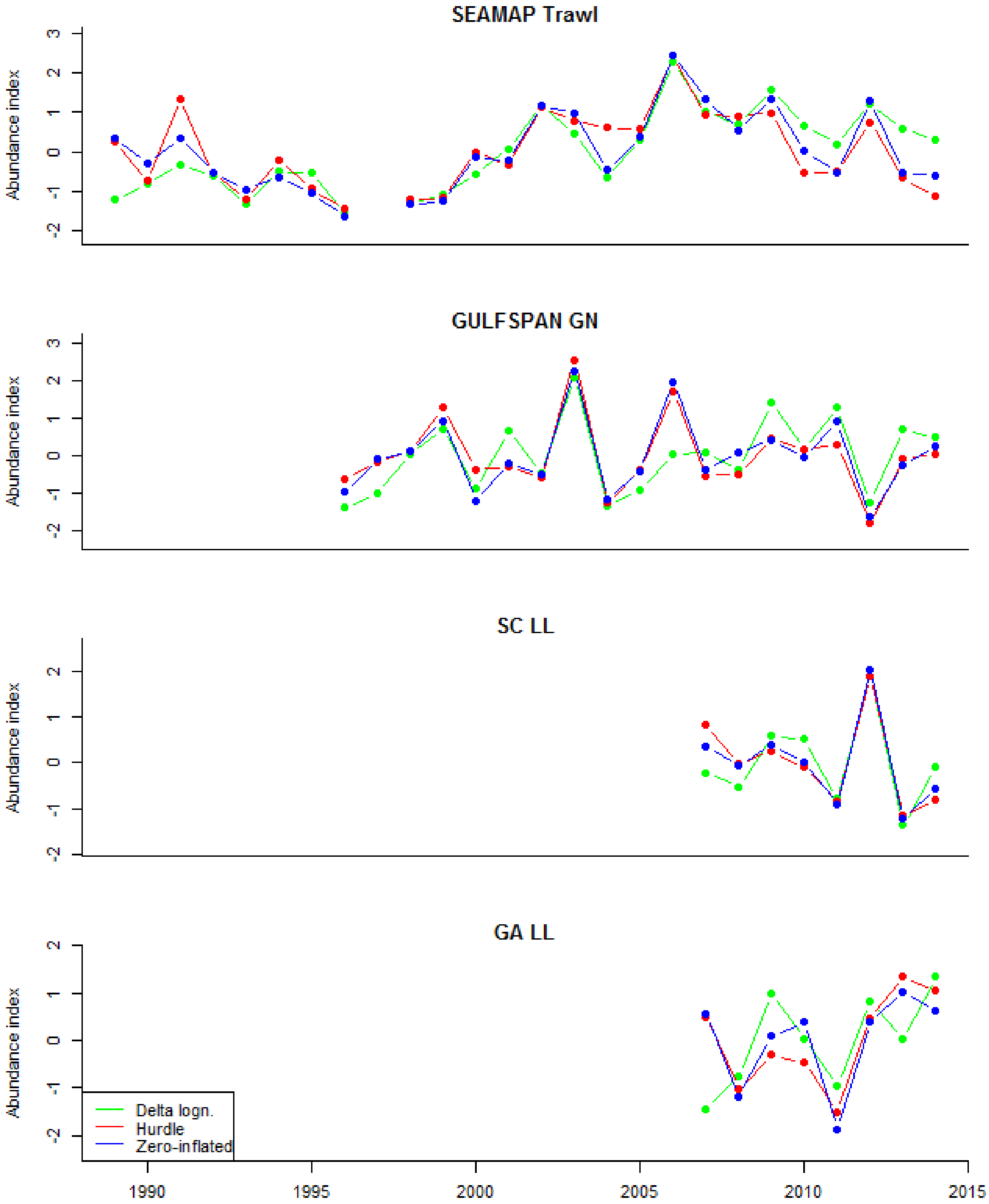
Appendix 4. Survey-based indices of abundance for the tiger shark calculated by one catch-per-unit-effort (CPUE) standardization methods, the delta-lognormal generalized linear models (GLMs). Survey abbreviations are as follows: Virginia Institute of Marine Science longline (VIMS LL), Southeast Fishery Science Center longline (SEFSC LL), South Carolina Red Drum longline (SC LL).



