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# Spatiotemporal Abundance Patterns and Ecological Drivers of A Nearshore U.S. Atlantic Fish and Invertebrate Assemblage

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# Spatiotemporal abundance patterns and ecological drivers of a nearshore U.S. Atlantic fish and invertebrate assemblage

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Doctor or Philosophy

by

Mark A. Stratton

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# APPROVAL SHEET

This dissertation is submitted in partial fulfillment of

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## DISSERTATION ABSTRACT

Taking an ecosystem approach to fisheries requires the consideration of relevant ecological processes within research and assessment frameworks. Processes affecting ecosystem productivity can be categorized as biophysical (climate variability, primary production), exploitative (fishing), or trophodynamic (food web interactions). This dissertation incorporates these three governing processes to characterize spatiotemporal diversity and population abundance trends for multiple demersal fish and invertebrate species that inhabit the nearshore zone (15-30 ft. depth) along portions of the U.S. Atlantic east coast.

Two large marine ecosystems (LMEs) encompass the U.S. East coast – the Southeast and Northeast U.S. Continental Shelf LMEs. The level of connectivity within and between these two ecosystems is well understood for some individual species, but not generally for the nearshore assemblage. The first research chapter of this dissertation is a spatial diversity analysis of 141 fish and invertebrate species that inhabit nearshore waters from Florida to New York. Latitudinal diversity patterns revealed multiple biotic ecotones, or areas of high species turnover. An ecotone was evident in northern spring near the Cape Hatteras border of the two LMEs, but this barrier dissipated as water temperatures homogenized and assemblage connectivity between ecosystems increased throughout the year. Multiple other biotic ecotones were evident within the Southeast U.S. LME and were explained by seasonality and the proximity and area of adjacent estuarine habitat.

The second and third research chapters of this dissertation focus on explaining temporal abundance trends for multiple nearshore fish and invertebrate species within the Southeast U.S. LME. For the second research chapter, abundance trends for 71 species were analyzed during 1990-2013 within a univariate time series modeling framework with the goal of determining the relative importance of climate variability and fishing pressure as governing influences on abundance. A decrease in bycatch mortality explained changes for multiple species, while climate variability governed the dynamics for others. Multivariate ordination revealed similar trends for groups of taxonomically related species, indicating governing processes act on species with similar life histories. An extension of results from the second research chapter, research chapter three explores trophic interactions between the bonnethead shark (*Sphyrna tiburo*) and five of its prey species within Southeast U.S. LME nearshore waters. Multivariate time series modeling supports a negative effect of bycatch on bonnetheads, and population-level predation effects of larger sharks on multiple prey species. Abundance trends for most prey species were also explained by environmental variability associated with the Pacific Decadal Oscillation, although trophic effects were stronger.

This body of work incorporates relevant ecological factors in characterizing diversity and abundance trends for fish and invertebrate species comprising the nearshore demersal assemblage within Southeast and Northeast U.S. LMEs. Results indicate seasonal connectivity between LMEs that require further exploration at multiple spatial scales. Abundance time series modeling for multiple species in the Southeast U.S. LME reveals that fishing and trophodynamics may be relatively more influential drivers than climate variability in this sub-tropical system.

## AUTHOR’S NOTE

Chapters 2 through 4 of this dissertation were written as manuscripts for publication in scientific journals. Each chapter is structured in general accordance with length and formatting guidelines of the respective journal. Citations for these chapters at the time of writing are as follows:

### CHAPTER 2

Stratton MA, Meynard CN, Latour RJ. *In prep*. Defining borders between Large Marine Ecosystems: Cape Hatteras as an example of a dynamic ecotone. For submission to the *Journal of Biogeography*.

### CHAPTER 3

Stratton MA, Nesslage GN, Latour RJ. *In review*. Multi-decadal climate and fishing predictors of abundance for U.S. South Atlantic coastal fishes and invertebrates. Submitted to *Fisheries Oceanography*.

### CHAPTER 4

Stratton MA, Peterson CD, Webster P, Latour RJ. *In prep*. A shark species and its prey: Relative importance of predation, fishing, and environmental variability to population growth rates. For submission to the *Canadian Journal of Fisheries and Aquatic Sciences*.

# Spatiotemporal abundance patterns and ecological drivers of a nearshore U.S. Atlantic fish and invertebrate assemblage

# CHAPTER 1

# Dissertation Introduction

This work is an examination of ecological patterns for the demersal fish and invertebrate assemblage inhabiting shallow nearshore waters (15-30 ft.) within portions of the Southeast and Northeast U.S. Continental Shelf Large Marine Ecosystems (LMEs). Within the study area, which ranged latitudinally from Cape Canaveral FL to the northeastern tip of Long Island NY, the nearshore coastal ocean is a dynamic aquatic environment. Like all habitats in nature that scientists have categorized for necessary simplification, nearshore ocean habitats are physically and biologically connected to adjacent habitats such as estuaries, shelf and open-ocean habitats, and even landscapes. Land-based or upwelled nutrients fuel biological production in the nearshore zone, while physical mixing by winds and tides facilitate efficient recycling of these nutrients back into the food web by lower trophic level organisms (Nixon, 1988). In part because they contain or are in close proximity to diverse habitat types inshore and offshore, nearshore coastal waters can be hotspots for biological production and diversity. Estuaries are traditionally thought of as the most important nursery areas for many marine species, yet nearshore habitats within the study area are preferred rearing habitat for multiple species compared to estuaries (Woodland *et al.*, 2012; Able *et al.*, 2013). Many economically important species utilize nearshore habitats at various life stages, thus this area of the ocean has inherent economic value to fisheries even if fishing is not a primary activity occurring within the zone at certain locales.

Link et al. (2010) describe three main processes that regulate the production dynamics of any marine ecosystem: biophysical (primary productivity, climate), exploitative (fishing), and trophodynamic (food web interactions). In each of the studies comprising this dissertation, the effects of one or more of these processes on nearshore species were considered. For chapter two, multiple biophysical variables were hypothesized to explain spatial diversity patterns. For chapter three, climate variability and fishing pressure were investigated as governing factors for abundance dynamics of dozens of demersal species. For chapter four, fishing, climate variability, and trophic interactions were considered concurrently in a multispecies time series model.

This body of work addresses multiple gaps in ecological knowledge within Southeast and Northeast U.S. LMEs pertinent to the field of fisheries ecology. First, comparative community-level studies between these two LMEs are lacking. Second, knowledge of multi-decadal effects of climate on fish and shellfish populations are limited within the Southeast U.S. LME. Third, multispecies modeling efforts within the Southeast U.S. LME are also limited. This dissertation begins to fill these knowledge gaps by leveraging data sets from two fishery-independent surveys that sample the nearshore demersal biological assemblage by bottom trawl along the U.S. East Coast. These surveys are the Southeast Area Monitoring and Assessment Program – South Atlantic (SEAMAP-SA), which operates from Cape Canaveral FL to Cape Hatteras NC, and the Northeast Area Monitoring and Assessment Program (NEAMAP), which operates from Cape Hatteras NC to southern New England. SEAMAP-SA sampling occurs within the Southeast U.S. LME (1989-present), while NEAMAP sampling occurs within the Northeast U.S. LME (2007-present). Data from both of these surveys have been utilized often by fishery researchers and managers for single species research and assessments, but these datasets have not yet been analyzed in-depth within a community or multispecies context.

Chapter two is a multispecies study comparing diversity patterns in the nearshore assemblage within the Southeast U.S. LME and the Mid-Atlantic portion of the Northeast U.S. LME. Species composition studies of estuarine and marine benthic invertebrates within and between these two ecosystems (Engle and Summers, 1999; Pappalardo *et al.*, 2015) have yielded greater understanding of the potential barriers to, and pathways of, biological connectivity in this area of the ocean. Chapter two adds to this body of biogeographic knowledge using the nearshore demersal assemblage as a model for characterizing and explaining spatiotemporal changes in diversity. Results from this study revealed seasonally dynamic patterns of biological connectivity between these two ecosystems that are defined within the LME framework as separate entities.

Chapter three focuses on temporal abundance patterns of multiple species within the Southeast U.S. LME. Using SEAMAP-SA from 1990-2013, the relative importance of climate indices and fishing indicators were modeled for 71 fish and invertebrate species. Enabled by a high percentage of data-rich stocks (Newman *et al.*, 2015), the effects of climate change and variability on fish stocks have been heavily researched in the adjacent Northeast U.S. LME (e.g., Araújo and Bundy, 2012; Collie et al., 2008; Nye et al., 2014). Within the Southeast U.S. LME, however, climate effects have been modeled for a more limited number of species (e.g., Colton et al., 2014; Garcia et al., 2007; Hare and Able, 2007; Harford et al., 2014; Munch and Conover, 2000). Chapter three continues to fill the climate-related knowledge gap for Southeast U.S. LME species while also determining the relative importance of fishing versus climate within a modeling framework.

Similar to the extent of knowledge for climate-related effects on marine species, understanding of upper trophic level food web patterns is much more limited in the Southeast U.S. LME compared to other U.S. LMEs. Robust and long-standing fish food habits time series in the Northeast U.S. LME (e.g., Garrison and Link, 2000) and North Pacific (Livingston *et al.*, 2017) have enabled researchers to investigate multispecies effects (e.g., Tsou and Collie, 2001; Tyrrell *et al.*, 2008; Link *et al.*, 2009). Such efforts have not been possible within the Southeast U.S. LME due to a lack of fish diet time series. There have been several fish diet studies conducted in the Southeast U.S. LME (reviewed by Marancik and Hare, 2005), however these studies were conducted at inconsistent locales and asynchronous points in time. A preliminary ecosystem model based on trophic guilds was constructed for the Southeast U.S. Atlantic (Okey and Pugliese, 2001), however this type of approach has limited applied use until the consistency and quantity of empirical food web data collection in the system increases.

In regions such as the Southeast U.S. LME with spatial and temporal mismatch in empirical food web data, as well as uncertainty in or lack of consumption rates for most predators, the types of multispecies models that can be applied to provide tactical advice (i.e., quantitative on short time scales; Collie *et al.*, 2016) to fishery managers are limited. In such cases, multispecies time series analysis using abundance data (Francis *et al.*, 2014) or other biological indicators (Torres *et al.*, 2017) is a viable alternative approach to more data intensive multispecies trophic models (e.g., Garrison et al., 2010). In chapter four of this dissertation, a multispecies time series model was applied to a specialist shark predator and multiple of its known crustacean prey species. Results from this study highlight the importance characterizing marine food webs to improve abundance predictions for lower trophic level species. Eventually this type of approach could be implemented in fishery assessment settings within the Southeast U.S. LME to inform management for commercially-targeted species.

The three studies comprising this dissertation take an ecosystem approach in characterizing biological patterns for the nearshore community within the study range. As holistic fisheries management approaches continue to be refined, ecosystem-oriented research is a necessary precursor to assessment and management. This collection of studies bolsters the foundation for further ecosystem-oriented research in coastal U.S. Atlantic waters.

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# CHAPTER 2

# Defining borders between Large Marine Ecosystems:

## Cape Hatteras as an example of a dynamic ecotone

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## ABSTRACT

Theoretical advances in the science of ecological boundaries have increased in recent years, promoting an upsurge of empirical studies in all system types including aquatic, marine, and land-water interfaces. In this empirical study of the fish and invertebrate assemblage inhabiting coastal marine waters of the U.S. Atlantic coast, a measure of β diversity and distance-based statistical techniques were used to identify biotic and environmental ecotones within Southeast and Northeast U.S. Large Marine Ecosystems (LMEs). We present evidence of multiple seasonally-modulated biotic ecotones. Of particular interest was an environmental and biotic transition zone associated with the Hatteras Front, an oceanographic feature near the border of these two LMEs. An ecological boundary near Cape Hatteras was evident during spring, but not during northern fall as a result of a diminished and spatially diverging temperature and salinity gradients. Seasonal modulation of this ecotone reflects inherent biological connectivity within the coastal ocean and across this purported biogeographic barrier. In addition to day length and temperature-induced seasonality, alongshore estuarine system heterogeneity (proximity, size) also explained notable variability in pairwise β diversity within biotic ecotones. While the LME framework provides a tenable platform for the study and management of some living marine resources at the ecosystem scale, our results indicate otherwise for the demersal coastal fish and invertebrate community within our area of study. We place our marine example in the context of the expanding theoretical literature of ecological boundaries. In particular, we echo the call for emphasis on characterizing temporal variability (not just spatial) of ecological boundaries, both on seasonal and interannual scales.

# INTRODUCTION

In marine environments, it is widely recognized that an ecosystem approach is necessary to successfully manage living resources, including fisheries. Ecosystem-based management and assessment were suggested in the 1992 United Nations Conference on Environment and Development (FAO, 1992), were already an integral part of the 2002 World Summit on Sustainable Development (Sherman, 2006), and continue to be refined in a multidisciplinary light (e.g., McLeod and Leslie, 2009). In this context, the network of Large Marine Ecosystems (LMEs) distributed globally in coastal seas is a viable framework for multidisciplinary research and tractable management of marine living resources at the ecosystem scale (Sherman, 1986, 1991). The LME system provides a spatial platform for taking an ecosystem approach to fisheries (EAF), which builds on existing fisheries principles and practices to enable more holistic research and management (Link, 2010). Under the current paradigm, boundaries between LMEs are delineated based on bathymetry, hydrography, productivity, and trophic interactions (Sherman and Hempel, 2009). However, because the LME framework is categorical by nature, some LME boundaries may not realistically represent the inherent connectivity between LMEs evident by the flow of materials (water, nutrients, etc.) and organisms between them (Rosenberg and Sandifer, 2009; Friedland *et al.*, 2012). Marine systems are intrinsically more dynamic than terrestrial ones (e.g., Kinlan and Gaines, 2003), thus a more flexible spatial framework may be needed for appropriate research and management of living marine resources in certain coastal systems. Since appropriate definitions of LME units will have consequences for marine resource management decisions, it becomes increasingly important to evaluate such boundaries in light of relevant ecological information.

Large Marine Ecosystem borders should, in theory, be transition zones with rapidly changing ecological characteristics, such that each unit can be managed relatively independent from the others. Such an area of transition may be described as an “ecotone”, a term that arose in the early 20th century describing ecological boundaries and transition zones (Yarrow and Marín, 2007). While theorists have devised many definitions and variations of the ecotone concept (e.g., Hufkens *et al.*, 2009; Erdôs *et al.*, 2011), an especially intuitive framework described by Fortin *et al.* (2000) discriminates between “biotic” and “environmental” ecotones. Environmental ecotones refer to areas with sharp physical gradients for attributes such as elevation and soils in terrestrial systems, or depth and nutrients in aquatic systems. Similarly, biotic ecotones are described by sharp gradients in community composition (i.e., species turnover) as measured by appropriate metrics. Measures of beta (β) diversity, designed to quantify such changes in community composition between two or more sampling units along a specified gradient (Anderson *et al.*, 2011; Legendre *et al.*, 2012), are especially suitable for the identification of biotic ecotones. While the ecotone concept is most intuitive in a static spatial context such as a boundary zone on a map, ecological systems are inherently dynamic, especially marine systems. Thus, in addition to spatial characterizations, the potentially dynamic temporal nature of both biotic and environmental ecotones should be considered (Kolasa and Zalewski, 1995; Cadenasso *et al.*, 2003a,b).

The U.S. Atlantic coast contains two Large Marine Ecosystems, the Northeast U.S. Continental Shelf LME (hereafter “Northeast U.S. LME”) and the Southeast U.S.

Continental Shelf LME ("Southeast U.S. LME"), with the line of latitude intersecting Cape Hatteras, NC as the delineation between them (Fig. 1). Cape Hatteras has traditionally been considered a biogeographic barrier primarily due to a sharp latitudinal temperature gradient (Hutchins, 1947; Fischer, 1960; Cerame-Vivas and Gray, 1966; Schopf, 1979) and limited water body mixing that imposes constraints on movement and dispersal for some species (Avise *et al.*, 1987; Palumbi, 1994; Baker *et al.*, 2008; McCartney *et al.*, 2013). However, Cape Hatteras apparently does not limit movement or dispersal of many other invertebrate species (Saunders *et al.*, 1986; Reeb and Avise, 1990; Wise *et al.*, 2004; Díaz-Ferguson *et al.*, 2009) and fishes (Nicholson, 1978; Jones and Quattro, 1999; Lankford Jr. *et al.*, 1999; McMillen-Jackson and Bert, 2004; Wuenschel *et al.*, 2012). At the community level, multiple studies investigating latitudinal breakpoints do not support the traditional model of Cape Hatteras as a strong biogeographic barrier, but do reveal transition zones at other locations along the U.S. Atlantic coast (Schwartz, 1989; Engle and Summers, 1999; Pappalardo *et al.*, 2015).

The primary goal of this study is to determine the level of continuity in community composition between two adjacent Large Marine Ecosystems, the Southeast and Northeast U.S. LMEs. We used a measure of β diversity to quantify seasonal and spatial changes in community composition for the coastal demersal fish and invertebrate assemblage. While we were particularly interested in evidence of a biotic ecotone near the LME border at Cape Hatteras, we also characterized transition areas along other portions of the U.S. Atlantic coast. For areas that we identified as biotic ecotones, we addressed the following questions:

1) How does spatial scale affect ecotone definition?

2) Are ecotones seasonally stable?

3) Which environmental gradients explain biological patterns?

We revealed biotic ecotones and pursued these questions using a flexible methodological approach considering multiple levels of spatial and temporal scale. We place our results in the context of system-specific considerations for study and management of living marine resources within coastal U.S. Atlantic waters, as well as contemplate the meaning and utility of the ecological boundary concept in the interconnected coastal ocean.

## METHODS

### Sampling platforms

We leveraged data from two fishery-independent bottom trawl surveys: the Northeast Area Monitoring and Assessment Program (NEAMAP; Bonzek *et al.*, 2015), and the Southeast Area Monitoring and Assessment Program – U.S. South Atlantic (SEAMAP-SA; Richardson and Boylan, 2013; SEAMAP-SA Data Management Work Group, 2014). NEAMAP is conducted twice a year during spring and fall within the Northeast U.S. LME, from Martha's Vineyard, MA to Cape Hatteras, NC. SEAMAP-SA is conducted three times a year (spring, summer, fall) within the Southeast U.S. LME from Cape Hatteras, NC to Cape Canaveral, FL. Specifications and deployment methods of trawl gear are similar between surveys (see Appendix I for additional details). For appropriate comparisons between surveys, we utilized six years of temporally overlapping data collected during daylight hours in spring (mid-April to mid-May) and fall (October to early November) from 2008-2013 and within a common depth range of 5 to 12-m (Fig. 1).

### Biological data treatment

For each species in each tow sample, we calculated the natural log-transformed biomass (wet weight in grams). We excluded species not captured every year during the study period based on the assumption that they were not sampled effectively by one or both survey gears (see Table S1 for a species list and total biomass by survey and season). We chose biomass rather than number of individuals for our abundance currency given the wide range of body sizes among species included in the analysis. Numerical abundance equates individuals and species with disparate body sizes, whereas biomass more appropriately weights individuals according to their gravimetric and energetic contributions to and impacts on the food web (Certain *et al.*, 2014). Log-transformed biomass data were converted to matrix form with individual tow samples as rows and species as columns. Each row containing log-transformed biomass values was standardized to sum to one in order to account for differences in seafloor area swept among tows (Shertzer *et al.*, 2009), which ranged from 1.5 to 5.3 hectares (mean 3.3, SD 0.6).

**β diversity**

We calculated pairwise beta diversity (i.e., between-samples) using Rao's quadratic entropy index (1982) following the framework of de Bello *et al.* (2010), which reduces the biases associated with the raw Rao indices. In this context, beta diversity was defined as the difference between gamma (regional, or two or more samples pooled together) and alpha (local) diversity, which had previously been corrected to reflect equivalent numbers:

$$\beta_{\mathrm{EqvAdd}} = \gamma_{\mathrm{Eqv}} - \alpha_{\mathrm{Eqv}} \tag{1}$$

Rao α diversity (i.e., within-sample) was calculated as

$$\alpha\ \mathrm{Rao} = \sum_{i=1}^{s} \sum_{j=1}^{s} d_{ij} p_{ic} p_{jc} \tag{2}$$

where $p_{ic}$ is the proportion of species $i$ in sample $c$ (i.e., the relative abundance of the $i$th species in the $c$th sampling unit or site), $s$ is the number of species (species richness) in the community, and $d_{ij}$ is the dissimilarity (or "distance") between each pair of species $i$ and $j$. For taxonomic diversity, $d_{ij}$ is an extraneous parameter and coded as a unity matrix with a null diagonal (0's for the diagonal, 1's for off-diagonals). As noted by

Pavoine *et al.* (2004), taxonomic α Rao is equivalent to the Simpson index: $D = \sum {p_i}^2$ (Maurer and McGill, 2011). Regional Rao γ diversity was calculated as

$$\gamma \text{ Rao} = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} P_i P_j \tag{3}$$

where $S$ is the total number of species in the region, and $P_i$ is the regional species relative abundance for species $i$ (same for $P_j$). $P_i$ is equal to the average of $p_{ic}$ across all samples:

$$P_i = \sum_{c=1}^{n} p_{ic} / n \tag{4}$$

This is the unweighted formulation of $P_i$ recommended by de Bello *et al.* (2010) for studies like ours seeking primarily to characterize diversity among habitats. To obtain meaningful β results, we transformed α and γ to their "numbers equivalents" (Jost, 2007):

$$\alpha_{\text{Eqv}} = \frac{1}{(1-\alpha)}; \tag{5}$$

$$\gamma_{\text{Eqv}} = \frac{1}{(1-\gamma)} \tag{6}$$

**Revealing ecotones**

Prior to applying statistical methods for identifying ecotones, we generated a one-dimensional transect (1-km interval) along the coastline from Cape Canaveral, FL to Cape Cod, MA (Wessel and Smith, 1996; ESRI, 2014). Each coastal trawl sampling location was assigned a value corresponding to the closest coastline transect point (see Appendix I for additional details). This 'coastline distance' variable was used as a spatial indicator instead of latitude, the latter of which did not appropriately capture variability in certain landscape variables for east-west orientated sections of coastline. We conducted separate analyses for spring and fall to capture seasonal variability of biotic and environmental ecotones.

We implemented a moving window approach to evaluate changes in β diversity and reveal biotic ecotones along the coastal transect. At a given point along the transect, we fitted a regression model on distance matrices (Legendre *et al.*, 1994) within a specified window size where pairwise β diversity was the response and pairwise coastline distance was the predictor. We repeated this ‘moving gradient window’ approach every 5-km along the coastline transect, and at multiple levels of scale from 100 to 400-km window widths in 10-km increments (Erdős *et al.*, 2013). Because simple linear regression is not appropriate for pairwise distance matrices (Anderson *et al.*, 2011), regression coefficients and confidence intervals were estimated using regression on distance matrices using permutation tests with 1,000 iterations (Goslee and Urban, 2007; Lichstein, 2007) and bootstrapping (Efron, 1983) with a 90% sampling rate without replacement (*n* = 500). Our ‘moving gradient window’ method is based on the ‘moving split window’ approach (Whittaker, 1960; Ludwig and Cornelius, 1987). Our method is also akin to analysis ‘Turnover analysis 3’ (‘T3’) described by Anderson *et al.* (2011), but within a moving window.

## Explaining variation in β diversity

To determine which aspects of the environment explained biotic ecotones, we analyzed the variance in β diversity within biotic ecotones using distance-based redundancy analysis (db-RDA; Legendre and Anderson, 1999). This technique partitions the variation of a response matrix with respect to two, three, or four explanatory tables (variable ‘groups’) using adjusted R-squared. For this approach, collinear variables do not have to be removed prior to distance-based transformation (in our case Euclidean) and subsequent variance partitioning (Oksanen *et al.*, 2016).

For db-RDA, we included four groups of explanatory variables (i.e., four tables) to explain variation in β diversity (Table 1): 1) temperature, 2) chlorophyll, 3) salinity, and 4) landscape variables. For some analyses, we replaced temperature with day length to test for seasonal differences. Temperature influences nearly all aspects of a poikilotherm's life history, including growth, reproduction, geographic distribution, and migration (Wootton, 1998). In large ocean basins, current-driven and latitudinal temperature gradients are important determinants of species richness and composition of marine faunal assemblages (Hutchins, 1947; Fischer, 1960; Schopf, 1979). At the ecosystem scale, chlorophyll concentration is a good predictor of upper trophic level biomass and fishery yields (Nixon, 1982, 1988; Houde and Rutherford, 1993; Friedland *et al.*, 2012). We included chlorophyll as an indicator of local changes in the diversity of fish and invertebrate predators due to shifts in overall food availability fueled by lower trophic level production (see Appendix I for additional details). We included salinity as a general indicator of differences between water masses not differentiable by temperature and chlorophyll, such as turbidity and sub-surface primary productivity, differences that may be reflected in β diversity.

We included multiple landscape variables parameterized using spatial datasets (Table 1, Appendix 1). Finer methodological details regarding how data for these variables were obtained or generated are described in Appendix 1. For each trawl sample, we calculated the distance to the nearest land feature (Wessel and Smith, 1996). 'Distance to land' is intended to capture changes in β diversity due to proximity to surf zone and nearshore habitats with faunal compositions potentially different than more offshore locations. Because many species captured by SEAMAP-SA and NEAMAP are estuarine-dependent to some extent, we also included a variable that quantified the distance to the nearest estuarine inlet (Wessel and Smith, 1996). ‘Distance to an estuary’ is intended to capture changes in diversity due to estuarine habitat utilization for life history processes such as spawning, feeding, and seeking refuge. Because estuary size and function vary, we also generated a variable that quantified the area of deepwater estuarine habitat (i.e., non-intertidal brackish or marine) within a given distance of the sampling site (2, 4, 8, 16, 32, or 64-km). All sampling sites were within 60-km of an estuarine system. Distance and area variables, as well as chlorophyll, were transformed to reduce skewness (Table 1).

To determine the relative importance of seasonal progression of β diversity within ecotones, we repeated variance partitioning for each biotic ecotone with data from both seasons included. We ran this analysis twice – once with temperature as an explanatory variable, and again with day length replacing temperature. Compared to date, day length is a more biologically-relevant proxy for time that captures seasonality (Horodysky *et al.*, 2015). As a final analysis, we conducted variance partitioning for all data points within each seasonal dataset. This analysis was the coarsest scale that considered which environmental variables were most important in structuring β diversity throughout the entire study range.

### Biomass and richness

For comparison to pairwise β diversity patterns along the coastal transect, we computed tow-level cumulative biomass and species richness. Cumulative biomass values included only species encountered every year and were scaled (centered on zero and divided by the standard deviation) separately for each survey to account for differences in catchability between gear types.

### Data and computing

NEAMAP data are available by request from Robert J. Latour at the Virginia Institute of Marine Science; SEAMAP-SA data are available online (SEAMAP-SA Data Management Work Group, 2014). We conducted all statistical analyses in R (R Core Team, 2016) using the following packages: *ecodist* (Goslee and Urban, 2007) for regression on distance matrices; *vegan* (Oksanen *et al.*, 2016) for variance partitioning; *venneuler* (Wilkinson, 2011), and *scales* (Wickham, 2016) for graphing; *geosphere* (Hijmans, 2015) for day length calculations; and *ade4* (Dray and Dufour, 2007), *doParallel* (Revolution Analytics and Weston, 2015), *plyr* (Wickham, 2011), *R.utils* (Bengtsson, 2016), and *reshape2* (Wickham, 2007) for data processing and computing. Code is available by request from the first author.

## RESULTS

The presence and location of biotic ecotones, as well as the strength of biotic and environmental gradients within these areas, were scale and season dependent. We chose to evaluate the presence of biotic and environmental ecotones at a moving window width of 190-km. At this window size, all slope values (i.e., estimated coefficients from regression on distance matrices) during both seasons were positive (Fig. 2). For our study system and dataset, this window size was at an intermediate scale that revealed a balanced contrast between areas of high versus low species turnover. At a finer scale (100-km), distinct areas of high turnover were difficult to discern, while broader scales (300 to 400-km) did not allow meaningful interpretation given the geography of the study system. For instance, the coastal bays of North Carolina are separated by capes less than 200-km apart, thus interpreting diversity patterns at window widths wider than this distance would obscure potential differences in diversity between these features. Implementing a moving window approach in other systems will require a window width appropriate to the nature of the system and scientific questions being pursued.

Seven biotic ecotones were evident at a 190-km window width, six during spring and one during fall (Fig. 2). Boundaries for each seasonal ecotone were set at 50% of the maximum slope value of the most prominent ecotone during that season. Although 50% was an arbitrary cutoff, it allowed categorization of ecotones with the strongest diversity gradients. The most prominent ecotone with the greatest slope of species turnover occurred near Cape Hatteras in spring (Fig. 2A). Spatial gradients in temperature and salinity were dramatic near Hatteras during spring (Fig. 3), indicating convergence of water masses in this location. However, a spatial mismatch in turnover of these two environmental variables compared to biological (i.e., β diversity) turnover resulted in low total variance explained by distance-based redundancy analysis (24%, Fig. 4). Biological turnover reached a peak approximately 20-km south of Cape Hatteras in spring, yet temperature and salinity turnover both peaked 15-km north of Cape Hatteras (Fig 5A). A peak in chlorophyll turnover overlapped spatially with the peak in β diversity turnover near Cape Hatteras, although its lower maximum slope value (Fig 5A) resulted in a proportion of variance explained comparable to temperature and salinity (Fig. 4).

In fall, biological turnover patterns near Cape Hatteras differed markedly compared to spring. Peak slope of β diversity in fall occurred farther south compared to in spring (Fig. 5B). The peak slope value in β diversity was approximately 40% less in fall (slope = 0.015) compared to spring (slope = 0.025), indicating that spatial changes in β diversity near Cape Hatteras were less dramatic in fall. Environmental turnover patterns also differed between seasons. In fall, salinity turnover was similar to β diversity turnover immediately south of Cape Hatteras (Fig. 5B). Temperature turnover, however, peaked farther north of Cape Hatteras in fall, while chlorophyll turnover patterns near Cape Hatteras were spatially similar.

Seasonal differences in biological and environmental turnover patterns were not limited to near Cape Hatteras. In spring, there were multiple distinct peaks in β diversity which we assigned as biological ecotones:  St. Augustine, St. Mary’s River, lower Onslow Bay, upper Onslow Bay, Cape Hatteras, and Virginia Beach (Fig. 2A, Fig. 6). Areas outside of these ecotone boundaries had low β diversity slope values, indicating that spatial gradients in species turnover were gradual rather than steep. In fall, the Winyah Bay ecotone was the only area along the coastline with β diversity slope values of comparable magnitude to spring ecotones (Fig. 2, Fig. 6). However, in fall, there were multiple biological transition zones of intermediate magnitude with peak slope values of approximately 0.014. While we do not describe these areas further, overall increased spatial heterogeneity of species turnover in fall appears to be a general property of the study system.

Within each of seven ecotones, the combination and relative importance of environmental variables explaining diversity patterns were idiosyncratic. Three different variance partitioning analyses were conducted for each ecotone. The first analysis included data only for the season during which the ecotone was evident (single-season analyses; Fig. 4, left column of Venn diagrams). The second analysis included both spring and fall data within the spatial boundaries delineated for the ecotone (Fig. 4, middle column). The third analysis differed from the second only in that temperature was replaced by day length as one of the explanatory variable tables (Fig. 4, right column). The second and third analyses (“dual-season” analyses) revealed the relative importance of temporal (i.e., seasonal) versus spatial shifts in community composition.

For single-season analyses, species turnover within five of seven ecotones was best explained by landscape variables that quantified changes in proximity to land, proximity to an estuary, and amount of available estuarine habitat. St. Augustine and upper Onslow Bay were the two exceptions; temperature, salinity, or chlorophyll explained more variation than landscape variables for these ecotones. For dual-season analyses, temperature and day length were largely redundant, indicating that at this spatial scale (i.e., 190-km window width), temperature and day length were equivalent proxies for seasonality. For most ecotones, seasonality explained an equal amount or more variation than landscape heterogeneity. For St. Augustine, upper Onslow Bay, and Cape Hatteras ecotones, seasonality explained notably more variation than any other variable. The total amount of variation explained within a given ecotone ranged from 19% for St. Augustine in spring to 79% for upper Onslow Bay in spring (Fig. 4). The amount of variation explained in single-season analyses was typically greater than for dual-season analyses; exceptions were St. Augustine and Cape Hatteras ecotones, which had the lowest amounts of variation explained compared to other ecotones.

Cumulative scaled biomass was greatest in northeast Florida, the North Carolina outer banks, and in spring, New York's Long Island (Fig. 3). Species richness was consistently higher south of Cape Hatteras, with hotspots in northeast Florida during spring and the southern outer banks of North Carolina. Richness gradually declined from a high in Onslow Bay to a low near the mouth of the Chesapeake Bay in spring. The location of biotic ecotones typically corresponded not with peaks and troughs in biomass and richness, but rather with areas where these two metrics were changing most rapidly (i.e., had the most turnover).

## DISCUSSION

Our main focus was to evaluate Cape Hatteras as the primary ecological boundary between the two Large Marine Ecosystems encompassing the U.S. Atlantic coast. This approach was in keeping with Kolasa's (2014) thesis emphasizing the importance of recognizing ecological entities (LMEs in this case) prior to evaluating the existence and properties of ecological boundaries between such entities. Biotic and environmental patterns near Cape Hatteras were highly seasonal. In spring the most apparent biotic and environmental ecotones occurred here, characterized by rapid turnover in β diversity, temperature, and salinity (Fig. 5). In fall, Cape Hatteras was not an obvious transition zone for the sampled biological community, nor was there a dramatic temperature or salinity gradient. The seasonally-dependent nature of these biological and environmental patterns are typical of temperate marine and terrestrial systems within which seasonal temperature fluctuations govern a multitude of biological and physical processes (Block *et al.*, 2011).

Seasonally divergent β diversity patterns are not conflicting, but instead reveal environmentally-modulated (Kolasa, 2014) connectivity between the Northeast and Southeast U.S. LMEs as biota move through and among coastal marine habitats during certain seasons. When coastal waters warm as spring turns to summer, many species with southern ranges migrate or settle (if young-of-the-year) northward and farther inshore for foraging, reproduction, and refuge (Epifanio and Garvine, 2001; Murdy *et al.*, 2013). As temperatures and day length decrease in late fall, these southern species reverse course, while some northern species may migrate southward and inshore in opposite fashion (e.g., Burr and Schwartz, 1986). While we did not analyze the seasonality of individual species distributions, these general migration patterns can be seen in our results as the location and magnitude of biotic ecotones changed dramatically between two seasonal snapshots. In spring, temperature explained 42% of all variation in β diversity (all data points included); this percentage dropped to 20% in fall as the diminished Hatteras temperature gradient expanded the thermal niche of many southern species. Dual season variance partitioning results reinforce the importance of seasonality of spatial diversity patterns driven by life history processes of species that comprise the assemblage. The impact of predictable seasonal migrations on ecosystem function has been an underappreciated dimension of biodiversity (Bauer and Hoye, 2014); future studies could investigate latitudinal energy flow across Cape Hatteras with specific emphasis on influential migratory predators.

Pappalardo *et al.* (2015) investigated species range boundaries for hundreds of benthic marine invertebrate species along the U.S. Atlantic coast. While they found some species ranges were restricted by current flow patterns near Cape Hatteras, this biogeographic boundary was highly permeable for most species. In other words, range boundaries typically did not occur there, except notably for deep-water species with long larval durations. For shallow-water invertebrates (< 20-m depth), reduced water transport near Cape Cod and the Bay of Fundy resulted in a higher percentage of species with range boundaries near these locations as compared to Cape Hatteras (Pappalardo *et al.*, 2015). Hale (2010) and Engle and Summers (1999) also report Cape Cod to be a clear faunal transition zone for estuarine and coastal benthic invertebrates. In their analysis of zoogeographic boundaries focusing on benthic estuarine invertebrates, Engle and Summers (1999) did not identify Cape Hatteras as a latitudinal breakpoint in community composition. They did, however, identify breakpoints that closely correspond to the lower Onslow Bay, Winyah Bay, and St. Mary's River biotic ecotones revealed in our study (compare our Fig. 6 to their Figure 3). Landscape heterogeneity, which considered the distance to and area of adjacent estuarine habitat, was important for explaining variance in beta diversity within each of these nearshore ecotones. Consistent results from these two studies support the notion that estuarine habitat acts to structure community composition similarly for a wide variety of taxa in this coastal ocean system.

In our study of shallow-water fishes and invertebrates with high motility, Cape Hatteras appears to impose range restrictions on species only when a strong temperature gradient exists in colder months. Once this temperature gradient diminished during the warm season, magnitudes of β diversity slopes near Cape Hatteras were dampened and shifted, indicating increased permeability across this biogeographic landmark and LME border. Interestingly, our study and Pappalardo *et al.* (2015) observed similar mismatches between biological versus temperature patterns near Cape Hatteras; peaks in temperature turnover (our study) or temperature-predicted species boundaries (Pappalardo *et al.*, 2015) occurred north of Cape Hatteras, whereas observed biotic turnover or species boundaries occurred south of Cape of Hatteras. This asynchrony, which is likely due to the dynamic nature of current conditions associated with the 'Hatteras Front' (Churchill and Berger, 1998; Savidge, 2002), deserves further study and highlights the importance of distinguishing between biotic and environmental ecotone concepts. In summary, Pappalardo *et al.* (2015) used different methodologies and biological communities to yield our same overall result: biological connectivity between the Southeast and Northeast U.S. LMEs is strong due to latitudinal permeability across Cape Hatteras within the coastal ocean. Thus, the boundary between these LMEs acts as a seasonally-modulated filter of the macrofaunal community shared by these two ecosystem entities (Kolasa and Zalewski, 1995; Fagan *et al.*, 2003).

