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39 Abstract

40 Relative abundance of many shark species in the Atlantic is assessed by compiling data from 41 several independently conducted, but somewhat spatially limited surveys. Although these localized 42 surveys annually sample the same populations, resulting trends in yearly indices often conflict with 43 one another, thereby hindering interpretation of abundance patterns at broad spatial scales. We 44 used delta-lognormal generalized linear models (GLMs) to generate indices of abundance for seven 45 Atlantic coastal shark species from six fishery-independent surveys along the U.S. east coast and 46 Gulf of Mexico from 1975 to 2014. These indices were further analysed using dynamic factor 47 analysis (DFA) to produce simplified, broad-scale common trends in relative abundance over the 48 entire sampled distribution. Effects of drivers including the North Atlantic Oscillation index, the Atlantic Multidecadal Oscillation index, annually averaged sea surface temperature, and species 49 50 landings were evaluated within the DFA model. The two decadal oscillations and species landings 51 were shown to affect shark distribution along southeast U.S. coast. Estimated common trends of 52 relative abundance for all large coastal shark species showed similar decreasing patterns into the 53 early 1990s, periods of sustained low index values thereafter, and recent indications of recovery. 54 Small coastal shark species exhibited more regional variability in their estimated common trends, 55 such that two common trends were required to adequately describe patterns in relative abundance 56 throughout the Gulf of Mexico and Atlantic. Overall, all species' (except the Gulf of Mexico blacktip 57 shark) time series concluded with an increasing trend, suggestive of initial recovery from past 58 exploitation.

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60 **Key words:** Coastal sharks; data conflict; dynamic factor analysis; index of abundance; generalized

61 linear models

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87 Introduction

88 While it is generally agreed upon within the scientific community that shark stocks rapidly 89 declined in abundance along the U.S. east coast beginning in the mid-1970s through the early 1990s 90 (Stevens et al. 2000; Cortés et al. 2002; Dulvy et al. 2014; Grubbs et al. 2016), the extent of that 91 decline has been contentiously debated in the scientific literature with varyingly pessimistic 92 outlooks. Studies quantifying population declines have largely been restricted to modelling effects 93 in a localized area from a single fishery-independent survey (e.g., Musick et al. 1993; Musick et al. 94 2000; Myers *et al.* 2007) or at a broader scale using fishery-dependent data (e.g., Baum *et al.* 2003; 95 Myers and Worm 2003; Baum and Myers 2004; Baum et al. 2005; Burgess et al. 2005a; b; Myers et 96 al. 2007; Baum and Blanchard 2010). In particular, substantial declines as reported by Baum et al. 97 (2003) and Baum and Myers (2004) were rebutted by Burgess *et al.* (2005a), resulting in additional 98 exchanges (Baum et al. 2005; Burgess et al. 2005b; see Field et al. 2009 for more extensive review). 99 These declines may hold economic and ecosystem-wide implications as effects of altered apex 100 predator abundance propagate down the food web via direct and indirect trophic cascades, where 101 sharks likely facilitate natural selection of their prey (Stevens *et al.* 2000; Scheffer *et al.* 2005; Baum 102 and Worm 2009; Ferretti et al. 2010; Heupel et al. 2014).

103 Shark exploitation along the southeast coast of the U.S. began in the mid-1970s coincident 104 with declining stock abundances of other commercially important species, and since sharks were 105 deemed an underutilized natural resource at that time, fishers were encouraged to focus on sharks 106 for commercial harvest (Musick et al. 1993; McCandless et al. 2014). Simultaneously, directed 107 recreational shark fisheries rapidly developed in response to public excitement stemming from the 108 release of the movie "Jaws" in 1975 (Musick et al. 1993; Cortés et al. 2006). Yet, many sharks are 109 inherently susceptible to fishing pressure due to their K-selected life history strategy (Musick et al. 110 2000; Stevens et al. 2000; Au et al. 2015). Large-bodied, coastal shark species were likely most 111 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 112 113 northwest Atlantic, which generally are not considered apex predators, have experienced less 114 dramatic declines in abundance (SEDAR 2007). These smaller species have comparably higher intrinsic population growth rates, and consequently are less susceptible to fishing pressure (Au et 115 116 *al.* 2015).

117 As a result of declines in large coastal shark stocks within the U.S., a shark fishery 118 management plan (FMP) was established by the National Marine Fishery Service (NMFS) in 1993, 119 which initiated the enactment of several commercial and recreational regulations in federal Atlantic 120 waters (SEDAR 2011). Prior to the implementation of management measures, shark population 121 dynamics were not the focus of extensive scientific investigation. The FMP noted a lack of species-122 specific data required to conduct individual stock assessments, which stimulated numerous life 123 history studies of shark stocks within the southeast U.S., and several state and federal agencies 124 began collecting relative abundance information either through directed surveys or as bycatch of 125 existing surveys (NMFS 1993). However, due to their sex- and size-specific migratory patterns and 126 the expansive spatial distributions of Atlantic coastal sharks, developing stock-wide 127 characterizations of relative abundance is challenging (Kohler *et al.* 1998; Castro 2011; 128 Simpfendorfer and Heupel 2012). At present, inferences about shark abundance in the Atlantic are 129 largely based on catch-per-unit-effort (CPUE) data obtained from several relatively spatially limited 130 surveys. When multiple independent surveys each sample a small or incomplete portion of a stock's 131 migratory range, it is not uncommon for the resulting trends in CPUE to be in conflict, which creates 132 uncertainty about true population trends (SEDAR 2013). Thus, developing representative 133 characterizations of stock-wide dynamics and patterns in relative abundance for sharks in the 134 Atlantic involves reconciling discrete, and often contradictory, fragments of information.