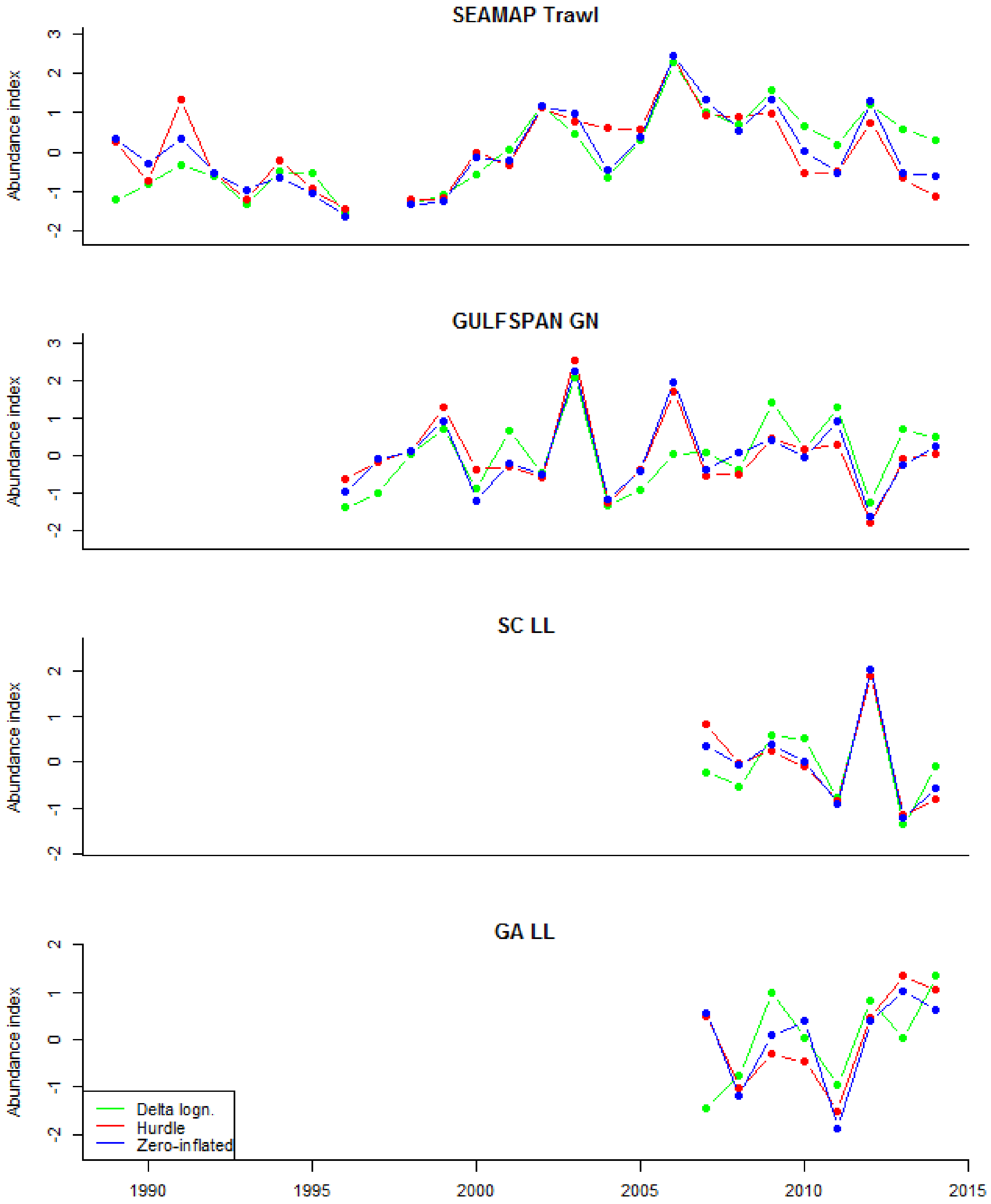
Appendix 5. Survey-based indices of abundance for the spinner shark calculated by one catch-per-unit-effort (CPUE) standardization methods, the delta-lognormal generalized linear models (GLMs). Survey abbreviations are as follows: Virginia Institute of Marine Science longline (VIMS LL), SouthEast Area Monitoring and Assessment Program trawl (SEAMAP Trawl), Southeast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN), South Carolina Red Drum longline (SC LL).



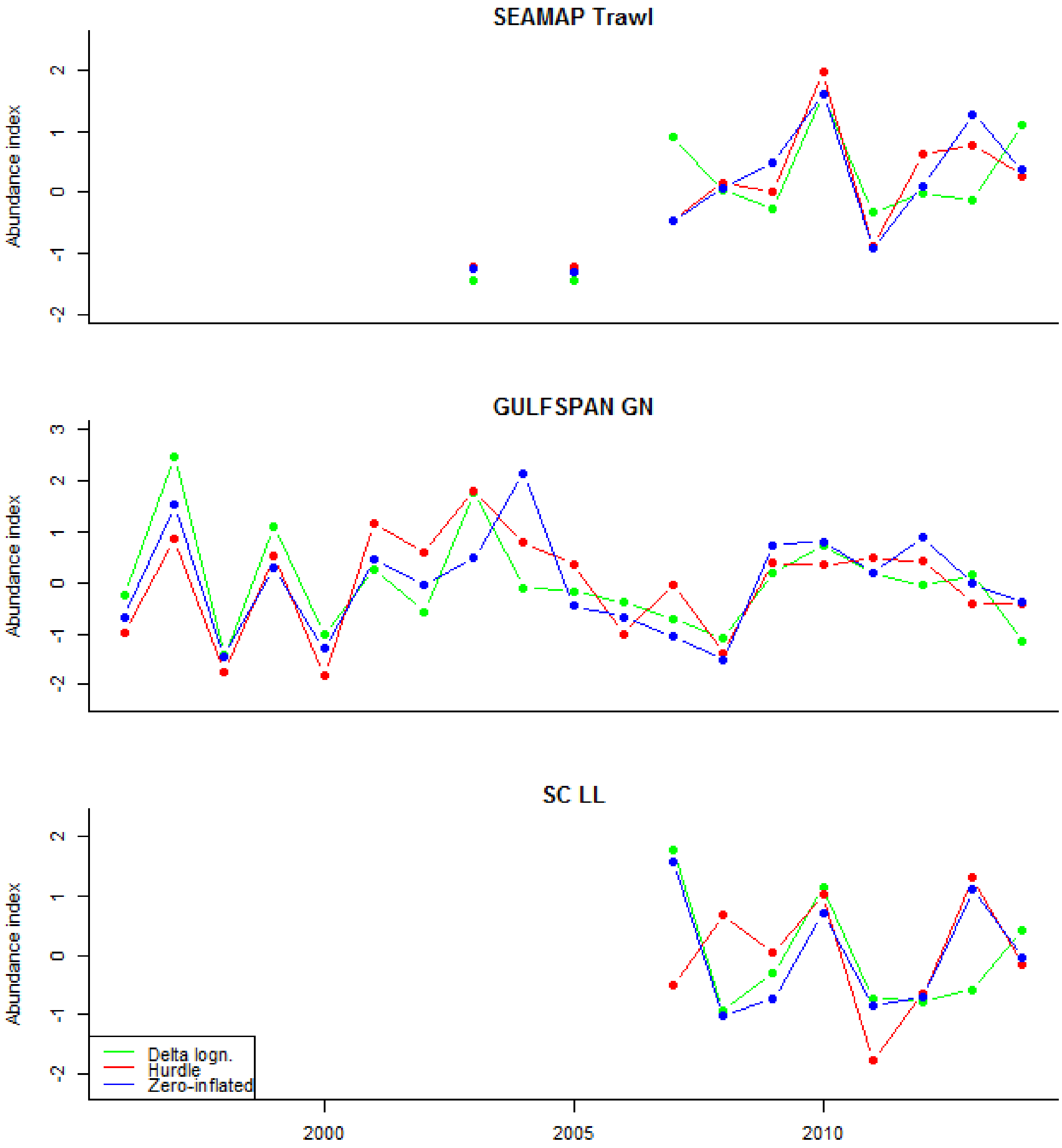
Appendix 6. Survey-based indices of abundance for the Atlantic sharpnose shark calculated by three catch-per-unit-effort (CPUE) standardization methods: 1) delta-lognormal generalized linear models (GLMs), 2) hurdle (or zero-altered) GLMs, and 3) zero-inflated GLMs. Survey abbreviations are as follows: Virginia Institute of Marine Science longline (VIMS LL), SouthEast Area Monitoring and Assessment Program trawl (SEAMAP Trawl), Southeast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN), South Carolina Red Drum longline (SC LL), and Georgia Red Drum longline (GA LL).