Ferro and Morrone (2014) argue that biogeographic transition zones should be defined based on evidence from multiple taxonomic clades. Although latitudinal coverage was relatively broad, an analysis leveraging inshore, coastal, and offshore fisheries survey datasets would complement the existing evidence from benthic macrofaunal studies to allow a more thorough understanding of the relative importance and permeability of ecological boundaries associated with Capes Hatteras and Cod. There are multiple ways to compartmentalize large-scale coastal marine systems (Spalding *et al.*, 2007); a given partition may be useful for the study and management of certain taxonomic groups, while irrelevant for another. For coastal marine fishes and invertebrates inhabiting the Southeast U.S. LME and southern portion of the Northeast U.S. LME, the Large Marine Ecosystem framework may not be a useful paradigm given the demonstrated biological connectivity northward across Cape Hatteras. As climate change continues to influence the structure of coastal marine biological communities (see "Temporal change" subsection below), the relevancy of the LME framework along the U.S. Atlantic coast may diminish.

### Across-shore dynamics

Within six of seven biotic ecotones (St. Augustine excluded), spatial changes in landscape variables explained the majority or a notable fraction of variation in β diversity. This result is consistent with the utilization of both estuarine and coastal habitats by many species within the study area (Able, 2005; Woodland *et al.*, 2012).

While we did not investigate estuary-ocean ecotones directly, the explanatory power of estuarine habitat variables indicates that the presence and amount of estuarine habitat is a primary determinant of coastal β diversity patterns at an intermediate geographic scale (~200-km). By quantifying the amount of adjacent estuarine habitat, we are incorporating 2-dimensional aspects of the system into our 1-dimensional transect approach (see Figure 1 in Kolasa, 2014). A true 2-dimensional approach leveraging existing estuarine, coastal, and offshore datasets could reveal both alongshore and across-shore ecotones within these two LMEs, but would require near-continuous spatial coverage and comparable temporal overlap between datasets. We would expect the magnitude and steepness of biological turnover for across-shore transects to be greater than that within the alongshore coastal ecotones revealed in this study. Examples of such across-shore zones could include salinity fronts (Lee *et al.*, 1991), steep bathymetric features (Jamieson *et al.*, 2011), and abrupt habitat shifts resulting from geomorphology (e.g., hardbottom reefs) or ecosystem engineers (e.g., seagrasses, coral reefs, marshes; Barnes and Hamylton, 2013; Kolasa, 2014). Although typically at a smaller scale than was the focus of our study, even heterogeneity within soft-bottom habitats can yield sharp biological gradients (Weston, 1988; Zajac *et al.*, 2003). Large estuaries may fit better within the conceptual model of a salinity-driver ecocline rather than an ecotone (Attrill and Rundle, 2002), the former of which can be described as a more gradual gradient zone which is relatively heterogeneous but environmentally more stable (van der Maarel, 1990). Our alongshore study area considered as a whole (i.e., at the coarsest of scales) also fits the ecocline conceptual model, whereby diversity patterns emerge from the overarching influence of a latitudinal temperature gradient. Within portions of the transect (i.e., windows), environmental effects were much more nuanced, reflecting the hierarchical nature of ecological boundaries and ecological systems in general (Yarrow and Salthe, 2008 and references therein).

### Temporal change

In their general framework for studying ecological boundaries, Cadenasso *et al.* (2003a,b) urged spatiotemporal variability, not just spatial variability, to be incorporated into measures of boundary structure and function (also see Kolasa and Zalewski, 1995). In our empirical study of coastal marine transition zones, we illustrate that seasonal temporal variability is essential for proper characterization of these boundaries. However, data were not available to conduct a robust temporal study characterizing interannual variability within biotic ecotones. As atmospheric $CO_2$ levels continue to rise, coastal and shelf water temperatures throughout the Southeast and Northeast U.S. LMEs are predicted to follow suite (Saba *et al.*, 2016). Within the latitudinal and depth range of our study area, coastal waters along the North Carolina outer banks, especially near the Hatteras Front, are expected to warm the fastest (Figure 5a in Saba *et al.*, 2016). While the effects of climate change on marine communities can be difficult to predict (Doney *et al.*, 2012), single-species distribution expansions have already been documented and forecasted within the Northeast U.S. LME (Nye *et al.*, 2009; Bell *et al.*, 2015; Hare *et al.*, 2016). These studies suggest that the ecological boundary near Cape Hatteras will become more permeable to some species if temperatures homogenize between LMEs. However, if waters immediately south of the Hatteras Front warm quickly but coastal Mid-Atlantic waters do not, then the Cape Hatteras ecological boundary may actually become less permeable. Few studies have characterized macrofaunal communities in the localized area influenced by the Hatteras Front (Magnuson *et al.*, 1981; Atkinson and Targett, 1983; Govoni and Spach, 1999). To truly understand the spatiotemporal patterns of this seasonally-modulated boundary on populations and communities of interest, additional high-frequency empirical studies are needed.

Increased permeability across the Cape Hatteras boundary may manifest as changes in migration phenology (e.g., Peer and Miller, 2014). For south-to-north migrating species, the seasonal window for utilizing Northeast U.S. LME habitats may widen, while the southern window for north-to-south migrating species may narrow. To complicate matters, many species have across-shelf migration patterns to overwintering grounds in deeper continental shelf waters (e.g., Kraus and Musick, 2000); throughout the Southeast and Northeast U.S. LMEs, shelf-edge bottom waters are expected to warm considerably faster than most adjacent shallow coastal habitat (Saba *et al.*, 2016). Given the inherent complexities of multi-species modeling of any kind, climate-driven forecast models developed for individual species (e.g., Hare *et al.*, 2010, 2012; Kohut *et al.*, 2013) should be the immediate focus for understanding how changing climate will affect living marine resources. Basic community-level forecasts using simple metrics such as species richness or gamma diversity could be developed based on amalgamated single-species projections.

### Management implications

For successful natural resources study and management, biological or ecological units must be defined at a scale appropriate for the process of interest (Post *et al.*, 2007). In a single-species fishery assessment setting, the biological unit is the fishery stock. All life history processes are assumed to be occurring within this defined unit, the spatial extent of which may cross various types of boundaries including ecosystem (e.g., LMEs delineations), sociopolitical (e.g., state/country borders), and management units (e.g., U.S. federal fishery management council regions). Single-species stock assessments in the United States should be and are typically flexible in the data and information that is included in an assessment proceeding, regardless of from which pre-defined management unit that information originated. However, investigations with more complexity such as those at the multispecies (Garrison *et al.*, 2010), community (Link *et al.*, 2011), or ecosystem (Link *et al.*, 2010) level, the appropriate scale at which processes of interest are occurring is more nebulous due to the dynamic nature of ecological processes within the marine realm (Lourie and Vincent, 2004). The Large Marine Ecosystem framework has provided a workable approach to the study and conservation of marine living marine resources for multiple decades (Sherman, 2009). However, certain coastal ocean areas with demonstrated biological interconnectedness such as the U.S. Atlantic coast would benefit from scientific sampling platforms that reflect the scale of ecosystem processes rather than pre-determined spatial management constructs. As living marine resources management continues to expand from single-species analyses to include more holistic, ecosystem-based tenants, the importance of ensuring a spatiotemporal match between data collection and dynamic ecological processes will intensify.

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**TABLES**

Table 1. Tow-level explanatory variables included in variance partitioning of β diversity.

| Group | Variable | Transformation | Data source | Interpretation |
|---|---|---|---|---|
| Temperature (‘Temp’) | Observed bottom temperature (˚C) | none | NEAMAP, SEAMAP-SA | Physiological limit to distribution; migratory cue |
| Chlorophyll (‘Chl’) | Satellite-estimated surface chlorophyll *a* concentration (mg $m^{-3}$) | log | Generated from Feldman and McClain (2014) | Proxy for primary productivity; influences food availability via bottom-up control |
| Salinity (‘Sal’) | Observed bottom salinity (Practical Salinity Units) | none | NEAMAP, SEAMAP-SA | Freshwater outflow, local productivity |
| Landscape (‘Land’) | Distance to land (km) | square-root | Generated from Wessel and Smith (1996) | Proximity to land |
|  | Distance to an estuary (km) | square-root | Generated from USFWS (2014) | Proximity to estuarine habitat |
|  | Area ($km^2$) of proximate deepwater estuarine habitat within 2, 4, 8, 16, 32, or 64-km | square-root | Generated from USFWS (2014) | Measure of estuarine habitat availability |
| Day length (‘DayLength’) | Photoperiod for a given latitude and date (hours) | none | Forsythe *et al.* (1995); not included in season-specific analyses | Migratory cue |

Table 2. Summary of environmental effects within biotic ecotones. Distance-based redundancy analysis was conducted once for each biotic ecotone at the window width and during the season in which the ecotone was most prominent (see Fig. 2). State abbreviations are Florida (FL), Georgia (GA), South Carolina (SC), North Carolina (NC), and Virginia (VA). Ecotones are displayed as blue polygons in Fig. 2 and mapped in Fig. 5. Predominant explanatory processes and strength of explanation are qualitative determinations based on variance partitioning results (Fig. 4), with consideration for the relative proportions of variance explained by variable groups and the total variance explained.

| LME | State | Biotic ecotone landmark | # | Season evident | Predominant explanatory processes | Strength of explanation |
|---|---|---|---|---|---|---|
| Southeast U.S. | FL | St. Augustine | 1 | Spring | Seasonality,<br>Productivity gradient | Weak |
| | FL/GA | St. Mary's River | 2 | Spring | Multiple | Moderate |
| | SC | Winyah Bay | 3 | Fall | Landscape heterogeneity<br>Seasonality | Moderate |
| | NC | Onslow Bay, lower | 4 | Spring | Landscape heterogeneity<br>Seasonality | Moderate |
| | NC | Onslow Bay, upper | 5 | Spring | Seasonality<br>Productivity gradient | Strong |
| Border | NC | Cape Hatteras | 6 | Spring | Seasonality<br>Productivity gradient<br>Salinity gradient | Weak |
| Northeast U.S. | NC/VA | Virginia Beach | 7 | Spring | Landscape heterogeneity<br>Seasonality | Moderate |

## FIGURES

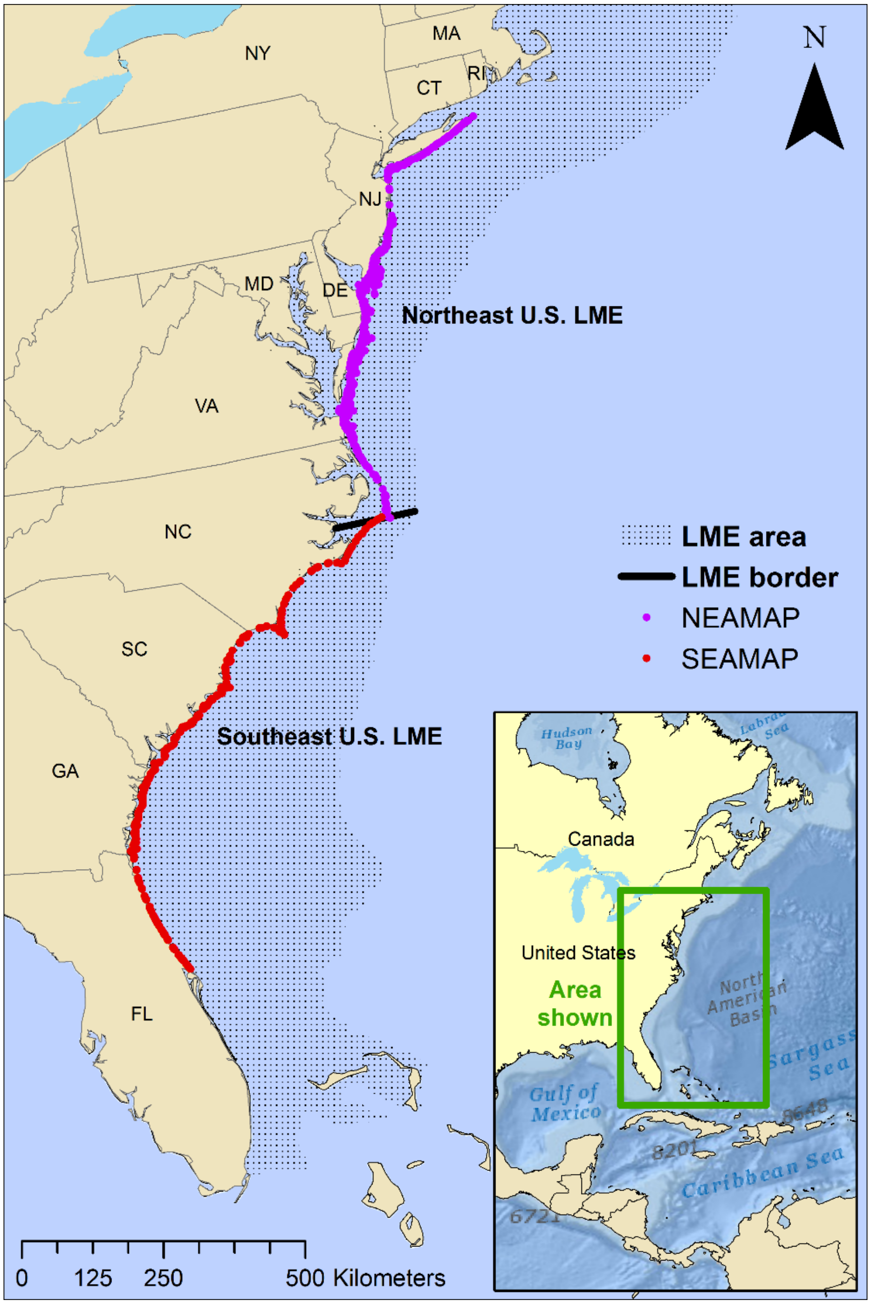


Figure 1. The study area included the nearshore coastal ocean within Southeast and Northeast U.S. LMEs from Cape Canaveral, Florida to Montauk, New York. Overlapping red and purple closed circles represent SEAMAP-SA and NEAMAP sampling sites, respectively; data are from spring and fall during 2008-2013 and within a 5 to 12-m depth range. Stippled areas are within LME boundaries (the Northeast U.S. LME extends farther north to the Bay of Fundy). The bold black line is the geographic boundary between LMEs located at the Cape Hatteras latitude line (35.4°N).

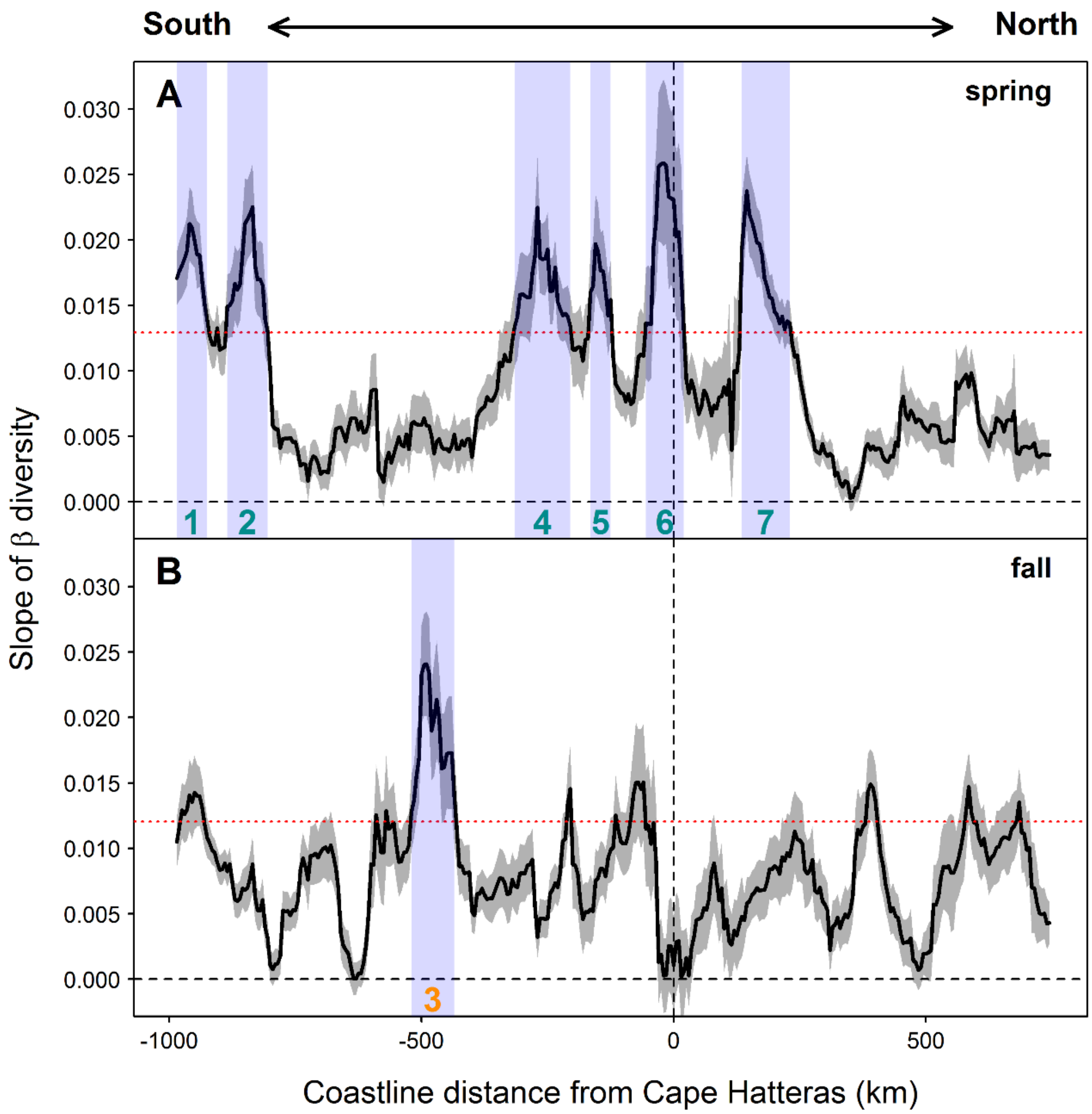


Figure 2. Slopes of β diversity (black lines) versus coastline transect distance at an intermediate and optimal moving window width size of 190-km. Spring (A, top) and fall (B, bottom) patterns were analyzed separately to depict seasonal differences. Bootstrapped 99% confidence intervals are shown as grey polygons encompassing slope estimates calculated at 5-km increments. Shaded blue polygons depict biotic ecotones that were further analyzed to determine which environmental variables explained biotic gradients. Ecotone boundaries were set at 50% of the maximum slope for that season (horizontal dotted red line). Number labels refer to ecotone names (Table 2): 1) St. Augustine, 2) St. Mary's River, 3) Winyah Bay, 4) lower Onslow Bay, 5) upper Onslow Bay, 6) Cape Hatteras, and 7) Virginia Beach.

Figure 3 (figure on following page). Bottom temperature, bottom salinity, surface chlorophyll *a*, scaled log cumulative biomass, and species richness patterns along a coastline transect centered near Cape Hatteras, NC during 2008-2013 and within a 5 to 12-m depth range. Values corresponding to SEAMAP-SA sampling sites (closed squares) are south of Cape Hatteras, whereas NEAMAP sites (closed circles) are north of this shared boundary between Southeast and Northeast U.S. LMEs. A loess smother with 99% confidence intervals are overlaid for each environmental variable in spring (cyan) and fall (orange). For the top three panels, shaded blue polygons depict biotic ecotones within which an environmental predictor was a good explanatory variable (see Table 2). Number labels refer to ecotone names (Table 2): 1) St. Augustine, 2) St. Mary's River, 3) Winyah Bay, 4) lower Onslow Bay, 5) upper Onslow Bay, 6) Cape Hatteras, and 7) Virginia Beach.

Figure 3 (caption on previous page)

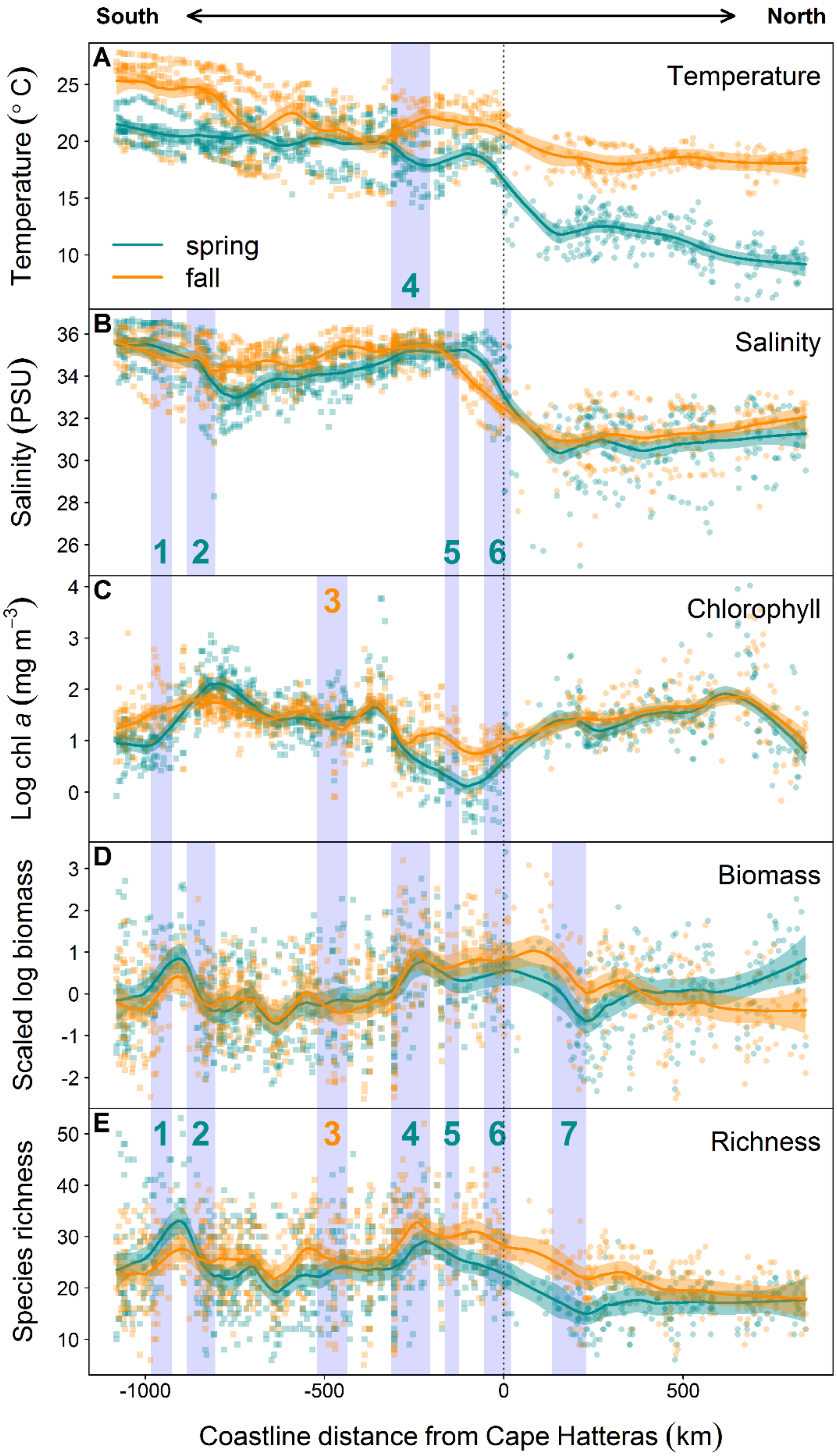
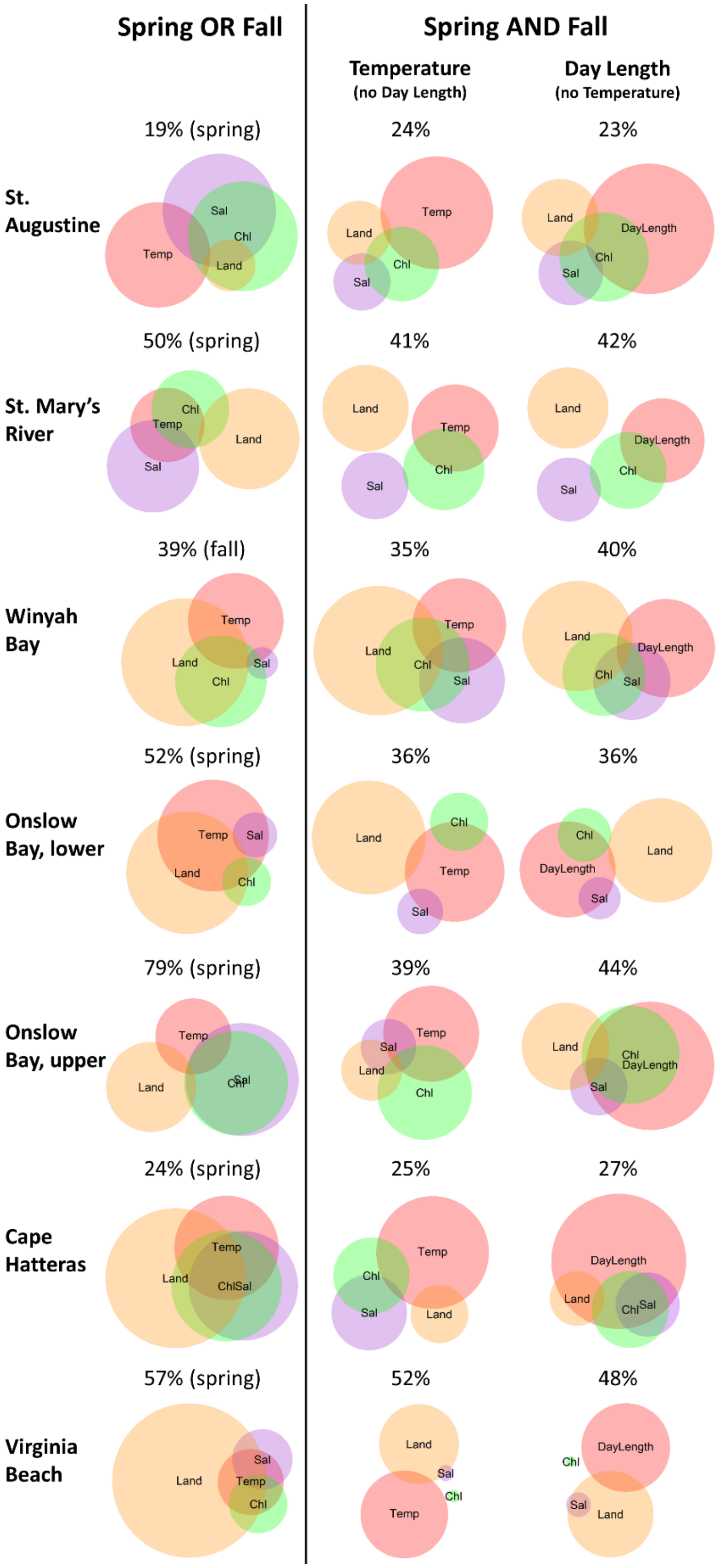


Figure 4 (figure on following page). Venn diagrams depicting the relative proportions of variance explained in β diversity by groups of environmental variables for each biotic ecotone. The left column shows season-specific analyses during the season in which the ecotone was evident (see Fig. 2). The middle column depicts partitioning results for all data (both seasons) within each ecotone, while the right column differs from the middle column only in that temperature was replaced with day length. Circle sizes are normalized to the total variation explained (percentages in parentheses) for individual analyses in each ecotone. Overlapping areas represent the proportion of variation concomitantly explained by two or more variable groups. Variable group abbreviations also listed in Table 1 are temperature (‘Temp’), chlorophyll (‘Chl’), salinity (‘Sal’), landscape (‘Land’), and day length (‘DayLength’).

Figure 4 (caption on previous page).



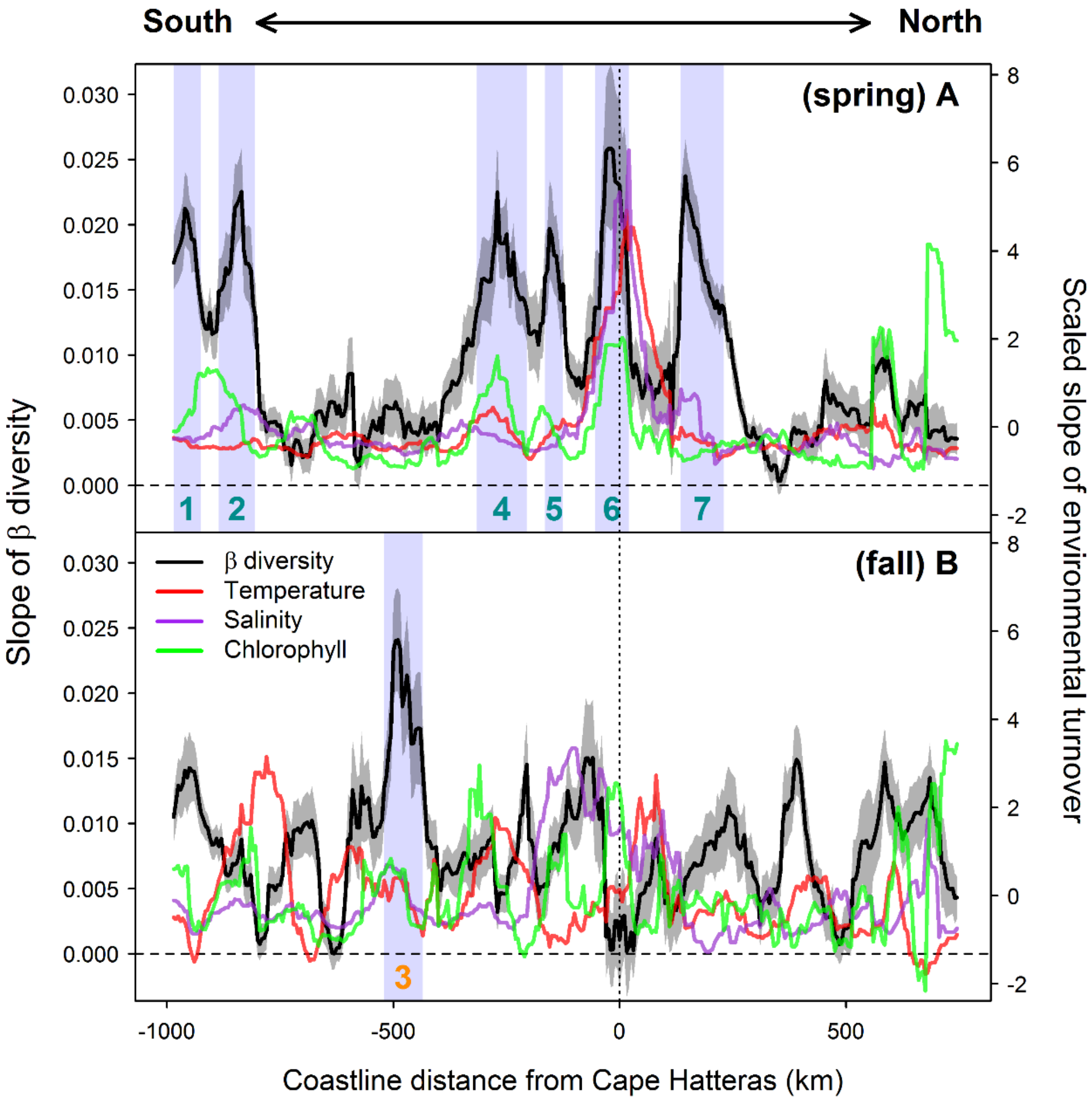


Figure 5. Slopes of β diversity (black lines) and turnover of bottom temperature (red lines), bottom salinity (purple lines), and chlorophyll (green lines) along a coastline transect distance at an intermediate and optimal moving window width size of 190-km. Environmental slopes were scaled by centering on the mean and dividing by the standard deviation. Shaded blue polygons depict biotic ecotones that were further analyzed to determine which environmental variables explained biotic gradients. Number labels refer to ecotone names (see Table 2 and Fig. 4): 1) St. Augustine, 2) St. Mary’s River, 3) Winyah Bay, 4) lower Onslow Bay, 5) upper Onslow Bay, 6) Cape Hatteras, and 7) Virginia Beach.

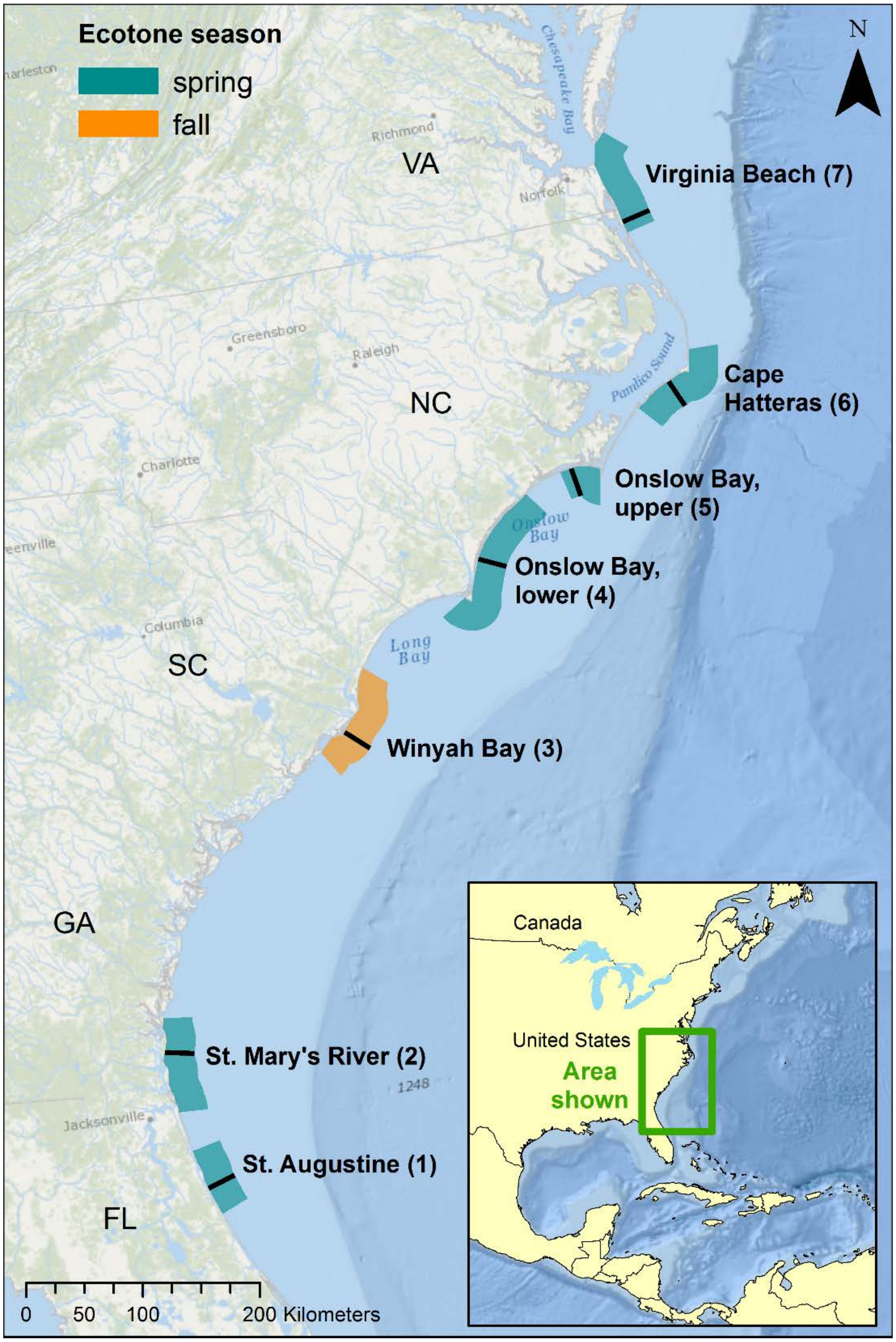


Figure 6. Locations of biotic ecotones revealed by moving gradient window analysis and summarized in Table 2. Winyah Bay was the only prominent ecotone in fall. Ecotone boundaries parallel to the coastline were set as a 25-km buffer for visual purposes only. Black lines depict the approximate location of peak slopes within ecotones.

## APPENDIX I

Additional methodological details for Chapter 2.