135 The objectives of the study were two-fold: i) develop simplified broad-scale trends of 136 relative abundance for seven Atlantic shark species by integrating data from multiple fishery-137 independent survey programs performed at differing spatial scales, and ii) investigate the effects of 138 hypothesized drivers (climatic, environmental, anthropogenic) on resultant broad-scale temporal 139 patterns of relative abundance. We acquired raw data from six fishery-independent surveys and 140 used those data to generate indices of relative abundance for seven species, including four large 141 coastal species (LCS; sandbar shark, *Carcharhinus plumbeus*, Carcharhinidae; blacktip shark, *C.* 142 limbatus, Carcharhinidae; spinner shark, C. brevipinna, Carcharhinidae; tiger shark, Galeocerdo 143 cuvier; Carcharhinidae) and three small coastal sharks (SCS; Atlantic sharpnose shark, 144 Rhizoprionodon terraenovae, Carcharhinidae; blacknose shark, C. acronotus, Carcharhinidae; 145 bonnethead, Sphyrna tiburo, Sphyrnidae). Large and small coastal shark designations distinguish 146 management units along the Atlantic coast of the U.S. as defined by NMFS (1993). The relative 147 abundance indices were jointly analysed for underlying common trends in abundance using 148 dynamic factor analysis (DFA), a multivariate dimension reduction approach for time series. We 149 subsequently examined the effects that broad-scale environmental and anthropogenic drivers had 150 on these species-specific relative abundances.

151 Methods

152 Data sources

153 Catch and effort data from six fishery independent shark surveys ranging from 1975-2014 154 were the basis for this study: the Virginia Institute of Marine Science Longline (VIMS LL), SouthEast 155 Area Monitoring and Assessment Program-South Atlantic Coastal Trawl Survey (SEAMAP-SA 156 Trawl), South Carolina Coastal Longline Survey (SC LL), Georgia Red Drum Longline Survey (GA LL), 157 Southeast Fisheries Science Centre Longline Survey (SEFSC LL), Gulf of Mexico Shark Pupping and 158 Nursery Gillnet Survey (GULFSPAN GN; Fig. 1; Table S1). Data for the SEAMAP-SA Trawl, SC LL, and 159 GA LL can be accessed from www.seamap.org (SEAMAP-SA Data Management Work Group). A 160 minimum of three independent survey-based indices of abundance were required for a given 161 species to be considered for analysis (with the exception of the tiger shark). Data from seven shark 162 species were analysed (Table S2).

163 *Indices of abundance*

164 Generalized linear models (GLMs; McCullaugh and Nelder 1989) were used to standardize 165 species-specific CPUE data from each survey program and provide estimated annual indices of 166 relative abundance. Preliminary explorations of each survey dataset revealed high frequencies of 167 zero observations, which were expected given the fishery-independent nature of the surveys and 168 low overall abundance of the focal species. Consequently, delta-lognormal GLMs were used to 169 generate species-specific relative abundance indices from each survey (Lo et al. 1992; Maunder and 170 Punt 2004: Cortés et al. 2006), where the survey observations were defined as number of sharks 171 captured per hook-hours, per net area-hours, or per area swept for longline, gillnet, and trawl 172 gears, respectively. For the purposes of the current study, we assumed that gear selectivity was 173 principally constant over time.

Delta-lognormal models contain two components (Pennington 1983). The binomial submodel is fitted to presence/absence data, where presence is defined as sampling events in which at least one target species was captured, and estimates the probability of encountering the target species. The lognormal submodel, fitted to the log-transformed nonzero observations, is used to estimate the mean CPUE. The general form of a delta-lognormal GLM is:

 $logit(\boldsymbol{\pi}_{\boldsymbol{B}}) = \boldsymbol{X}_{\boldsymbol{B}}\boldsymbol{\beta}_{\boldsymbol{B}} + \boldsymbol{\varepsilon}_{\boldsymbol{B}}, \text{ where } \boldsymbol{\varepsilon}_{\boldsymbol{B}} \sim N(0, \sigma_{\boldsymbol{B}}^2)$

179 $\boldsymbol{\mu}_{CPUE} = \boldsymbol{X}_{CPUE} \boldsymbol{\beta}_{CPUE} + \boldsymbol{\varepsilon}_{CPUE}, \text{ where } \boldsymbol{\varepsilon}_{CPUE} \sim N(0, \sigma_{CPUE}^2)$ (1)

180 where π_B represents the probability that each observation (i.e., sampling event) is non-zero, μ_{CPUE} is 181 the log-transformed CPUE, and in both submodels, *X* is the design matrix, β is the vector of estimated parameters, and ε is the associated observation error. Predicted indices of relative abundance were generated using estimated marginal means (Searle *et al.* 1980), and back transformed bias correction followed Lo *et al.* (1992). The resulting predictions over years from both submodels were multiplied to generate a final annual index of relative abundance. Uncertainty estimates for the annual indices were generated from 1000 nonparametric bootstrapped samples (Efron and Tibshirani 1993). All analyses of survey data were performed with the software package R (version 3.1.1, R Core Development Team 2014).

189 Akaike's Information Criterion (AIC, Akaike 1973, Burnham and Anderson 2002) was used 190 to discriminate among model parameterizations containing different combinations of covariates. 191 The covariates examined varied by survey (Table S1), while year was included in all models to 192 ensure estimation of annual abundance indices. Year, month/season, and station/area were treated 193 as categorical variables, and levels of those categorical variables were excluded from analyses if the 194 species of interest was not present during at least two sampling events. Latitude, longitude, and 195 depth were standardized and treated as continuous variables. Scatter plot matrices and variance 196 inflation factors (VIFs) were used to assess correlation and collinearity of covariates. Covariates 197 with correlation coefficient of large magnitudes (≥ 0.7) or that produced large VIFs (> 10) were not 198 mutually included in any model. Graphical residual analysis, deviance explained, and dispersion 199 analysis were used to assess model fit. Resulting indices of abundance were standardized (Z-200 scored) prior to implementation into the dynamic factor analysis model.