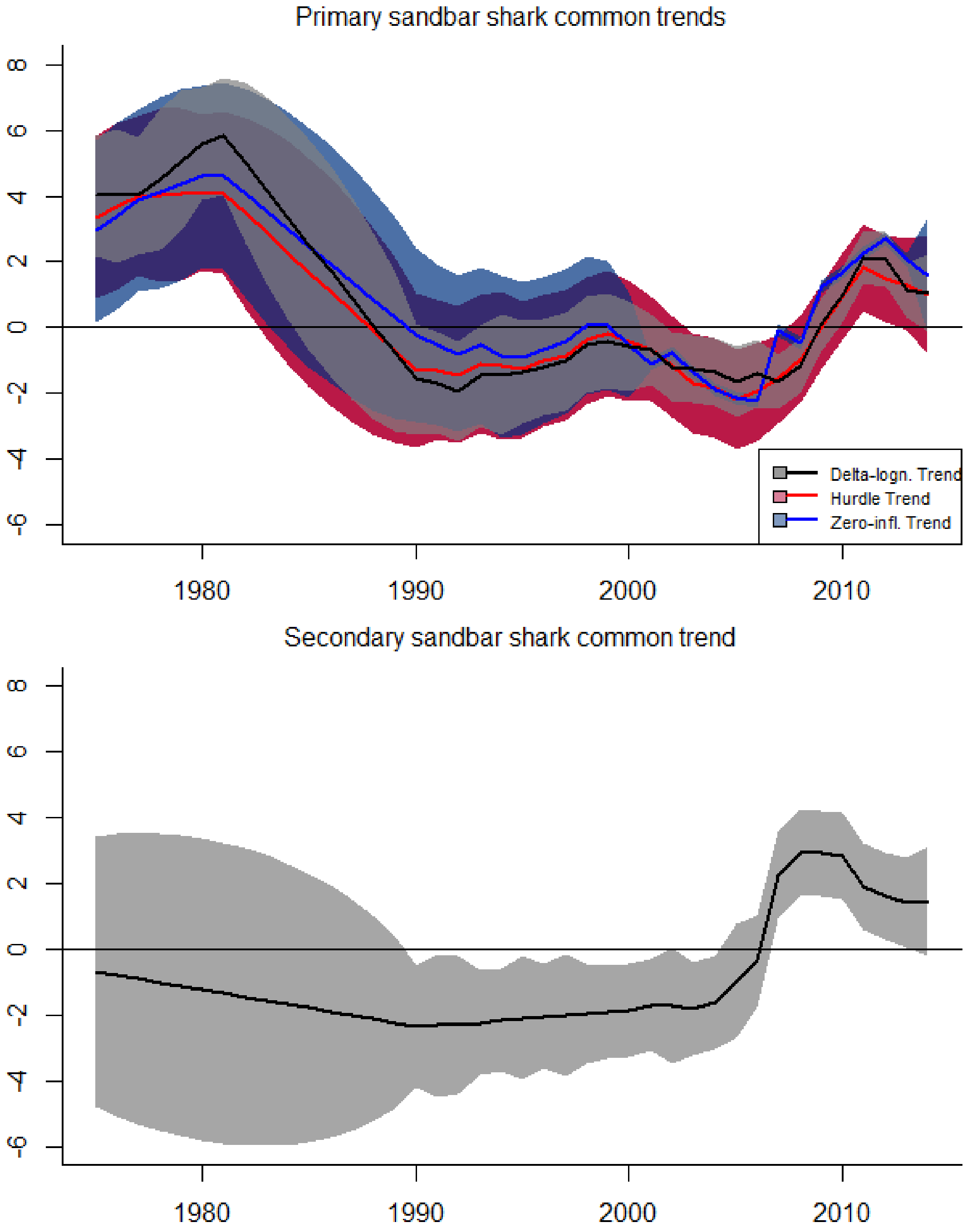
Appendix 7. Survey-based indices of abundance for the blacknose shark calculated by three catch-per-unit-effort (CPUE) standardization methods: 1) delta-lognormal generalized linear models (GLMs), 2) hurdle (or zero-altered) GLMs, and 3) zero-inflated GLMs. Survey abbreviations are as follows: SouthEast Area Monitoring and Assessment Program trawl (SEAMAP Trawl), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN), South Carolina Red Drum longline (SC LL), and Georgia Red Drum longline (GA LL).