### *Sampling platforms*

The Northeast Area Monitoring and Assessment Program (NEAMAP) is conducted by Virginia Institute of Marine Science (Gloucester Point, VA) personnel twice annually (spring, fall) within the Northeast U.S. LME from Martha's Vineyard, MA to Cape Hatteras, NC. The Southeast Area Monitoring and Assessment Program – U.S. South Atlantic (SEAMAP-SA) is conducted by South Carolina Department of Natural Resources (Charleston, SC) personnel thrice annually (spring, summer, fall) within the Southeast U.S. LME from Cape Hatteras, NC to Cape Canaveral, FL. NEAMAP began in fall 2007 and SEAMAP-SA in 1989. Specifications and deployment methods of trawl gear are similar between surveys. NEAMAP deploys a "box" trawl from a 27-m stern-dragger at a target speed of 3-kt (Bonzek *et al.*, 2015), while SEAMAP-SA simultaneously deploys two "tongue" trawls from a 23-m St. Augustine shrimp trawler at a target speed of 2-kt (Stender and Barans, 1994). Tow time for both surveys is typically 20 min, after which the catch is brought onboard, sub-sampled (if necessary), all individuals identified to species and quantified, and additional information (allometrics, reproductive status/tissue, otoliths, and stomach contents) obtained from certain species and specimens. NEAMAP employs a stratified random design across 15 strata in waters between 6.1-m and 36.6-m depth contours. SEAMAP-SA employs a stratified fixed station design, whereby a pre-determined number of fixed stations are chosen for seasonal sampling from a pool of all possible stations within each of 6 subregions (Fig. 1). For appropriate comparisons between surveys, we utilized six years of temporally overlapping data collected during daylight hours in spring (mid-April to mid-May) and fall (October to early November) from 2008-2013 and within a common depth range of 5 to 12-m. Bottom temperature and salinity data used in this analysis were collected at each sampling location by NEAMAP and SEAMAP-SA personnel using a hydrographic profiler.

### *Coastline transect*

For use in statistical analysis and generation of additional explanatory variables, a coastline transect was generated from the tip of Cape Canaveral, FL to the tip of Cape Cod, MA. At a resolution of 1:1,000,000, the transect was traced as a polyline in ArcGIS (ESRI, 2014) from a shoreline polygon shapefile ("GSHHS_f_L1.shp") available from the Global Self-consistent Hierarchical, High-resolution Geography database (v. 2.3.2) provided by the National Geophysical Data Center (Wessel and Smith, 1996). The "Create Random Points" tool in ArcGIS was then used to generate shapefile containing points at 1-km intervals along the polyline. Using the transect points as near features, a "Near Table" was generated for all sampling points. The "Join Field" tool was then used to assign the closest transect point to the trawl points feature attribute table.

### *Chlorophyll*

Satellite-estimated surface chlorophyll (chl) *a* data were obtained from the National Aeronautics and Space Administration (NASA) Goddard Space Flight Center (GSFC) OceanColor Group website (Feldman and McClain, 2014) using Marine Geospatial Ecology Tools (Roberts *et al.*, 2010) within ArcGIS (ESRI, 2014). Raster images of chl *a* concentration (mg $m^{-3}$) were collected by NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) instrument carried by the Aqua satellite. NASA

MODIS data were obtained using the “Create Rasters for NASA OceanColor L3 SMI Product” script available via Marine Geospatial Ecology Tools (Roberts *et al.*, 2010). Downloaded images had an 8-day temporal resolution, a 4-km spatial resolution, were in the World Geodetic System 1984 coordinate system, and limited to between 82˚ and 70˚W longitude and 28˚ and 42˚N latitude. This spatial extent encompassed all trawl survey sample locations included in the study.

Each survey tow was assigned a chl *a* estimate with the best spatial and temporal alignment. Each 8-day raster dataset was masked to exclude raster cells that overlapped with inshore estuarine waters, which potentially have markedly different and unrepresentative chl *a* signatures compared to neighboring nearshore waters within which survey trawls were conducted. This was done by creating an equal area grid with the exact spatial extent and number of columns and rows as each downloaded raster file. All cells that overlapped any amount of inshore water were then selected and removed, and the remaining fishnet containing only nearshore and offshore waters was used as a template to mask chl *a* raster datafiles. The mask template consistently excluded certain 4-km cells within which survey trawls were conducted, notably those cells close to land features that contained both nearshore and inshore waters separated by narrow barrier islands. To reduce the number of trawl survey tows without assigned chl *a* estimates, focal statistics (mean within a 3 by 3 rectangle) were calculated for each raster file so that values for these “no data” cells could be extrapolated based on values from immediately adjacent cells containing only nearshore waters. Focal statistics were saved as separate files. While extrapolating average values for “no data” cells from immediately adjacent cells using focal statistics likely introduced some bias, the amount of bias introduced is likely less than if masked cells that were confounded by inshore readings were allowed to retain their original values.

ArcGIS ModelBuilder was used to automate the assignment of chl *a* estimates to trawl survey tow starting points. For points that spatiotemporally aligned with raster cells containing no chl *a* estimate, either due to incomplete satellite coverage or masking as described above, chl *a* values were assigned using the “Raster Calculator” tool with a conditional statement specifying a hierarchy of alternative datasets in the case of a null value. In order of preference, alternative datasets were:

1) Aligned 8-day raster file with focal statistics calculated,
2) Raster file from the previous or following 8-day period, whichever was *nearer* in time to the trawl survey sampling date,
3) Alternative 2 with focal statistics calculated,
4) Raster file from the previous or following 8-day period, whichever was *farther* in time to the trawl survey sampling date,
5) Alternative 4 with focal statistics calculated,
6) A seasonal raster file calculated as an average of all 8-day raster files that overlapped in time with sampling dates for either survey during the appropriate season,
7) Alternative 6 with focal statistics calculated.

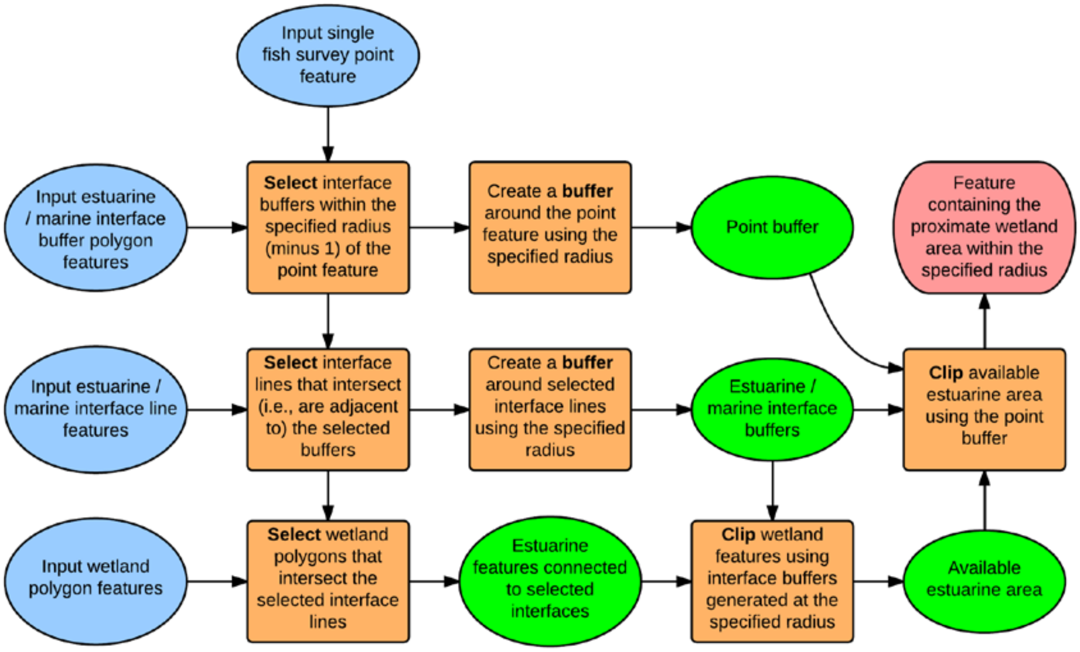
Although the file that was used to assign a each point its chl *a* estimate was not recorded, rarely was there loss of satellite coverage for a given raster cell within the nearshore zone for three consecutive 8-day periods. Thus few trawl survey tows, if any, were assigned a chl *a* value based on seasonal average datasets (alternatives 6 and 7) that had much coarser temporal resolution.

### *Landscape variables*

Prior to making distance and area calculations, all point and polygon shapefiles were projected to North American Datum 1983 Albers. Using the “Near” tool in ArcGIS, ‘distance to land’ was calculated as the geodesic distance from the starting coordinates of each trawl survey location to the nearest land feature. Land features were obtained from the same shoreline polygon shapefile (“GSHHS_f_L1.shp”) described above.

Distance to an estuarine inlet or river mouth (hereafter “estuarine/marine interface”) was calculated as the geodesic distance from the start of each trawl survey tow to the nearest estuarine/marine interface, circumventing any hindering land features. Estuarine/marine interfaces were drawn according to the topology of features within the National Wetlands Inventory database (USFWS, 2014). Wetlands data for each coastal state from Florida north to Massachusetts were downloaded and merged into a single shapefile. Within the study area, an interface line was drawn for each instance where any deepwater polygon with “ATTRIBUTE = 'M%'” (“M” denotes marine) intersected a polygon with “ATTRIBUTE = 'E%'” (“E” denotes estuarine). The topology and attributes of some polygons were manually altered to correct obvious attribute misspecifications within the downloaded data or to simplify interface line construction. Ephemeral interfaces that open and closed due to sediment movement (manmade or natural) were identified using Google Earth (accessed 10 Dec 2014) and excluded from analysis. 1-km buffers were then created around interface lines, and the portions of the buffers that overlapped land or wetland polygons were erased. The purpose of creating interface buffers was to reduce the number of intersections between land features and nearest distance path lines. The “Near” tool was then used to calculate the geodesic distance of each trawl survey location to the edge of the closest interface buffer. Using the original trawl coordinates and spatial coordinates of the closest interface feature location output from the “Near” analysis, the “Points to Line” script was used to generate path lines from each trawl location to the nearest interface feature. Path lines that intersected land features were manually altered to circumvent those features; line lengths (geodesic distances) were then automatically recalculated within the attribute table.

Also using National Wetlands Inventory data, the amount of proximate estuarine area was calculated for each trawl survey point at radii of 2, 4, 8, 16, 32, and 64-km. These radii were chosen based on a frequency histogram of distances to an estuary (not shown), which indicated log-normally distributed data and a maximum distance of 60-km. First, six subset shapefiles of survey points were generated, one for each radius, by selecting points with a distance to the nearest estuarine/marine interface equal to or less than the specified radius minus 1. One was subtracted from each distance to account for the 1-km buffer surrounding each interface used in distance calculations. ArcGIS ModelBuilder was then used to automate calculations of proximate estuarine area to each point. To speed processing, features within the shapefile containing wetlands data were split according to watershed using watershed designations from the National Wetlands Inventory database. Certain watersheds were combined or split according to natural connectivity among coastal deepwater areas. For features within a given watershed, features of a certain wetland type – subtidal estuarine deepwater or intertidal estuarine wetland – were merged into a single feature, resulting in two feature polygons for each watershed. For a given point feature, the amount of proximate wetland area was calculated using the following workflow:



This workflow was iterated for each point feature within each of the six subset point datafiles. Following the model run for given subset datafile, output shapefiles were merged. Deepwater estuarine features were then selected and saved as a separate table containing area calculations. Total estuarine area was calculated by merging features within the original merged file based on the unique identifiers of point features. Ultimately, only deepwater estuarine area calculations were used in statistical analyses.

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# APPENDIX I:  SUPPLEMENTARY TABLES

Table S1. Total biomass (grams) captured (sum for 2008-2013) for species considered for inclusion in diversity analysis. A species was excluded from analysis if it was not captured during all six years of the study period by either NEAMAP or SEAMAP.

| | NEAMAP | | SEAMAP | | Excluded? |
|---|---|---|---|---|---|
| Scientific Name | Spring | Fall | Spring | Fall | |
| *Acanthostracion quadricornis* | 0 | 0 | 3,208 | 4,329 | Yes |
| *Achirus lineatus* | 0 | 0 | 212 | 0 | Yes |
| *Acipenser oxyrinchus* | 539,214 | 497,150 | 101,810 | 24,680 | No |
| *Aetobatus narinari* | 0 | 0 | 1,045,800 | 222,405 | No |
| *Albunea paretii* | 0 | 0 | 3 | 81 | Yes |
| *Alectis ciliaris* | 0 | 380 | 0 | 65 | Yes |
| *Alopias vulpinus* | 295,100 | 537,700 | 236,410 | 0 | No |
| *Alosa aestivalis* | 1,045,208 | 0 | 859 | 3 | No |
| *Alosa mediocris* | 7,533 | 5,050 | 0 | 0 | No |
| *Alosa pseudoharengus* | 250,107 | 45 | 0 | 0 | No |
| *Alosa sapidissima* | 137,227 | 400 | 318 | 0 | No |
| *Alpheus heterochaelis* | 0 | 0 | 0 | 2 | Yes |
| *Aluterus monoceros* | 0 | 0 | 0 | 2,912 | Yes |
| *Aluterus schoepfii* | 0 | 495 | 0 | 12 | Yes |
| *Ammodytes americanus* | 4 | 15 | 0 | 0 | Yes |
| *Anchoa* sp. | 561,896 | 2,939,614 | 756,265 | 1,243,815 | No |
| *Ancylopsetta ommata* | 0 | 15 | 55,920 | 6,300 | No |
| *Anisotremus virginicus* | 0 | 0 | 0 | 45 | Yes |
| *Archosargus probatocephalus* | 24,356 | 398,526 | 457,544 | 127,072 | No |
| *Arenaeus cribrarius* | 0 | 0 | 7,973 | 13,642 | No |
| *Ariomma regulus* | 0 | 0 | 0 | 175 | Yes |
| *Ariopsis felis* | 0 | 0 | 884 | 40,082 | No |
| *Astroscopus guttatus* | 0 | 16,307 | 0 | 162 | No |
| *Astroscopus y-graecum* | 0 | 0 | 671 | 713 | Yes |
| *Bagre marinus* | 0 | 0 | 4,595 | 62,981 | No |
| *Bairdiella chrysoura* | 129,971 | 1,300,138 | 380,329 | 807,810 | No |
| *Balistes capriscus* | 854 | 5,547 | 1,958 | 550 | No |
| *Bothus ocellatus* | 24 | 0 | 0 | 0 | Yes |
| *Brevoortia smithi* | 0 | 0 | 3,684 | 25,919 | No |
| *Brevoortia tyrannus* | 206,947 | 64,480 | 771,233 | 149,240 | No |
| *Calappa flammea* | 0 | 0 | 1,414 | 965 | No |
| *Callinectes ornatus* | 0 | 0 | 470 | 1,775 | No |
| *Callinectes sapidus* | 3,099 | 5,593 | 22,654 | 26,979 | No |
| *Cancer borealis* | 30 | 130 | 0 | 0 | Yes |

| | NEAMAP | | SEAMAP | | Excluded? |
|---|---|---|---|---|---|
| Scientific Name | Spring | Fall | Spring | Fall | |
| *Caranx bartholomaei* | 0 | 0 | 11 | 97 | Yes |
| *Caranx crysos* | 0 | 18,101 | 20,771 | 139,346 | No |
| *Caranx hippos* | 0 | 1,128 | 43,193 | 10,366 | No |
| *Carcharhinus acronotus* | 0 | 0 | 586,400 | 814,272 | No |
| *Carcharhinus brevipinna* | 0 | 2,990 | 55,800 | 192,957 | Yes |
| *Carcharhinus isodon* | 0 | 0 | 7,420 | 6,375 | Yes |
| *Carcharhinus leucas* | 0 | 0 | 0 | 137,600 | Yes |
| *Carcharhinus limbatus* | 0 | 0 | 198,260 | 415,900 | No |
| *Carcharhinus obscurus* | 5,500 | 0 | 4,280 | 0 | Yes |
| *Carcharhinus plumbeus* | 22,720 | 168,463 | 20,090 | 164,028 | No |
| *Carcharias taurus* | 113,660 | 588,570 | 1,223,150 | 337,530 | No |
| *Centropristis philadelphica* | 0 | 0 | 1,998 | 33,644 | No |
| *Centropristis striata* | 29,653 | 15,437 | 9,352 | 11,768 | No |
| *Chaetodipterus faber* | 90 | 9,363 | 18,287 | 255,366 | No |
| *Chaetodon ocellatus* | 0 | 7 | 0 | 37 | Yes |
| *Chilomycterus schoepfii* | 11,575 | 33,533 | 469,837 | 97,912 | No |
| *Chloroscombrus chrysurus* | 0 | 337 | 7,567,154 | 5,766,950 | No |
| *Citharichthys arctifrons* | 120 | 35 | 0 | 0 | Yes |
| *Citharichthys macrops* | 0 | 0 | 17,067 | 31,179 | No |
| *Citharichthys spilopterus* | 0 | 0 | 135 | 8,604 | No |
| *Clupea harengus* | 19,459 | 294 | 0 | 0 | No |
| *Cryptodromiopsis antillensis* | 0 | 0 | 7 | 25 | Yes |
| *Cynoscion nebulosus* | 458 | 4,257 | 1,869 | 10,632 | No |
| *Cynoscion nothus* | 750 | 0 | 606,982 | 595,121 | No |
| *Cynoscion regalis* | 2,833,860 | 14,248,284 | 987,558 | 1,719,882 | No |
| *Dasyatis americana* | 2,480 | 22,105 | 1,291,699 | 1,223,708 | No |
| *Dasyatis centroura* | 22,114 | 409,185 | 2,072,240 | 1,143,079 | No |
| *Dasyatis sabina* | 4,575 | 26,647 | 17,980 | 465,412 | No |
| *Dasyatis say* | 1,220,033 | 177,730 | 4,471,999 | 5,041,504 | No |
| *Decapterus punctatus* | 0 | 1,845 | 9,992 | 38,091 | No |
| *Diodon hystrix* | 0 | 0 | 1,481 | 0 | Yes |
| *Diplectrum formosum* | 0 | 0 | 651 | 534 | No |
| *Diplodus holbrookii* | 0 | 0 | 0 | 385 | Yes |
| *Dorosoma petenense* | 0 | 0 | 36 | 0 | Yes |
| *Dorosoma cepedianum* | 0 | 0 | 279 | 0 | Yes |
| *Doryteuthis* sp. | 396,068 | 366,453 | 173,490 | 66,396 | No |
| *Echeneis naucrates* | 0 | 50 | 5,171 | 8,402 | No |
| *Elops saurus* | 0 | 0 | 0 | 6,618 | Yes |
| *Enchelyopus cimbrius* | 0 | 503 | 0 | 0 | Yes |
| *Engraulis eurystole* | 0 | 3,546 | 0 | 0 | Yes |
| *Epinephelus itajara* | 0 | 0 | 43,000 | 0 | Yes |
| *Epinephelus morio* | 0 | 0 | 0 | 118 | Yes |

| | NEAMAP | | SEAMAP | | Excluded? |
|---|---|---|---|---|---|
| Scientific Name | Spring | Fall | Spring | Fall | |
| *Etropus* sp. | 660 | 591 | 50,841 | 85,125 | No |
| *Etrumeus teres* | 25 | 712 | 2,645 | 9 | No |
| *Eucinostomus* sp. | 0 | 719 | 40 | 23,548 | No |
| *Farfantepenaeus aztecus* | 205 | 25,201 | 5,516 | 276,663 | No |
| *Farfantepenaeus duorarum* | 2 | 40 | 92,647 | 8,324 | No |
| *Gibbesia neglecta* | 0 | 0 | 8,298 | 4,290 | No |
| *Ginglymostoma cirratum* | 0 | 0 | 159,700 | 0 | Yes |
| *Gobiesox strumosus* | 0 | 0 | 6 | 0 | Yes |
| *Gobiosoma bosc* | 0 | 0 | 47 | 0 | Yes |
| *Gymnachirus melas* | 0 | 0 | 0 | 354 | Yes |
| *Gymnura altavela* | 0 | 1,702,812 | 1,543,773 | 4,874,277 | No |
| *Gymnura micrura* | 19,852 | 355,146 | 1,280,113 | 1,855,084 | No |
| *Haemulon aurolineatum* | 0 | 0 | 566 | 8 | Yes |
| *Harengula jaguana* | 0 | 0 | 10,537 | 40,684 | No |
| *Helicolenus dactylopterus* | 0 | 312 | 0 | 0 | Yes |
| *Hemitripterus americanus* | 1,288 | 0 | 0 | 0 | Yes |
| *Hepatus epheliticus* | 0 | 0 | 12,707 | 4,154 | No |
| *Hippocampus erectus* | 15 | 0 | 23 | 57 | No |
| *Hippoglossina oblonga* | 8,658 | 415 | 0 | 0 | No |
| *Homarus americanus* | 8,276 | 5,403 | 0 | 0 | No |
| *Hyperoglyphe perciformis* | 106 | 0 | 119 | 0 | Yes |
| *Hypleurochilus geminatus* | 0 | 0 | 3 | 24 | Yes |
| *Hypsoblennius hentz* | 0 | 0 | 141 | 0 | Yes |
| *Labrisomus nuchipinnis* | 0 | 0 | 15 | 0 | Yes |
| *Lagocephalus laevigatus* | 0 | 0 | 160 | 732 | Yes |
| *Lagodon rhomboides* | 247 | 31,740 | 500,010 | 2,501,213 | No |
| *Larimus fasciatus* | 3,880 | 27,984 | 2,741,161 | 1,614,255 | No |
| *Leiostomus xanthurus* | 2,328,809 | 13,369,196 | 11,439,894 | 13,625,825 | No |
| *Lepophidium profundorum* | 611 | 1,065 | 0 | 0 | Yes |
| *Leucoraja* sp. | 28,072,852 | 5,196,521 | 2,930 | 0 | No |
| *Limulus polyphemus* | 3,568,661 | 2,667,649 | 2,069,207 | 5,103,106 | No |
| *Litopenaeus setiferus* | 3,031 | 83,632 | 848,414 | 3,125,323 | No |
| *Lobotes surinamensis* | 0 | 0 | 3,276 | 10,650 | Yes |
| *Lolliguncula brevis* | 170 | 79,813 | 178,052 | 311,995 | No |
| *Lophius americanus* | 43,774 | 523 | 0 | 0 | Yes |
| *Lutjanus campechanus* | 0 | 0 | 0 | 502 | Yes |
| *Lutjanus griseus* | 0 | 0 | 0 | 1,399 | Yes |
| *Lutjanus synagris* | 0 | 0 | 317 | 219 | Yes |
| *Melanogrammus aeglefinus* | 0 | 100 | 0 | 0 | Yes |
| *Menidia menidia* | 0 | 0 | 0 | 30 | Yes |
| *Menippe mercenaria* | 0 | 0 | 8,902 | 4,808 | No |
| *Menticirrhus* sp. | 662,746 | 4,300,925 | 4,074,883 | 3,831,779 | No |

| | NEAMAP | | SEAMAP | | Excluded? |
|---|---|---|---|---|---|
| Scientific Name | Spring | Fall | Spring | Fall | |
| *Merluccius bilinearis* | 104,791 | 5,984 | 0 | 0 | No |
| *Metoporhaphis calcarata* | 0 | 0 | 2 | 0 | Yes |
| *Micropogonias undulatus* | 1,668,427 | 17,227,948 | 16,876,441 | 11,743,668 | No |
| *Mobula hypostoma* | 0 | 0 | 569,960 | 419,540 | No |
| *Mola mola* | 0 | 0 | 100,000 | 0 | Yes |
| *Morone americana* | 55 | 0 | 0 | 0 | Yes |
| *Morone saxatilis* | 521,764 | 4,932,090 | 0 | 0 | No |
| *Mugil cephalus* | 0 | 0 | 106 | 635 | Yes |
| *Mugil curema* | 0 | 1,140 | 0 | 4,688 | Yes |
| *Mullus auratus* | 0 | 15 | 0 | 0 | Yes |
| *Mustelus canis* | 2,896,017 | 1,400,981 | 1,346,042 | 83,541 | No |
| *Myliobatis freminvillei* | 187,416 | 751,086 | 18,413,498 | 1,570,508 | No |
| *Narcine brasiliensis* | 0 | 0 | 8,020 | 5,110 | Yes |
| *Octopus vulgaris* | 0 | 0 | 780 | 3,284 | Yes |
| *Ogcocephalus parvus* | 0 | 0 | 0 | 24 | Yes |
| *Ogcocephalus rostellum* | 0 | 0 | 4 | 263 | No |
| *Oligoplites saurus* | 0 | 0 | 191 | 264 | Yes |
| *Ophichthus gomesii* | 0 | 0 | 0 | 824 | Yes |
| *Ophidion* sp. | 250 | 4,358 | 407 | 595 | No |
| *Opisthonema oglinum* | 2,033 | 85,372 | 732,509 | 452,846 | No |
| *Opsanus tau* | 0 | 0 | 587 | 801 | Yes |
| *Orthopristis chrysoptera* | 5,793 | 40,947 | 432,366 | 775,402 | No |
| *Paralichthys albigutta* | 0 | 0 | 7,073 | 24,426 | No |
| *Paralichthys dentatus* | 876,335 | 434,554 | 82,133 | 229,356 | No |
| *Paralichthys lethostigma* | 0 | 0 | 97,125 | 77,691 | No |
| *Paralichthys squamilentus* | 0 | 0 | 17 | 169 | Yes |
| *Pareques umbrosus* | 0 | 0 | 0 | 25 | Yes |
| *Penaeus monodon* | 0 | 0 | 0 | 190 | Yes |
| *Peprilus paru* | 9,052 | 208,793 | 1,087,859 | 1,405,855 | No |
| *Peprilus triacanthus* | 1,936,253 | 5,527,240 | 767,129 | 1,001,585 | No |
| *Persephona mediterranea* | 0 | 0 | 8,146 | 1,211 | No |
| *Petrolisthes galathinus* | 0 | 0 | 1 | 21 | Yes |
| *Pilumnus sayi* | 0 | 0 | 47 | 65 | Yes |
| *Platylambrus granulata* | 0 | 0 | 5 | 0 | Yes |
| *Podochela riisei* | 0 | 0 | 4 | 0 | Yes |
| *Pogonias cromis* | 181,950 | 22,231 | 63,980 | 13,897 | No |
| *Pollachius virens* | 47 | 0 | 0 | 0 | Yes |
| *Polyonyx gibbesi* | 0 | 0 | 2 | 0 | Yes |
| *Pomatomus saltatrix* | 79,395 | 1,612,382 | 528,149 | 1,128,806 | No |
| *Porcellana sayana* | 0 | 0 | 2 | 5 | Yes |
| *Porcellana sigsbeiana* | 0 | 0 | 41 | 0 | Yes |
| *Porichthys plectrodon* | 0 | 0 | 135 | 0 | Yes |

| Scientific Name | NEAMAP<br>Spring | <br>Fall | SEAMAP<br>Spring | <br>Fall | Excluded? |
|---|---|---|---|---|---|
| *Portunus gibbesii* | 0 | 81 | 131,533 | 19,986 | No |
| *Portunus sayi* | 0 | 0 | 25 | 127 | Yes |
| *Portunus spinimanus* | 0 | 0 | 26,420 | 7,112 | No |
| *Priacanthus arenatus* | 0 | 0 | 8 | 4 | Yes |
| *Prionotus carolinus* | 31,336 | 23,245 | 707,449 | 28,948 | No |
| *Prionotus evolans* | 566,376 | 328,959 | 7,827 | 104,268 | No |
| *Prionotus ophryas* | 0 | 0 | 0 | 44 | Yes |
| *Prionotus rubio* | 0 | 0 | 1,207 | 3,901 | No |
| *Prionotus scitulus* | 0 | 0 | 9,645 | 47,589 | No |
| *Prionotus tribulus* | 0 | 0 | 16,729 | 12,386 | No |
| *Pseudopleuronectes americanus* | 280,881 | 10,922 | 0 | 0 | No |
| *Rachycentron canadum* | 0 | 0 | 47,837 | 8,732 | No |
| *Raja eglanteria* | 9,401,178 | 2,201,354 | 1,260,994 | 1,072,769 | No |
| *Rhinobatos lentiginosus* | 0 | 0 | 15,909 | 4,042 | No |
| *Rhinoptera bonasus* | 113,438 | 5,539,013 | 9,510,086 | 6,007,754 | No |
| *Rhizoprionodon terraenovae* | 7,170 | 14,300 | 2,053,511 | 927,932 | No |
| *Rimapenaeus constrictus* | 99 | 0 | 3,228 | 2,390 | No |
| *Sardinella aurita* | 0 | 565 | 161,905 | 11,003 | No |
| *Sciaenops ocellatus* | 0 | 78,212 | 14,800 | 27,170 | No |
| *Scomber japonicus* | 0 | 64 | 0 | 0 | Yes |
| *Scomber scombrus* | 1,668 | 0 | 0 | 0 | Yes |
| *Scomberomorus cavalla* | 0 | 0 | 3,627 | 237,763 | No |
| *Scomberomorus maculatus* | 0 | 7,794 | 273,589 | 289,540 | No |
| *Scomberomorus regalis* | 0 | 1,160 | 0 | 0 | Yes |
| *Scophthalmus aquosus* | 550,657 | 209,441 | 113,873 | 84,454 | No |
| *Scorpaena brasiliensis* | 0 | 0 | 0 | 63 | Yes |
| *Scorpaena calcarata* | 0 | 0 | 30 | 62 | Yes |
| *Selar crumenophthalmus* | 0 | 3,047 | 74 | 124 | Yes |
| *Selene setapinnis* | 236 | 164,295 | 730,363 | 900,108 | No |
| *Selene vomer* | 0 | 667 | 171 | 161,555 | No |
| *Seriola rivoliana* | 0 | 0 | 0 | 28 | Yes |
| *Seriola zonata* | 0 | 0 | 50 | 0 | Yes |
| *Sicyonia brevirostris* | 0 | 0 | 83 | 0 | Yes |
| *Sicyonia laevigata* | 0 | 0 | 1 | 0 | Yes |
| *Sphoeroides maculatus* | 54,572 | 36,732 | 43,974 | 142,823 | No |
| *Sphoeroides nephelus* | 0 | 0 | 27 | 0 | Yes |
| *Sphyraena barracuda* | 0 | 0 | 0 | 4,970 | Yes |
| *Sphyraena borealis* | 0 | 29,679 | 0 | 0 | No |
| *Sphyraena guachancho* | 0 | 0 | 17,435 | 25,534 | No |
| *Sphyrna lewini* | 0 | 0 | 78,396 | 53,331 | No |
| *Sphyrna tiburo* | 0 | 0 | 1,770,276 | 1,207,759 | No |
| *Sphyrna zygaena* | 0 | 1,810 | 0 | 0 | Yes |

| | NEAMAP | | SEAMAP | | Excluded? |
|---|---|---|---|---|---|
| Scientific Name | Spring | Fall | Spring | Fall | |
| *Squalus acanthias* | 3,584,700 | 108,187 | 133,614 | 0 | No |
| *Squatina dumeril* | 8,554 | 284,690 | 144,000 | 11,890 | No |
| *Squilla empusa* | 380 | 815 | 36,923 | 10,776 | No |
| *Stellifer lanceolatus* | 0 | 65 | 831,690 | 1,204,467 | No |
| *Stenotomus* sp. | 1,335,057 | 799,555 | 629,235 | 1,694,263 | No |
| *Stephanolepis hispida* | 0 | 196 | 86 | 1,444 | No |
| *Syacium papillosum* | 0 | 0 | 63 | 1,751 | Yes |
| *Symphurus plagiusa* | 12,995 | 6,358 | 50,259 | 49,438 | No |
| *Symphurus urospilus* | 0 | 0 | 0 | 28 | Yes |
| *Syngnathus floridae* | 0 | 0 | 15 | 0 | Yes |
| *Syngnathus fuscus* | 0 | 122 | 41 | 6 | Yes |
| *Syngnathus louisianae* | 0 | 0 | 336 | 44 | No |
| *Syngnathus springeri* | 0 | 0 | 750 | 0 | Yes |
| *Synodus foetens* | 26 | 11,144 | 607,592 | 1,137,058 | No |
| *Tautoga onitis* | 14,514 | 49,929 | 0 | 0 | Yes |
| *Torpedo nobiliana* | 53,260 | 0 | 0 | 0 | Yes |
| *Trachinotus carolinus* | 0 | 464 | 21,424 | 188,593 | No |
| *Trachinotus falcatus* | 0 | 335 | 0 | 0 | Yes |
| *Trachurus lathami* | 10 | 12,419 | 10,844 | 0 | No |
| *Trichiurus lepturus* | 21,970 | 30,901 | 680,703 | 1,217,559 | No |
| *Trinectes maculatus* | 17,054 | 52,018 | 151,179 | 86,068 | No |
| *Umbrina coroides* | 0 | 0 | 1,697 | 564 | Yes |
| *Upeneus parvus* | 0 | 0 | 237 | 310 | No |
| *Urophycis chuss* | 41,819 | 790 | 0 | 0 | No |
| *Urophycis earllii* | 0 | 0 | 1,145 | 289 | Yes |
| *Urophycis floridana* | 0 | 0 | 5,074 | 2,744 | No |
| *Urophycis regia* | 746,560 | 863,310 | 161,309 | 9,407 | No |
| *Xiphopenaeus kroyeri* | 0 | 0 | 2,268 | 29,035 | No |

# CHAPTER 3

# Multi-decadal climate and fishing predictors of abundance for U.S. South Atlantic coastal fishes and invertebrates

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## ABSTRACT

Abundance of marine stocks fluctuate in response to both internal processes (e.g., density-dependence) and exogenous drivers, including the physical environment, fishing, and trophodynamic interactions. In the United States, research investigating ecosystem drivers has been focused in data-rich systems, primarily in the North Atlantic and North Pacific. To develop a more holistic understanding of important ecosystem drivers in the Southeast U.S. continental shelf Large Marine Ecosystem, we applied generalized linear and dynamic linear modelling to investigate the effects of climate and fishing covariates on the relative abundance trends of 71 demersal fish and invertebrate species sampled by a coastal trawl survey during 1990-2013. For the assemblage as a whole, fishing effects predominated over climate effects. In particular, changes in trawling effort within the penaeid shrimp fishery governed abundance trends of bony fishes, invertebrates, and elasmobranchs, a likely result of temporal changes in bycatch mortality. Changes in trawling intensity induced changes in overall community composition and appear to have altered trophic interactions among particular species. Among climate indices investigated, the Pacific Decadal Oscillation and the Western Bermuda High Index were most prevalent in well supported dynamic linear models. Observed annual abundance trends were synchronous among some taxonomically-related species, highlighting similar responses to exogenous influences based on life history. This study strengthens the foundation for generating hypotheses and advancing ecosystem-based fisheries research within the region.

## INTRODUCTION

Fisheries scientists have long recognized that ecological processes can cause fluctuations in population abundance (Baird, 1873; Helland-Hansen and Nansen, 1909), but only in recent decades have ecological considerations been widely investigated by fisheries researchers and broadly considered within fisheries management. This focal shift has been in large part due to the establishment and continued refinement of long-term surveys and an ecosystem-based fisheries management (EBFM) framework (Bianchi and Skjoldal, 2008; Link, 2010; Belgrano and Fowler, 2011; Christensen and Maclean, 2011). Although EBFM is being incorporated into policy at the highest levels of United States (MSRA, 2007; Exec. Order No. 13547, 2010) and international governments (Day *et al.*, 2008; Jennings and Rice, 2011), lack of scientific support still hampers the integration of ecosystem processes in fisheries management of stocks worldwide (Skern-Mauritzen *et al.*, 2016).

Taking an ecosystem approach to fisheries (EAF), the bottom-up analog to EBFM (Link, 2010), requires fundamental understanding of the exogenous factors that influence living marine resources. Link *et al.* (2010) describe a 'triad' of exogenous factors or processes that regulate population dynamics of marine biota at scales from species to ecosystems: 1) biophysical, 2) trophodynamic, and 3) exploitative. Biophysical factors include climate effects, as well as planktonic production, which are largely governed by environmental conditions (Miller, 2004). Trophodynamic processes affect population dynamics either through bottom-up or top-down forcing depending on a species' role in the food web. Population impacts from exploitation are typically through direct harvests, but fishing activities can also alter stock productivity via habitat alteration (Jennings and

Kaiser, 1998), fishing-induced evolution (Enberg *et al.*, 2012), or trophic re-organization (Pusceddu *et al.*, 2014). For individual fish stocks, the amalgamated effects of the triad of processes determine abundance by influencing vital rates including growth, survival, recruitment, and reproductive output (Ottersen *et al.*, 2004; Lehodey *et al.*, 2006; Shelton and Mangel, 2011; Hollowed *et al.*, 2013).

The first exogenous factor in the triad includes biophysical factors such as primary and secondary planktonic production, which are relevant to early life stages of many marine fish and invertebrate populations. The match-mismatch hypothesis (Cushing, 1974, 1975) is a well-known mechanism by which planktonic production affects early life stages of fish populations. If ocean environmental conditions are favorable such that planktonic food resources are abundantly available, high larval growth and survival should result in a strong year-class if density-dependence is negligible. To maximize this synchrony, many marine species have evolved to spawn during periods of high primary and secondary productivity (Turner *et al.*, 1979; Sherman *et al.*, 1984; Cushing, 1990). At the ecosystem scale, lower trophic level production correlates with fisheries yields, demonstrating consistent bottom-up effects at broad spatial scales (Friedland *et al.*, 2012).

Climate is a biophysical factor that not only influences lower trophic level interactions within populations, but may also directly impact growth and survival. For instance, the larvae of broadcast spawners are largely at the mercy of ocean currents, deviations in which could result in strong year-classes if larvae are advected to suitable habitat (or vice versa if not) (Houde, 1989). For species with limited larvae dispersal, deviations in local environmental conditions may directly influence growth rates and potentially survival if conditions are especially deleterious. Anomalous environmental conditions can influence adult survival as well, for instance mortality events associated with severely cold conditions (Hurst, 2007). Such variability in local or regional ocean environmental conditions are often linked to atmospheric climate oscillations at much broader scales, perhaps even in a distant ocean or climate basin. The phenomenon of broad-scale linkage in planetary circulation patterns is termed 'teleconnection' (Bridgman and Oliver, 2006). Climate indices amalgamate climate conditions at spatial and temporal scales appropriate for investigating the dynamics of marine populations at a regional scale (Stenseth *et al.*, 2003).