201 Dynamic factor analysis

Dynamic factor analysis is a multivariate dimension reduction technique designed for relatively 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 short time series (Zuur *et al.* 2003a; b; Holmes *et al.* 2014). The general form of a DFA model can be written:

207 208

$$y_{t} = \Gamma \alpha_{t} + Dx_{t} + \varepsilon_{t}, \text{ where } \varepsilon_{t} \sim MVN(0, H)$$

$$\alpha_{t} = \alpha_{t-1} + \eta_{t}, \text{ where } \eta_{t} \sim MVN(0, Q)$$
(2)

where the top equation represents the observation component, and the second equation represents the process or state component. The $(n \times 1)$ vector y_t is comprised of abundance indices at time t, a_t is the vector $(m \times 1)$ of common trends (m < n) that are modelled as stochastic random walks, Γ is the matrix $(n \times m)$ of estimated factor loadings on the common trend(s), x_t is the vector $(k \times 1)$ of drivers, *D* holds the corresponding coefficients $(n \times k)$, and *H* and *Q* denote the variance-covariance matrices associated with the observation error vector ε_t $(n \times 1)$ and process error vector η_t $(m \times 1)$, 215 respectively (Zuur et al. 2003a; b; Holmes et al. 2014). The process component of DFA fits 216 autocorrelated common trends to accommodate the time series nature of the indices and resulting 217 trends (Stachura *et al.* 2014). Factor loadings (elements of the Γ matrix) indicate the strength of the 218 influence of each survey index on the resulting common trend. Values higher in magnitud $\gtrsim 0$.2) denote a stronger effect of the given survey on the corresponding common trend. Since the indices 219 220 were Z-scored, the resulting factor loadings, common trends, and fitted values were unitless (Zuur 221 et al. 2003b). Significance of factor loadings and drivers were defined as 95% confidence intervals 222 (CIs) that did not overlap zero.

To ensure that the model was identifiable, *Q* was set to the identity matrix (*I*) and *H*, which specifies the variance-covariance structure between 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 (Holmes *et al.* 2014). Model implementation occurred using the statespace multivariate autoregressive modelling package 'MARSS' (Holmes *et al.* 2013) in R (version 3.1.1).

230 Models were fitted in two-steps (Supplement 1). First, all combinations of one, two, or three 231 common trends and the four covariance matrix structures were explored in the absence of drivers, 232 and corrected Akaike's Information Criterion (AICc) for low sample sizes was used for model 233 selection (Holmes et al. 2014), along with graphical evaluation. An additional quantitative measure 234 of model fit, which was calculated as the sum of the squared residuals (*r*) of the fitted trend divided by the sum of the squared observations $(\sum r_t^2 / \sum \hat{y}_t^2)$ for each survey, was also used to compare 235 236 models. Lower quantities (defined as ≤ 0.6) were interpreted as indicative of better model fit, while 237 higher values indicated that all or several years were poorly estimated by the resulting fitted trend 238 (Zuur et al. 2003b). For comparative purposes, these values were averaged for all surveys of a given 239 species. Second, the effect of broad-scale drivers were investigated in the most supported model 240 from the first step. The mean fit value, combined with AICc and graphical analyses that assessed 241 agreement between the fitted trend and raw indices of abundance, were collectively used to select 242 the most parsimonious model that best described the indices of relative abundance.

Four drivers were examined: (1) the North Atlantic Oscillation (NAO) index, (2) the Atlantic Multidecadal Oscillation (AMO) index, (3) global, 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/; GISTEMP Team 2016; Fig. 2a), and (4) species landings (provided by E. Cortés, NMFS, Panama City, FL; Fig. 2b). The NAO, which is a 248 measure of pressure difference over the North Atlantic Ocean, and AMO, which encompasses basin-249 wide sea surface temperature, circulation patterns, and sea level pressure, were selected as 250 environmental drivers because they directly impact climate patterns and have been shown to affect 251 fish survival and ecosystem organization through bottom-up control in the southeast U.S. Atlantic 252 coast and Gulf of Mexico (Stenseth *et al.* 2002 and references therein; Collie et al. 2008; Nye et al. 253 2009; Nye et al. 2014; Karnauskas et al. 2015). Annually averaged SST was included because 254 several studies have shown that shark movement is influenced by temperature patterns (e.g., 255 Merson and Pratt 2001; McCandless et al. 2005; Castro 2011). Since AMO and SST were highly 256 positively correlated by definition (correlation coefficient = 0.85), they were not mutually included 257 in any DFA model. Lastly, species-specific landings, pooled across the Atlantic and Gulf of Mexico, 258 were included to examine the effect of top-down pressure on species relative abundance. Drivers 259 were limited to broad-scale processes, as the corresponding effect should encompass the spatial 260 range employed by all surveys. Landings were prepared following procedures routinely applied in 261 shark stock assessments (E. Cortés, personal communication). Dynamic factor analysis requires 262 complete time series of drivers, and landings time series did not encompass the temporal span of 263 the index data for the blacktip shark and tiger shark (first five years had no landings data for each 264 species). Hence, hindcasting over missing years was performed by calculating an average catch from the first five years of observed landings data. 265

266 **Results**

267 *Indices of abundance*

Delta-lognormal GLMs provided acceptable fits to raw survey data as determined by graphical residual analysis, variance inflation factors, dispersion analysis, and estimated parameter values and standard errors. Location and month were the covariates that were most frequently included in the most supported GLMs for each species when generating indices of abundance, followed by depth, when available (Table S3). For all species, superimposed standardized indices of relative abundance display obvious data conflict (Fig. 3), such that visual interpretation of broadscale patterns in species relative abundances is challenging.

275 Dynamic factor analysis

Time series of relative abundance were well-fitted by the DFA models for all species, with the exception of spinner shark (Tables 1, S4, S5; Figs. S1 and S2). Similarly, either one or two common trends were identified for each species. A diagonal covariance structure was empirically supported for all species, suggesting that no covariance exists between survey indices for the focal species. Furthermore, DFA models were optimally fitted when variances for each survey index within the covariance matrices were assumed to be equal for each species, except for Atlantic sharpnose shark, where a unique variance was estimated for each survey and no covariance was included in the model.

284 The DFA results for the large coastal sharks showed consistent trends in relative abundance 285 across species. For example, the sandbar shark common trend (Fig. 4a) indicated that relative 286 abundance peaked in the early 1980s, decreased until the early 1990s, remained low for several 287 years, and exhibited a modest recovery in the late 2000s. This common trend was well supported 288 by the VIMS LL, SEFSC LL, and GA LL, as indicated by statistically significant factor loadings, with a 289 negative loading by the SC LL (Fig. 4b), such that the SC LL showed a generally decreasing trend 290 from 2007-2014 (Fig. S1). The NAO, which was included in the optimal DFA model for sandbar 291 shark, had a significantly negative effect on the VIMS LL and a positive effect on the GA LL indices of 292 abundance for the sandbar shark (Table S5).