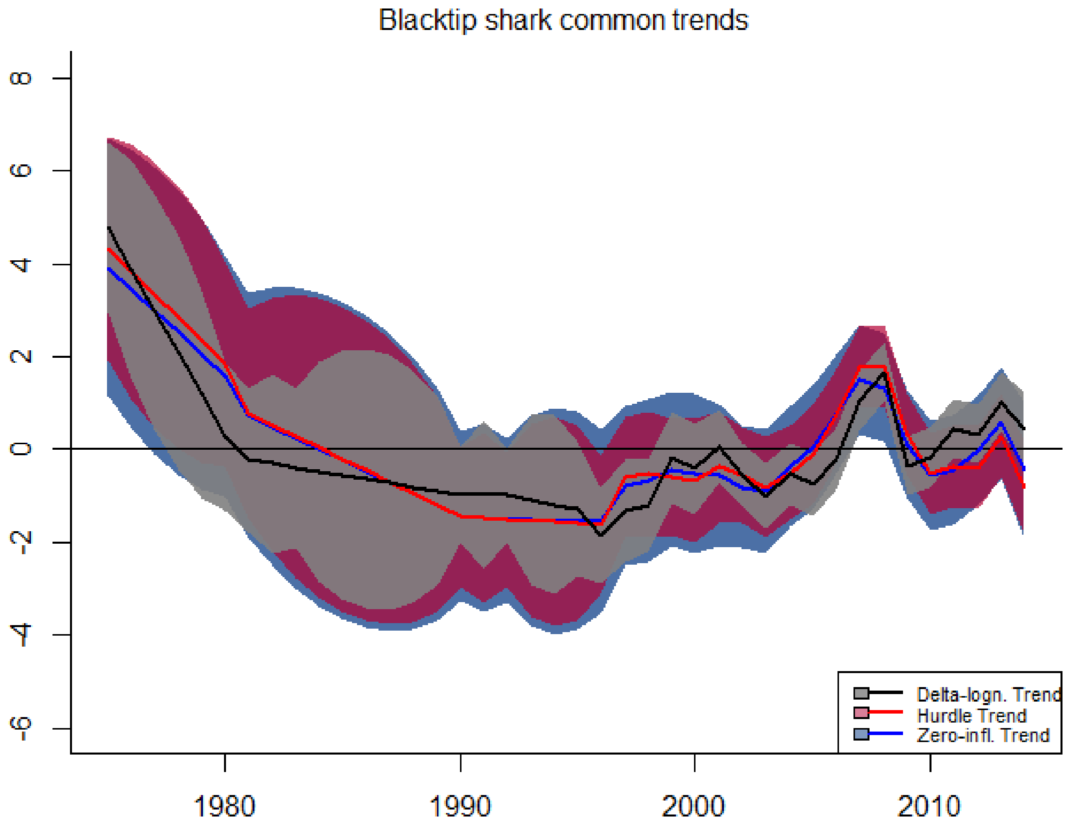
Appendix 8. Survey-based indices of abundance for the bonnethead shark calculated by three catch-per-unit-effort (CPUE) standardization methods: 1) delta-lognormal generalized linear models (GLMs), 2) hurdle (or zero-altered) GLMs, and 3) zero-inflated GLMs. Survey abbreviations are as follows: SouthEast Area Monitoring and Assessment Program trawl (SEAMAP Trawl), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN), South Carolina Red Drum longline (SC LL), and Georgia Red Drum longline (GA LL).



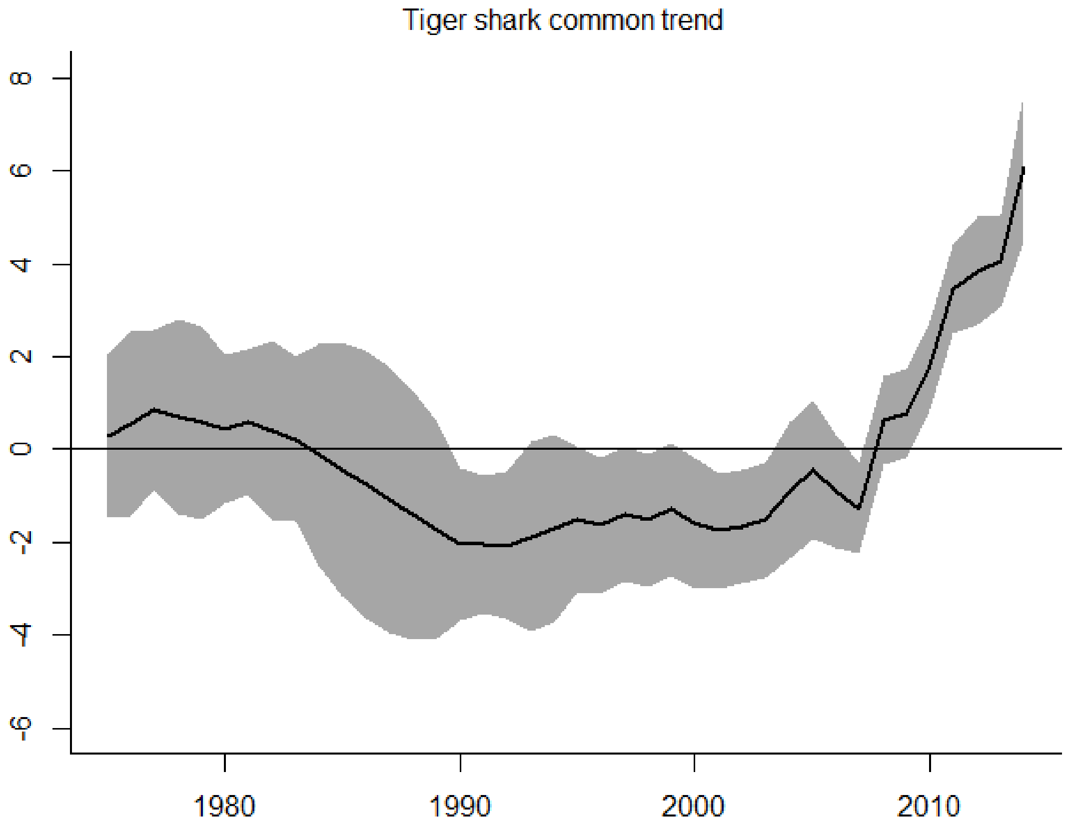
Appendix 9. Survey-based indices of abundance for the finetooth shark calculated by three catch-per-unit-effort (CPUE) standardization methods: 1) delta-lognormal generalized linear models (GLMs), 2) hurdle (or zero-altered) GLMs, and 3) zero-inflated GLMs. Survey abbreviations are as follows: SouthEast Area Monitoring and Assessment Program trawl (SEAMAP Trawl), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN), South Carolina Red Drum longline (SC LL).