In addition to affecting population vital rates, dynamic ocean conditions also alter species ranges, as well as spawning and migration phenology as individuals seek habitat closer to physiological optima (Collie *et al.*, 2008; Drinkwater *et al.*, 2010; Peer and Miller, 2014). Spatial distribution shifts in response to seasonal cycles, multi-decadal oscillations, or longer-term change in environmental conditions can influence availability of fish to fishers and surveys, possibly biasing abundance estimates (Ottersen *et al.*, 2004; Blanchard *et al.*, 2008; Nye *et al.*, 2009). Understanding the mechanisms for how climate variability affects vital rates, abundance, and the distribution of fish and shellfish stocks remains a considerable challenge.

The second exogenous factor in the triad is bottom-up or top-down trophodynamic interactions that may affect stock abundance. An outburst of available prey may allow a predator species to increase energy reserves, thus resulting in increased reproductive potential (bottom-up effect) (Buchheister *et al.*, 2015; Mcbride *et al.*, 2015). Alternatively, a species that experiences predation will undergo an overall population size reduction (top-down effect). Accounting for predation mortality can be critical for setting appropriate management reference points (Tyrrell *et al.*, 2011), especially for forage fishes (Tyrrell *et al.*, 2008). Compared to local scale studies, the effects of multi-trophic interactions are more difficult to quantify at larger spatial scales that encompass entire populations due to intensive data requirements.

The third process in the Link *et al.* (2010) triad of exogenous population-regulating factors is exploitation, or fishing. Fisheries removals (harvest and discards) directly increase mortality and decrease stock abundance, and can influence certain vital rates such as reproductive output (Jennings *et al.*, 2001). Although the most direct effects of fishing on stocks are typically top-down through direct removals, damage to essential habitat or reduction in prey resources caused by fishing or fishing gear can reduce the productivity of higher trophic level stocks (Auster and Langton, 1999; Smith *et al.*, 2013). Of the triad of drivers, only the effects from fishing can be effectively managed; natural processes such as climate and trophodynamics are observable but not alterable at the spatial scale of a biological population.

Within the U.S. Southeast continental shelf Large Marine Ecosystem (hereafter "Southeast U.S. LME"), multiple studies have leveraged time series data for investigating exogenous impacts on fish and invertebrate populations, primarily focusing on climate effects and individual species (Lam *et al.*, 1989; Parker Jr. and Dixon, 1998; Munch and Conover, 2000; Belcher and Jennings, 2004; Hare and Able, 2007; Garcia *et al.*, 2007; Eggleston *et al.*, 2010; Hare *et al.*, 2010, 2012; Colton *et al.*, 2014; Munyandorero, 2014; Harford *et al.*, 2014). However, ecosystem-oriented research that considers multiple species and long-term driving factors is lacking within the Southeast U.S. LME relative to other ecosystems in the U.S. and globally (McFadden and Barnes, 2009; Hollowed *et al.*, 2013), especially studies focused on multiple species and driving factors. The impetus for our study was to expand the body of knowledge regarding how the triad of exogenous population drivers impact biological populations within the Southeast U.S. LME. In particular, we sought to determine the utility of multiple climate indices and metrics of fishing mortality for predicting abundance dynamics of a large suite of coastal fish and invertebrate stocks as measured by a fishery-independent trawl survey. While we do postulate mechanistic underpinnings for the dynamics of certain species in response to exogenous factors, this work should be viewed as a springboard for future investigations at finer levels of scale.

## METHODS

### Biological sampling

An important data source for coastal stocks in the Southeast U.S. LME is the Southeast Area Monitoring and Assessment Program – U.S. South Atlantic (SEAMAP-SA) (SEAMAP-SA Data Management Work Group, 2014). This fishery-independent bottom trawl survey has been conducted by South Carolina Department of Natural Resources (Charleston, SC) personnel thrice annually (spring, summer, and fall) since 1989 within the Southeast U.S. LME from Cape Hatteras, NC to Cape Canaveral, FL. SEAMAP-SA employs a stratified fixed station design, whereby a pre-determined number of fixed stations are chosen for seasonal sampling from a pool of all possible stations distributed across six sampling regions and within a depth range of 15-30 ft. (Fig. 7). At each sampling station, two tongue trawl nets (13.5-m wingspan) are towed on the bottom for 20 minutes from a 23-m St. Augustine shrimp trawler. For this study, catches in both nets were considered a single sample and pooled for analysis. The catch is brought on-board, sub-sampled (if necessary) and sorted, all individuals identified to species and enumerated, and allometric data collected for certain priority species.

### Statistical modeling

We evaluated the influences of climate and fishing factors on Southeast U.S. LME coastal fish populations using generalized and dynamic linear models. We first generated standardized indices of relative abundance for each species using generalized linear models with technical tow-level covariates, followed by an investigation of drivers of abundance using dynamic linear models with climate and fishing covariates. All statistical analyses were conducted in R (R Core Team, 2015) (see Appendix II for specific packages used).

We focused on species that were captured by SEAMAP-SA in all 24 years of the study period from 1990–2013. Species not captured perennially could either have low abundance (true rarity) or low survey catchability; in either case, we did not estimate annual abundances for these rarely caught species. We examined availability and abundance information for each species during each sampling season (spring, Apr.-May; summer, Jul.-Aug.; fall, Oct.-Nov.) and within each sampling region. If a species was largely absent from a sampling region or during a particular season (i.e., low or no availability), those trawl sets were eliminated to reduce the number of uninformative zeros that occurred due to sampling outside that species' seasonal or spatial range (Austin and Meyers, 1996; Martin *et al.*, 2005).

## Standardized abundance indices

To generate standardized annual indices of relative abundance, we modeled numbers of individuals per tow with covariates using generalized linear models (GLMs) (Nelder and Wedderburn, 1972) and zero-inflated generalized linear models (ZIGLMs) (Lambert, 1992; Hall, 2000). Multispecies surveys that sample across long ecological gradients often incur design, survey, and observer errors for individual species, thus possibly resulting in zero-inflated data (Kuhnert *et al.*, 2005). Zero-inflated models account for zeros unexpected in reference to the specified underlying probability distribution (false zeros). Within both GLM and ZIGLM frameworks, we considered Poisson and negative binomial probability distributions (Fig. S1, Table S2; see Appendix II for additional details). For most species, a zero-inflated negative binomial model was most appropriate; a negative binomial distribution was more appropriate than a Poisson for all species. At this stage of analysis, the following technical covariates were considered: year, season, sampling region, depth, total biomass of other species in trawl, effort (as an offset), and if the catch was subsampled (Table S3). We fitted main effects models (i.e., no covariate interactions included) for all possible combinations of technical covariates and retained the model with the lowest AIC$_c$ value (Sugiura, 1978).

For each species' most supported GLM, we estimated annual relative abundances by averaging the marginal mean predictions for each year (Searle *et al.*, 1980). Uncertainty for predictions were estimated via year-stratified bootstrapping ($n = 15{,}000$) (Efron, 1983) as the percent coefficient of variation (CV) (Gotelli and Ellison, 2004). We also generated bias-corrected and accelerated ($BC_a$) 95% confidence intervals (CIs) for comparison to forecast uncertainty estimated from dynamic linear models (see below). If a species time series had 6 or more (≥ ¼ of the time series) predictions with CVs $\geq 100\%$, that species was eliminated from further analysis. We also removed individual annual predictions with CVs $\geq 200\%$.

## Climate and fishing covariates

We hypothesized multiple climate and fishing factors to be potential drivers of abundance. The majority of climate covariates consisted of indices that describe climate anomalies or oscillations derived from spatial differences in atmospheric pressure or sea surface temperature (SST). Many of these indices are recognized teleconnections and all are known to confer variability to ocean conditions within the Southeast U.S. LME (Table 3; Fig. S2, see Appendix II). Cold-season covariates included the North Atlantic Oscillation (NAO), the Pacific Decadal Oscillation (PDO), the Pacific North American Pattern in winter (PNA$_W$), and the Southern Oscillation Index (SOI). We lagged cold-season covariates 0 and 1 years, where lag 0 included data for winter months (Dec.–Mar.)

immediately prior to SEAMAP-SA sampling. For example, the value for a lag 1 cold-season covariate was an average of monthly values during December of $year_t$ through March of $year_{t+1}$, with corresponding observed biological effects during spring through fall $year_{t+2}$. We hypothesized winter conditions associated with these climate oscillations impact larval or juvenile growth and survival (e.g., Hare and Able, 2007) at lags 0 or 1, and migration phenology at lag 0.

Warm-season covariates included the Atlantic Multi-decadal Oscillation (AMO), the Pacific North American Pattern in summer ($PNA_S$), the Western Bermuda High Index (WBHI; Diem, 2013), and average sea bottom temperature (SBT). We also considered the Atlantic Warm Pool (AWP), which is a measure of the area of SST warmer than 28.5°C in the Western Central Atlantic Ocean (Wang *et al.*, 2006), but ultimately excluded this metric based on its high correlation with the AMO (Wang *et al.*, 2008) during the study period ($R = 0.9$). We hypothesized summer conditions associated with these climate oscillations may impact growth and recruitment of early life stages at lags 0 or 1, and migration phenology at lag 0. Warm-season covariates were lagged differently based on seasonality of GLM predictions and the extent of knowledge regarding age composition in SEAMAP-SA catches. If a species' standardized GLM index included only spring data, we lagged warm-season covariates 1 and 2 years (no lag 0). If an index included summer or fall data, warm-season covariates were lagged 0 and 1 years. If an index included summer but not fall data, warm-season lag 0 indices were recalculated as an average of monthly covariate values from May–July rather than May–September. Additionally, we included lag 2 warm-season covariates for species whose primary abundance signal are known or assumed to include age 2 animals (Table S4). We lagged SBT 0 years to account for temperature-driven changes in availability resulting from interannual differences in migration phenology (see Appendix II, Fig. S3).

Fishing covariates included annual shrimp fishery effort (relevant to all species), landings (data available for 35 of 71 species), and estimated instantaneous fishing mortality (estimates for 9 species) (see Appendix II, Figs. S4 and S5). We included shrimp fishery effort, input as log-transformed total annual commercial trips, as a proxy for relative changes in bycatch mortality within the penaeid shrimp fishery (Walter and Isley 2014). Empirical bycatch mortality estimates for all species were unavailable for the duration of the study period. Fishery effort quantified as total annual trips does not account for potential temporal changes in fleet characteristics (e.g., vessel size, hours fished per trip, number of nets) that could influence general bycatch rates for the fishery. However, total annual trips was the best available bycatch proxy given that fishery logbook data spanning the study period were not available. We obtained annual commercial and recreational fishery landings data (input as log-transformed total biomass) from the Atlantic Coastal Cooperative Statistics Program (ACCSP 2015). Fishing mortality estimates were gleaned from stock assessment reports for recently assessed species. We lagged all fishing covariates up to 3 years depending on known or assumed maximum age; most fishes had lags of 1–3 years and most invertebrates 1–2 years (see Table S4 for exceptions). For appropriate scale comparisons, all climate and fishing covariates were *z*-scored (subtracted the mean and divided by the standard deviation) prior to dynamic linear modeling.

## Modeling climate and fishing effects

We investigated climate and fishing drivers of abundance for each remaining species' time series using univariate dynamic linear models (DLMs) (Pole *et al.*, 1994; Lamon III *et al.*, 1998; Scheuerell *et al.*, 2002). Each log-transformed abundance observation $y$ in year $t$ was modeled as

$$y_t = \mathbf{F}_t{}^{\mathrm{T}}\boldsymbol{\theta}_t + \boldsymbol{v}_t \tag{7}$$

where $\mathbf{F}_t$ and $\boldsymbol{\theta}_t$ are vectors of regression variables and parameters, respectively, $\boldsymbol{v}_t$ are observation errors with $\boldsymbol{v}_t \sim N(0, r)$, and

$$\boldsymbol{\theta}_t = \boldsymbol{\theta}_{t-1} + \mathbf{w}_t \tag{8}$$

where $\mathbf{w}_t$ are process errors with $\mathbf{w}_t \sim \mathrm{MVN}(\mathbf{0}, \mathbf{Q})$ (Holmes *et al.*, 2014).

For each species, we fitted DLMs for all possible combinations of climate and fishing covariates with a minimum of zero covariates (intercept-only model) up to one climate and one fishing covariate (maximum two covariates per model). To reduce multicollinearity, two-covariate models were not fitted if they contained combinations of covariates that were significantly correlated (Pearson's product-moment correlation test, $\alpha = 0.1$). For each unique combination of covariates, we considered multiple variance parameterizations for process and observation errors (Table 4). For models with covariates, process errors in $\mathbf{w}_t$ were either 1) assumed independent and identically distributed or 2) assumed independent but potentially distributed differently. For all models, the **Q** diagonal element corresponding to intercept process error variance was fixed at zero. Observation error variance ($r$) was either estimated within the DLM, or fixed at the average annual percent coefficient of variation estimated from GLM bootstrapping. For each species, we retained for further analysis all converged models (maximum 10,000 iterations, convergence tolerance = 0.9) with $\Delta\mathrm{AIC}_c$ values $\leq 10$, where $\Delta\mathrm{AIC}_c = \mathrm{AIC}_c - \min(\mathrm{AIC}_c)$. Among species, unique combinations of covariates ranged from 23 to 136 and the total model set size including error variance parameterization options ranged from 70 to 488 (Table S4).

For assessing performance of individual models, we obtained expected values of one-year forecasted abundances with corresponding variances (in log space) calculated using a Kalman filter algorithm. We checked forecast errors for egregious violations of normality and independence using Student's $t$-Tests and autocorrelation function ($\alpha = 0.05$), respectively. We assessed forecast bias by calculating the Root Mean Squared Error (RMSE) for each forecast series in log space (Hyndman and Koehler, 2006):

$$\mathrm{RMSE} = \sqrt{\sum_{t=1}^{n}(Y_t - f_t)^2/n} \qquad (9)$$

where $f$ is the forecast for observation $Y$ at time $t$.

For each retained model, we determined the persistence of its combination of covariates by comparing time-truncated models to vet the staying power of a given parameter within models as years were 'peeled' off the time series (Mohn, 1999; Miller *et al.*, 2016). This approach is analogous to examining retrospective patterns in a stock assessment model. We generated time-truncated datasets by removing one year of data either at the proximal or terminal end of the time series. We define 'persistence' of a given covariate as

$$\varphi_i = \sum_{j=1}^{J}\left(\frac{c_{ij}}{m}\right)w_j \qquad (10)$$

where $c_{ij}$ is the number of occurrences of covariate $i$ in $m$ truncated models based on full time series (non-truncated) model $j$, and $w_j$ is the Akaike weight ($\mathrm{AIC}_w$; Burnham and Anderson 2002) for non-truncated model $j$. φ is a percentage bounded by 0 and 1. We fixed

$m$ at 10; 5 proximal year peels and 5 terminal year peels. For the purposes of calculating φ, lag identities were removed from covariates. For instance, if model 1 contained 'lag 0 SOI' and model 2 contained 'lag 1 SOI', $c_i$ would be 'SOI' for both.

To quantify the overall importance of a covariate to all species or a group of species, we define 'prevalence' as

$$\Phi_i = \frac{\sum \varphi_i}{\sum \varphi} \tag{11}$$

where $\sum \varphi_i$ is the sum of persistence (Eq. 10) values for covariate $i$ across species, and $\sum \varphi$ is the grand sum of persistence values across species and all covariates. To identify covariates with consistently significant unidirectional effects, we quantified an Akaike-weighted index describing the 'frequency of significance' for time-dynamic regression parameter estimates as

$$\Gamma_{i,\alpha} = \sum_{j=1}^{J} \left( \frac{(pos - neg)_{ij,\alpha}}{T_j} \right) w_j \tag{12}$$

where $pos$ and $neg$ are the number of years in which potentially time-varying coefficient estimates for $z$-scored covariate $i$ in model $j$ were significantly different from zero at alpha level $\alpha$, $T$ is the length of time series (always 24 years), and $w_j$ is defined as in Eq. 10. Lag identities were removed from covariates prior to calculating Γ, which is bounded by -1 and 1. Frequency of significance also implicitly incorporates covariate persistence (Eq. 10); covariates not present in all non-truncated models for a given species are penalized proportional to the sum of the Akaike weights for models in which the covariate was absent. Species that had significant parameter estimates with different signs that counteract one another (i.e., sign-switching) will have reduced frequency of significance values. Time-varying parameter estimates that switch signs may indicate a change in the mechanistic relationship between the variate and covariate. However, given the exploratory nature of the study, we were only interested in characterizing covariate effects with consistent unidirectional effects through time.

### Multivariate analysis

To compare temporal abundance patterns among species, we conducted multivariate ordination using *z*-scored marginal mean GLM predictions. To visualize community-level patterns in abundance changes, we conducted principal components analysis (PCA) with GLM-generated indices of relative abundance where each year was a separate descriptor. Sand perch (*Diplectrum formosum*) and dusky flounder (*Syacium papillosum*) were excluded from this analysis due to extremely low log-space predictions for certain years; these data points were also excluded in DLMs for these species.

## RESULTS

### Linear modeling

Of the 101 coastal fish and invertebrate species modeled using GLMs (Table S5), we investigated climate and fishing effects for 71 species that had acceptable CVs for ¾ of the 24 year time series (Table 5). Shrimp fishery effort was the most prevalent covariate in dynamic linear models for all broad taxonomic groups, indicating this was the most important covariate in weighted time series models (Table 6). This proxy for bycatch mortality was much more prevalent than any climate effect. Shrimp fishery effort prevalence ($\Phi$; Eq. 11) was 26%, 35%, and 44% for bony fishes, invertebrates, and elasmobranchs, respectively. Shrimp fishery effort had moderate ($75\% < \varphi \geq 50\%$) to high ($\varphi \geq 75\%$) persistence (Eq. 10) in time-truncated models for 12 and 15 species, respectively, indicating that this covariate was retained in the best model more than 50% of the time after removal of up to five years of data from the start or end of the 24 year time series. For comparison, all eight climate variables combined had just 9 species with moderate persistence. Furthermore, of the 27 species with moderate to high persistence for shrimp fishery effort, 20 had frequency of significance (Eq. 12) values greater than 60% ($|\Gamma| \geq 0.6$), indicating that estimated regression coefficients for this covariate differed from zero during at least 60% of years in the time series (Fig. 8). For species with direct harvest data, a 'landings' covariate was also relatively prevalent (22%) in models among bony fishes (Table 6). For three species (*Centropristis striata*, *Chaetodipterus faber*, and *Menticirrhus littoralis*) landings had a frequency of significance of at least 70% (Fig. 8). However, the relationship between landings and *C. striata* and *M. littoralis* was positive, indicating possible spurious effects. Strong persistence or frequency of significance for a covariate does not verify a mechanistic relationship, but does provide evidence of a possible linkage between the exogenous factor and relative abundance that should be vetted further through additional investigation.

Compared to fishing covariates, climate covariates were much less predominant in species models despite the consideration of eight different climate indices versus three fishing covariates. Among warm-season climate covariates the Western Bermuda High Index (WBHI) was the most common in DLMs, with 10% overall prevalence (Table 6), persistence greater than 50% for three species, and moderate frequency of significance ($|\Gamma| \geq 0.5$) for four species (Fig. 8). The Pacific North American Pattern in summer ($\text{PNA}_\text{S}$) was second-most prevalent for warm-season climate covariates, while the Atlantic Multi-decadal Oscillation (AMO) and sea bottom temperature anomalies (SBT) were least prevalent. $\text{PNA}_\text{S}$ was persistent in more than 50% of weighted models for three species (Table 6). Prevalence values for cold-season climate covariates were also relatively low for most taxon groups, although the Pacific Decadal Oscillation (PDO) was more prevalent in invertebrate models (14%). Three species exhibited negative associations with and had moderate frequency of significance for the PDO: *Callinectes similis*, *Portunus spinimanus*, and *Centropristis striata* (Fig. 8).

Five crustacean species had positive associations with shrimp fishery effort (Fig. 8), relationships which are counterintuitive given that these species are also vulnerable to bycatch. These patterns suggest possible indirect effects potentially from increased predation by *S. tiburo* (Fig. 9). Assumptions of forecast error normality ($t$-tests, $\alpha = 0.05$) and independence (not strongly autocorrelated at lags 1-10) were met for each species' most supported model ($\Delta\text{AIC}_c = 0$), results from which are depicted in Fig. S6. Forecast bias, measured as Root Mean Squared Error (RMSE), varied more so between species (range 0.23 to 1.81, where zero indicates no bias) than within models for a given species (Table S6).

## Species comparisons

A biplot of the first two principal components explaining the most variation (cumulative 31%) in multispecies abundance predictions illustrates time series trend commonalities among species and taxon groups (Fig. 10). Notable groupings include five crustacean species (top; *Arenaeus cribrarius*, *Callinectes sapidus*, *C. similis*, *Portunus spinimanus*, and *Squilla empusa*), four skate and ray species (middle-left; *Dasyatis sabina*, *D. say*, *Gymnura micrura*, and *R. eglanteria*), and two common small coastal sharks (bottom; *Rhizoprionodon terranovae*, *Sphyrna tiburo*). Species in quadrant 1 (top right) were more abundant earlier in the time series, species in quadrant 2 (top left) were abundant during the middle 2000s, while species in quadrant 3 (bottom left) were more abundant later in the time series. *Doryteuthis* spp. exhibited an abundance trajectory different from most other species with peaks near 2000 and 2010 (quadrant 4, bottom right). A higher number of species with negative PC1 values is consistent with an overall increase in community abundance throughout the time series (Richardson and Boylan, 2014). A biplot of the descriptor axes (i.e., years) indicate a period of most rapid change in community abundances during the 2000s, especially during 2001 to 2004 (Fig. 11). Based on biplot species groupings, DLM forecasts and regression coefficient estimates for *S. tiburo* and the five aforementioned crustaceans are compared in Fig. 9 (see Discussion).

## DISCUSSION

The overall goal for this work was to expand general understanding of how exogenous factors influence abundance dynamics for coastal fishes and invertebrates within the Southeast U.S. LME. Results indicate that each of the factors described by Link *et al.* (2010) – trophodynamic, exploitative, and biophysical – exert influence on the abundance dynamics of several species we examined. In many cases taxonomically-related species exhibited synchronous abundance trends and associations with covariates, suggesting that working knowledge of life history characteristics provides guidance for explaining these connections. In all cases, our results and interpretations should be viewed as a foundation for future ecosystem-based research within the region at finer spatial and temporal scales for each species or taxonomic/trophic group.

### Indirect fishing effects on trophodynamics

During the study period, shrimp fleet effort decreased due to an economic downturn in the fishery (SEDAR, 2014). Five crustaceans and one bony fish species exhibited a positive relationship with shrimp fishery effort that was persistent and significant (Fig. 8): *Arenaeus cribrarius*, *Callinectes sapidus, C. similis, Portunus spinimanus, Squilla empusa*, and *Urophycis floridana*. While there are no empirical shrimp bycatch time series available for the U.S. South Atlantic penaeid shrimp fishery, Scott-Denton *et al.* (2012) and Brown (2014) provide a snapshot summary of bycatch trends during the late 2000's. In North Carolina, *C. sapidus, S. empusa, U. floridana,* and portunid crabs comprised a total of 9% of non-shrimp biomass caught in commercial shrimp trawl gear from July 2007 to June 2008 (Brown, 2014). Throughout the U.S. South Atlantic region, *C. sapidus* and non-identified 'crustaceans' comprised 19% of all non-shrimp biomass during July 2007 through December 2010 (Scott-Denton *et al.*, 2012). Although bycatch reduction devices (BRDs), which include turtle excluder devices, have been used within this fishery within federal waters since 1997/8 (ASMFC, 2011), these species or groups remain frequently captured within the fishery. Due to the small maximum body size attained by these species and empirical evidence that they are in fact bycatch, the positive relationship between abundance and shrimp fishery effort that we found is counterintuitive.

A possible explanation for the positive relationship between trawling effort and abundance of the five crustaceans is that the rebound of the bonnethead shark (*Sphyrna tiburo*) has resulted in increased top-down control on these species. The shrimp fleet effort time series may be acting as proxy for the abundance dynamics of this predator known to feed primarily on crustaceans, especially portunid crabs (Cortés *et al.* 1996; MAS, unpublished data). The most recent *S. tiburo* stock assessment attributes an overall population increase after 2000 in large part to bycatch reduction following BRD implementation (SEDAR, 2013b). Results from the current study support this conclusion; *S. tiburo* abundance was higher overall in the 2000's compared to the 1990's (Fig. 9A), and shrimp fishery effort was a moderately persistent ($\varphi \geq 50\%$) negative predictor with moderate frequency of significance ($|\Gamma| = 0.7$) in the well-fit ($\mathrm{RMSE} = 0.29$) most supported model for this species. Based on opposing trends of *S. tiburo* and its prey species (Fig. 9), multi-species modeling is warranted for these trophically-related species. While the bonnethead is likely not the only predator for these species, it may be acting as a general proxy for increases in abundance of higher trophic level predators (e.g., *Raja eglanteria*, *Gymnura micrura*) following a reduction in shrimp fishery effort and overall bycatch risk for the assemblage.

One alternative hypothesis for the decline in crustacean abundance within the nearshore zone is that an overall decrease in bycatch discards by the shrimp fishery has reduced the amount of carrion available to portunid crabs whose diets include scavenged food. In theory, increased food availability and decreased energy expenditure on food handling would increase growth rates and potentially reproductive output. The carrion reduction hypothesis could be tested via manipulative experiments and inferences based on more robust bycatch data, especially prior to when BRDs were mandated. Johnson (2006) demonstrated that blue crabs strongly preferred bycatch carrion to natural prey, lending support for this hypothesis. Changes in bottom-up (carrion reduction) and top-down (predation increase) trophodynamics could have synergistically led to an overall decline of one or more of these ecologically-important crustacean species.

### Direct fishing effects

Biomass removals from fishing result in a direct decrease in population abundance, yet only one species out of 35, Atlantic spadefish (*Chaetodipterus faber*), had a moderate and negative frequency of significance for the covariate ‘Landings’ (Fig. 8). Stock status of *C. faber* has not been formally assessed, but results indicate that landings may be great enough to elicit a population-level change in abundance. The covariate fishing mortality (‘Total *F*’) (Fig. S5) was not persistent in models of any species for which estimated time series were available from stock assessments (Table 6). Overall null results for the fishing covariates ‘Landings’ and ‘Total *F*’ could be due to 1) bottom-up environmental conditions or top-down trophodynamics being overriding drivers of abundance dynamics, 2) the magnitude of landings not being high enough to elicit a detectable population response (i.e., low exploitation rate), or 3) SEAMAP-SA not being a representative index for the stock. For species with landings but which are not actively managed, the first and second hypotheses are plausible; the third is not testable without additional data sources. Of the nine species for which estimated 'Total *F*' time series were available, weakfish (*C. regalis*), summer flounder (*P. dentatus*), butterfish (*P. triacanthus*), bluefish (*P. saltatrix*), and scup (*Stenotomus*) were based primarily on data from more northerly areas, thus hypothesis three is likely for these species. While Atlantic sharpnose (*R. terranovae*) and bonnethead (*S. tiburo*) are recognized to exhibit separate Gulf of Mexico and Atlantic stocks, the most recent update assessment for each of these species combined these two regions based on precedent from the previous benchmark assessment (SEDAR, 2013a,b). The spatial mismatch between SEAMAP-SA and assessments for these two coastal sharks may have resulted in null 'Total *F*' results.

Shrimp fleet effort exhibited a persistent negative association with moderate to strong frequency of significance for fourteen species – nine bony fish, four elasmobranch, and one invertebrate species (Fig. 8). All of these species except two (*Persephona mediterranea* and *Prionotus carolinus*) are documented bycatch species in the region within the penaeid shrimp trawl fishery (Scott-Denton *et al.*, 2012; Brown, 2014). In all cases, estimated abundances for these species were higher during the second half of the time series during which shrimp fleet effort and overall bycatch risk were lower than during the 1990's. Although decreases in effort occurred concomitantly with BRD mandates intended to reduce bycatch mortality, decreased effort may be driving abundance increases for these species more so than BRDs given that they still remain vulnerable to bycatch in shrimp fishery gears despite BRD requirements. Elasmobranchs in particular have benefited from this decrease in fishery activity, indicated by prevalence of 44% for shrimp fishery effort (Table 6) and overall negative associations with ‘Effort’ in all cases (Fig. 8).

### Biophysical effects

Compared to fishing effects, many fewer species exhibited abundance changes in response to climate. Among warm-season climate variables, none had outstanding prevalence within species models. Among cold-season climate variables, the Pacific Decadal Oscillation (PDO) was most prevalent in invertebrate models, although moderately so, but this covariate had only moderate persistence in time-truncated models for just three species. The one climate variable that quantified local environmental conditions, sea bottom temperature (SBT), had particularly low prevalence values among all taxon groups. Taken together, these unremarkable climate results are in stark contrast to studies in temperate Northeast U.S. LME waters, where oscillatory climate patterns and directional ocean warming have been extensively documented to be causing dramatic ecological shifts in multiple populations that are major players in the food web (Collie *et al.*, 2008; Araújo and Bundy, 2012; Nye *et al.*, 2014). Climate forcing appears to be inherently less impactful to the assemblage within subtropical waters of the Southeast U.S. LME compared to temperate Atlantic waters to the north.

Although no species had a strong frequency of significance for the PDO, this teleconnection was moderately prevalent (14%) within invertebrate models. The PDO and SOI are related measures of the complex air-sea interactions characteristic of El Niño Southern Oscillation (ENSO) events in the tropical Pacific, which confer variability in atmospheric and ocean conditions across the globe including within the southeast U.S. Atlantic (Alexander *et al.*, 2002). The influence of PDO on precipitation, river discharge, and estuarine salinity regimes have been demonstrated for a coastal Georgia river (Sheldon and Burd, 2014) and the Chesapeake Bay (Xu *et al.*, 2012), but we are not aware of any studies linking the PDO to dynamics of living marine resources in the southeast U.S. Our results indicate that, among cold-season climate indices, the PDO may be the best amalgamation of winter weather conditions impactful to several coastal invertebrates within the Southeast U.S. LME. The influence of this climate signal on demersal populations in the region deserves further investigation.

In the Northeast U.S. LME, taxonomic and abundance shifts in planktonic communities have been shown to respond to temperature-related changes induced by multi-decadal climate oscillations and directional ocean warming (Pershing *et al.*, 2005; Greene and Pershing, 2007; Morse *et al.*, 2017). Shifts in abundance and composition in lower trophic levels can have cascading effects for higher trophic level organisms, both big (Wishner *et al.*, 1995) and small (Beaugrand *et al.*, 2003). Bottom-up trophodynamic effects on fish populations in the Southeast U.S. LME have been studied (Weinstein *et al.*, 1981; Yoder, 1983; Govoni *et al.*, 2013), however evaluating hypotheses regarding lower trophic effects on long-term trends in Southeast U.S. LME fish and invertebrate populations requires more robust planktonic data sets with temporal sampling regularity. We are not aware of any local *in situ* or regional satellite-based studies examining long-term changes in primary productivity, phytoplankton composition, or zooplankton within the ecosystem. In the future, as SEAMAP-SA and remote sensing time series extend and overlap over a longer time frame, this issue may be more thoroughly addressed.

### Migration phenology

Sampling effort for the SEAMAP-SA coastal trawl survey is focused on the most biodiverse and biomass-rich areas of soft-bottom habitat within the nearshore zone of the Southeast U.S. LME coastal ocean. The survey does not sample estuarine or offshore habitats that many nearshore species also utilize during certain seasons. To limit the potential bias in abundance estimates given this sampling limitation, we only investigated species with an acceptable level of uncertainty in annual abundance estimates and only in seasons where there were perennially consistent catches. Additionally, we recognize that only relative and not absolute indices of abundance can be derived from SEAMAP-SA and other similar datasets within specialized habitat zones. If our estimated relative abundance indices were generally biased, we would have expected higher prevalence of the local environmental covariate sea bottom temperature (SBT), which was included to detect any annual anomalies in migration phenology induced by seasonal temperature cues. Out of 71 species, SBT did not have high prevalence for any species group, nor was it persistent or have strong frequency of significance for any species. This null result suggests that the SEAMAP-SA dataset may be largely robust to bias in relative abundance estimates stemming from timing differences in seasonal weather patterns. Nevertheless, we agree with Blanchard *et al.* (2008) that coordinating sampling methods, timing, and coverage of fisheries surveys that are spatial neighbors should be further emphasized.

## Conclusions

Our results suggest that changes in trawling intensity for the penaeid shrimp fishery have been the most influential determining factor for multi-species patterns of change within the nearshore Southeast U.S. LME since 1990. Trawling effort and assumed bycatch was high early in the time series, dropped precipitously from 1999 to 2005, and plateaued at a relatively low level thereafter (Fig. S2). The period of most rapid change in community composition occurred during the same time frame (Fig. 11), resulting in an overall increase in abundance for the majority of nearshore species. BRD implementation at the onset of this period of rapid change likely accelerated relative abundance rebounds for many of these species. Prevalence of trawling effort in species-specific DLM results lend support for fishing-induced shifts in overall community abundance and composition. Due to some level of fishing-induced restructuring apparent in the nearshore food web, we reiterate the call by Marancik and Hare (2007) for the establishment of long-term diet sampling programs in the Southeast U.S. LME; such programs have enabled informative multi-species modeling efforts in the Northeast U.S. Shelf (Link *et al.*, 2012) and North Pacific (Livingston *et al.*, 2017).

During the same time frame that shrimp trawling intensity was rapidly decreasing, the PDO and SOI underwent rapid but short-lived phase shifts (Mills and Walsh, 2013). The AMO also entered a positive phase around the year 2000 (Nye *et al.*, 2014), thus further adding to possible confounded effects of fishing and climate. Longer biological time series are needed to clarify the impacts of these low-frequency climate signals on fish abundance. In the interim, the simplest explanation is that direct anthropogenic impacts from fishing have exerted the most influence on this system.

## Future directions

Although we detected fishing, climate, and indirect trophodynamic effects, the majority of species exhibited inconsistent or undetectable responses to climate and fishing covariates. The overall lack of explanatory power for any given species is likely a product of simultaneous and complex forcing from fishing, the physical environment, biological interactions, and density-dependent effects, often making it difficult to establish unequivocal linkages between changes in the physical environment and stock abundance (Ottersen *et al.*, 2004; Megrey *et al.*, 2009; Rijnsdorp *et al.*, 2009; Deyle *et al.*, 2013). Investigating ecosystem linkages is made more challenging by incomplete life history and catch information. In the Southeast U.S. LME, future species-specific analyses investigating exogenous drivers would benefit from more complete age composition data, greater extent of diet characterization (especially for upper trophic level predators), and species-specific bycatch rates.

Specific to climate impacts, a more refined understanding is needed of how teleconnections influence local-scale oceanographic conditions relevant to populations in coastal waters of the Southeast U.S. LME (e.g., temperature, salinity, wind, and planktonic productivity). Broad-scale climate indices amalgamate these local variables and thus have their advantages in ecological modeling (Stenseth *et al.*, 2003). However, organisms respond to conditions in their proximate environment at much finer temporal and spatial scales than annual climate indices can capture. As such, future climate-fisheries studies within the region should not only investigate correlations between large-scale climate effects and populations, but the effects of large-scale climate forcing on specific oceanographic conditions that may in turn produce a detectable population-level effect.