293 The blacktip shark showed a similar common trend to sandbar shark, although the initial 294 recovery began sooner in the time series (Fig. 4c). The trend was significantly and positively driven 295 by the VIMS LL, SEAMAP-SA Trawl, and SEFSC LL surveys, while the GULFSPAN GN and SC LL 296 negatively loaded on the blacktip shark trend (Fig. 4d), suggesting that the latter indices were 297 following an opposing signal of relative abundance as compared to the estimated common trend 298 (Fig. S1). The GULFSPAN GN primarily captured immature blacktip shark, such that the Gulf of 299 Mexico juvenile trend was decreasing. The short SC LL and GA LL indices of relative abundance 300 (2007–2014) showed generally increasing patterns whereas the common trend showed a minimal 301 decline during those years (Fig. S1), explaining the negative factor loadings. The AMO was included 302 in the optimal DFA model for the blacktip shark and had a significantly negative effect on the VIMS 303 LL index of abundance and a positive effect on the GULFSPAN GN and SC LL indices (Table S5).

The tiger shark trend also showed a decrease in abundance into the early 1990s, followed by a period of low relative abundance (Fig. 4e). However, in the early 2000s, the relative abundance of tiger shark began to increase much more rapidly than the other large coastal species. Factor loadings indicated that the VIMS LL and SEFSC LL both significantly positively influenced the common trend (Fig. 4f). The optimal DFA model for the tiger shark included the NAO index, which had a significantly negative effect on the SEFSC LL index, and landings, which showed a significantly positive effect on the SEFSC LL index (Table S5).

The spinner shark time series was much shorter (Fig. 4g), and raw indices of abundance showed little contrast in relative abundance across years, resulting in low and insignificant factor loadings (Fig. 4h). Nevertheless, the common trend was positively driven by the VIMS LL and
negatively driven by the GULFSPAN GN indices of relative abundance (85% CIs excluded zero). The
resulting trend reflected an increase of relative abundance from the late-1990s to 2014.

316 The small coastal complex showed more regionally distinctive trends in relative abundance, 317 as all species exhibited two common trends or opposing factor loadings (Table 1; Fig. 5). The first 318 Atlantic sharpnose shark trend showed moderately stable relative abundances until the mid-2000s, 319 followed by a subsequent increase (Fig. 5a). This first trend was primarily driven by the SEFSC LL, 320 which principally samples the Gulf of Mexico. However, it was also significantly driven by sampling 321 off the coast of Virginia by the VIMS LL (Fig. 5b). The secondary trend was largely uninformed prior 322 to the late 1980s, showed a steady increase in abundance into the mid-2000s, and a moderate 323 decline to 2014. This second trend was significantly driven by the SEAMAP-SA Trawl and SC LL, 324 which both sample in the Atlantic.

325 Although the optimal blacknose DFA model produced a single trend that showed a clear 326 decrease in abundance from the mid-1990s into the 2010s (Fig. 5c), the factor loadings indicated 327 opposing trends in relative abundance based on region (Fig. 5d). The common trend was 328 significantly positively influenced by the SEFSC LL and GULFSPAN GN, indicating that the common 329 trend was representative of a decline in blacknose shark abundance within the Gulf of Mexico. 330 Contrarily, the SEAMAP-SA Trawl had a significantly negative factor loading, suggesting that 331 blacknose shark sampled along the Atlantic coast underwent an increase in relative abundance (Fig. 332 S2). The NAO index was included in the optimal blacknose shark model, and had a significantly 333 negative effect on the GULFSPAN GN index and a positive effect on the SC LL index (Table S5).

Despite the two common trends estimated for the bonnethead (Fig. 5e), only the primary trend was indicative of the pattern of abundance of bonnethead in the Atlantic. The second common trend was included to better accommodate the increase in SC and GA LL survey indices (Fig. S2), explaining the broad uncertainty prior to 2007. Since the GULFSPAN GN showed low and insignificant factor loadings (Fig. 5f), it is difficult to draw inferences about patterns in relative abundance of bonnethead within Gulf of Mexico.

340 Discussion

341 *Indices of abundance*

Spatial and temporal covariates were important explanatory variables of local shark relative abundance for all species examined. Considering the broad seasonal migratory patterns of several shark species (Speed 2010 and references therein), it is expected that CPUE of the surveys in this study will change with month/season. Similarly, as sampling areas (or other measures of 346 spatial sampling distribution) represent environmental variability, their importance in explaining 347 CPUE patterns is not surprising since target species will distribute according to preferred habitat 348 types. Additionally, depth also reflects habitat suitability, and when this covariate was available, it 349 too was important in explaining changing CPUE of sampled species. Results from the delta-350 lognormal GLMs collectively showed that CPUE was variable across space, season, and depth, even 351 within the relatively small areas covered by the surveys. Consequently, obtaining conflicting 352 patterns in indices is likely, which motivates the need for data reconciliation to develop a robust 353 understanding of relative abundance.

354 *Large coastal abundance*

The drastic decline in LCS stocks has been extensively debated (i.e. Baum et al. 2003; Baum 355 356 and Myers 2004; Baum et al. 2005; Burgess et al. 2005a; b; Grubbs et al. 2016). Postulated declines 357 of 60-99% relative to virgin conditions have been suggested for several coastal shark species into 358 the 1990s and 2000s (Musick et al. 1993; Baum et al. 2003; Baum and Myers 2004; SEDAR 2006; 359 Myers et al. 2007; SEDAR 2007; Baum and Blanchard 2010; SEDAR 2011; 2012). However, the 360 patterns of relative abundance described in the current study provide a more optimistic outlook and more closely align with results presented by Carlson et al. (2012), where spinner shark and 361 362 tiger shark, among other species, were shown to have increased in abundance by 14% and 3%, 363 respectively, following enactment of the shark FMP. Those results showed preliminary recovery 364 and stabilization of some LCS stocks by 2009 within the commercial bottom longline fishery 365 (Carlson *et al.* 2012).