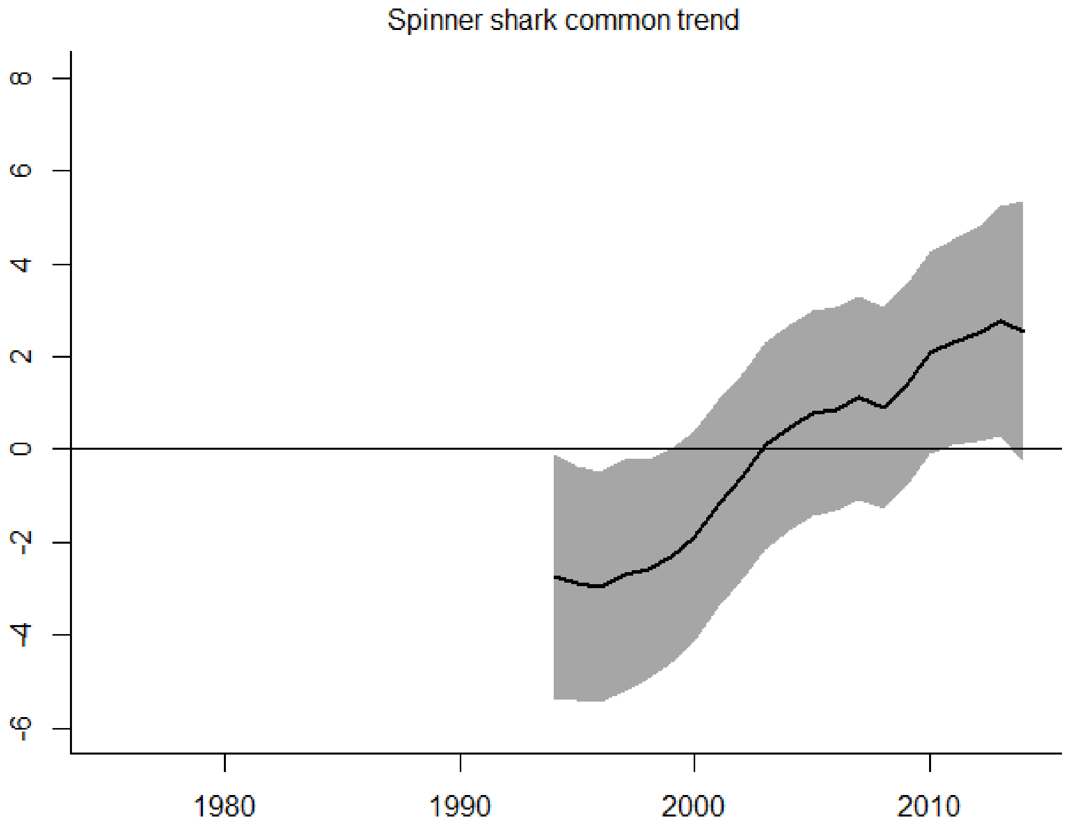
Appendix 10. Dynamic factor analysis common trends in abundance with shaded 95% confidence intervals (CIs) estimated for the sandbar shark from three index standardization methods: 1) delta-lognormal generalized linear models (GLMs; black), 2) hurdle GLMs (red), and 3) zero-inflated GLMs (blue).



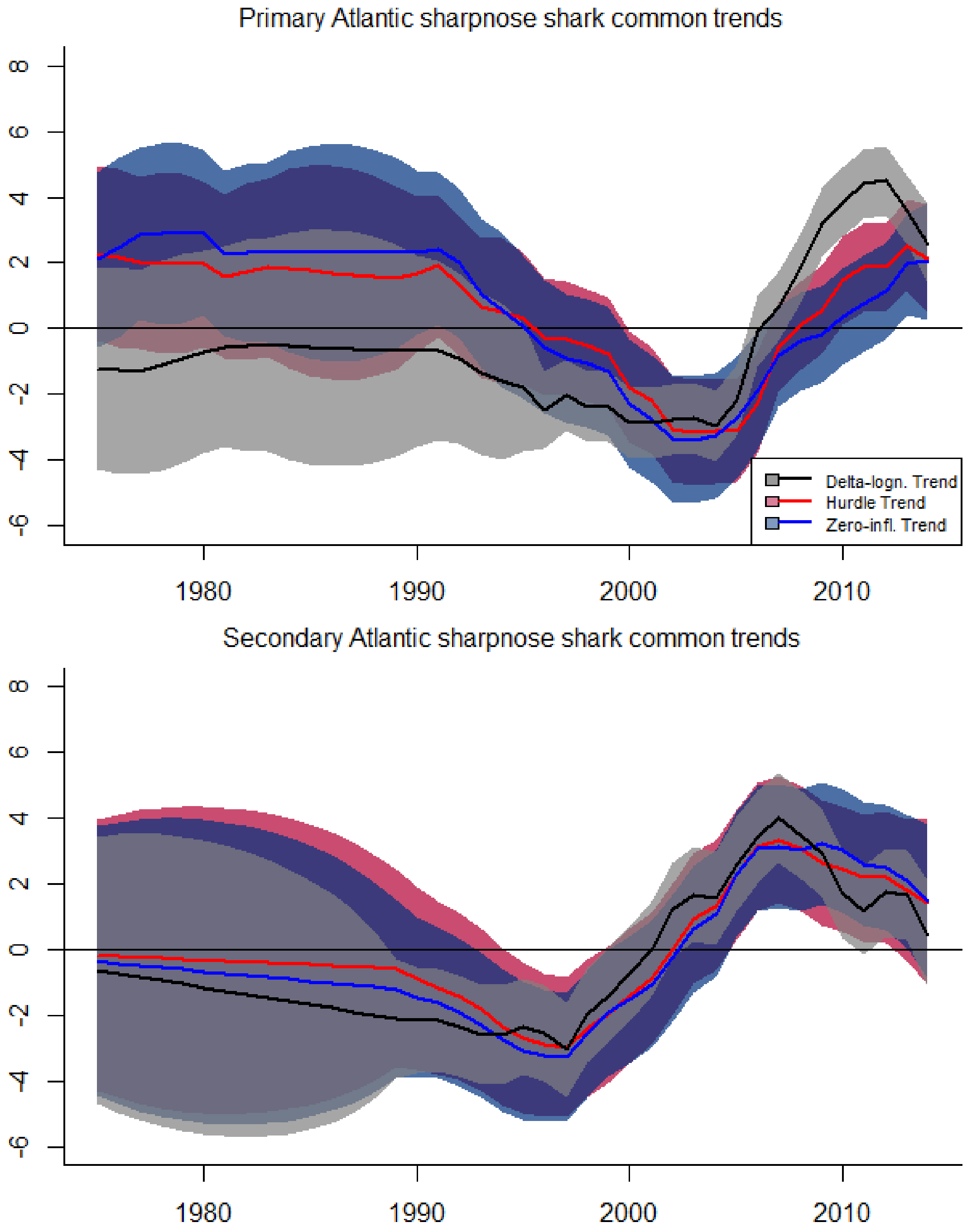
Appendix 11. Dynamic factor analysis common trends in abundance with shaded 95% confidence intervals (CIs) estimated for the blacktip shark from three index standardization methods: 1) delta-lognormal generalized linear models (GLMs; black), 2) hurdle GLMs (red), and 3) zero-inflated GLMs (blue).