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# TABLES

Table 3. Descriptions of climate covariates included in dynamic linear models. Correlations values ($R$, + or −) are for the period of 1988–2013. Time series for climate covariates are depicted in Figs. S2 and S3.

| **Covariate** | **Calculation** | **Impacts to southeast U.S. Atlantic meteorological conditions** |
|---|---|---|
| Atlantic Multi-decadal Oscillation (AMO) | Area-weighted average of North Atlantic SST from 0–70°N latitude, detrended and unsmoothed (NCAR, 2013); average of monthly values during May–Sep | + (−) phase: ↑ (↓) SST, ↑ (↓) precipitation during Aug – Oct, ↑ (↓) tropical cyclone activity (Enfield *et al.*, 2001; Wang *et al.*, 2008). Correlated with NAO (0.44,−) and $\text{PNA}_W$ (0.43,+). |
| North Atlantic Oscillation (NAO) | Principal component (PC)-based sea level pressure anomalies over the Atlantic sector (20–80°N, 90°W–40°E) (NCAR, 2015); average of monthly winter (Dec–Mar) values | + (−) phase: ↑ (↓) temperatures (Joyce, 2002; Bridgman and Oliver, 2006); correlated with AMO (0.44,−) |
| Pacific Decadal Oscillation (PDO) | Statistical reconstruction of *in situ* SST in the North Pacific Ocean (NCDC, 2015); average of monthly winter (Dec–Mar) values | + (−) phase: ↓ (↑) temperatures and possibly ↑ (↓) precipitation in winter (Mantua and Hare, 2002; SCO, 2015); correlated with $\text{PNA}_W$ (0.50,+) and SOI (0.61,−) |
| Pacific North-American Pattern, summer ($\text{PNA}_S$) and winter ($\text{PNA}_W$) | Anomalies in the 500mb geopotential height field observed over the western and eastern U.S. (CPC, 2015a); average of monthly summer ($\text{PNA}_S$; May–Sep) and winter ($\text{PNA}_W$; Dec–Mar) values | $\text{PNA}_S$: ↑ (↓) warm-season precipitation (Henderson and Vega, 1996); correlated with WBHI (0.34,−)<br>$\text{PNA}_W$: + (−) phase: ↓ (↑) winter temperatures (Leathers *et al.*, 1991; SCO, 2015); correlated with AMO (0.43,+), PDO (0.50,+) and SOI (0.50,−) |
| Southern Oscillation Index (SOI) | Normalized sea level pressure differences between Tahiti and Darwin, Australia (CPC, 2015b); average of monthly winter (Dec–Mar) values | + (−) phase: La Niña (El Niño); ↑ (↓) temperatures and ↓ (↑) precipitation in winter (Joyce, 2002); correlated with PDO (0.57,−) and $\text{PNA}_W$ (0.50,−). Driven by sea surface temperature (Bridgman and Oliver, 2006). |
| Western Bermuda High Index (WBHI) | Pressure differences (850-hPa heights) between the Blake Plateau (30°N, 75°W) and New Orleans (30°N, 92°W) (Kalnay *et al.*, 1996); average of monthly values during May–Sep (see Appendix II) | + (−) phase: ↑ (↓) summer precipitation, similar to the better known Bermuda High Index (BHI) (Henderson and Vega, 1996; Diem, 2013); correlated with $\text{PNA}_S$ (0.34,−) |
| Sea Bottom Temperature (SBT) anomaly | SEAMAP-SA tow-level data; annual average of $z$-scored anomalies for each combination of season and sub-region combination (see Appendix II) | Proxy for temporal changes in availability of species due to variation in temperature-induced seasonal or extreme event migration patterns |

Table 4. Variance parameterizations for each unique combination of covariates. Process error variances for covariates were specified on the diagonal of the $\mathbf{Q}$ matrix (see Eq. 8). Observation error variance $r$ (see Eq. 7) was either estimated by dynamic linear modeling or fixed at the average annual coefficient of variation estimated from GLM bootstrapping.

| **No. of covariates** | **Q options** | **$r$ options** | **Model set size** |
|---|---|---|---|
| Zero (intercept-only model) | 1) Intercept $\mathbf{Q}$ estimated | 1) estimated, 2) fixed | 2 |
| One (1 climate or 1 fishing) | 1) Covariate $\mathbf{Q}$ estimated | 1) estimated, 2) fixed | 3 |
| Two (1 climate and 1 fishing) | 1) Covariate $\mathbf{Q}$'s estimated, assumed equal<br>2) Covariate $\mathbf{Q}$'s estimated, assumed unequal | 1) estimated, 2) fixed | 4 |

Table 5. Species for which climate and fishing effects were investigated using dynamic linear models. Species for three genera (*Eucinostomus*, *Stenotomus*, *Doryteuthis*) were grouped for analysis due to difficulties of rapid on-board survey taxonomic identification. Species identification numbers are referenced in Table 6.

| | Latin name | Common name | | Latin name | Common name |
|---|---|---|---|---|---|
| Bony fishes | | | Bony fishes cont'd | | |
| 1 | *Ancylopsetta ommata* | Ocellated flounder | 38 | *Sphyraena guachancho* | Guaguanche |
| 2 | *Bairdiella chrysoura* | Silver perch | 39 | *Stellifer lanceolatus* | Star drum |
| 3 | *Centropristis philadelphica* | Rock sea bass | 40 | *Stenotomus* spp. | Scup / Longspine porgy |
| 4 | *Centropristis striata* | Black sea bass | 41 | *Stephanolepis hispida* | Planehead filefish |
| 5 | *Chaetodipterus faber* | Atlantic spadefish | 42 | *Syacium papillosum* | Dusky flounder |
| 6 | *Chilomycterus schoepfii* | Striped burrfish | 43 | *Symphurus plagiusa* | Blackcheek tonguefish |
| 7 | *Chloroscombrus chrysurus* | Atlantic bumper | 44 | *Synodus foetens* | Inshore lizardfish |
| 8 | *Citharichthys macrops* | Spotted whiff | 45 | *Trachinotus carolinus* | Florida pompano |
| 9 | *Citharichthys spilopterus* | Bay whiff | 46 | *Trichiurus lepturus* | Atlantic cutlassfish |
| 10 | *Cynoscion nothus* | Silver seatrout | 47 | *Trinectes maculatus* | Hogchoker |
| 11 | *Diplectrum formosum* | Sand perch | 48 | *Urophycis floridana* | Southern hake |
| 12 | *Echeneis naucrates* | Sharksucker | Elasmobranchs | | |
| 13 | *Etropus crossotus* | Fringed flounder | 49 | *Dasyatis sabina* | Atlantic stingray |
| 14 | *Etropus cyclosquamus* | Shelf flounder | 50 | *Dasyatis say* | Bluntnose stingray |
| 15 | *Eucinostomus* spp. | Mojarras | 51 | *Gymnura micrura* | Smooth butterfly ray |
| 16 | *Lagodon rhomboides* | Pinfish | 52 | *Mustelus canis* | Smooth dogfish |
| 17 | *Larimus fasciatus* | Banded drum | 53 | *Raja eglanteria* | Clearnose skate |
| 18 | *Leiostomus xanthurus* | Spot | 54 | *Rhinoptera bonasus* | Cownose ray |
| 19 | *Menticirrhus americanus* | Southern kingfish | 55 | *Rhizoprionodon terraenovae* | Atlantic sharpnose shark |
| 20 | *Menticirrhus littoralis* | Gulf kingfish | | | |
| 21 | *Micropogonias undulatus* | Atlantic croaker | 56 | *Sphyrna tiburo* | Bonnethead shark |
| 22 | *Opisthonema oglinum* | Atlantic thread herring | Invertebrates | | |
| 23 | *Orthopristis chrysoptera* | Pigfish | 57 | *Arenaeus cribrarius* | Speckled swimming crab |
| 24 | *Paralichthys albigutta* | Gulf flounder | 58 | *Callinectes ornatus* | Ornate blue crab |
| 25 | *Paralichthys dentatus* | Summer flounder | 59 | *Callinectes sapidus* | Blue crab |
| 26 | *Paralichthys lethostigma* | Southern flounder | 60 | *Callinectes similis* | Lesser blue crab |
| 27 | *Peprilus paru* | Harvestfish | 61 | *Doryteuthis* spp. | Inshore squids |
| 28 | *Peprilus triacanthus* | Butterfish | 62 | *Hepatus epheliticus* | Calico box crab |
| 29 | *Pomatomus saltatrix* | Bluefish | 63 | *Litopenaeus setiferus* | Northern white shrimp |
| 30 | *Prionotus carolinus* | Northern searobin | 64 | *Lolliguncula brevis* | Atlantic brief squid |
| 31 | *Prionotus evolans* | Striped searobin | 65 | *Ovalipes ocellatus* | Lady crab |
| 32 | *Prionotus tribulus* | Bighead searobin | 66 | *Ovalipes stephensoni* | Coarsehand lady crab |
| 33 | *Sardinella aurita* | Spanish sardine | 67 | *Pagurus pollicaris* | Flatclaw hermit crab |
| 34 | *Scomberomorus cavalla* | King mackerel | 68 | *Persephona mediterranea* | Mottled purse crab |
| 35 | *Scomberomorus maculatus* | Spanish mackerel | 69 | *Portunus gibbesii* | Iridescent swimming crab |
| 36 | *Scophthalmus aquosus* | Windowpane | 70 | *Portunus spinimanus* | Blotched swimming crab |
| 37 | *Selene setapinnis* | Atlantic moonfish | 71 | *Squilla empusa* | Mantis shrimp |

Table 6. Prevalence $\Phi$ (Eq. 11) of climate and fishing covariates in time-truncated dynamic linear models, and species with at least 50% persistence $\varphi$ (Eq. 10) for a given covariate. Species identification numbers referenced for persistence are specified in Table 5. Landings and total fishing mortality information were available for 35 and 9 species, respectively. Prevalence percentages are calculated separately for all species ('All'), bony fishes (BF), elasmobranchs (E), and invertebrates (I). Species with persistence $\varphi \geq 75\%$ are bolded and those with $\varphi = 100\%$ are also asterisked.

| **Type** | **Covariate** | **No. of species** | **Prevalence $\Phi$** | | | | **Species with persistence $\varphi \geq 0.5$** |
|---|---|---|---|---|---|---|---|
| | | | All | BF | E | I | **(numbers refer to species in Table 5)** |
| Warm | WBHI | 71 | 10% | 11% | 10% | 8% | 1, 29, 46 |
| | PNA$_\text{S}$ | 71 | 8% | 8% | 8% | 9% | 5, 6, 62 |
| | AMO | 71 | 5% | 5% | 5% | 4% | |
| | SBT | 71 | 4% | 5% | 3% | 4% | |
| Cold | PDO | 71 | 9% | 8% | 8% | 14% | 4 |
| | SOI | 71 | 7% | 6% | 5% | 9% | 30 |
| | PNA$_\text{W}$ | 71 | 7% | 7% | 6% | 7% | 28 |
| | NAO | 71 | 4% | 5% | 1% | 3% | |
| Fishing | Shrimp fishery effort | 71 | 30% | 26% | 44% | 35% | BF: 1, 6, **7**, **12**, 16, 17, 21, **28**, **30**, **31**, **37**, 43, 45, 46, **48**<br>E: **49**, 50, **51**, **52**, 53, 56<br>I: **57***, **59**, **60***, **68**, **70**, **71** |
| | Landings | 35 | 19% | 22% | 5% | 11% | **4**, **5**, 20, 36 |
| | Total *F* | 9 | 10% | 10% | 12% | | |
| Intercept | None | 71 | 4% | 4% | 3% | 4% | |

## FIGURES

Figure 7. Six SEAMAP-SA stratified sampling regions (bounded by black bars) within the Southeast U.S. LME (stippled area). From south to north, region names are Florida (1), Georgia (2), South Carolina (3), Long Bay (4), Onslow Bay (5), and Raleigh Bay (6). Individual sampling sites are depicted as overlapping dark blue dots.

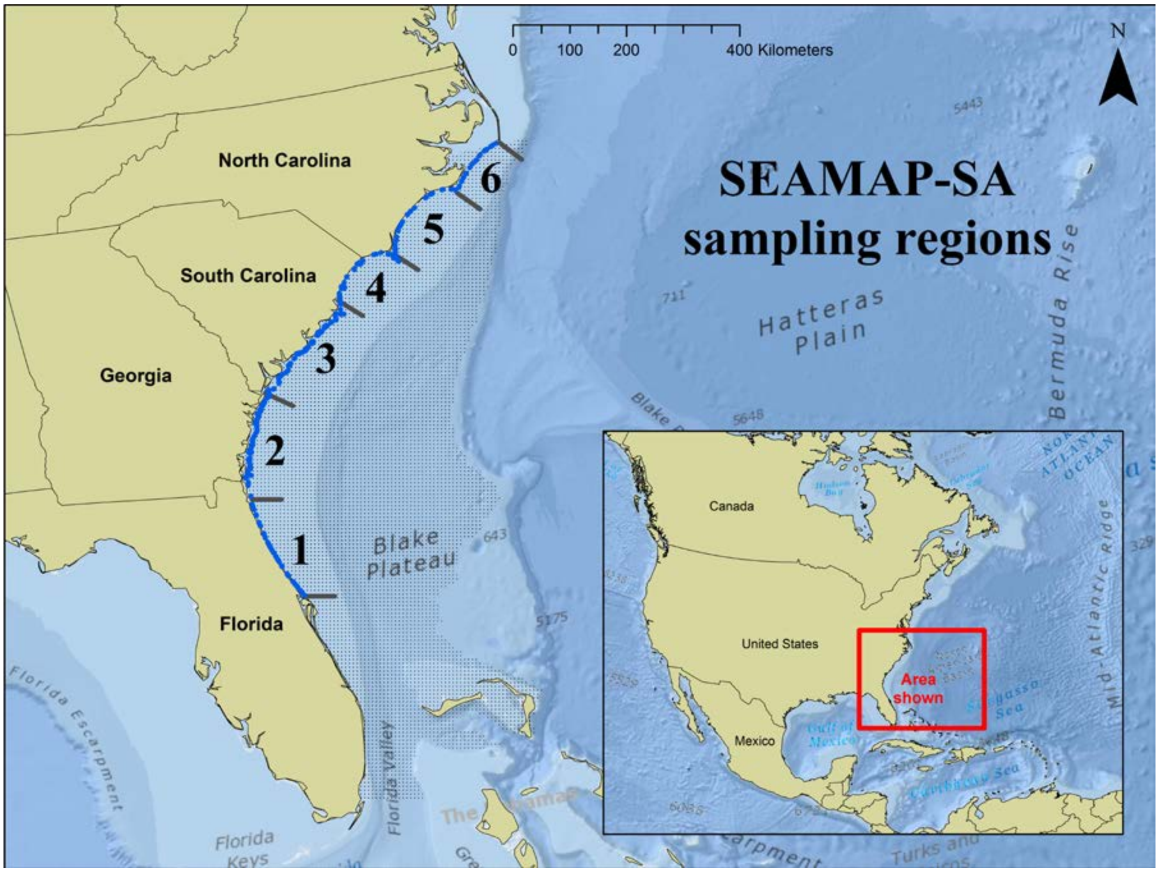
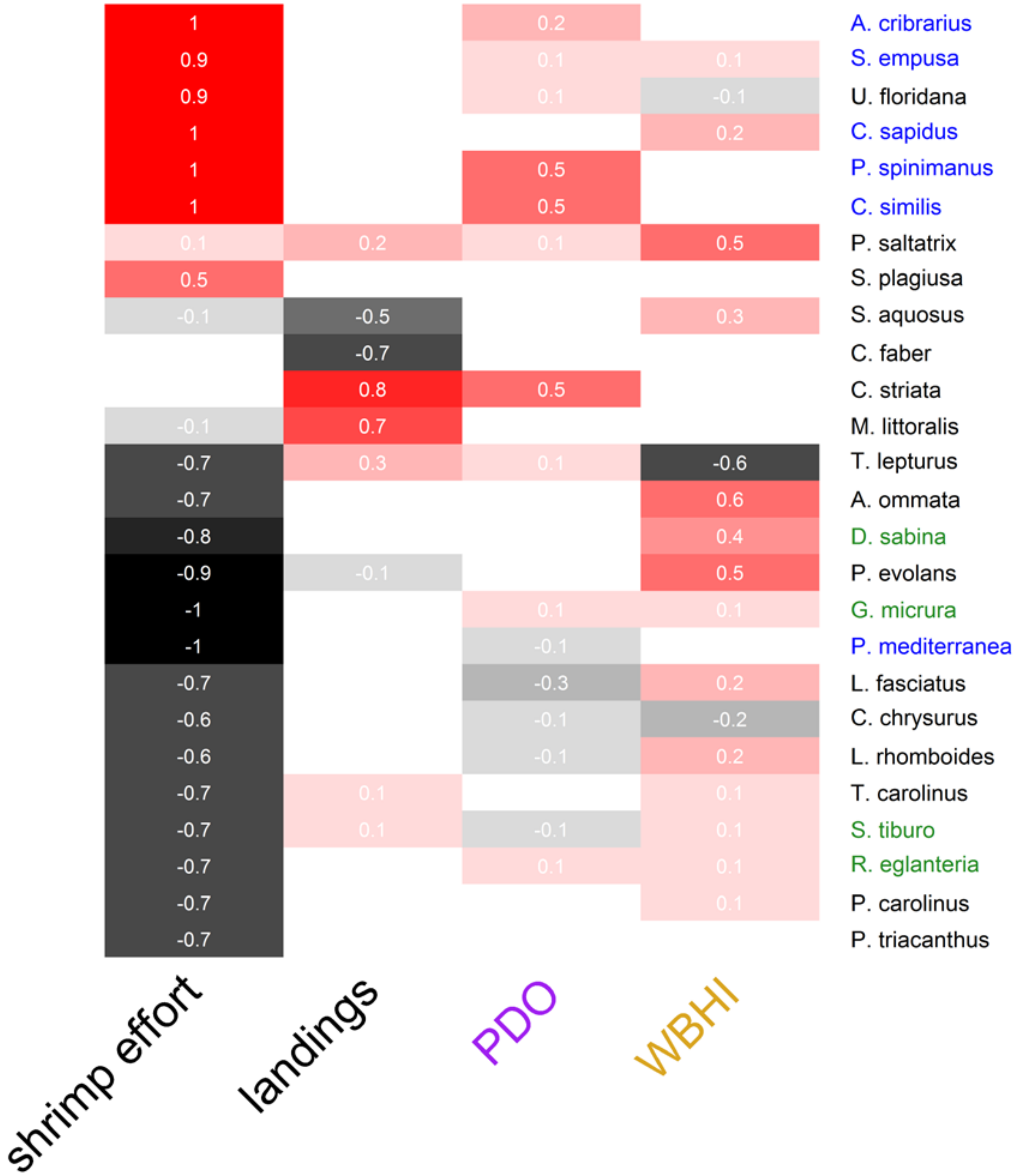


Figure 8. Heatmap of frequency of significance ($\Gamma$) for each species with persistence ($\varphi$; Eq. 10) values $\geq 0.5$ and frequency of significance ($\Gamma$; Eq. 12) values $\geq 0.5$ or $\leq -0.5$ for at least one covariate. Red and black shaded blocks indicate an overall positive and negative explanatory effect on abundance, respectively. Intensity of shading and magnitude of values shown within blocks correspond to frequency of significance for each species-covariate relationship. Covariates on the x-axis are highlighted to indicate warm-season (orange), cold-season (purple), or fishing (black) effects. Species names colors indicate broad taxon type as bony fishes (black), elasmobranchs (green), or invertebrates (blue).



| shrimp effort | landings | PDO | WBHI | |
|---|---|---|---|---|
| 1 | | 0.2 | | A. cribrarius |
| 0.9 | | 0.1 | 0.1 | S. empusa |
| 0.9 | | 0.1 | -0.1 | U. floridana |
| 1 | | | 0.2 | C. sapidus |
| 1 | | 0.5 | | P. spinimanus |
| 1 | | 0.5 | | C. similis |
| 0.1 | 0.2 | 0.1 | 0.5 | P. saltatrix |
| 0.5 | | | | S. plagiusa |
| -0.1 | -0.5 | | 0.3 | S. aquosus |
| | -0.7 | | | C. faber |
| | 0.8 | 0.5 | | C. striata |
| -0.1 | 0.7 | | | M. littoralis |
| -0.7 | 0.3 | 0.1 | -0.6 | T. lepturus |
| -0.7 | | | 0.6 | A. ommata |
| -0.8 | | | 0.4 | D. sabina |
| -0.9 | -0.1 | | 0.5 | P. evolans |
| -1 | | 0.1 | 0.1 | G. micrura |
| -1 | | -0.1 | | P. mediterranea |
| -0.7 | | -0.3 | 0.2 | L. fasciatus |
| -0.6 | | -0.1 | -0.2 | C. chrysurus |
| -0.6 | | -0.1 | 0.2 | L. rhomboides |
| -0.7 | 0.1 | | 0.1 | T. carolinus |
| -0.7 | 0.1 | -0.1 | 0.1 | S. tiburo |
| -0.7 | | 0.1 | 0.1 | R. eglanteria |
| -0.7 | | | 0.1 | P. carolinus |
| -0.7 | | | | P. triacanthus |

Figure 9 (figure on following page). Annual time series of logged relative abundance (left panels) and covariate parameter estimates (right panels) for the bonnethead shark (*S. tiburo*) and five crustacean prey species. Only DLMs with the highest $\mathrm{AIC}_w$ are illustrated. Left panels show GLM-standardized annual abundance observations (open or closed blue circles) that are bracketed by bootstrapped 95% CIs (vertical dotted lines); DLM forecasts (solid black line) are bracketed by approximate 95% prediction intervals (purple polygon). Model fits quantified as Root Mean Squared Error (RMSE) are reported following $\mathrm{AIC}_w$ values. Right panels show corresponding covariate parameter estimates that were significant at $\alpha = 0.05$ and $\alpha = 0.01$ if shown with open and closed circles, respectively. Shrimp fleet effort is abbreviated as ‘Effort’ and Pacific Decadal Oscillation as ‘PDO’. Integers in parentheses adjacent to covariate abbreviations indicate year lag. Colors of species names highlighted to indicate broad taxon type as elasmobranchs (green) or invertebrates (blue).

Figure 9 (caption on previous page).

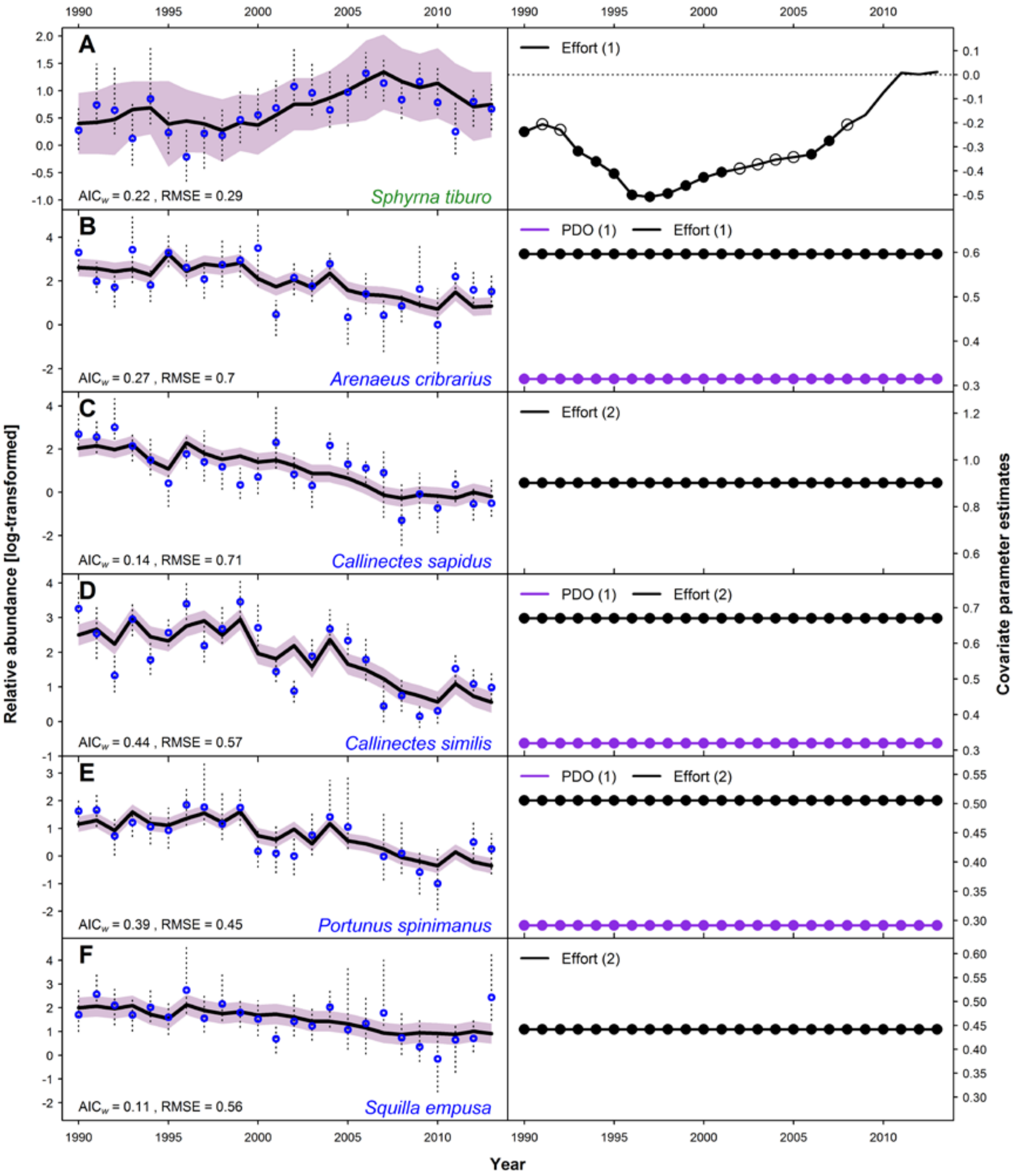


Figure 10. PCA biplot of species abundance trends for 69 species. Species in right quadrants I and IV were more abundant earlier in the time series, while species in left quadrants II and III exhibit higher recent abundances. Species scores are comparable to year scores depicted in Fig. 11, although note scale differences between axes.

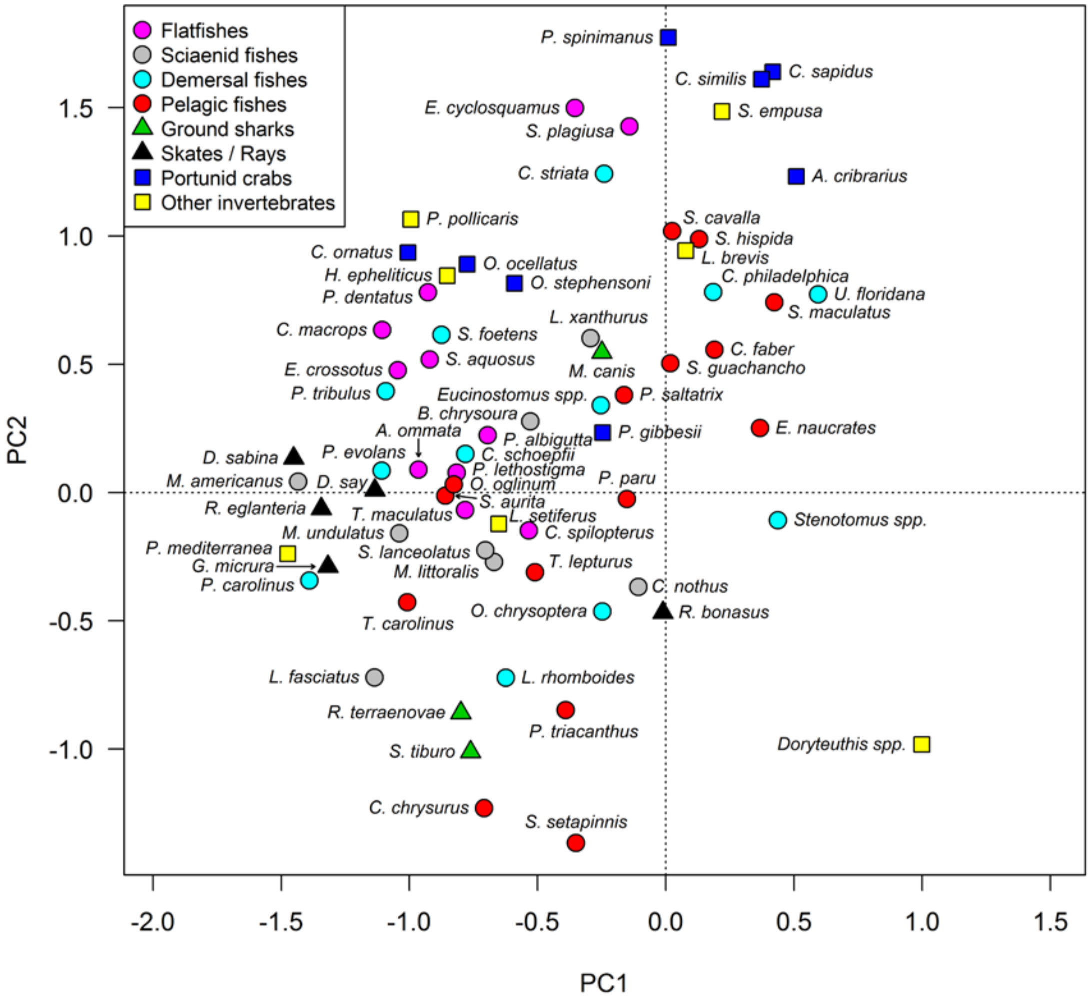
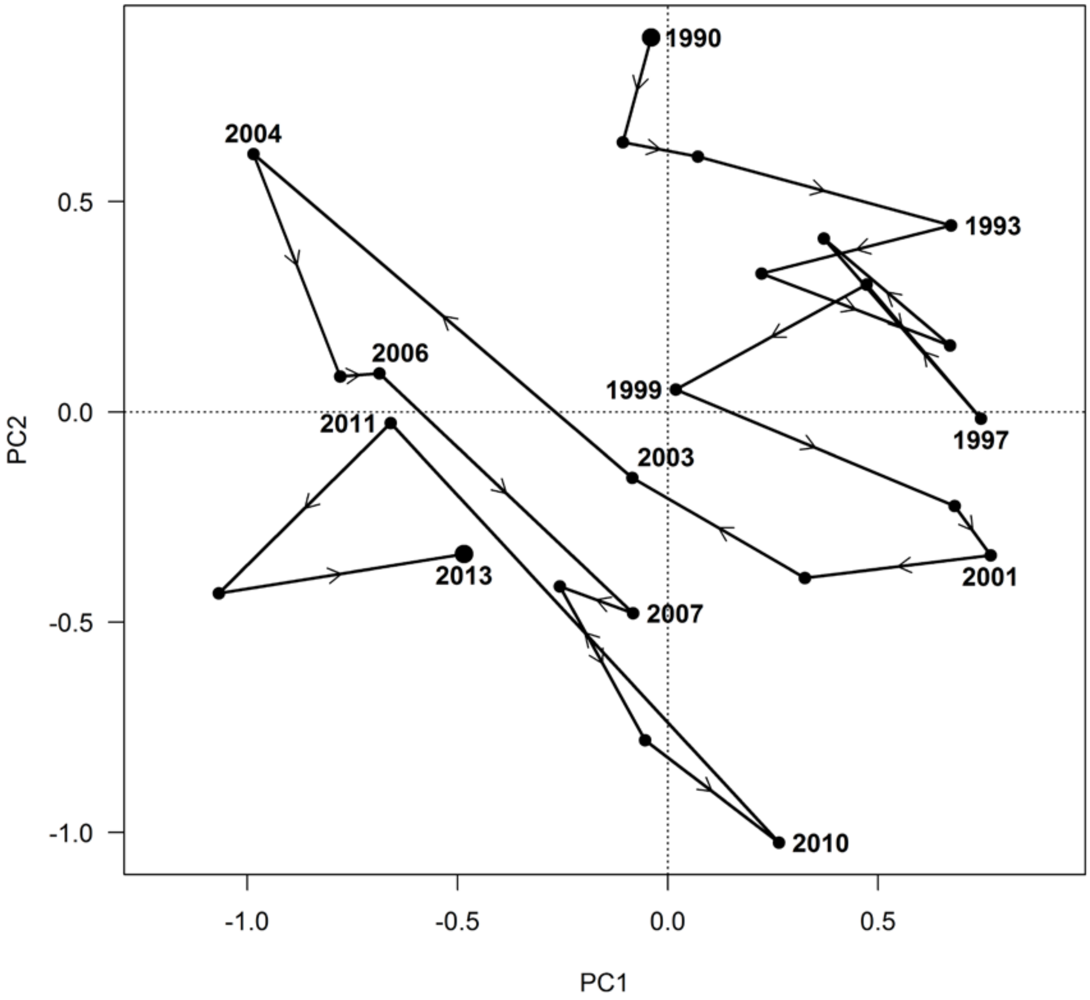


Figure 11. PCA biplot illustrating the evolution of community abundance trends through time. Year scores are comparable to species scores depicted in Fig. 10, although note scale differences between axes.



## APPENDIX II

Additional methods and results for Chapter 3.

### *Generalized linear modeling*

To generate standardized annual indices of relative abundance, we modeled numbers of individuals per tow with covariates using generalized linear models (GLMs) (Nelder and Wedderburn, 1972) and zero-inflated generalized linear models (ZIGLMs) (Lambert, 1992; Hall, 2000). We tested four model frameworks: negative binomial GLM (NBGLM), Poisson GLM (PGLM), zero-inflated negative binomial GLM (ZINB), and zero-inflated Poisson GLM (ZIP) (Table S2; McCullagh and Nelder 1989; Zuur *et al.* 2009; Hilbe 2011). Multispecies surveys that sample across long ecological gradients often incur design, survey, and observer errors for individual species, thus possibly resulting in zero-inflated data (Kuhnert *et al.*, 2005). Zero-inflated models handle these types of errors by accounting for excess zeros not expected in reference to the specified underlying probability distribution. Zero-inflated models are also called 'mixture' models because they incorporate zeros into both the binomial ('true' or 'false' zeros) and count processes (Zuur *et al.*, 2009; Hilbe, 2011).

We implemented a decision tree to identify the optimal model framework for each species (Fig. S1). We only considered technical covariates at this stage of analysis; we investigated climate and fishing covariates afterward using dynamic linear models. Technical covariates included year, season, sampling region, depth, total biomass of other species in trawl, effort, and if the catch was subsampled (Table S3). To determine if a species dataset was zero-inflated, we used Akaike's Information Criterion (AIC) (Akaike, 1973) to compare a fully saturated main effects ZINB (i.e., all appropriate technical covariates included for count and binomial processes, no interactions) to a main effects ZINB with a saturated count process and an intercept (no covariates) binomial process. A difference in AIC between the models ($\mathrm{AIC}_{saturated} - \mathrm{AIC}_{intercept}) \geq 4$ indicated limited support for a ZIGLM framework, thus a GLM framework was selected. For zero-inflated datasets, we conducted a likelihood ratio test ($\alpha = 0.05$) to determine if the saturated ZIP was overdispersed compared to the saturated ZINB (Zuur *et al.*, 2012). This test requires nested models and is appropriate here because a ZIP is a special nested case of a ZINB (Hilbe, 2011). For non- zero-inflated datasets, we calculated dispersion for the PGLM as the ratio of squared and summed Pearson residuals to the residual degrees of freedom (McCullagh and Nelder, 1989); we considered a PGLM unacceptably overdispersed if dispersion $> 2$. Once we determined the optimal GLM framework for each species, we took an information-theoretic approach (Burnham and Anderson, 2002) to model selection with the goal of identifying the most parsimonious combination of technical covariates. We fitted main effects models for all possible combinations of technical covariates and retained the model with the lowest $\mathrm{AIC}_c$ value (Sugiura, 1978).

For each species' best GLM, we estimated annual relative abundances by averaging the marginal mean predictions for each year (Searle *et al.*, 1980). We estimated uncertainty for predictions via year-stratified bootstrapping ($n = 15{,}000$) (Efron, 1983) as the percent coefficient of variation (CV) (Gotelli and Ellison, 2004). We also generated bias-corrected and accelerated ($BC_a$) 95% confidence intervals (CIs) for comparison to forecast uncertainty estimated from dynamic linear models. If a species' time series had 6 or more (≥ ¼ of the time series) predictions with CVs $\geq 100\%$, we eliminated that species from further analysis. We also removed individual annual predictions with CVs $\geq 200\%$.

*Descriptions of dynamic linear model (DLM) covariates*

**Western Bermuda High Index (WBHI)**. Diem (2013) describes the original method for calculating this index, which is similar to the more commonly known Bermuda High Index. We obtained 850-hPa geopotential-height data from the NCEP/NCAR Reanalysis dataset (Kalnay *et al.*, 1996) of NOAA's Earth System Research Laboratory. During the period of 1948–2014, we calculated the monthly pressure difference between a location over the Blake Plateau (30˚N, 75˚W) and New Orleans (30˚N, 92˚W). To remove seasonality, we normalized (i.e., *z*-scored) the time series month by month (Trenberth, 1984; Sheldon and Burd, 2014). To remove any remaining residual autocorrelation, we fit an autoregressive integrated moving average (ARIMA) using the 'auto.arima' function with default specifications (Hyndman and Khandakar, 2008) in R (R Core Team, 2015). We used the residuals from this model as the final time series after conducting Durbin-Watson and Breusch-Godfrey (Zeileis and Hothorn, 2002), portmanteau goodness-of-fit (Mahdi and McLeod, 2012), and runs (Wuertz, 2013) tests, none of which indicated non-independence. Diem (2013) calculated annual WBHI values as an average of monthly values from Jun–Aug, whereas our average included monthly values from May–Sep. We expanded our annual average to include May and Sep to match more closely the warm-season month range for other environmental covariates (Apr–Sep).

**Sea bottom temperature (SBT) anomaly**. We calculated the normalized average annual bottom temperature for each of 18 season / sub-region combinations (Fig. S3) using the SEAMAP-SA survey dataset. We tailored this covariate based on the season(s) and region(s) included in the best fit GLM for each species. For example, if a species' best fit GLM included only summer and fall trawls occurring in the Florida region, then we calculated SBT as the average of the two annual anomaly time series that included the appropriate combination of levels (summer-FL, fall-FL). We normalized each subset time series again prior to DLM fitting.