366 Thus far, studies estimating LCS stock declines have relied on independent and fragmented 367 information, typically only analysing data from a single survey, where changes in regional 368 distribution may be interpreted as changes in abundance. Indices of abundance from disparate 369 surveys frequently result in conflicting information due to high levels of uncertainty and the 370 variable timing of sampling relative to environmentally driven shark migrations (Grubbs 2010). 371 Additionally, complex life cycles, which include size- and sex-specific habitat and movement 372 patterns, result in indices of relative abundance that may only be representative of a portion of the 373 species' life cycle (Kohler et al. 1998; Castro 2011; Simpfendorfer and Heupel 2012). For example, 374 sandbar sharks mate within the coastal waters of Florida during June and July (Portnoy et al. 2007; 375 Baremore and Hale 2012). A year later, gravid females migrate northward along the Atlantic coast 376 to pup in bays and estuaries during late spring and early summer, after which they migrate back 377 offshore (Grubbs et al. 2007; McCandless et al. 2005, Baremore and Hale 2012). Neonates remain in 378 these nurseries throughout the summer (McCandless et al. 2005; Conrath and Musick 2010), and

overwinter off the coast of North Carolina (Grubbs *et al.* 2007; 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.* 2007; 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).

385 In the current study, CPUE data from several surveys were analysed outside the context of a 386 stock assessment model to reconcile data conflict and provide representative trends of broad-scale 387 relative abundance, where increased abundance suggests preliminary recovery of LCS species. All 388 LCS species followed similar trends in relative abundance, with high levels at the beginning of the 389 time series, followed by a decline until the early 1990s, and signs of recovery in the mid-2000s. 390 Given the low intrinsic population growth rates of many shark species (Au et al. 2015), it is 391 reasonable to assume that efficacy of management regulations would not immediately translate 392 into stock recovery (Musick et al. 2000). The results of the current study support that reasoning 393 since relative abundance trends of all large coastal species remained depressed following 394 implementation of the 1993 shark FMP. The duration of low relative abundance varied by species 395 however, and relative abundances of those with younger ages-at-maturity (Table S2) showed 396 quicker recoveries than those with older ages at first reproduction.

The sandbar shark period of extended low abundance may have also been related to statewide fisheries targeting young and late juvenile animals, since state and federal management was not formally linked until 2009 (Grubbs 2010). Within Atlantic state waters, sandbar shark utilize large estuaries as nursery areas along the coast (Merson and Pratt 2001; Grubbs *et al.* 2007; McCandless *et al.* 2005), facilitating survival to maturity (Heupel and Hueter 2002; Heupel *et al.* 2007). Hence, given the critical role that state waters play in the lifespan of several shark species, it is necessary to consider the synergistic effects of federal and state management regulations.

404 The recent increase in the blacktip shark trend was gradual and showed a great deal of 405 variability, which could be attributed to various management measures, such as the staggered 406 mandatory implementation of bycatch reduction devices (BRDs) within the shrimp trawl fishery (SEDAR 2013; mandated in 1997 in the southeast Atlantic coast, 1998 in the western Gulf of 407 408 Mexico, and 2004 in the eastern Gulf of Mexico; Scott-Denton *et al.* 2012). Despite surveys sampling 409 two genetically distinct stocks of blacktip shark (Keeney et al. 2005), a single common trend was 410 selected to encompass abundance patterns in both the Atlantic and the Gulf of Mexico, potentially 411 indicating that sufficient data were not available within either or both stocks to distinguish

412 alternative relative abundance patterns, or that both stocks were following a similar trend in 413 relative abundance. The tiger shark recovery was extremely large in magnitude, likely reflective of 414 the relatively high fecundity of these sharks, in which females produce an average of 41 pups every 415 two years in the Atlantic (Castro 2011) or three years in the Pacific Ocean (Whitney and Crow 416 2007). While the spinner shark common trend was shorter due to the limited length of each time 417 series included, the modest increase in relative abundance corresponds with that of the other large 418 coastal species, despite larger uncertainty in the resulting estimated trend.

419 Small coastal abundance

420 Due to a higher capacity to recover (Au et al. 2015), SCS species underwent declines of 421 generally smaller magnitudes than LCS species. Stock assessments have suggested declines of 35-422 55% relative to virgin abundance for Atlantic sharpnose shark and bonnethead (SEDAR 2007; 423 2013), compared to an estimated 80-85% decline in Atlantic and Gulf of Mexico blacknose shark 424 (SEDAR 2011). In contrast, Myers et al. (2007) suggested seemingly exponential increases in 425 mesopredator abundances, particularly Atlantic sharpnose shark, coinciding with declining LCS 426 abundances. In the current study, with the exception of the Gulf of Mexico blacknose shark, relative 427 population declines were minimal and followed by substantial increases that were much smaller in 428 magnitude than those predicted by Myers *et al.* (2007).

429 While the large coastal species typically undergo extensive migrations between the Atlantic 430 Ocean and the Gulf of Mexico, it is likely that gene flow around the Florida peninsula is restricted in 431 small coastal species due to comparatively localized movement patterns (Kohler *et al.* 1998). Both 432 the Gulf of Mexico stocks of blacknose shark and bonnethead are considered genetically separate 433 stocks (Portnov et al. 2014). Bonnethead have been shown to exhibit variation in life history 434 parameters on a much smaller spatial scale along the Atlantic coast (Frazier *et al.* 2013) and within 435 the Gulf of Mexico (Lombardi-Carlson et al. 2003). Ultimately, while Atlantic sharpnose shark 436 within the southeast U.S. coast and within the Gulf of Mexico represent a single genetic stock 437 (SEDAR 2013), it has been suggested that migrations between the U.S. east coast and Gulf of Mexico 438 are rare for the species (Kohler *et al.* 1998). It is not surprising to note that there appears to be 439 more localized variability in small coastal shark abundance as demonstrated by the increased 440 number of common trends estimated for the Atlantic sharpnose shark and conflicting factor 441 loadings in the blacknose shark.

442 Regional increases in the Atlantic sharpnose shark, blacknose shark, and bonnethead 443 common trends also correspond with localized management implementation such as BRDs. For 444 example, following the 1998 BRD mandate in the southeast Atlantic coast (Scott-Denton *et al.* 445 2012), abundance of the Atlantic stocks of Atlantic sharpnose shark, blacknose shark, and 446 bonnethead, all significantly driven by the SEAMAP-SA Trawl, increased. Similarly, the Atlantic 447 sharpnose shark trend in the Gulf of Mexico showed an abrupt increase following the mandatory 448 implementation of BRDs in the eastern Gulf in 2004 (Scott-Denton et al. 2012). All small coastal 449 shark stocks showed overall increased abundance into the 2010s except the Gulf of Mexico 450 blacknose shark, which are known to be largely susceptible to bycatch within the shrimp trawl 451 fishery and likely further depleted than the Atlantic stock (SEDAR 2011). Additional survey data 452 within the Gulf of Mexico will greatly aid interpretations of coast-wide patterns of relative 453 abundance in the bonnethead.