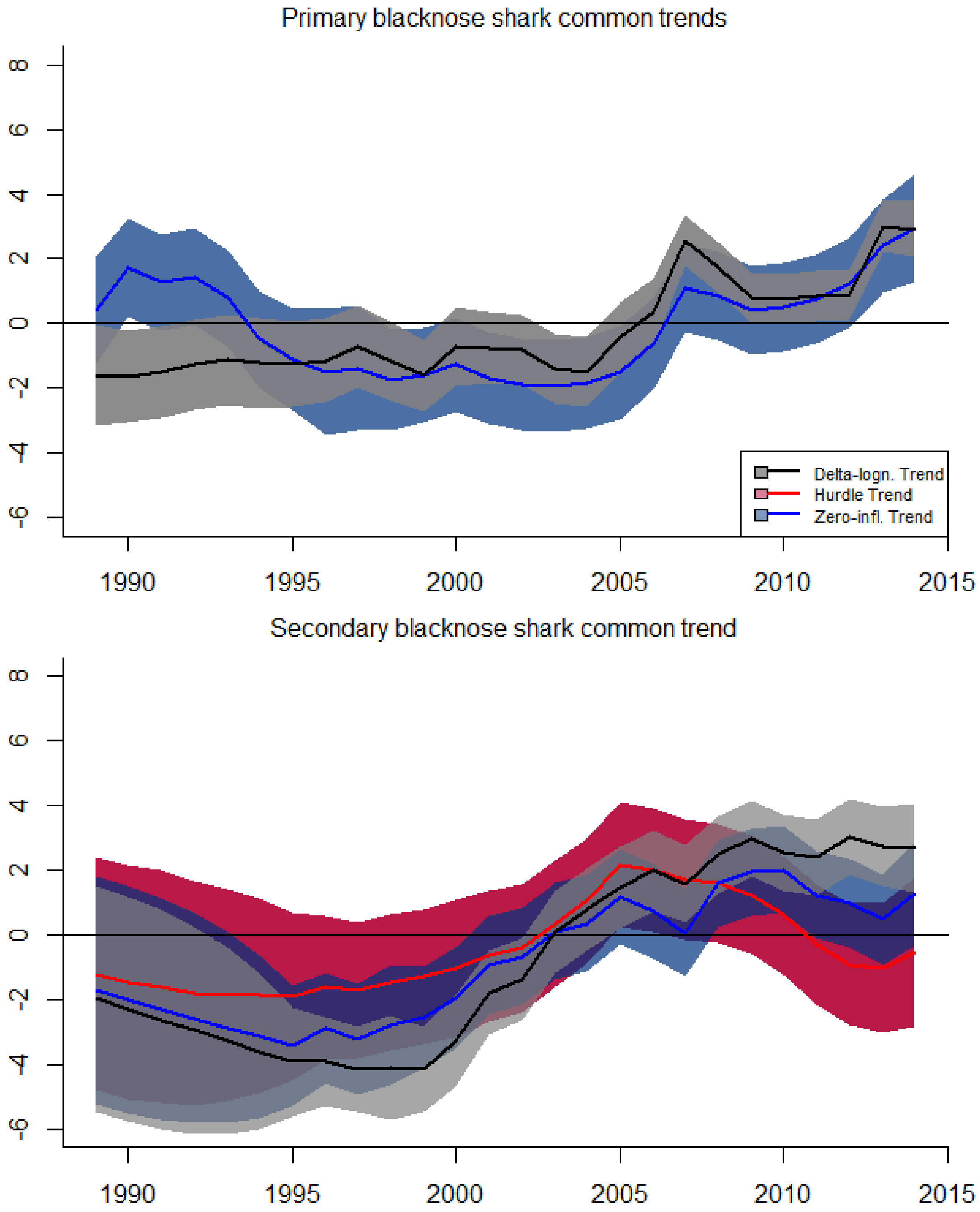
Appendix 12. Dynamic factor analysis common trends in abundance with shaded 95% confidence intervals (CIs) estimated for the tiger shark from the delta-lognormal generalized linear model (GLM) index standardization method.