**Shrimp fishery effort**. We obtained commercial penaeid shrimp fishery effort (cumulative trips per calendar year) from the 2014 South Atlantic King Mackerel stock assessment (Walter and Isley, 2014). Moderate to strong correlations of shrimp fishery effort to bycatch discards for four recently assessed species support the hypothesis that shrimp fishery effort is an appropriate proxy for bycatch mortality (Fig. S4). These species are the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (SEDAR, 2013a), bonnethead shark (*Sphyrna tiburo*) (SEDAR, 2013b), Atlantic croaker (*M. undulatus*) (ASMFC, 2010), and Spanish mackerel (*Scomberomorus maculatus*) (SEDAR, 2012). Because these four species represent diverse morphologies and water column habitat preferences (2 demersal sharks, 1 demersal finfish, and 1 pelagic finfish), we reasoned that this correlative pattern should hold for other species in our analysis. It should be noted that the U.S. South Atlantic and Gulf of Mexico stocks of *R. terraenovae* and *S. tiburo* are separate, yet were assessed using a combined stock approach for expediency (SEDAR, 2013a,b). Bycatch discard trends for these two species include Gulf of Mexico data, which likely skews effort/discard correlations for these two species. Shrimp fishery effort only includes U.S. South Atlantic data.

**Fishery landings**. We obtained non-confidential recreational and commercial landings data (biomass harvested per calendar year) from the Atlantic Coastal Cooperative

Statistics Program (ACCSP, 2015) (Fig. S5). For the majority of species we included landings data within both the U.S. South Atlantic and Mid-Atlantic regions under the assumption that population connectivity exists between the two regions until demonstrated otherwise. We excluded MA data for black seabass (*Centropristis striata*) and summer flounder (*Paralichthys dentatus*), which are considered separate SA and MA stocks (Wilk *et al.*, 1980; Roy *et al.*, 2012) and managed accordingly (SEFSC, 2013; Terceiro, 2015). We also limited blue crab (*Callinectes sapidus*) landings to U.S. South Atlantic states because this species exhibits low regional connectivity between major estuaries along the U.S East Coast (Miller *et al.*, 2010).

**Fishing mortality**. As an alternative to fishery landings time series, we obtained estimates of instantaneous annual fishing mortality ($F$) for a subset of species that were recently assessed (Fig. S5): *Centropristis striata* (SEFSC, 2013), *Paralichthys dentatus* (Terceiro, 2015), *Peprilus triacanthus* (NEFSC, 2013), *Pomatomus saltatrix* (NEFSC, 2015a), *Rhizoprionodon terranovae* (SEDAR, 2013a), *Scomberomorus cavalla* (SEDAR, 2014), *Scomberomorus maculatus* (SEDAR, 2012), *Sphyrna tiburo* (SEDAR, 2013b), and *Stenotomus chrysops* (NEFSC, 2015b). Because fishing mortality is derived in part from landings data, no model was fit that contained both of these counfounded variables. Although *Stenotomus* analyses were conducted at the genus level, *S. chrysops* was assumed to constitute the majority of *Stenotomus* SEAMAP-SA catches. For *P. dentatus*, *P. triacanthus*, and *S. chrysops* age-structured assessment models, $F$ was calculated as the maximum $F$ value across ages.

### *Computing*

We conducted all statistical analyses in R (R Core Team, 2015) using the following packages: *MASS* and *pscl* (Jackman, 2015) for generalized linear modeling; *MARSS* (Holmes *et al.*, 2012) for dynamic linear modeling; *forecast* (Hyndman and Khandakar, 2008) for forecast accuracy; *AICcmodavg* (Mazerolle, 2015), *lmtest* (Zeileis and Hothorn, 2002), and *qpcR* (Spiess, 2014) for model selection; *boot* (Canty and Ripley, 2015) for bootstrapping; *vegan* (Oksanen *et al.*, 2015) for ordination; *gplots* (Warnes *et al.*, 2015), *gstat* (Pebesma, 2004), *lattice* (Sarkar, 2008), *RColorBrewer* (Neuwirth, 2014), and *sp* (Pebesma and Bivand, 2005) for plotting; *doBy* (Højsgaard and Halekoh, 2014), *formula.tools* (Brown, 2015), *plyr* (Wickham, 2011), *reshape2* (Wickham, 2007), and *timeSeries* (Wuertz *et al.*, 2015) for data manipulation and programming.

# APPENDIX II: SUPPLEMENTARY FIGURES

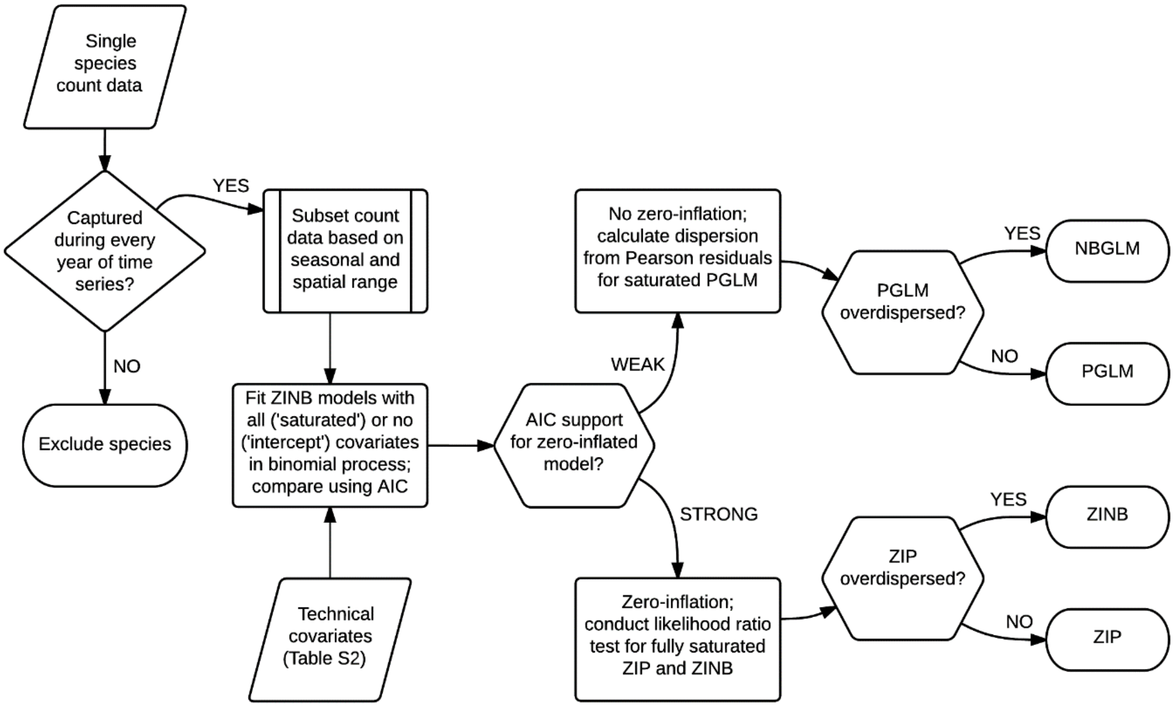


Figure S1. Decision-tree for selecting the optimal generalized linear model framework. Four model framework outcomes were possible: negative binomial GLM (NBGLM), Poisson GLM (PGLM), zero-inflated negative binomial GLM (ZINB), or zero-inflated Poisson GLM (ZIP).

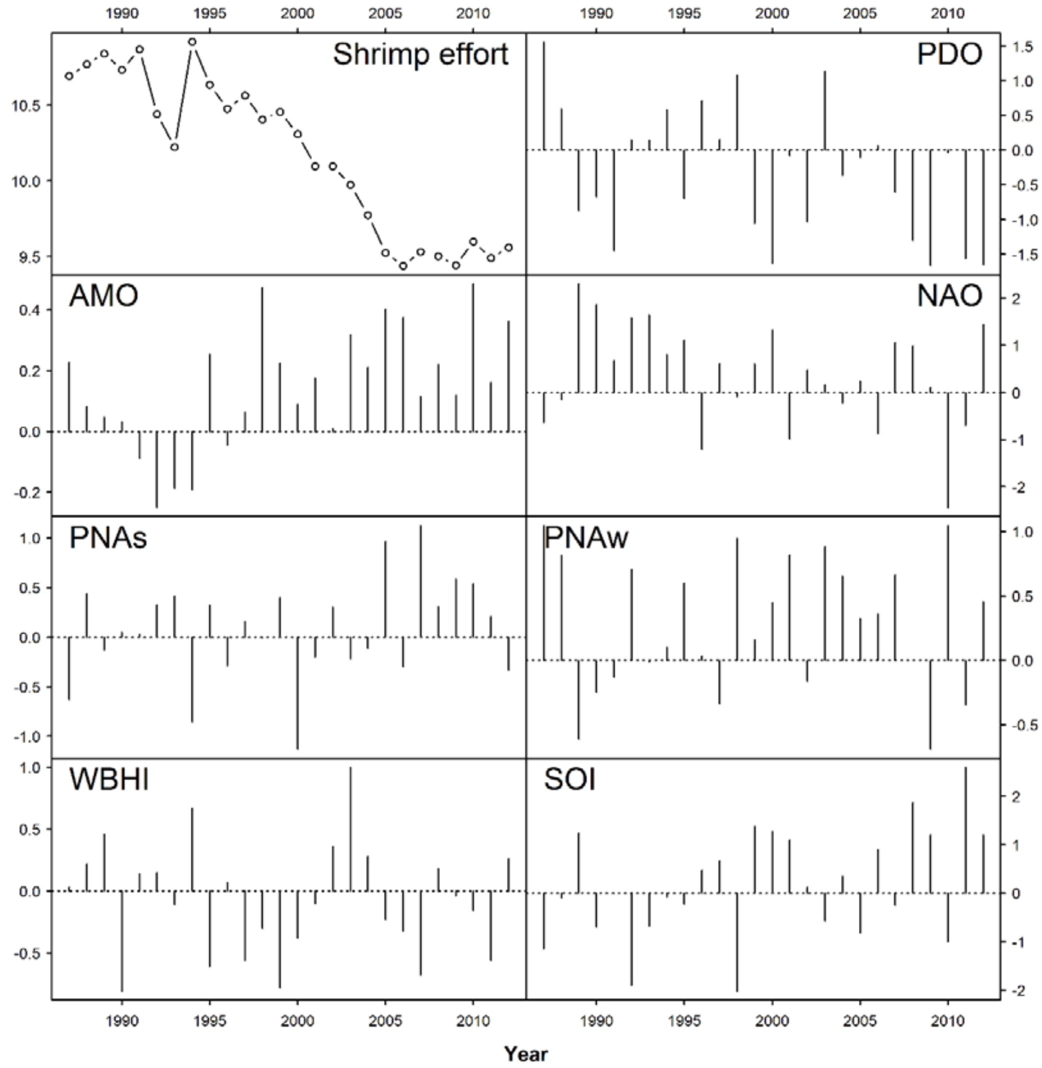


Figure S2. Time series for shrimp fishery effort (log-transformed cumulative fishing trips) and climate indices (non-normalized) during the study period. Abbreviations are as in Table 3.

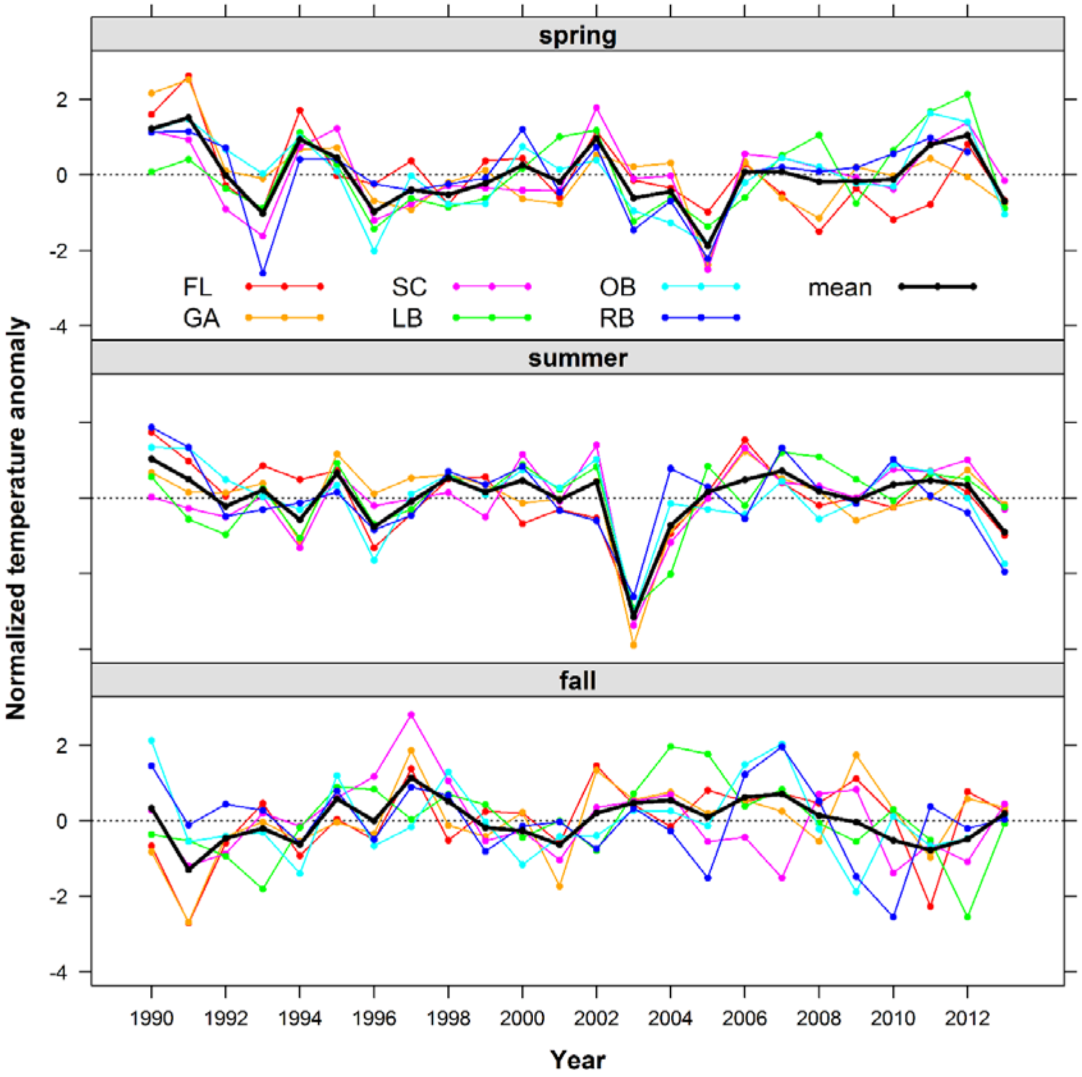


Fig. S3. Normalized annual sea bottom temperature across region and season SEAMAP survey stratifications. Region abbreviations match those in Fig. 1 (FL = Florida, GA = Georgia, SC = South Carolina, LB = Long Bay, OB = Onslow Bay, RB = Raleigh Bay). Cold temperatures during summer 2003 have been attributed to anomalous stratification and upwelling (Aretxabaleta *et al.*, 2006).

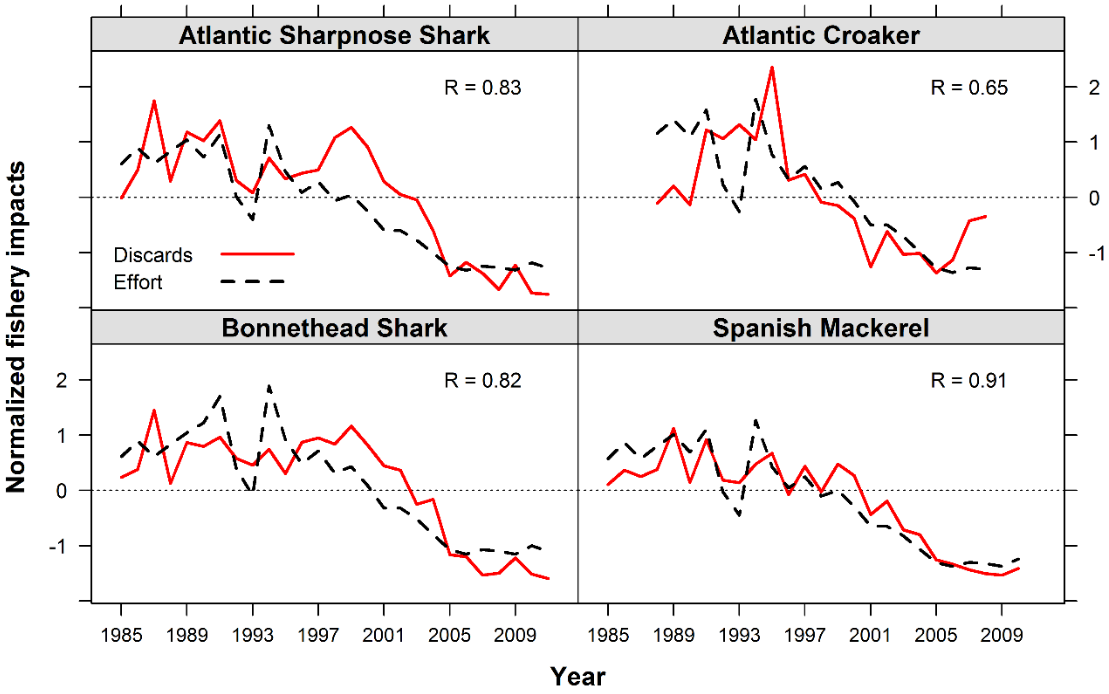


Figure S4. Normalized annual shrimp fishery discards and shrimp fishery effort for four recently assessed species. “R” values indicate the Pearson correlations between the two time series for each species.

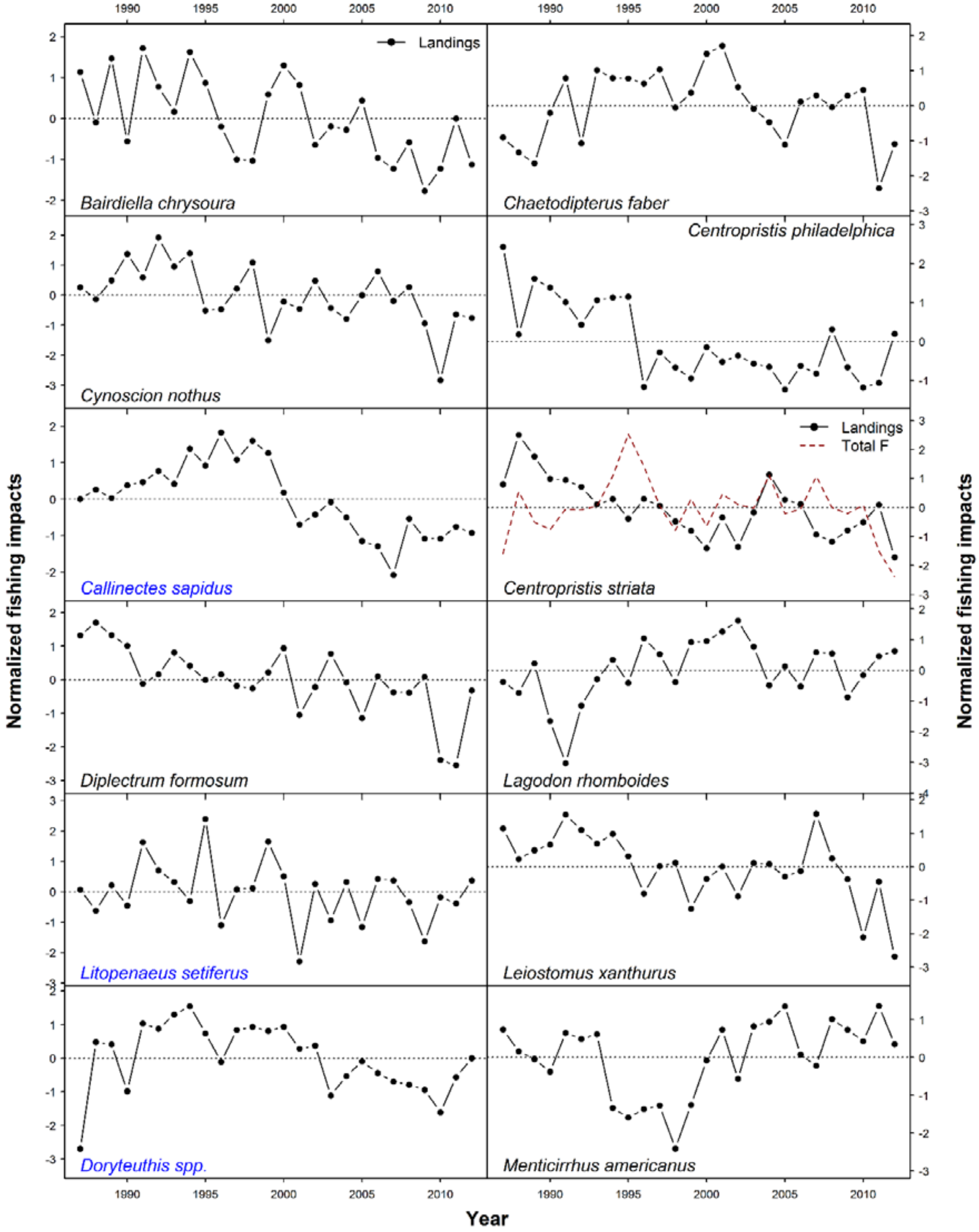


Figure S5. (page 1 of 3). Normalized landings and fishing mortality time series.

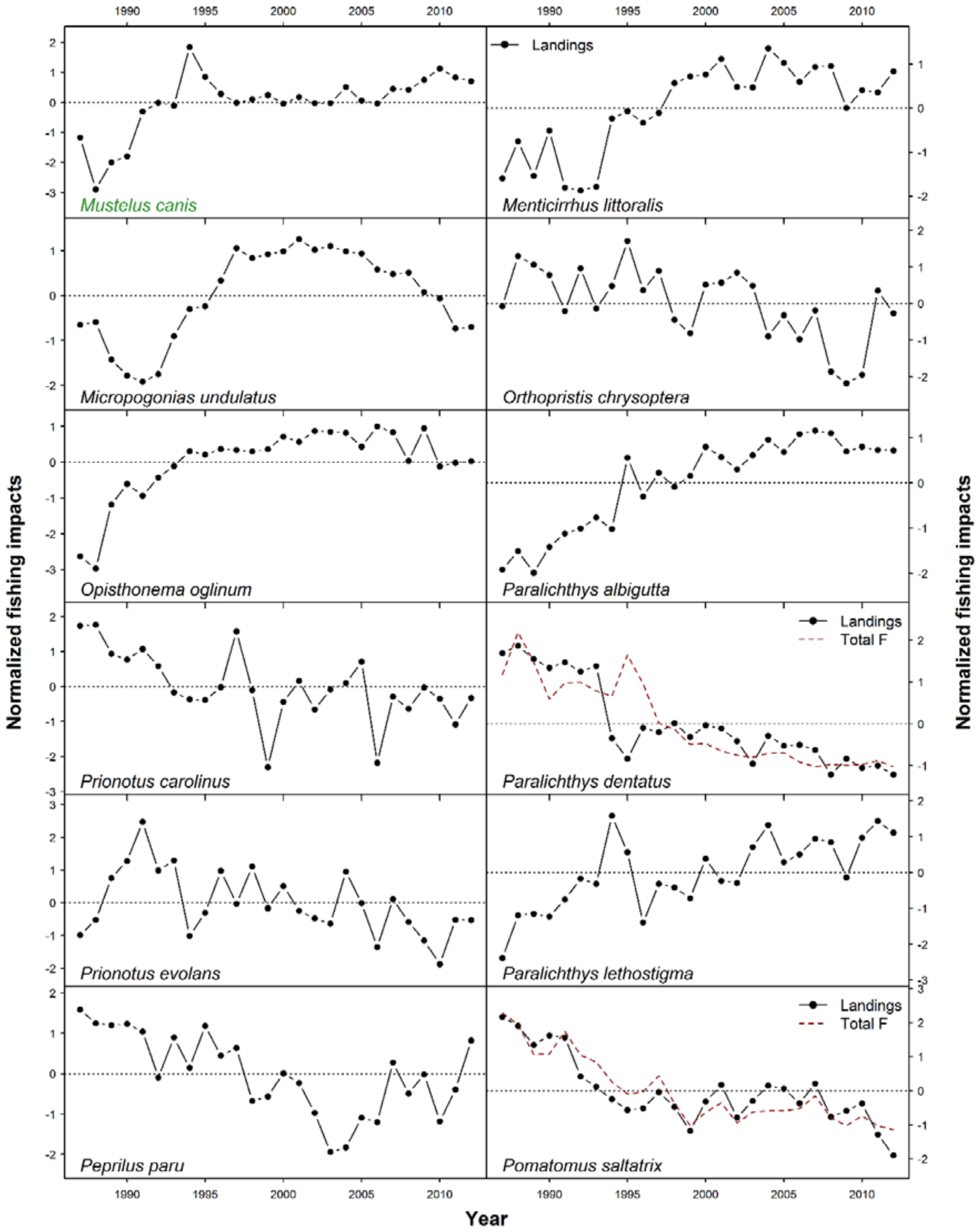


Figure S5 (page 2 of 3). Normalized landings and fishing mortality time series.

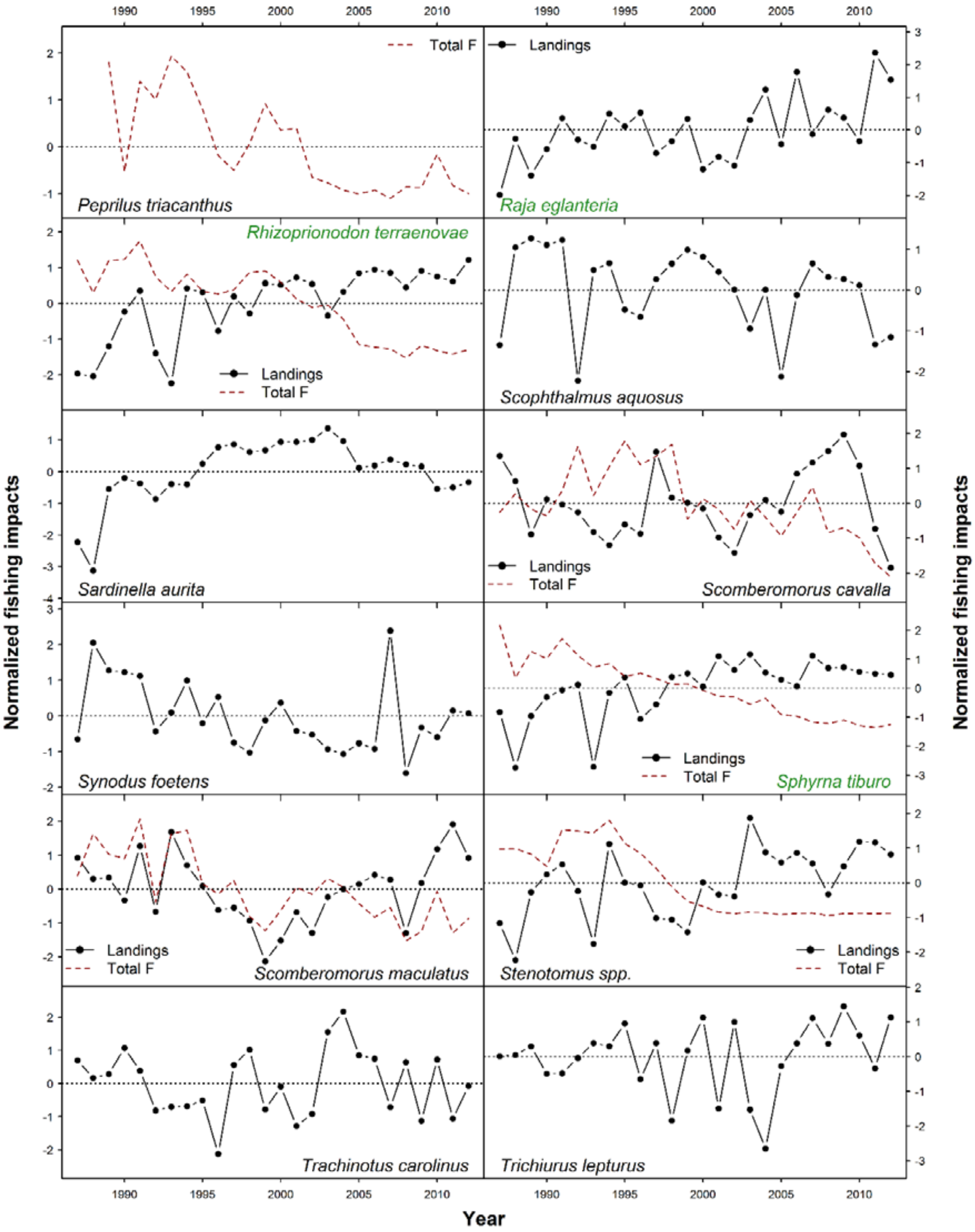


Figure S5 (page 3 of 3). Normalized landings and fishing mortality time series.

Figure S6. (9 pages of panels to follow) Annual time series of logged relative abundance (left panels) and covariate parameter estimates (right panels). The final six panels on the final page depict species whose best model contained no covariates. Only DLMs with the highest AIC$_w$ are illustrated. Left panels show GLM-standardized annual abundance observations (open or closed blue circles) that are bracketed by bootstrapped 95% CIs (vertical dotted lines); DLM forecasts (solid black line) are bracketed by approximate 95% prediction intervals (purple polygon). For visual purposes, abundance observations with anomalously low lower CI bounds are shown as closed blue circles without CIs depicted. Prediction bias quantified as Root Mean Squared Error (RMSE) is reported following AIC$_w$ values. Right panels (except for intercept models) show corresponding covariate parameter estimates, some of which were time-dynamic; values are significant at $\alpha = 0.05$ and $\alpha = 0.01$ if shown with open and closed circles, respectively. Covariate abbreviations are as in Table 3; shrimp fleet effort is denoted as “Effort”. Integers in parentheses adjacent to covariate abbreviations indicate lag (0, 1, 2, or 3). Colors of species names highlighted to indicate broad taxon type as bony fishes (black), elasmobranchs (green), or invertebrates (blue).

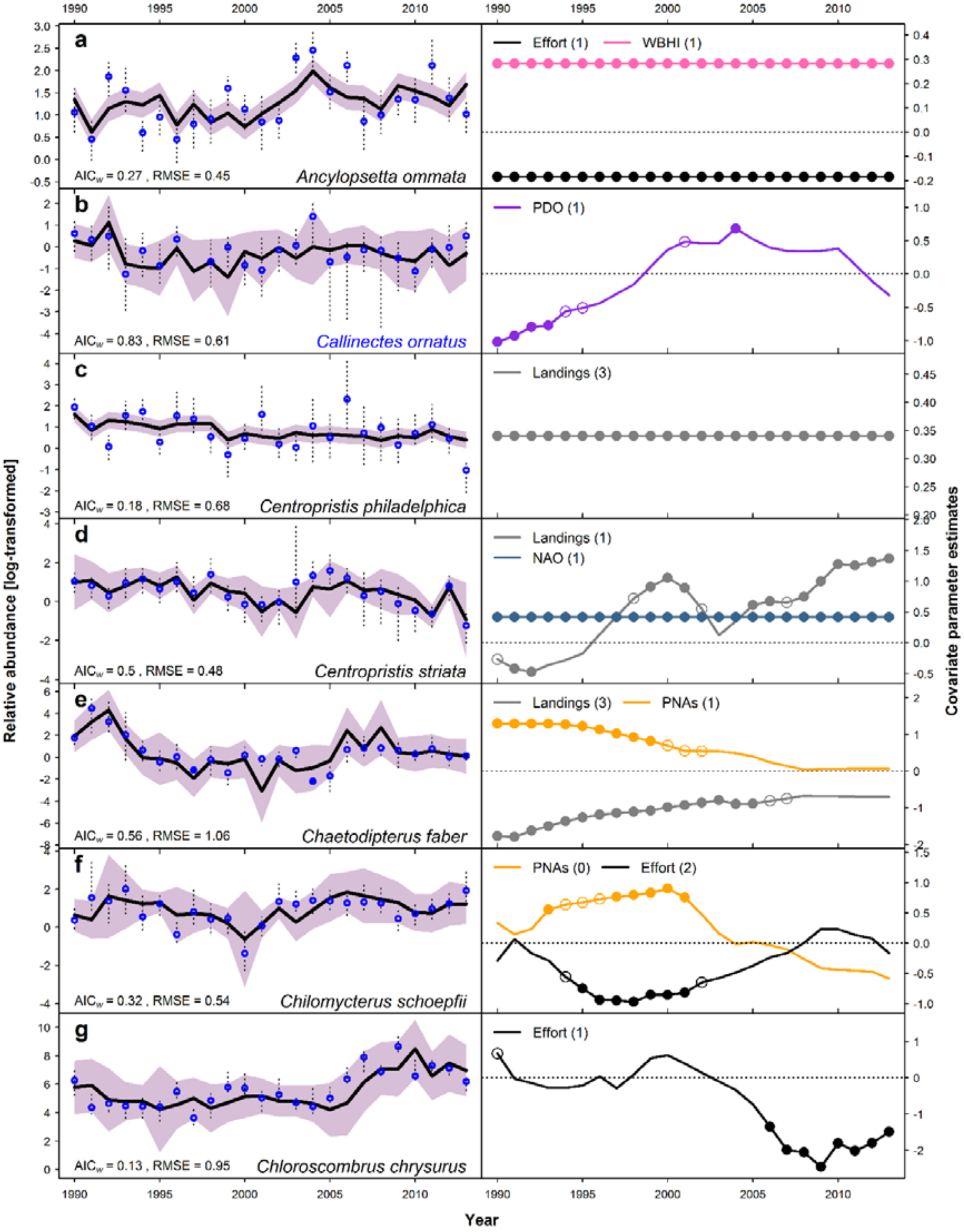


Figure S6 (page 1 of 9).

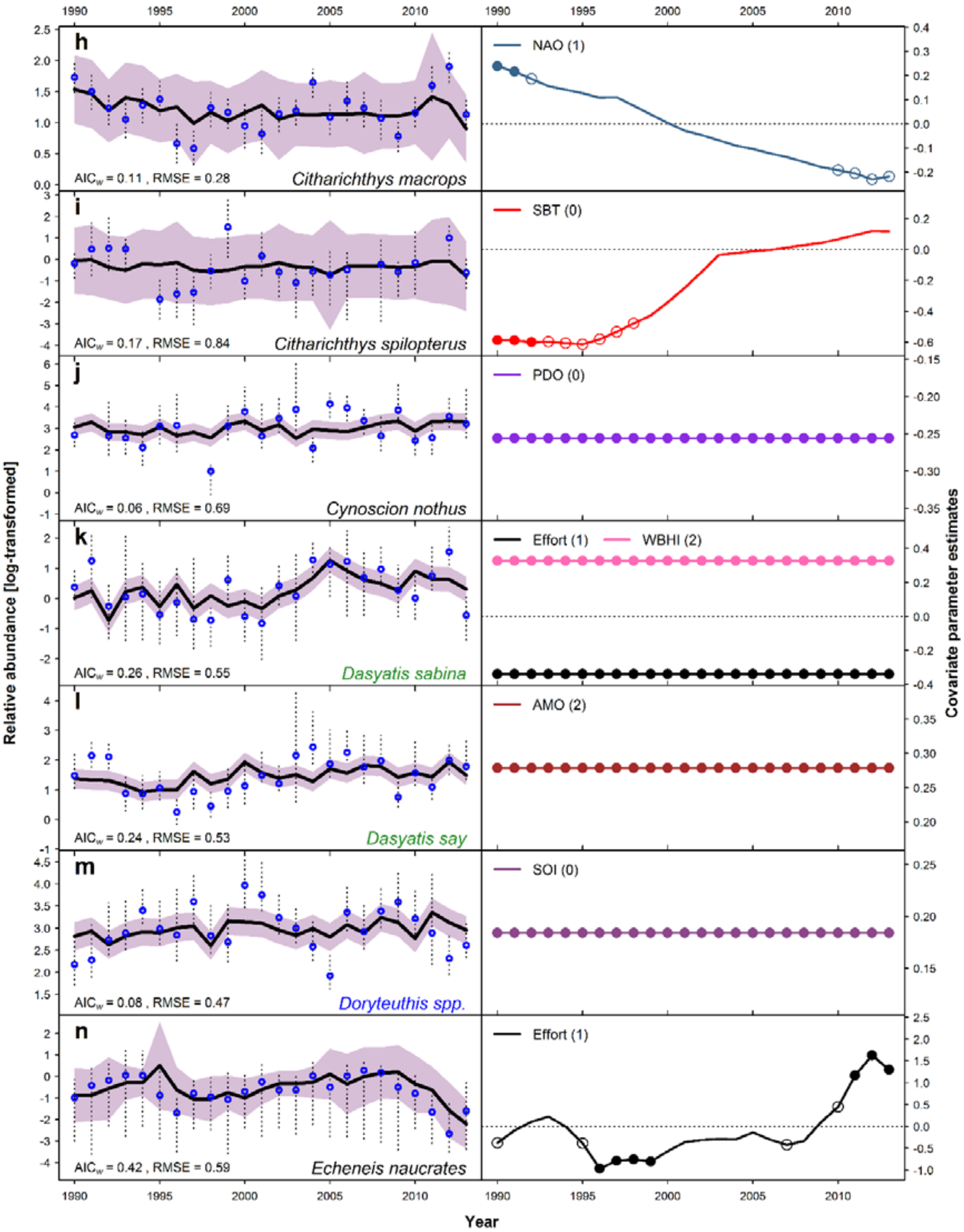


Figure S6 (page 2 of 9).