454 *Dynamic factor analysis drivers*

Although several studies have linked small- and meso-scale shark distributions to climatic 455 456 indices (Carlson 1999; Cotton et al. 2005; Brodziak and Walsh 2013; Hoffmayer et al. 2014; Mitchell 457 et al. 2014; Báez 2015), studies have rarely examined whether broad-scale relative stock 458 abundance is affected by multidecadal oscillations. Although Perry et al. (2005) noted that slower 459 growing species (like sharks) are less likely to undergo distributional shifts due to changing 460 environmental conditions and are thus, more susceptible to changes in climate, conclusions from 461 the current study suggest that when immediate environmental conditions are unfavourable, the 462 coastal shark species examined may redistribute to more suitable conditions. For instance, although 463 blacknose sharks rarely migrate northward into Virginia waters and instead reside off the coast of 464 North and South Carolina during summer (Castro 2011 and references therein, Ulrich *et al.* 2007), 465 due to extremely warm water temperatures in the southeastern U.S. coast in the summer of 2015 466 (positive AMO and NAO indices), the VIMS LL captured 16 blacknose sharks compared to only eight 467 specimens previously recorded between 1973 and 2014. Similar accounts of distributional shifts in 468 sharks due to unfavourable environmental conditions have been documented (Wiley and Simpfendorfer 2007; Nye et al. 2009; Sunday et al. 2012). Last et al. (2011) investigated the change 469 470 in species composition along the coast of Tasmania, Australia, an area subjected to extreme 471 temperature increases over the past 60 years, and found that five out of 10 elasmobranch species 472 examined exhibited distributional changes.

In the current study, during years when the AMO index was in its warm phase, reflective of increased rainfall in Florida and heightened hurricane activity in the Atlantic Ocean, relative abundance of blacktip shark was below average off the coast of Virginia and above average off South Carolina. Blacktip sharks may therefore restrict their northward migration and reside in more southerly areas due to unfavourable environmental conditions associated with above average AMO index values. Additionally, the GULFSPAN GN, a latitudinally constant juvenile survey within
which 95% of blacktip shark captured were of neonatal or juvenile life stage, showed a positive
association with the AMO, suggesting better recruitment years and potentially higher nursery
habitation in the Gulf of Mexico in years when the AMO index is positive.

482 Positive NAO index values also result in increased temperatures and rainfall off the 483 southeast coast of the United States, and such environmental conditions corresponded with below 484 average sandbar shark relative abundance off Virginia and above average relative abundance off 485 Georgia. As such, environmental conditions associated with positive NAO values may lead to 486 restricted northward migration of the sandbar shark. A similar explanation likely underlies climate 487 induced distributional changes of the blacknose shark, in which relative abundance is higher off 488 South Carolina and nursery utilization and recruitment was inhibited within the Gulf of Mexico 489 during years with above average NAO values. Because the tiger shark range is so large and vast 490 migrations are common (Kohler *et al.* 1998; Lea *et al.* 2015), the data in this study are likely still 491 representative of localized relative abundance, such that tiger shark distribution patterns may shift 492 from the Gulf of Mexico to areas outside of those sampled by surveys when the NAO index is low. 493 Further empirical research will be necessary to fully understand the underlying physiological 494 linkages governing the species-specific responses to these climatic drivers.

495 Given the functionally equivalent patterns of common trends generated from models with 496 and without climatic drivers, it is reasonable to conclude that the overall abundance of coastal 497 shark stocks was not altered by environmental and anthropogenic drivers, as similarly noted by Bigelow et al. (1999) in a pelagic shark. Rather, effects of climatic drivers within the optimal DFA 498 499 models were survey-specific and likely indicative of localized distributional reorganization, while 500 the estimated DFA trends reflect underlying patterns in relative abundance over broad geographic 501 scales. These regional distributional changes due to climatic forcing may be the mechanism 502 underlying local ecosystem reorganization noted by several studies (Stenseth et al. 2002 and 503 references therein; Collie et al. 2008; Nye et al. 2009; 2014; Karnauskas et al. 2015).

While it is expected that any substantial top-down forcing would affect shark stock abundance, the estimated harvest effects differed by survey or location when included in the optimal DFA model. For example, overall tiger shark landings did not significantly affect CPUE off the coast of Virginia but were positively related to the SEFSC LL relative abundance in the Gulf of Mexico. Landings from the Atlantic and Gulf of Mexico were necessarily pooled for analysis. Lack of spatially resolved harvest information, potential changes in the distribution of tiger shark fishing and bycatch over the 40-year span of the current study, a lack of information regarding differential habitat use, and vast migratory patterns (Lea *et al.* 2015) creates uncertainty in understanding true
impacts of tiger shark landings along the southeast U.S. coast. In years when tiger shark abundance
along the southeast U.S. was high, they were more available to both survey gear and commercial
fishermen, reflective of the close correlation between the DFA common trend and tiger shark
landings.

516 Dynamic factor analysis modelling

517 Resulting broad-scale trends in relative abundance were successfully generated for the 518 species examined, as indicated by model diagnostics and the alignment between the common 519 trends, species' life history parameters, and historical management measures. Marine ecological 520 applications of DFA models have indeed increased in recent years (Chen et al. 2006; Azevedo et al. 521 2008; Katara et al. 2011; Tam et al. 2013; Colton et al. 2014; Stachura et al. 2014; Thorson et al. 522 2015; Buchheister et al. 2016) which signifies the general applicability of the method. Dynamic 523 factor analysis models provide the necessary flexibility for fisheries time series data, 524 accommodating for temporal autocorrelation short and nonstationary time series, as well as time 525 series with missing values.