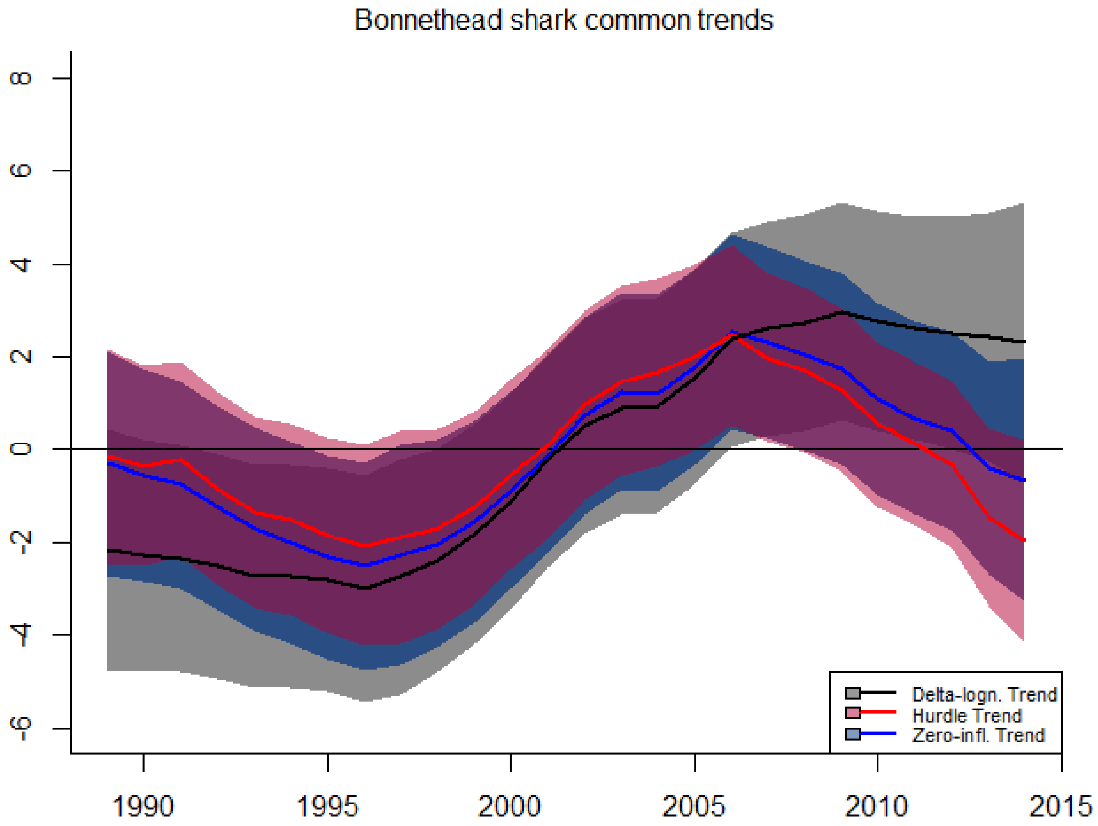
Appendix 13. Dynamic factor analysis common trends in abundance with shaded 95% confidence intervals (CIs) estimated for the spinner shark from the delta-lognormal generalized linear model (GLM) index standardization method.



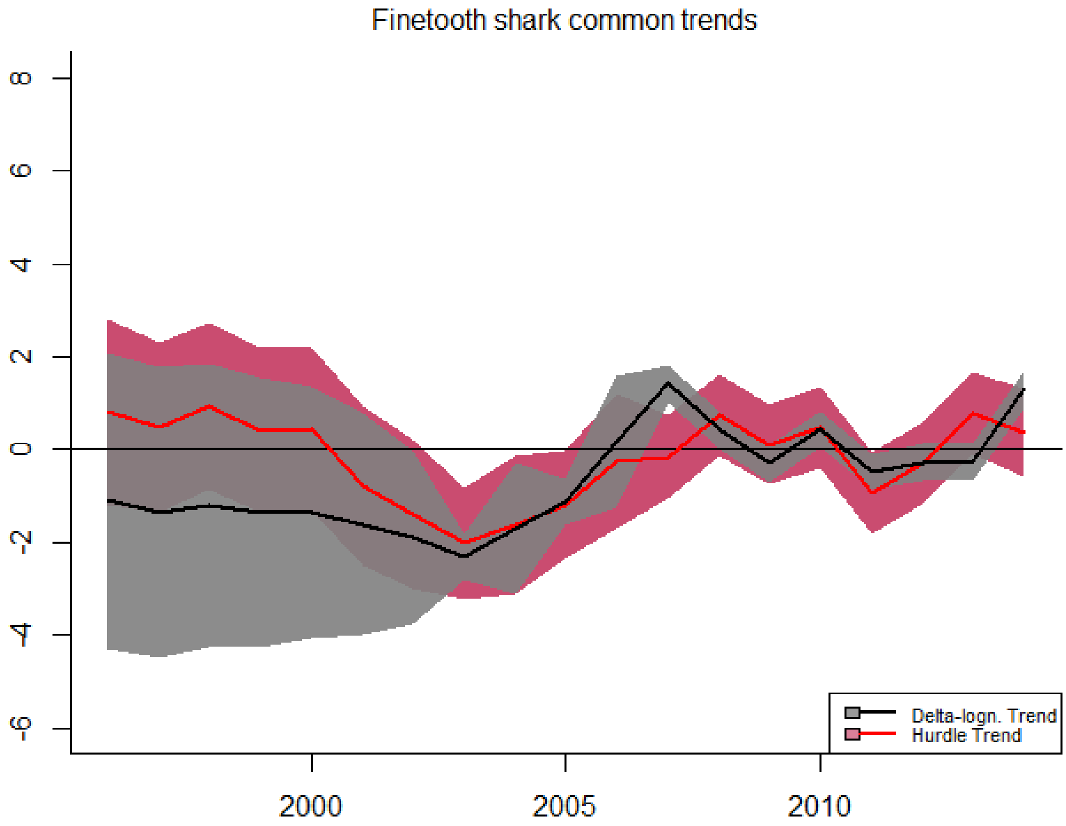
Appendix 14. Dynamic factor analysis common trends in abundance with shaded 95% confidence intervals (CIs) estimated for the Atlantic sharpnose shark from three index standardization methods: 1) delta-lognormal generalized linear models (GLMs; black), 2) hurdle GLMs (red), and 3) zero-inflated GLMs (blue).