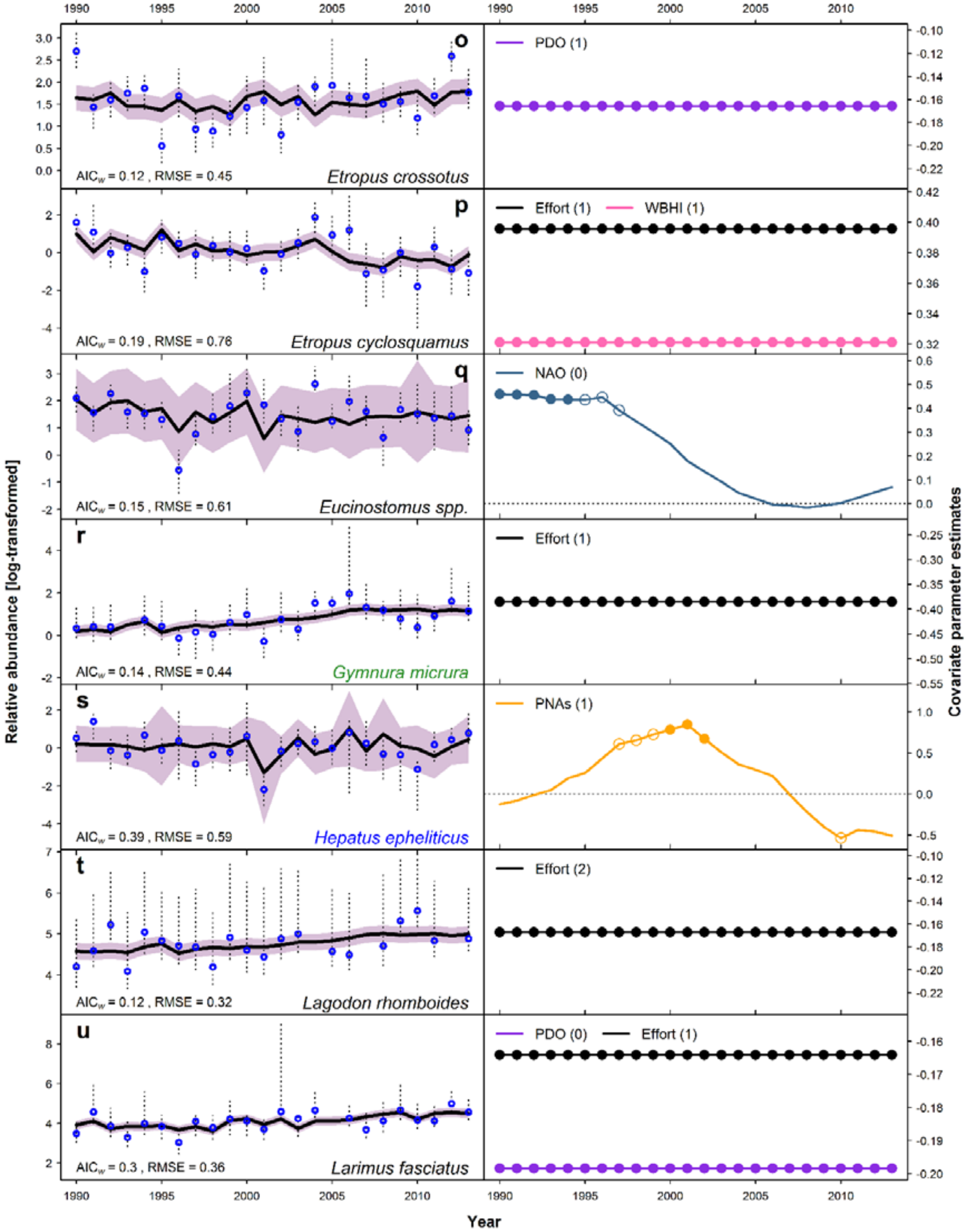


Figure S6 (page 3 of 9).

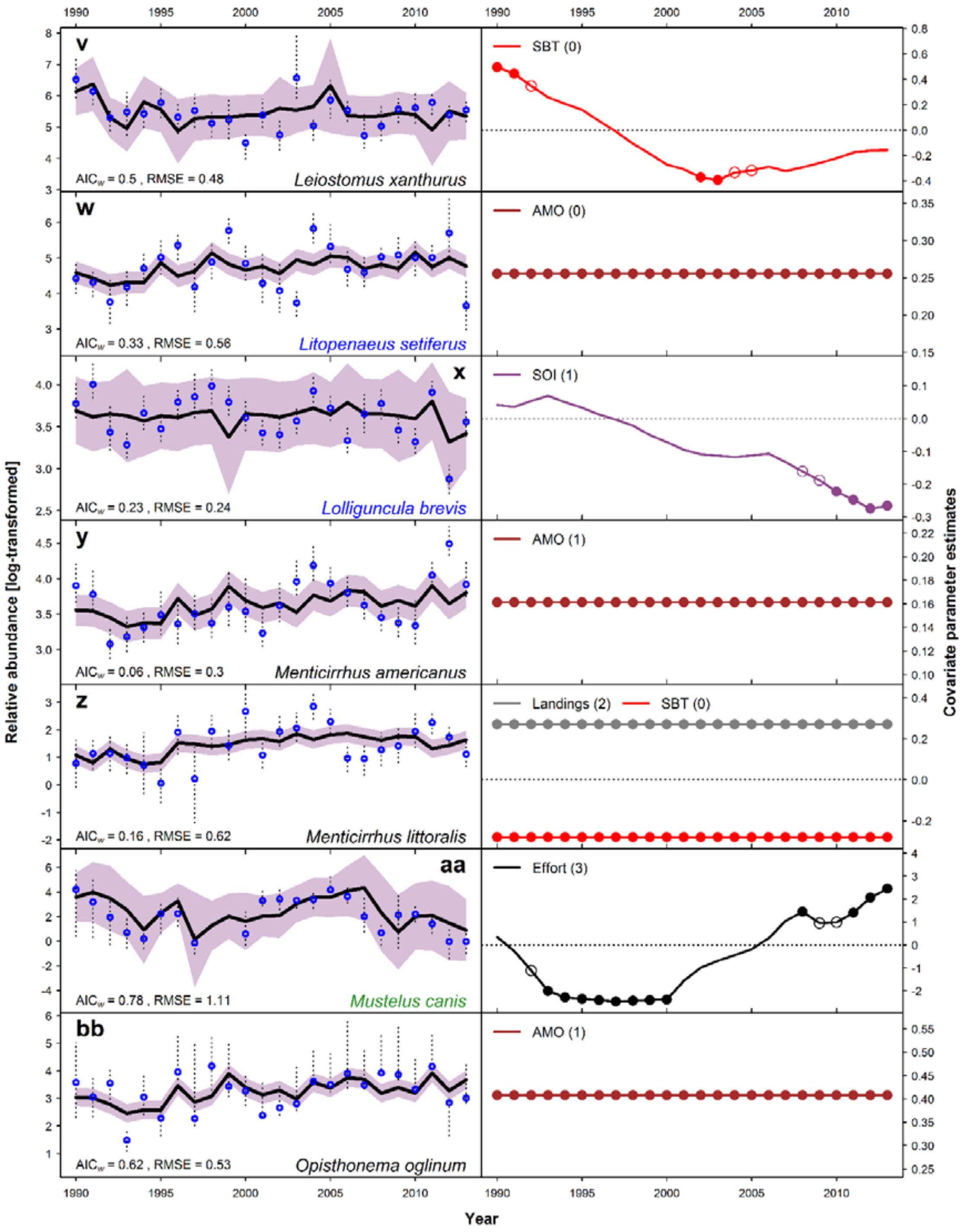


Figure S6 (page 4 of 9).

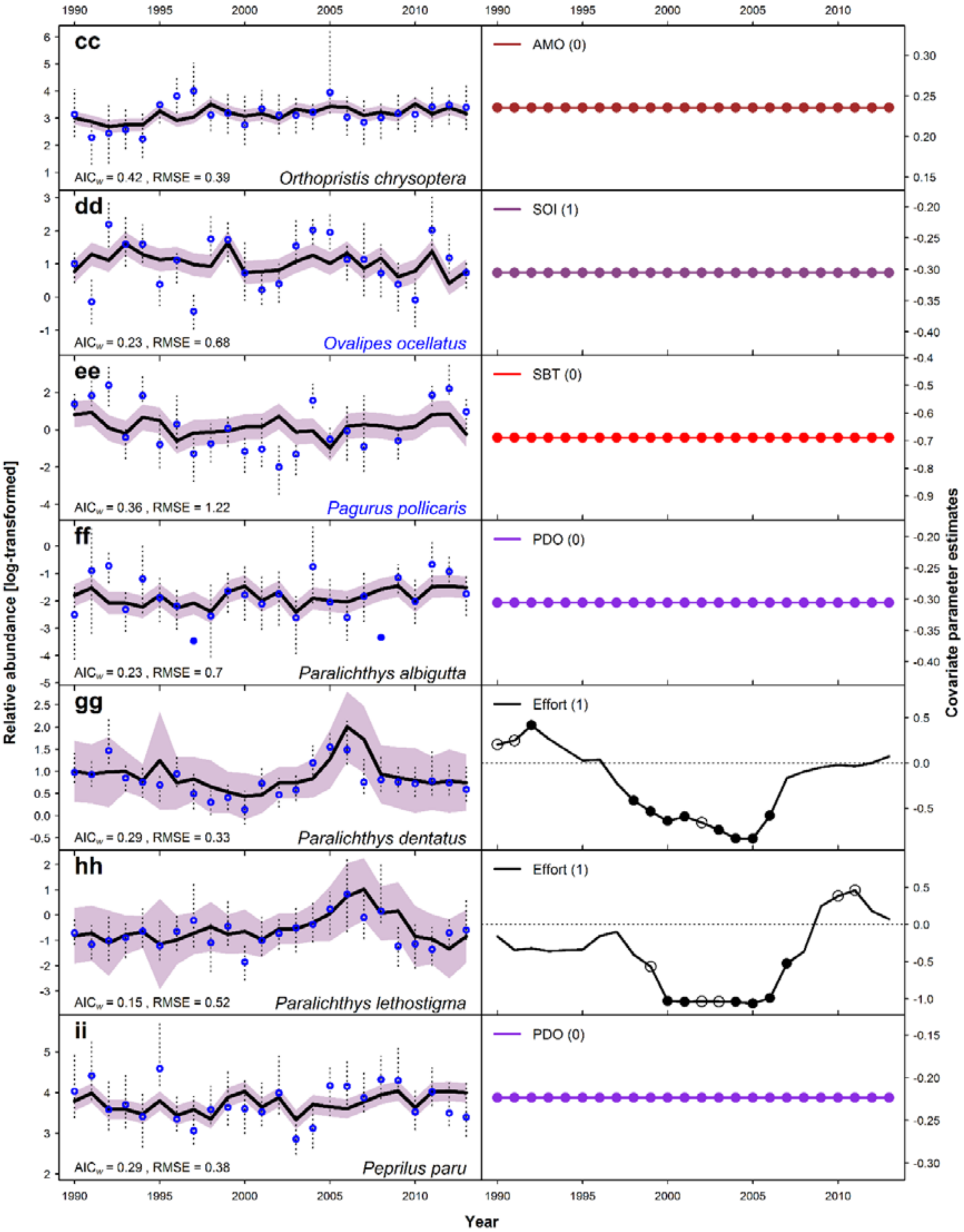


Figure S6 (page 5 of 9).

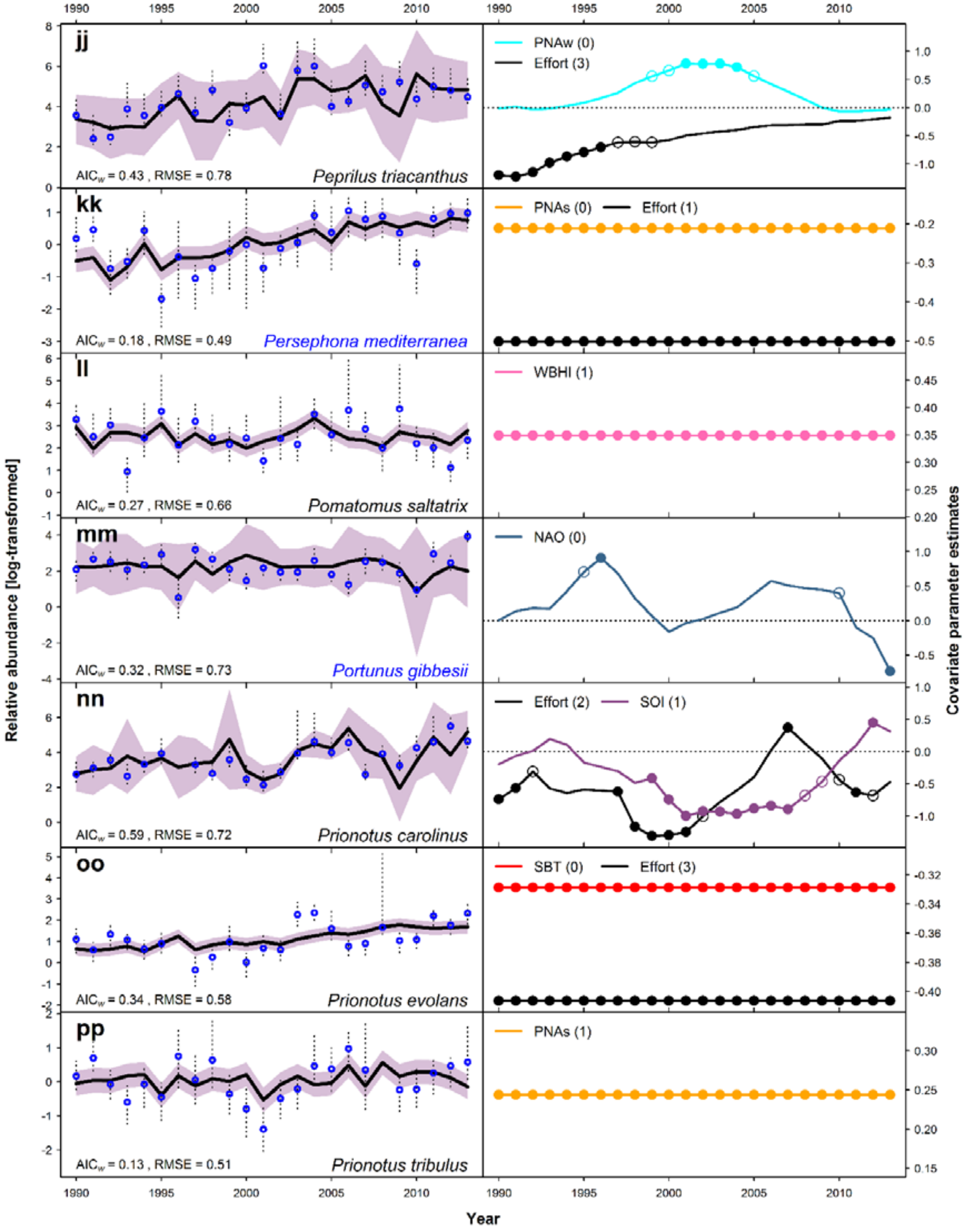


Figure S6 (page 6 of 9).

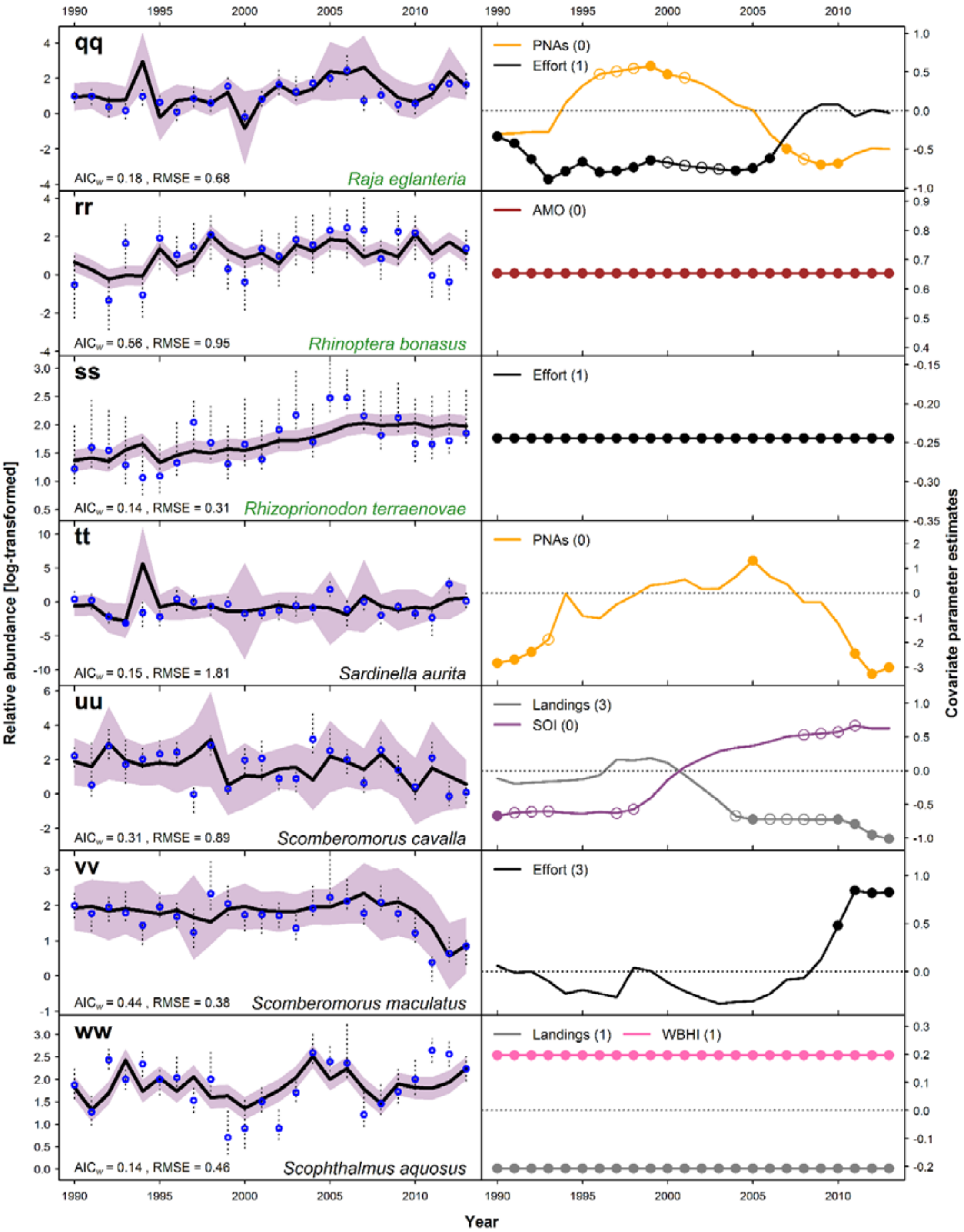


Figure S6 (page 7 of 9).

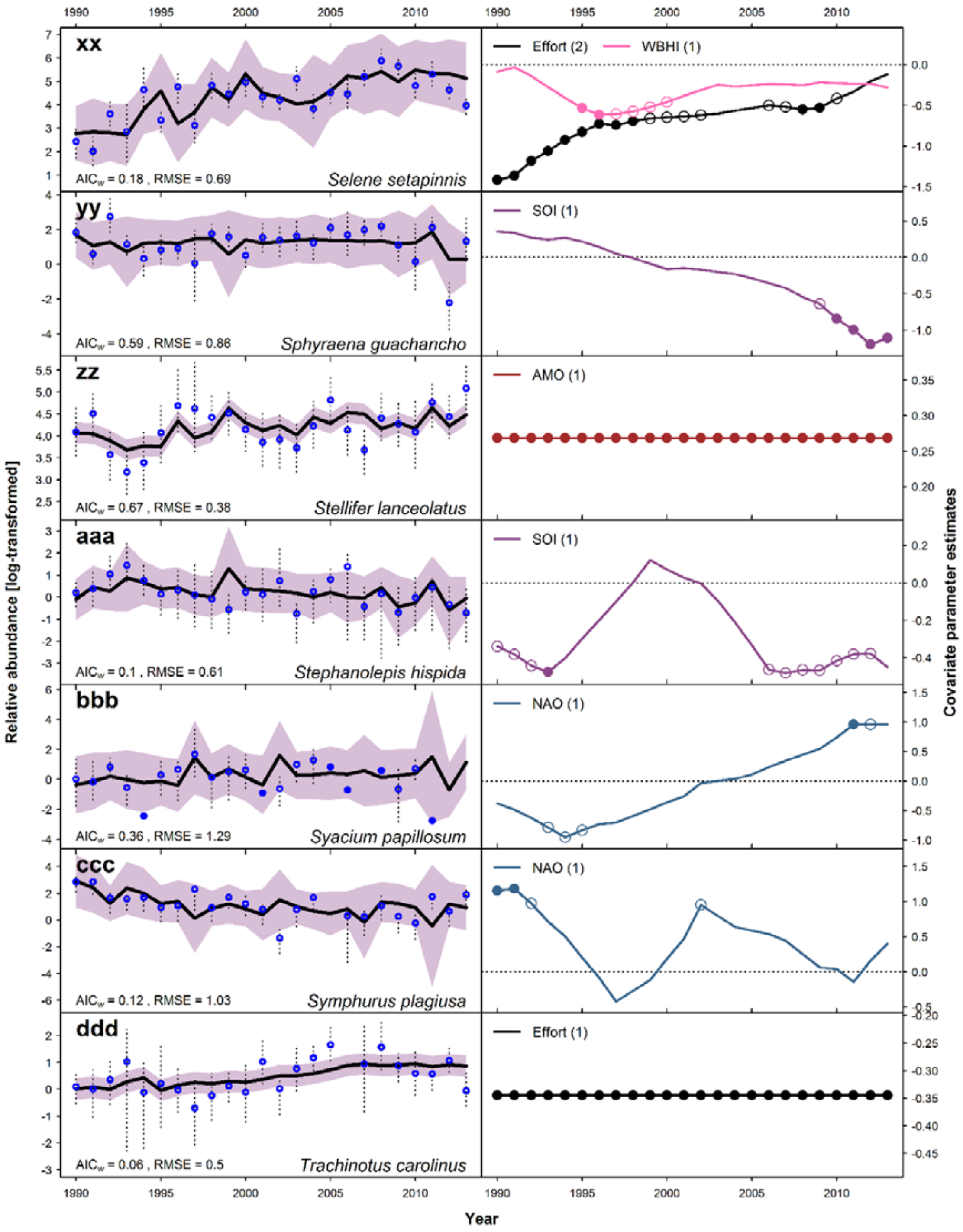
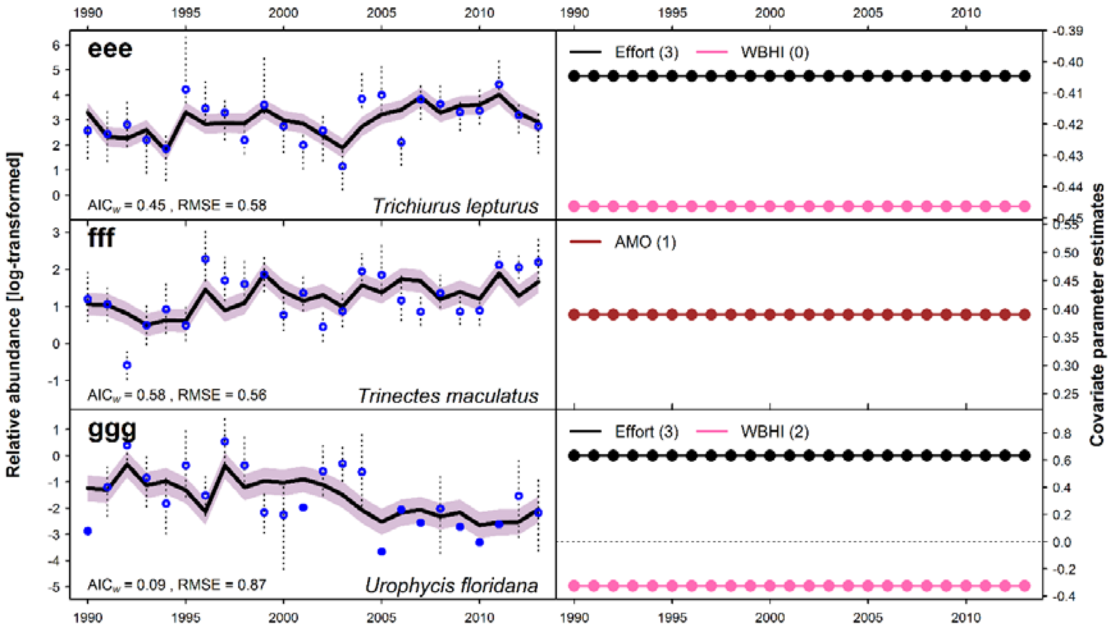


Figure S6 (page 8 of 9).



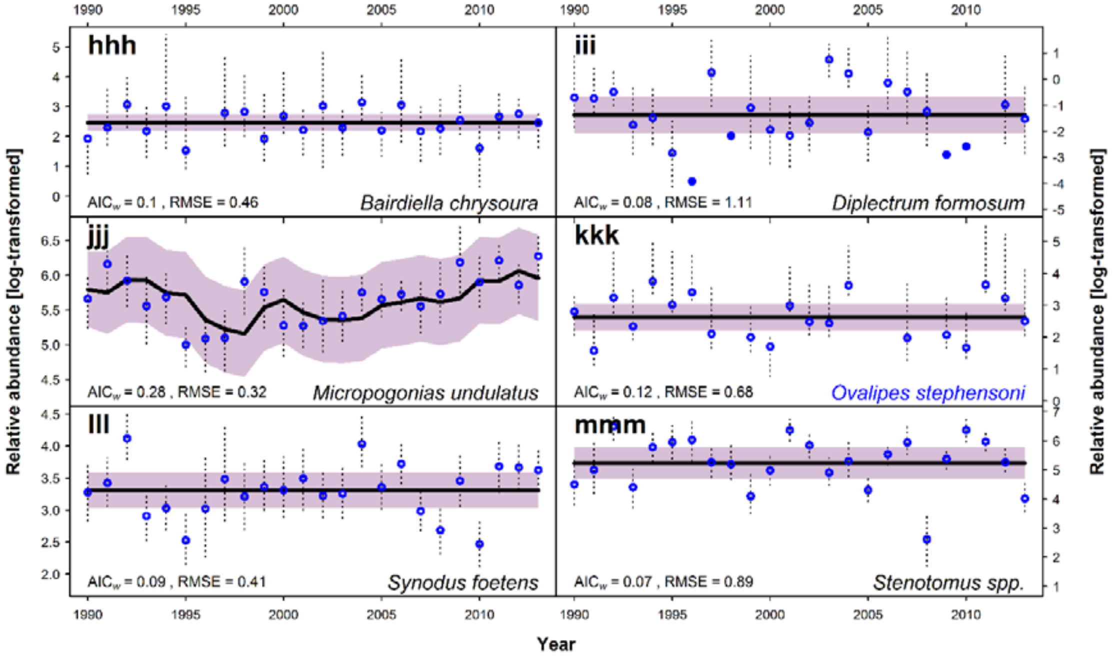


Figure S6 (page 9 of 9).

## APPENDIX II: SUPPLEMENTARY TABLES

Table S2. Supporting mathematics for GLM frameworks. Assumed known values include the number of fish $y$ in trawl set $i$, and covariates $X$ and $Z$. Estimated parameters include the mean $\mu$, a dispersion parameter $k$, the probability $\pi$ of a false zero, intercepts $\alpha$ and $\nu$, and regression parameters $\beta$ and $\gamma$.

| GLM framework | Probability mass function(s) | Link function(s) | Expected mean, $E(Y_i)$ | Variance, $\text{var}(Y_i)$ |
|---|---|---|---|---|
| Poisson (PGLM) | $f_P(y_i;\ \mu_i) = \frac{\mu^{y_i} e^{-\mu_i}}{y_i!}$ | $\mu_i = e^{\alpha+\beta_1 X_{i1}+\cdots+\beta_q X_{iq}}$ | $\mu_i$ | $\mu_i$ |
| Negative binomial (NBGLM) | $f_{NB}(y_i; k, \mu_i) = \frac{\Gamma(y_i+k)}{\Gamma(k)\Gamma(y_i+1)}\left(\frac{k}{\mu_i+k}\right)^k \left(1-\frac{k}{\mu_i+k}\right)^k$ ,<br>where $\Gamma(y_i+1) = (y_i+1)!$ | $\mu_i =$ [as above] | $\mu_i$ | $\mu_i + \frac{\mu_i^2}{k}$ |
| Zero-inflated Poisson (ZIP) | $f(y_i = 0) = \pi_i + (1-\pi_i)e^{-\mu_i}$ ,<br>$f(y_i \mid y_i > 0) = (1-\pi_i) f_P(y)$ | $\mu_i =$ [as above]<br>$\pi_i = \frac{e^{\nu+\gamma_1 Z_{i1}+\cdots+\gamma_q Z_{iq}}}{1+e^{\nu+\gamma_1 Z_{i1}+\cdots+\gamma_q Z_{iq}}}$ | $\mu_i(1-\pi_i)$ | $(1-\pi_i)(\mu_i+\pi_i\mu_i^2)$ |
| Zero-inflated negative binomial (ZINB) | $f(y_i = 0) = \pi_i + (1-\pi_i)\left(\frac{k}{\mu_i+k}\right)^k$ ,<br>$f(y_i \mid y_i > 0) = (1-\pi_i) f_{NB}(y)$ | $\mu_i =$ [as above]<br>$\pi_i =$ [as above] | $\mu_i(1-\pi_i)$ | $(1-\mu_i)\left(\mu_i+\frac{\mu_i^2}{k}\right)+$<br>$\mu_i^2(\pi_i^2+\pi_i)$ |

Table S3. Tow-level technical covariates included in generalized linear models. 'Count' and 'binomial' columns describe within which zero-inflated GLM process a covariate was considered. Only 'count' covariates were included in non- zero-inflated GLMs.

| Covariate | Count | Binomial | Description | Rationale |
|---|---|---|---|---|
| Year | X | X | Categorical; 24 years | Reference effect |
| Season | X | X | Categorical; spring, summer, fall | Captures intra-annual variation |
| Region | X | X | Categorical; see Fig. 7 | Captures latitudinal and sub-regional habitat variation |
| Depth | X | X | Water column depth (m) at tow start (range: 2 – 20) | Captures variation in vertical habitat; important for species that are more pelagic in nature |
| Other biomass | X | X | Log-transformed total catch biomass minus biomass of modeled species (range varies by species) | Accounts for potential changes in species-specific catchability as a function of multispecies biomass and composition |
| Effort | X |  | Log-transformed area ($m^2$) of seafloor swept, calculated as net wingspan (13.5 m) × 2 nets × distance towed (m) determined from coordinate-based great circle distances (Nychka *et al.*, 2015) (range: 9.76 – 10.95) | Accounts for variation in effort; implemented as an offset scaling variable; not included in binomial process because the range of values is small |
| Subsample |  | X | Categorical; Was the total catch subsampled? (T / F) | Accounts for false zeros in zero-inflated models due to subsampling |

Table S4 (on following two pages). DLM covariate lag specifications for each species based on known or assumed longevity or age-selectivity of the SEAMAP-SA trawl survey. The number of covariate and model combinations differed between species due to differing number of lags included as well as availability of landings and fishing mortality time series. The final model set size was larger than the number of covariate combinations because multiple parameterizations of process ($\mathbf{Q}$ diagonals) and observation ($r$) error variances were hypothesized.

| Species | Climate lags | | Fishing lags | No. of covariate combinations | Final model set size |
|---|---|---|---|---|---|
| | Warm | Cold | | | |
| *Ancylopsetta ommata* | 0 1 | 0 1 | 1 2 3 | 47 | 150 |
| *Arenaeus cribrarius* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Bairdiella chrysoura* | 0 1 2 | 0 1 | 1 2 3 | 97 | 338 |
| *Callinectes ornatus* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Callinectes sapidus* | 0 1 2 | 0 1 | 1 2 | 72 | 242 |
| *Callinectes similis* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Centropristis philadelphica* | 0 1 | 0 1 | 1 2 3 | 82 | 284 |
| *Centropristis striata* | 0 1 | 0 1 | 1 2 3 | 126 | 454 |
| *Chaetodipterus faber* | 0 1 2 | 0 1 | 1 2 3 | 106 | 374 |
| *Chilomycterus schoepfii* | 0 1 2 | 0 1 | 1 2 3 | 55 | 176 |
| *Chloroscombrus chrysurus* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Citharichthys macrops* | 0 1 | 0 1 | 1 | 26 | 70 |
| *Citharichthys spilopterus* | 0 1 | 0 1 | 1 | 26 | 70 |
| *Cynoscion nothus* | 0 1 | 0 1 | 1 2 3 | 86 | 300 |
| *Dasyatis sabina* | 0 1 2 | 0 1 | 1 2 3 | 55 | 176 |
| *Dasyatis say* | 0 1 2 | 0 1 | 1 2 3 | 55 | 176 |
| *Diplectrum formosum* | 0 1 | 0 1 | 1 2 3 | 86 | 300 |
| *Doryteuthis* spp. | 0 1 | 0 1 | 1 2 | 62 | 208 |
| *Echeneis naucrates* | 0 1 | 0 1 | 1 2 3 | 47 | 150 |
| *Etropus crossotus* | 0 1 | 0 1 | 1 | 26 | 70 |
| *Etropus cyclosquamus* | 0 1 | 0 1 | 1 | 26 | 70 |
| *Eucinostomus* spp. | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Gymnura micrura* | 0 1 2 | 0 1 | 1 2 3 | 55 | 176 |
| *Hepatus epheliticus* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Lagodon rhomboides* | 0 1 | 0 1 | 1 2 3 | 85 | 296 |
| *Larimus fasciatus* | 0 1 | 0 1 | 1 2 3 | 47 | 150 |
| *Leiostomus xanthurus* | 0 1 | 0 1 | 1 2 3 | 83 | 288 |
| *Litopenaeus setiferus* | 0 | 0 | 1 | 23 | 70 |
| *Lolliguncula brevis* | 0 1 | 0 1 | 1 | 26 | 70 |
| *Menticirrhus americanus* | 0 1 | 0 1 | 1 2 3 | 92 | 324 |
| *Menticirrhus littoralis* | 0 1 | 0 1 | 1 2 3 | 79 | 272 |
| *Micropogonias undulatus* | 0 1 | 0 1 | 1 2 3 | 84 | 292 |
| *Mustelus canis* | 0 1 2 | 0 1 | 1 2 3 | 100 | 350 |
| *Opisthonema oglinum* | 0 1 | 0 1 | 1 2 3 | 81 | 280 |
| *Orthopristis chrysoptera* | 0 1 | 0 1 | 1 2 3 | 83 | 288 |
| *Ovalipes ocellatus* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Ovalipes stephensoni* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Pagurus pollicaris* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Paralichthys albigutta* | 0 1 | 0 1 | 1 2 3 | 78 | 268 |

| Species | Climate lags |  | Fishing lags | No. of covariate combinations | Final model set size |
|---|---|---|---|---|---|
|  | Warm | Cold |  |  |  |
| *Paralichthys dentatus* | 0 1 | 0 1 | 1 2 3 | 109 | 386 |
| *Paralichthys lethostigma* | 0 1 | 0 1 | 1 2 3 | 87 | 304 |
| *Peprilus paru* | 0 1 | 0 1 | 1 2 | 62 | 208 |
| *Peprilus triacanthus* | 0 1 2 | 0 1 | 1 2 3 | 69 | 230 |
| *Persephona mediterranea* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Pomatomus saltatrix* | 0 1 2 | 0 1 | 1 2 3 | 127 | 452 |
| *Portunus gibbesii* | 0 1 2 | 0 1 | 1 2 | 42 | 126 |
| *Portunus spinimanus* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Prionotus carolinus* | 0 1 | 0 1 | 1 2 3 | 86 | 300 |
| *Prionotus evolans* | 0 1 | 0 1 | 1 2 3 | 82 | 284 |
| *Prionotus tribulus* | 0 1 | 0 1 | 1 2 3 | 47 | 150 |
| *Raja eglanteria* | 0 1 2 | 0 1 | 1 2 3 | 104 | 366 |
| *Rhinoptera bonasus* | 0 1 2 | 0 1 | 1 2 3 | 55 | 176 |
| *Rhizoprionodon terraenovae* | 0 1 2 | 0 1 | 1 2 3 | 131 | 468 |
| *Sardinella aurita* | 0 1 | 0 1 | 1 2 3 | 83 | 288 |
| *Scomberomorus cavalla* | 0 | 0 | 1 2 3 | 70 | 244 |
| *Scomberomorus maculatus* | 0 1 | 0 1 | 1 2 3 | 124 | 446 |
| *Scophthalmus aquosus* | 0 1 | 0 1 | 1 2 3 | 92 | 324 |
| *Selene setapinnis* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Sphyraena guachancho* | 0 1 | 0 1 | 1 2 3 | 47 | 150 |
| *Sphyrna tiburo* | 0 1 2 | 0 1 | 1 2 3 | 132 | 472 |
| *Squilla empusa* | 0 1 | 0 1 | 1 2 | 36 | 108 |
| *Stellifer lanceolatus* | 0 1 | 0 1 | 1 2 3 | 47 | 150 |
| *Stenotomus* spp. | 0 1 | 0 1 | 1 2 3 | 123 | 442 |
| *Stephanolepis hispida* | 0 1 | 0 1 | 1 2 3 | 47 | 150 |
| *Syacium papillosum* | 0 1 | 0 1 | 1 2 3 | 47 | 150 |
| *Symphurus plagiusa* | 0 1 | 0 1 | 1 2 3 | 47 | 150 |
| *Synodus foetens* | 0 1 | 0 1 | 1 2 3 | 87 | 304 |
| *Trachinotus carolinus* | 0 1 | 0 1 | 1 2 3 | 94 | 332 |
| *Trichiurus lepturus* | 0 1 | 0 1 | 1 2 3 | 89 | 312 |
| *Trinectes maculatus* | 0 1 | 0 1 | 1 2 3 | 47 | 150 |
| *Urophycis floridana* | 0 1 2 | 0 1 | 1 2 3 | 55 | 176 |