Despite the appealing flexibility of DFA modelling, we note that the application in the 526 527 current study was limited. Although several coastal species are known to represent genetically 528 distinct stocks in the Atlantic and within the Gulf of Mexico (e.g., Portnov *et al.* 2014), we chose to include all survey indices in the same DFA model, regardless of location. We assumed that if the two 529 530 stocks showed differences in relative abundance trends over time, model selection would favour 531 estimation of two common trends, as in the Atlantic sharpnose shark. Since sharks represent 532 relatively "data limited" species, we did not have sufficient positive observations to build age- or 533 size-structure into analyses. As such, limited size ranges were likely disproportionately represented 534 in the common trend, depending on the gear configurations and sampling domains of surveys that 535 most contributed to the resulting trend. Likewise, gear-selectivity was not accounted for within the 536 DFA models. Although it can be beneficial to include multiple gear types within an analysis to 537 ensure that each species was adequately represented (e.g. bonnethead; Ulrich et al. 2007), 538 aggregating data from gears with different selectivities implies that resulting trends of relative 539 abundance may not explicitly represent the true patterns in length-frequency of the stock. A similar 540 argument can be made regarding potential incongruence among the estimated common trends and 541 the cumulative age composition of each stock. Representative selectivity functions for each DFA 542 common trend may be calculated by averaging the selectivity functions of each gear implemented 543 (if known), where the relative contribution of the selectivity function for each survey is weighted by

544 the corresponding factor loading. However, when size and age classes are pooled and if we assume 545 that gear selectivity and length-distribution of the catch has been largely constant over time (or 546 varies randomly), then the effect of correcting CPUE from a single survey based on the 547 corresponding gear selectivity would effectively scale the predicted estimate of relative abundance. 548 By standardizing (z-scoring) indices of relative abundance prior to DFA modelling, the effect of 549 scaling the indices to account for gear selectivity is essentially removed. Standardization also 550 removes the effect of scaling differences due to gear-specific catchability (q), where catchability is 551 the proportionality constant relating CPUE to total abundance (N; CPUE = qN; Quinn and Deriso 552 1999). Without known selectivity functions or catchability estimates for each survey, these 553 methods represent a best attempt to handle available data. Furthermore, a hierarchical model also 554 designed to reconcile conflicting indices of abundance was shown to be largely insensitive to 555 variability in gear selectivity (Conn 2010). Given additional data, DFA models may be run on 556 separate age- or size-classes or comparable gear types.

557 Conclusions

558 Availability of fisheries-independent data for shark species within the U.S. appears to be 559 much greater than comparable data available elsewhere in the world. Largely, global magnitudes of 560 shark stock declines in open ocean areas and other regions of the world are based on estimated 561 fisheries catch (i.e., Stevens et al. 2000; Clarke et al. 2006; Worm et al. 2013; Dulvey et al. 2014; 562 Davidson et al. 2016) or density-dependent data (i.e., Baum et al. 2003; Baum and Myers 2004; 563 Baum and Blanchard 2010), and vulnerability is assessed by life history information as opposed to 564 quantitative assessments of stock abundance (e.g., Field et al. 2009; Worm et al. 2013; Dulvy et al. 565 2014). The global status of these stocks is further complicated by the presence of illegal, 566 unreported, and unregulated fishing (Clarke et al. 2006), which is concentrated in the Indo-West 567 Pacific region where management is generally absent (Stevens et al. 2000; Field et al. 2009; Lam 568 and de Mitcheson 2011). Consequently, the currently available analyses of global shark stocks are 569 generally accompanied by operational challenges (e.g., lack of accurate landings and discard 570 information, unknown alterations in fishery-dependent fishing procedures, reliance on a single 571 index of relative abundance) and fail to provide comprehensive quantitative evidence supporting 572 claims of stock status and abundance trends. As a result, population dynamics information on 573 sharks is relatively limited (Field *et al.* 2009). A recent study by Worm *et al.* (2013) created a global 574 compilation of estimated values of fishing mortality for 21 assessed shark stocks (representing 17 575 species). Out of the 13 coastal stocks included, 11 observations of exploitation rate were obtained 576 from stocks within the U.S., emphasizing the scarcity of such information elsewhere.

577 Despite the general paucity of fisheries-independent shark survey data worldwide, a few 578 investigations of coastal shark trends in relative abundance have been made, indicating the regional 579 specificity in shark abundance trends over time. Protective beach nets in Australia and South Africa 580 have produced a relatively long time series of survey information (Dudley and Simpfendorfer 2006; 581 Reid *et al.* 2011). In southeast Australia, significant declines between 1950 and 2010 were reported 582 for four taxonomic shark groups, including Carcharhinid sharks that were pooled due to a lack of 583 species specific reporting prior to 1998. Three groups, including tiger shark, showed no significant 584 change in relative abundance, and one group showed a significant increase in relative abundance 585 (Reid et al. 2011). In South Africa, out of the 14 pelagic and coastal species for which indices of 586 relative abundance could be generated, only three showed significant declines in relative 587 abundance from 1978 to 2003, and one species, the tiger shark, showed a statistically significant 588 increase in relative abundance (Dudley and Simpfendorfer 2006). A compilation of opportunistic 589 data from the Mediterranean Sea showed large declines in abundance for five species comprising 590 four families, such that authors considered these large shark species to be functionally extinct 591 (Ferretti et al. 2008).

592 Management implementation is improving across the globe, as the International Plan of 593 Action for Sharks (IPOA-Sharks), a voluntary call for shark management from independent states, 594 was established in 1999. However, the IPOA-Sharks program currently does not include formal 595 enforcement of accountability and adoption of the program has been slow (Davis and Worm 2013). 596 Global shark landings have decreased in recent years, although further investigation revealed that 597 decreasing catch was reflective of reduced shark abundance as opposed to implementation of 598 conservative harvest policies (Davidson *et al.* 2016).

In conjunction with declines in the eastern U.S., global declines in shark catch and bycatch have been reported into the early 2000s (e.g., Stevens *et al.* 2000; Dulvy *et al.* 2014). The method presented in the current study does not enable us to estimate the magnitude of stock decline for the species examined from 1975 to the early 1990s. Nevertheless, after a relatively protracted period of low abundances following management implementation, common trends produced for the four large coastal species presented show increases in abundance, indicative of preliminary signs of recovery in U.S. Atlantic coastal shark stocks.