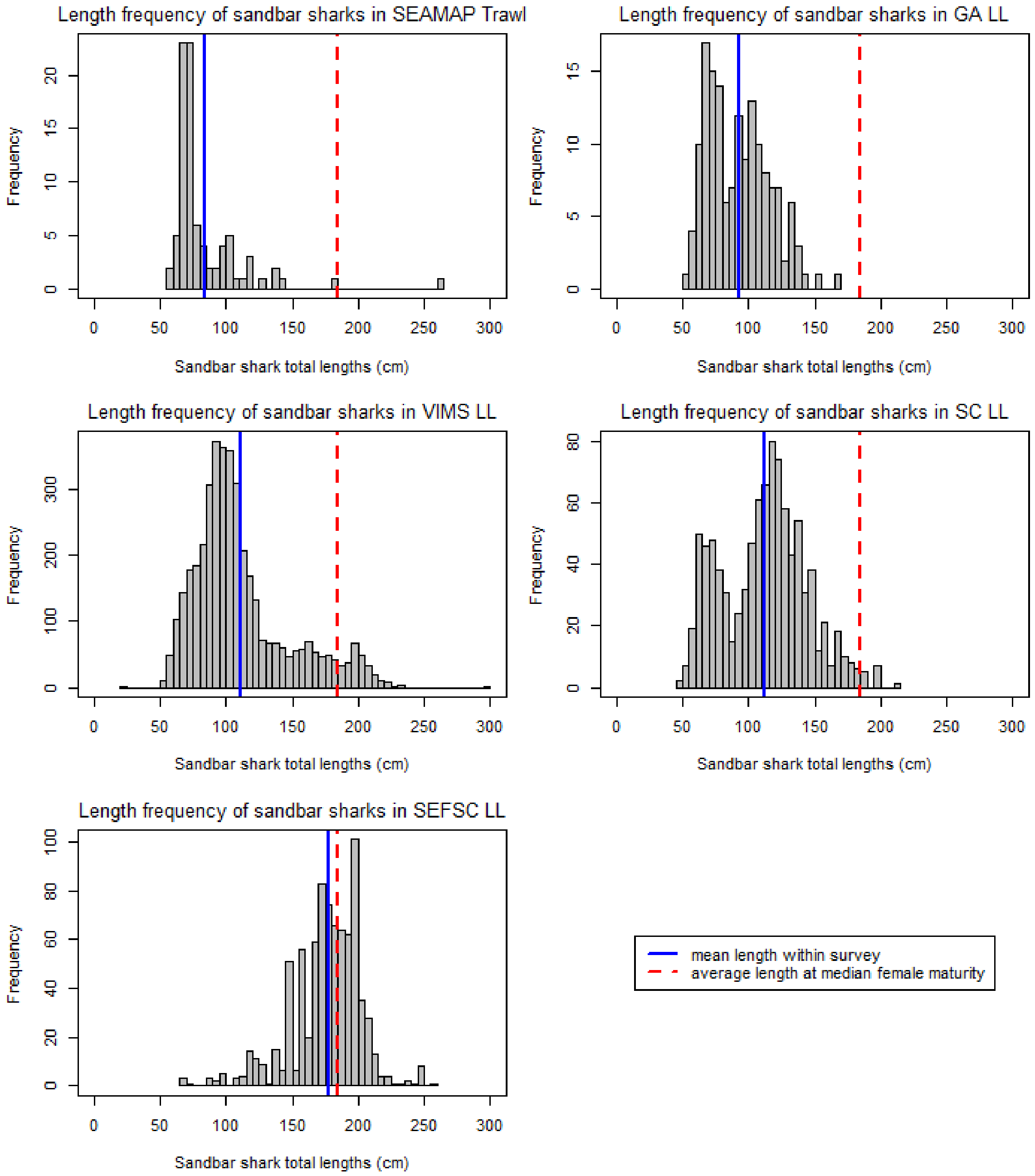
Appendix 15. Dynamic factor analysis common trends in abundance with shaded 95% confidence intervals (CIs) estimated for the blacknose shark from three index standardization methods: 1) delta-lognormal generalized linear models (GLMs; black), 2) hurdle GLMs (red), and 3) zero-inflated GLMs (blue).



Appendix 16. Dynamic factor analysis common trends in abundance with shaded 95% confidence intervals (CIs) estimated for the bonnethead shark from three index standardization methods: 1) delta-lognormal generalized linear models (GLMs; black), 2) hurdle GLMs (red), and 3) zero-inflated GLMs (blue).



Appendix 17. Dynamic factor analysis common trends in abundance with shaded 95% confidence intervals (CIs) estimated for the finetooth shark from two index standardization methods: 1) delta-lognormal generalized linear models (GLMs; black) and 2) hurdle GLMs (red).



Appendix 18. Length-frequency distributions of sandbar sharks captured in the Virginia Institute of Marine Science longline (VIMS LL), SouthEast Area Monitoring and Assessment Program trawl (SEAMAP Trawl), Southeast Fishery Science Center longline (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery gillnet (GULFSPAN GN), South Carolina Red Drum longline (SC LL), and Georgia Red Drum longline (GA LL). The blue vertical line represents the average length captured within the given survey while the red dashed line represents the average length at median female maturity. Note the changing scale of the y-axis.

# VITA

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