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874 Tables and Figures

875 Table 1. The optimal dynamic factor analysis (DFA) models fitted to indices of abundance derived from delta-876 lognormal GLMs for each species. The number of common trends is denoted by *m*. Covariance matrix 877 structure refers to the *H* covariance matrix which specifies observation error. Mean Fit is a relative measure 878 of model fit calculated by summing the squared residuals of the fitted DFA common trends and dividing by 879 the sum of the squared observations (delta-lognormal indices) for each survey, and averaging the values for 880 each species. Larger values (≥0.6) indicate poor overall fit (Zuur et al. 2003b). Survey abbreviations as 881 follows: Virginia Institute of Marine Science Longline Survey (VIMS LL), South Carolina Coastal Longline 882 Survey (SC LL), Georgia Red Drum Longline Survey (GA LL), SouthEast Area Monitoring and Assessment 883 Program-South Atlantic Coastal Trawl Survey (SEAMAP-SA Trawl), SouthEast Fishery Science Centre 884 Longline Survey (SEFSC LL), Gulf of Mexico Shark Pupping and Nursery Gillnet Survey (GULFSPAN GN).

0)	т	Н	Drivers	Surveys	ΔAICc	Mean Fit
Sandbar	1	diagonal	NAO	VIMS LL	0.000	0.1856
shark		and equal		SEFSC LL		
				SC LL		
T				GA LL		
Blacktip	1	diagonal	AMO	VIMS LL	2.3613	0.3736
shark		and equal		SEAMAP Trawl		
				SEFSC LL		
				GULFSPAN GN		
				SC LL		
				GA LL		
Spinner	1	diagonal	none	VIMS LL	1.0727	0.8118
shark		and equal		SEFSC LL		
				GULFSPAN GN		
				SC LL		
Tiger shark	1	diagonal	NAO +	VIMS LL	2.5255	0.3206
		and equal	landings	SEFSC LL		
Atlantic	2	diagonal	none	VIMS LL	0.000	0.4905
sharpnose		and		SEAMAP Trawl		
shark		unequal		SEFSC LL		
				GULFSPAN GN		

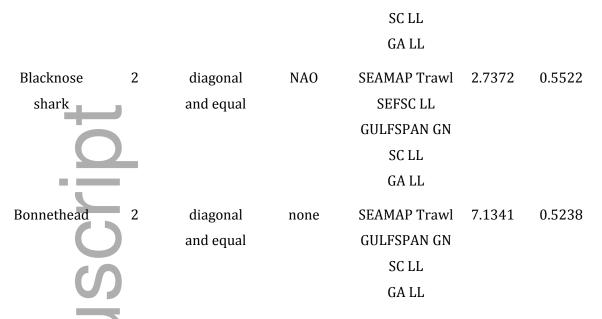


Figure 1. Map of representative stations/sites sampled (for the 2012 sampling year) within each survey:
Virginia Institute of Marine Science Longline Survey (VIMS LL), South Carolina Coastal Longline Survey (SC
LL), Georgia Red Drum Longline Survey (GA LL), SouthEast Area Monitoring and Assessment Program-South
Atlantic Coastal Trawl Survey (SEAMAP-SA Trawl), SouthEast Fishery Science Centre Longline Survey (SEFSC
LL), Gulf of Mexico Shark Pupping and Nursery Gillnet Survey (GULFSPAN GN). Map generated using the
rworldmap package in R (South 2011). Note that the SEFSC LL sampling has excluded the southeast coast
during the years 2001, 2003, and 2007.

Figure 2. Standardized (Z-scored) drivers examined within the dynamic factor analysis (DFA) models from
1975-2014. a) Environmental drivers include North Atlantic Oscillation index (NAO), Atlantic Multidecadal
Oscillation (AMO), and annually averaged sea surface temperature (SST), while b) anthropogenic drivers
included species-specific landings.

Figure 3. Standardized indices of abundance for a) sandbar shark, b) blacktip shark, c) tiger shark, d) spinner
shark, e) Atlantic sharpnose shark, f) blacknose shark, and g) bonnethead, representative of data conflict.
Survey abbreviations are as follows: Virginia Institute of Marine Science Longline Survey (VIMS LL),
SouthEast Area Monitoring and Assessment Program-South Atlantic Coastal Trawl Survey (SEAMAP-SA
Trawl), SouthEast Fishery Science Centre Longline Survey (SEFSC LL), Gulf of Mexico Shark Pupping and
Nursery Gillnet Survey (GULFSPAN GN), South Carolina Coastal Longline Survey (SC LL), Georgia Red Drum
Longline Survey (GA LL).

Figure 4. 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 for a) sandbar shark, c) blacktip shark, e) tiger shark, and g) spinner shark, and factor loadings for b) sandbar shark, d) blacktip shark, f) tiger shark, and h) spinner shark are shown. Factor loadings greater than 0.2 correspond to indices that had a relatively strong influence
on the resulting common trend, and negative factor loadings denote indices that follow an opposite trend to
the DFA common trend.

Figure 5. 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 for the a) Atlantic sharpnose shark, c) blacknose shark, and e) bonnethead, and factor loadings for the b) Atlantic sharpnose shark, d) blacknose shark, and f) bonnethead are shown. Factor loadings greater than 0.2 correspond to indices that had a relatively strong influence on the resulting common trend, and negative factor loadings denote indices that follow an opposite trend to the DFA common trend.

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918 Supporting information legend

919 <u>Supplement 1: dynamic factor analysis model fitting</u>

- 920 <u>Supplement 2: additional tables and figures</u>
- 921 Table S1. Summary of surveys included in the analyses.
- 922 Table S2. Life history information for shark species included in analyses.

923 Table S3. Covariates included in optimal delta-lognormal generalized linear model used to calculate indices of

- abundance for each species-survey combination.
- 925 Figure S1. Fitted dynamic factor analysis trends superimposed on survey-based delta-lognormally generated
- 926 indices of relative abundance for large coastal shark species.
- 927 Figure S2. Fitted dynamic factor analysis trends superimposed on survey-based delta-lognormally generated
- 928 indices of relative abundance for small coastal shark species.
- 929 Table S4. Dynamic factor analysis model fitting for each species.
- 930 Table S5. Dynamic factor analysis model results for each species.