Table S5 (continues for four pages). Results of generalized linear model fitting. Model types are negative binomial generalized linear models (NBGLM) and zero-inflated negative binomial GLMs (ZINB). Variable abbreviations within model formulas correspond to technical covariates described in Table S3: number of fish (N), year (Y), season (S), region (R) depth (D), other biomass (B), effort (E), and subsample (sub). Variables to the right of the vertical bar character for ZINBs were those included in the binomial process for these models. Seasons are spring (Sp), summer (Su), and fall (Fa). Regions (shown in Fig. 7) are Florida (FL), Georgia (GA), South Carolina (SC), Long Bay (LB), Onslow Bay (OB), and Raleigh Bay (RB). Column 'N' contains sample sizes (number of tows). Dispersion values further from 1 indicate increasing overdispersion. Column 'DLM' indicates if a species was considered for further analysis via dynamic linear modeling based on annual coefficients of variation. Species for three genera (*Eucinostomus*, *Stenotomus*, *Doryteuthis*) were grouped for analysis due to difficulties of rapid on-board survey taxonomic identification.

| Species | Model type | Formula for most-supported model | Seasons | Regions | N | Dispersion | DLM |
|---|---|---|---|---|---|---|---|
| Bony fishes | | | | | | | |
| *Acanthostracion quadricornis* | ZINB | N ~ Y + S + D + B + offset(E) \| S + D + B + sub | Sp Su Fa | LB | 1023 | 0.92 | N |
| *Ancylopsetta ommata* | ZINB | N ~ Y + D + offset(E) \| Y + R + D + B + sub | Su | GA SC LB OB | 1700 | 1.25 | Y |
| *Archosargus probatocephalus* | ZINB | N ~ Y + R + D + offset(E) \| R + D + sub | Sp | FL OB RB | 847 | 1.16 | N |
| *Ariopsis felis* | ZINB | N ~ Y + S + R + offset(E) \| S + R | Su Fa | FL GA SC LB | 3454 | 1.13 | N |
| *Bagre marinus* | ZINB | N ~ Y + S + R + B + offset(E) \| Y + S + R + D | Sp Su Fa | FL GA SC | 4159 | 0.79 | N |
| *Bairdiella chrysoura* | ZINB | N ~ Y + R + B + offset(E) \| Y + R + sub | Sp | FL GA SC LB OB RB | 2213 | 1.09 | Y |
| *Brevoortia tyrannus* | ZINB | N ~ Y + R + B + offset(E) \| Y + R + D + B | Sp | FL GA SC LB OB RB | 2213 | 1.15 | N |
| *Caranx crysos* | ZINB | N ~ Y + R + D + B + offset(E) \| Y + R + B + sub | Su | FL GA SC LB OB RB | 2224 | 1.21 | N |
| *Caranx hippos* | ZINB | N ~ Y + S + D + B + offset(E) \| S + sub | Sp Su Fa | FL | 1084 | 0.89 | N |
| *Centropristis philadelphica* | ZINB | N ~ Y + R + D + B \| Y + R + B + sub | Fa | FL GA SC LB OB RB | 2220 | 1.41 | Y |
| *Centropristis striata* | ZINB | N ~ Y + D + B \| Y + S + B | Sp Su Fa | LB OB | 2021 | 0.96 | Y |
| *Chaetodipterus faber* | ZINB | N ~ Y + D + B + offset(E) \| R + B + sub | Sp | FL GA | 896 | 0.98 | Y |
| *Chilomycterus schoepfii* | ZINB | N ~ Y + R + B \| Y + sub | Sp | GA SC LB OB RB | 1851 | 1.01 | Y |
| *Chloroscombrus chrysurus* | ZINB | N ~ Y + S + R + B \| Y + S + R + D + B | Sp Su Fa | FL GA | 2686 | 1.57 | Y |
| *Citharichthys macrops* | ZINB | N ~ Y + S + R + B \| Y + R + B + sub | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.37 | Y |
| *Citharichthys spilopterus* | ZINB | N ~ Y + S + R + D + B \| Y + D + B + sub | Su Fa | GA SC | 2050 | 1.03 | Y |
| *Cynoscion nothus* | ZINB | N ~ Y + R + D + B + offset(E) \| Y + R + D + B + sub | Su | FL GA SC LB OB | 2062 | 1.15 | Y |
| *Cynoscion regalis* | ZINB | N ~ Y + R + B \| Y + R + B + sub | Fa | FL GA SC LB OB RB | 2220 | 1.27 | N |
| *Decapterus punctatus* | ZINB | N ~ Y + offset(E) \| R | Su | FL GA SC LB OB RB | 2224 | 1.31 | N |

| Species | Model type | Formula for most-supported model | Seasons | Regions | N | Dispersion | DLM |
|---|---|---|---|---|---|---|---|
| *Diplectrum formosum* | ZINB | N ~ Y + D + offset(E) \| S + R + D + B + sub | Su Fa | GA SC LB | 2732 | 1.32 | Y |
| *Echeneis naucrates* | ZINB | N ~ Y + S + R + D + B + offset(E) \| Y + S + R + sub | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.01 | Y |
| *Etropus crossotus* | ZINB | N ~ Y + R + B \| Y + R + B + sub | Fa | FL GA SC LB OB RB | 2220 | 1.4 | Y |
| *Etropus cyclosquamus* | ZINB | N ~ Y + R + D + B \| R + B + sub | Su | FL GA SC LB OB RB | 2224 | 1.4 | Y |
| *Eucinostomus* spp. | ZINB | N ~ Y + D + B + offset(E) \| Y + R + B + sub | Fa | FL GA SC LB OB RB | 2220 | 1.24 | Y |
| *Lagodon rhomboides* | ZINB | N ~ Y + S + R + D + B + offset(E) \| S + R + B + sub | Sp Su Fa | LB OB RB | 2498 | 1.06 | Y |
| *Larimus fasciatus* | ZINB | N ~ Y + R + B \| Y + R + D + B + sub | Su | FL GA SC LB OB RB | 2224 | 2.11 | Y |
| *Leiostomus xanthurus* | ZINB | N ~ Y + S + R + B + offset(E) \| Y + S + R + B + sub | Sp Su Fa | FL GA SC LB OB RB | 6657 | 2.84 | Y |
| *Menticirrhus americanus* | ZINB | N ~ Y + S + R + B + offset(E) \| R + D + B | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.43 | Y |
| *Menticirrhus littoralis* | NBGLM | N ~ Y + S + B + offset(E) | Sp Su Fa | FL | 1084 | 0.94 | Y |
| *Menticirrhus saxatilis* | ZINB | N ~ Y + S + R + B + offset(E) \| Y + S + R + B + sub | Sp Su Fa | LB OB RB | 2498 | 1.2 | N |
| *Micropogonias undulatus* | ZINB | N ~ Y + S + R + B + offset(E) \| Y + S + R + B + sub | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.08 | Y |
| *Opisthonema oglinum* | ZINB | N ~ Y + S + R + D + B + offset(E) \| Y + S + R + D | Su Fa | FL GA SC LB OB RB | 4444 | 2.23 | Y |
| *Orthopristis chrysoptera* | ZINB | N ~ Y + S + R + D + B \| Y + S + R + D | Sp Su Fa | LB OB RB | 2498 | 1.07 | Y |
| *Paralichthys albigutta* | NBGLM | N ~ Y + S + R + B + offset(E) | Sp Su Fa | FL OB | 2082 | 1.26 | Y |
| *Paralichthys dentatus* | ZINB | N ~ Y + S + R + D + B \| Y + S + R + B + sub | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.22 | Y |
| *Paralichthys lethostigma* | ZINB | N ~ Y + S + R + B \| Y + S + B | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.08 | Y |
| *Peprilus paru* | ZINB | N ~ Y + R + D + B + offset(E) \| Y + R + D + B | Fa | FL GA SC LB OB RB | 2220 | 1.53 | Y |
| *Peprilus triacanthus* | ZINB | N ~ Y + R + B \| Y + R + D + B + sub | Sp | FL GA SC LB OB RB | 2213 | 1.62 | Y |
| *Pomatomus saltatrix* | ZINB | N ~ Y + R + B + offset(E) \| Y + R + B + sub | Sp | FL GA SC LB OB RB | 2213 | 1.47 | Y |
| *Prionotus carolinus* | ZINB | N ~ Y + S + D + offset(E) \| Y + S + R + B + sub | Sp Su | GA SC LB OB RB | 3713 | 1.48 | Y |
| *Prionotus evolans* | ZINB | N ~ Y + R + D + B \| Y + S + R + sub | Su Fa | FL GA SC LB OB RB | 4444 | 1.28 | Y |
| *Prionotus rubio* | ZINB | N ~ Y + R + D + B \| D + B + sub | Su | FL GA SC LB OB RB | 2224 | 1.26 | N |
| *Prionotus scitulus* | ZINB | N ~ Y + S + R + B \| S + R + B + sub | Su Fa | FL GA SC LB OB RB | 4444 | 1.38 | N |
| *Prionotus tribulus* | ZINB | N ~ Y + S + R + B + offset(E) \| Y + S + R + B + sub | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.43 | Y |
| *Rachycentron canadum* | ZINB | N ~ Y + S + R + D + B \| Y + S + R + sub | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.09 | N |
| *Sardinella aurita* | NBGLM | N ~ Y + S + D + B + offset(E) | Sp Fa | FL GA SC LB OB RB | 4433 | 1.17 | Y |
| *Scomberomorus cavalla* | ZINB | N ~ Y + B + offset(E) \| Y + R | Fa | FL GA SC LB OB | 2058 | 1.29 | Y |

| Species | Model type | Formula for most-supported model | Seasons | Regions | N | Dispersion | DLM |
|---|---|---|---|---|---|---|---|
| *Scomberomorus maculatus* | ZINB | N ~ Y + S + R + D + B + offset(E) \| Y + S + R | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.56 | Y |
| *Scophthalmus aquosus* | ZINB | N ~ Y + S + R + B \| Y + S + R + sub | Sp Su Fa | SC LB OB RB | 3971 | 1.31 | Y |
| *Selene setapinnis* | ZINB | N ~ Y + S + D + B \| D + B + sub | Sp Su Fa | FL | 1084 | 1.42 | Y |
| *Selene vomer* | ZINB | N ~ Y + S + R + D + B \| Y + S + R + D + B | Su Fa | FL GA SC LB OB RB | 4444 | 1.74 | N |
| *Sphoeroides maculatus* | ZINB | N ~ Y + S + R \| Y + S + R + D + B + sub | Sp Su Fa | GA SC LB OB RB | 5573 | 1.05 | N |
| *Sphyraena guachancho* | ZINB | N ~ Y + R + D + offset(E) \| Y + R + sub | Fa | FL GA SC LB OB | 2058 | 0.92 | Y |
| *Stellifer lanceolatus* | ZINB | N ~ Y + S + R + B + offset(E) \| Y + S + R + D + B + sub | Sp Su Fa | FL GA SC LB OB | 6180 | 1.03 | Y |
| *Stenotomus* spp. | NBGLM | N ~ Y + S + R + B | Su Fa | LB OB RB | 1672 | 1.16 | Y |
| *Stephanolepis hispida* | ZINB | N ~ Y + S + R + D + B \| Y + S + R + B + sub | Su Fa | FL GA SC LB OB RB | 4444 | 1.2 | Y |
| *Syacium papillosum* | ZINB | N ~ Y + D + B + offset(E) \| R + D + B + sub | Su | FL GA SC LB OB RB | 2224 | 1.71 | Y |
| *Symphurus plagiusa* | ZINB | N ~ Y + R + D + B \| Y + S + R + B + sub | Sp Fa | GA SC LB OB RB | 3711 | 1.21 | Y |
| *Synodus foetens* | ZINB | N ~ Y + R + D + offset(E) \| Y + S + R + B + sub | Su Fa | FL GA SC LB OB RB | 4444 | 1.08 | Y |
| *Trachinotus carolinus* | ZINB | N ~ Y + R + D + B + offset(E) \| Y + R + D + sub | Fa | FL GA SC LB OB RB | 2220 | 0.86 | Y |
| *Trichiurus lepturus* | ZINB | N ~ Y + S + B \| Y + S + D + B | Su Fa | FL GA SC LB OB | 4120 | 2.06 | Y |
| *Trinectes maculatus* | NBGLM | N ~ Y + S + R + D + B | Sp Su Fa | FL GA SC LB OB | 6180 | 1.6 | Y |
| *Urophycis floridana* | NBGLM | N ~ Y + R + D + B + offset(E) | Sp | GA SC LB OB | 1698 | 1.33 | Y |
| *Urophycis regia* | ZINB | N ~ Y + R + offset(E) \| Y + B | Sp | SC LB OB RB | 1317 | 1 | N |
| Elasmobranchs | | | | | | | |
| *Aetobatus narinari* | ZINB | N ~ Y + S + offset(E) \| S + R | Sp Su Fa | FL GA SC LB | 5182 | 1.02 | N |
| *Carcharhinus acronotus* | ZINB | N ~ Y + S \| R | Su Fa | FL GA SC LB OB | 4120 | 1.09 | N |
| *Dasyatis americana* | ZINB | N ~ Y + S + R + D + B \| Y + S + B + sub | Sp Su Fa | GA SC LB OB RB | 5573 | 1.11 | N |
| *Dasyatis centroura* | ZINB | N ~ Y + S + R + D + B \| Y + S + R + D | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.11 | N |
| *Dasyatis sabina* | ZINB | N ~ Y + R + B \| Y + R + D | Fa | GA SC LB OB RB | 1860 | 0.97 | Y |
| *Dasyatis say* | ZINB | N ~ Y + S + R + B + offset(E) \| Y + S + B | Sp Fa | LB OB RB | 1661 | 1.35 | Y |
| *Gymnura altavela* | ZINB | N ~ Y + S + D + offset(E) \| Y + S + D + sub | Sp Su Fa | RB | 477 | 0.86 | N |
| *Gymnura micrura* | ZINB | N ~ Y + S + R + D + B \| Y + S + R + D + sub | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.09 | Y |
| *Mustelus canis* | ZINB | N ~ Y + R + D + offset(E) \| Y + R | Sp | LB OB RB | 826 | 1.32 | Y |
| *Myliobatis freminvillei* | ZINB | N ~ Y + S + R + B \| Y + S + R + B | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.3 | N |

| Species | Model type | Formula for most-supported model | Seasons | Regions | N | Dispersion | DLM |
|---|---|---|---|---|---|---|---|
| *Raja eglanteria* | ZINB | N ~ Y + R + D + B + offset(E) \| Y + R + D | Sp Fa | FL GA SC LB OB RB | 4433 | 1.01 | Y |
| *Rhinoptera bonasus* | ZINB | N ~ Y + S + R + D + B \| Y + S + D + sub | Sp Fa | FL GA SC LB OB RB | 4433 | 1.07 | Y |
| *Rhizoprionodon terraenovae* | ZINB | N ~ Y + S + R + D + offset(E) \| Y + S + R + D + sub | Su Fa | FL GA SC LB OB RB | 4444 | 1.13 | Y |
| *Sphyrna lewini* | ZINB | N ~ Y + D + B \| S + R + B | Su Fa | FL GA SC | 2772 | 0.86 | N |
| *Sphyrna tiburo* | ZINB | N ~ Y + S + R + D + B + offset(E) \| Y + S + R + D + sub | Sp Su Fa | FL GA SC LB | 5182 | 1.2 | Y |
| Invertebrates | | | | | | | |
| *Arenaeus cribrarius* | ZINB | N ~ Y + S + R + B + offset(E) \| Y + R + D + B | Su Fa | FL OB RB | 1712 | 1.13 | Y |
| *Calappa flammea* | ZINB | N ~ Y + R + D \| R + D + B + sub | Su | FL GA SC LB OB | 2062 | 0.92 | N |
| *Callinectes ornatus* | ZINB | N ~ Y + S + B \| Y + S + R + D + B | Su Fa | FL GA SC LB OB | 4120 | 1.23 | Y |
| *Callinectes sapidus* | ZINB | N ~ Y + R + D + B \| Y + R + D + B + sub | Su | FL GA SC LB OB RB | 2224 | 1.02 | Y |
| *Callinectes similis* | NBGLM | N ~ Y + S + R + D + B | Su Fa | GA SC LB OB | 3398 | 1.66 | Y |
| *Doryteuthis* spp. | ZINB | N ~ Y + S + R + D + B \| Y + S + R + D + B + sub | Sp Fa | GA SC LB OB RB | 3711 | 1.24 | Y |
| *Farfantepenaeus aztecus* | ZINB | N ~ Y + R + B \| Y + R + B + sub | Su | FL GA SC LB OB RB | 2224 | 1.06 | N |
| *Farfantepenaeus duorarum* | ZINB | N ~ Y + R + D + B + offset(E) \| Y + R + B | Sp | FL GA SC LB OB RB | 2213 | 1.13 | N |
| *Gibbesia neglecta* | ZINB | N ~ Y + S + R + B \| Y + R + B + sub | Sp Su Fa | FL GA SC | 4159 | 1.46 | N |
| *Hepatus epheliticus* | ZINB | N ~ Y + R + B \| Y + S + D + B | Sp Su | FL GA SC | 2774 | 1.07 | Y |
| *Litopenaeus setiferus* | NBGLM | N ~ Y + R + D + B | Fa | FL GA SC LB OB | 2058 | 1.04 | Y |
| *Lolliguncula brevis* | ZINB | N ~ Y + S + R + B + offset(E) \| Y + R + sub | Sp Su Fa | FL GA SC LB OB RB | 6657 | 1.21 | Y |
| *Menippe mercenaria* | ZINB | N ~ Y + S + D + B \| Y + S + R + D + B + sub | Sp Su Fa | GA SC LB OB | 5096 | 1.05 | N |
| *Ovalipes ocellatus* | ZINB | N ~ Y + S + R + B \| Y + S + R + B + sub | Su Fa | GA SC LB OB RB | 3722 | 1.38 | Y |
| *Ovalipes stephensoni* | ZINB | N ~ Y + S + R \| Y + S + R + B + sub | Sp Su Fa | GA SC LB OB RB | 5573 | 1.23 | Y |
| *Pagurus pollicaris* | ZINB | N ~ Y + R + D + B + offset(E) \| Y + R + B + sub | Fa | FL GA SC LB OB RB | 2220 | 1.58 | Y |
| *Persephona mediterranea* | ZINB | N ~ Y + S + R + D + B + offset(E) \| Y + S + R + D + B + sub | Sp Su | FL GA SC LB OB RB | 4437 | 1.13 | Y |
| *Portunus gibbesii* | NBGLM | N ~ Y + R + B + offset(E) | Sp | FL GA SC LB OB RB | 2213 | 1.5 | Y |
| *Portunus spinimanus* | ZINB | N ~ Y + S + R + D + B \| Y + R + D + B + sub | Sp Su Fa | GA SC LB OB | 5096 | 1.32 | Y |
| *Rimapenaeus constrictus* | ZINB | N ~ Y + S + R + B + offset(E) \| Y + S + R + sub | Sp Fa | GA SC LB | 2732 | 0.96 | N |
| *Squilla empusa* | ZINB | N ~ Y + S + R + B \| Y + S + B + sub | Sp Su Fa | GA SC | 3075 | 0.87 | Y |
| *Xiphopenaeus kroyeri* | ZINB | N ~ Y + R + D + B + offset(E) \| Y + R + D + B + sub | Fa | FL GA SC | 1385 | 0.92 | N |

Table S6 (continues for nine pages). Results of dynamic linear model (DLM) fitting. Covariate lag values are in parenthesis following covariate abbreviations (see Table 3). AIC weights ($\text{AIC}_w$) were calculated from retained models with $\Delta\text{AIC}_c$, $\leq 10$ although only models with $\Delta\text{AIC}_c$ values $< 2$ are tabulated. Models with $\text{AIC}_w$ cells highlighted darker shades of green have more support (i.e., closer to 1) relative to other models for the same species. Models with Root Mean Squared Error (RMSE) cells highlighted darker shades of red have more forecast bias (higher RMSE). $\mathbf{Q}_{est}$ and $\boldsymbol{r}_{est}$ columns contain estimates of process error variance(s) and observation error variance, respectively. Reference the main text and Table 4 for details regarding how process and observation error variances were parameterized.

| Species | Model | Covariates (lags) | $\Delta\text{AIC}_c$ | $\text{AIC}_w$ | RMSE | $\text{Q}_{est}$ | $r$ | $r_{est}$ |
|---|---|---|---|---|---|---|---|---|
| Bony fishes | | | | | | | | |
| *Ancylopsetta ommata* | | | | | | | | |
| | 1 | WBHI (1), Effort (1) | 0 | 0.164 | 0.45 | 0 | fixed | 0.214 |
| | 2 | WBHI (1) | 0.74 | 0.114 | 0.49 | 0 | fixed | 0.214 |
| | 3 | WBHI (1), Effort (3) | 0.93 | 0.103 | 0.46 | 0 | fixed | 0.214 |
| | 4 | WBHI (1), Effort (2) | 0.96 | 0.102 | 0.46 | 0 | fixed | 0.214 |
| *Bairdiella chrysoura* | | | | | | | | |
| | 1 | | 0 | 0.062 | 0.46 | 0 | est. | 0.208 |
| | 2 | AMO (0) | 0.97 | 0.038 | 0.44 | 0 | est. | 0.19 |
| | 3 | Landings (3) | 1.41 | 0.031 | 0.44 | 0 | est. | 0.194 |
| | 4 | NAO (1) | 1.64 | 0.027 | 0.44 | 0 | est. | 0.196 |
| | 5 | PNAs (2) | 1.74 | 0.026 | 0.44 | 0 | est. | 0.197 |
| | 6 | PNAs (1) | 1.76 | 0.026 | 0.44 | 0 | est. | 0.197 |
| *Centropristis philadelphica* | | | | | | | | |
| | 1 | Landings (3) | 0 | 0.088 | 0.68 | 0 | fixed | 0.387 |
| | 2 | PNAs (1), Landings (3) | 0.87 | 0.058 | 0.66 | 0 | fixed | 0.387 |
| | 3 | WBHI (1), Landings (3) | 1.52 | 0.042 | 0.67 | 0 | fixed | 0.387 |
| | 4 | SOI (1), Landings (3) | 1.83 | 0.036 | 0.67 | 0 | fixed | 0.387 |
| | 5 | PNAs (0), Landings (3) | 1.91 | 0.034 | 0.67 | 0 | fixed | 0.387 |
| *Centropristis striata* | | | | | | | | |
| | 1 | NAO (1), Landings (1) | 0 | 0.348 | 0.48 | 0.101 | est. | 0.0659 |
| | 2 | PDO (0), Landings (1) | 1 | 0.211 | 0.46 | 0 | est. | 0.21 |
| | 3 | PDO (0), Landings (1) | 1.76 | 0.144 | 0.46 | 0 | fixed | 0.398 |
| *Chaetodipterus faber* | | | | | | | | |
| | 1 | PNAs (1), Landings (3) | 0 | 0.389 | 1.06 | 0.046 | fixed | 0.477 |
| *Chilomycterus schoepfii* | | | | | | | | |
| | 1 | PNAs (0), Effort (2) | 0 | 0.260 | 0.54 | 0.073 | est. | 0.0627 |
| | 2 | PNAs (0) | 0.95 | 0.162 | 0.64 | 0.0547 | fixed | 0.312 |
| | 3 | WBHI (1) | 1.71 | 0.111 | 0.67 | 0.0905 | fixed | 0.312 |
| *Chloroscombrus chrysurus* | | | | | | | | |
| | 1 | Effort (1) | 0 | 0.095 | 0.95 | 0.32 | fixed | 0.312 |
| | 2 | Effort (2) | 0.67 | 0.068 | 1.02 | 0.39 | fixed | 0.312 |
| | 3 | PDO (0), Effort (1) | 0.85 | 0.062 | 0.79 | 0 | est. | 0.621 |
| | 4 | WBHI (1), Effort (2) | 1.18 | 0.053 | 0.89 | 0.0535 | fixed | 0.312 |
| | 5 | WBHI (0), Effort (1) | 1.22 | 0.052 | 0.79 | 0 | est. | 0.631 |
| | 6 | | 1.47 | 0.045 | 0.96 | 0.369 | fixed | 0.312 |

| Species | Model | Covariates (lags) | $\Delta AIC_c$ | $AIC_w$ | RMSE | $Q_{est}$ | $r$ | $r_{est}$ |
|---|---|---|---|---|---|---|---|---|
| | 7 | WBHI (0), Effort (2) | 1.49 | 0.045 | 0.8 | 0 | est. | 0.638 |
| | 8 | Effort (2), SBT (0) | 1.7 | 0.041 | 0.93 | 0.0766 | fixed | 0.312 |
| | 9 | PNAw (0), Effort (2) | 1.71 | 0.040 | 0.8 | 0 | est. | 0.644 |
| | 10 | WBHI (1), Effort (2) | 1.73 | 0.040 | 0.8 | 0 | est. | 0.645 |
| *Citharichthys macrops* | | | | | | | | |
| | 1 | NAO (1) | 0 | 0.092 | 0.28 | 0.00445 | est. | 0.0664 |
| | 2 | SBT (0) | 0.34 | 0.077 | 0.25 | 0 | fixed | 0.14 |
| | 3 | | 0.39 | 0.075 | 0.32 | 0 | fixed | 0.14 |
| | 4 | SBT (0) | 0.61 | 0.067 | 0.25 | 0 | est. | 0.0843 |
| | 5 | NAO (1) | 1.7 | 0.039 | 0.29 | 0.00335 | fixed | 0.14 |
| | 6 | | 1.79 | 0.037 | 0.32 | 0 | est. | 0.0999 |
| | 7 | PDO (0) | 1.88 | 0.036 | 0.31 | 0 | fixed | 0.14 |
| | 8 | NAO (0) | 1.96 | 0.034 | 0.31 | 0 | fixed | 0.14 |
| *Citharichthys spilopterus* | | | | | | | | |
| | 1 | SBT (0) | 0 | 0.135 | 0.84 | 0.0257 | fixed | 0.577 |
| | 2 | | 0.89 | 0.087 | 0.83 | 0 | fixed | 0.577 |
| | 3 | PDO (0) | 1.5 | 0.064 | 0.79 | 0 | fixed | 0.577 |
| | 4 | WBHI (1) | 1.74 | 0.057 | 0.8 | 0 | fixed | 0.577 |
| | 5 | SOI (1) | 1.95 | 0.051 | 0.83 | 0.0182 | fixed | 0.577 |
| *Cynoscion nothus* | | | | | | | | |
| | 1 | PDO (0) | 0 | 0.044 | 0.69 | 0 | fixed | 0.451 |
| | 2 | | 0.4 | 0.036 | 0.74 | 0 | fixed | 0.451 |
| | 3 | Effort (1) | 0.59 | 0.033 | 0.7 | 0 | fixed | 0.451 |
| | 4 | SOI (0) | 0.65 | 0.032 | 0.7 | 0 | fixed | 0.451 |
| | 5 | AMO (1) | 0.76 | 0.030 | 0.7 | 0 | fixed | 0.451 |
| | 6 | Effort (3) | 0.85 | 0.029 | 0.7 | 0 | fixed | 0.451 |
| | 7 | Effort (2) | 1.24 | 0.024 | 0.71 | 0 | fixed | 0.451 |
| | 8 | PDO (1) | 1.34 | 0.023 | 0.71 | 0 | fixed | 0.451 |
| | 9 | PNAw (0) | 1.63 | 0.020 | 0.72 | 0 | fixed | 0.451 |
| | 10 | SOI (1) | 1.68 | 0.019 | 0.72 | 0 | fixed | 0.451 |
| | 11 | Landings (2) | 1.74 | 0.018 | 0.72 | 0 | fixed | 0.451 |
| *Diplectrum formosum* | | | | | | | | |
| | 1 | | 0 | 0.051 | 1.11 | 0 | est. | 1.24 |
| | 2 | SBT (0) | 0.44 | 0.041 | 1.09 | 0 | est. | 1.11 |
| | 3 | NAO (0) | 0.85 | 0.033 | 1.06 | 0 | est. | 1.13 |
| | 4 | NAO (1) | 1.43 | 0.025 | 1.08 | 0 | est. | 1.16 |
| | 5 | PDO (1), Landings (2) | 1.57 | 0.023 | 1.02 | 0.0529 | fixed | 0.639 |
| | 6 | PDO (1) | 1.71 | 0.022 | 1.08 | 0 | est. | 1.18 |
| | 7 | WBHI (1) | 1.75 | 0.021 | 1.09 | 0 | est. | 1.18 |
| | 8 | SBT (0) | 1.78 | 0.021 | 1.09 | 0 | fixed | 0.639 |
| *Echeneis naucrates* | | | | | | | | |
| | 1 | Effort (1) | 0 | 0.318 | 0.59 | 0.172 | est. | 0.0876 |
| | 2 | Effort (2) | 1.01 | 0.192 | 0.64 | 0.171 | est. | 0.0966 |

| Species | Model | Covariates (lags) | $\Delta\text{AIC}_c$ | $\text{AIC}_w$ | RMSE | $Q_{est}$ | $r$ | $r_{est}$ |
|---|---|---|---|---|---|---|---|---|
| | 3 | | 1.06 | 0.187 | 0.57 | 0.279 | est. | 0.0246 |
| *Etropus crossotus* | | | | | | | | |
| | 1 | PDO (1) | 0 | 0.097 | 0.45 | 0 | fixed | 0.214 |
| | 2 | | 0.33 | 0.082 | 0.48 | 0 | fixed | 0.214 |
| | 3 | NAO (1) | 1.01 | 0.058 | 0.46 | 0.00441 | fixed | 0.214 |
| | 4 | SBT (0) | 1.66 | 0.042 | 0.48 | 0 | fixed | 0.214 |
| *Etropus cyclosquamus* | | | | | | | | |
| | 1 | WBHI (1), Effort (1) | 0 | 0.150 | 0.76 | 0 | fixed | 0.557 |
| | 2 | PDO (1), Effort (1) | 0.3 | 0.129 | 0.76 | 0 | fixed | 0.557 |
| | 3 | PDO (1) | 0.96 | 0.093 | 0.83 | 0.017 | fixed | 0.557 |
| | 4 | Effort (1) | 1.35 | 0.077 | 0.82 | 0 | fixed | 0.557 |
| *Eucinostomus* spp. | | | | | | | | |
| | 1 | NAO (0) | 0 | 0.101 | 0.61 | 0.0115 | fixed | 0.31 |
| | 2 | | 0.64 | 0.073 | 0.63 | 0 | fixed | 0.31 |
| | 3 | WBHI (1) | 1.34 | 0.052 | 0.61 | 0 | fixed | 0.31 |
| | 4 | PNAw (0) | 1.74 | 0.042 | 0.62 | 0 | fixed | 0.31 |
| | 5 | WBHI (0) | 1.78 | 0.042 | 0.62 | 0 | fixed | 0.31 |
| | 6 | PDO (0) | 1.89 | 0.039 | 0.63 | 0.00621 | fixed | 0.31 |
| *Lagodon rhomboides* | | | | | | | | |
| | 1 | Effort (2) | 0 | 0.083 | 0.32 | 0 | est. | 0.103 |
| | 2 | Effort (3) | 0.97 | 0.051 | 0.33 | 0 | est. | 0.108 |
| | 3 | WBHI (0), Effort (2) | 1.37 | 0.042 | 0.31 | 0 | est. | 0.0935 |
| | 4 | Effort (1) | 1.67 | 0.036 | 0.33 | 0 | est. | 0.112 |
| | 5 | | 1.7 | 0.035 | 0.36 | 0 | est. | 0.13 |
| | 6 | WBHI (0), Effort (3) | 1.97 | 0.031 | 0.31 | 0 | est. | 0.0962 |
| | 7 | Effort (2), SBT (0) | 1.99 | 0.031 | 0.32 | 0 | est. | 0.0963 |
| *Larimus fasciatus* | | | | | | | | |
| | 1 | PDO (0), Effort (1) | 0 | 0.145 | 0.36 | 0 | est. | 0.127 |
| | 2 | PDO (0) | 0.61 | 0.107 | 0.39 | 0 | est. | 0.15 |
| | 3 | Effort (2) | 1.76 | 0.060 | 0.4 | 0 | est. | 0.158 |
| | 4 | WBHI (0), Effort (2) | 1.88 | 0.057 | 0.37 | 0 | est. | 0.138 |
| *Leiostomus xanthurus* | | | | | | | | |
| | 1 | SBT (0) | 0 | 0.218 | 0.48 | 0.0193 | est. | 0.11 |
| | 2 | SBT (0) | 1.7 | 0.094 | 0.47 | 0.017 | fixed | 0.238 |
| *Menticirrhus americanus* | | | | | | | | |
| | 1 | AMO (1) | 0 | 0.039 | 0.3 | 0 | fixed | 0.128 |
| | 2 | AMO (0), Landings (3) | 0.3 | 0.033 | 0.28 | 0 | fixed | 0.128 |
| | 3 | AMO (1), Landings (3) | 0.69 | 0.027 | 0.28 | 0 | fixed | 0.128 |
| | 4 | AMO (0), Landings (3) | 0.73 | 0.027 | 0.28 | 0 | est. | 0.0757 |
| | 5 | AMO (1), Landings (2) | 0.96 | 0.024 | 0.28 | 0 | fixed | 0.128 |
| | 6 | AMO (0) | 1.03 | 0.023 | 0.31 | 0 | fixed | 0.128 |
| | 7 | Effort (3) | 1.09 | 0.022 | 0.31 | 0 | fixed | 0.128 |
| | 8 | Effort (2) | 1.31 | 0.020 | 0.31 | 0 | fixed | 0.128 |

| Species | Model | Covariates (lags) | $\Delta AIC_c$ | $AIC_w$ | RMSE | $Q_{est}$ | $r$ | $r_{est}$ |
|---|---|---|---|---|---|---|---|---|
| | 9 | AMO (1), Landings (3) | 1.39 | 0.019 | 0.28 | 0 | est. | 0.0778 |
| | 10 | AMO (1), Landings (1) | 1.46 | 0.019 | 0.29 | 0 | fixed | 0.128 |
| | 11 | Effort (1) | 1.5 | 0.018 | 0.31 | 0 | fixed | 0.128 |
| | 12 | AMO (1) | 1.55 | 0.018 | 0.3 | 0 | est. | 0.0896 |
| | 13 | Landings (3) | 1.57 | 0.018 | 0.31 | 0 | fixed | 0.128 |
| | 14 | NAO (1), Landings (3) | 1.58 | 0.018 | 0.29 | 0 | fixed | 0.128 |
| | 15 | | 1.68 | 0.017 | 0.33 | 0.00268 | fixed | 0.128 |
| | 16 | PDO (0) | 1.7 | 0.016 | 0.3 | 0.0165 | est. | 0.055 |
| | 17 | PDO (0) | 1.82 | 0.016 | 0.32 | 0 | fixed | 0.128 |
| | 18 | AMO (1), Landings (2) | 1.83 | 0.016 | 0.28 | 0 | est. | 0.0793 |
| *Menticirrhus littoralis* | | | | | | | | |
| | 1 | SBT (0), Landings (2) | 0 | 0.087 | 0.62 | 0 | fixed | 0.289 |
| | 2 | SBT (0), Landings (1) | 0.25 | 0.077 | 0.63 | 0 | fixed | 0.289 |
| | 3 | SBT (0), Landings (3) | 0.74 | 0.060 | 0.61 | 0 | fixed | 0.289 |
| | 4 | WBHI (1) | 1.75 | 0.036 | 0.65 | 0.0775 | fixed | 0.289 |
| | 5 | PNAs (0), Landings (3) | 1.84 | 0.035 | 0.58 | 0 | fixed | 0.289 |
| *Micropogonias undulatus* | | | | | | | | |
| | 1 | | 0 | 0.125 | 0.32 | 0.0251 | est. | 0.0502 |
| | 2 | Effort (2) | 0.59 | 0.094 | 0.31 | 0.0101 | est. | 0.0634 |
| | 3 | Effort (3) | 0.8 | 0.085 | 0.3 | 0.00833 | est. | 0.0666 |
| | 4 | Effort (1) | 1.28 | 0.067 | 0.33 | 0.0167 | est. | 0.0578 |
| *Opisthonema oglinum* | | | | | | | | |
| | 1 | AMO (1) | 0 | 0.451 | 0.53 | 0 | fixed | 0.299 |
| *Orthopristis chrysoptera* | | | | | | | | |
| | 1 | AMO (0) | 0 | 0.209 | 0.39 | 0 | est. | 0.152 |
| | 2 | AMO (0), Landings (3) | 1.71 | 0.088 | 0.38 | 0 | est. | 0.143 |
| *Paralichthys albigutta* | | | | | | | | |
| | 1 | PDO (0) | 0 | 0.114 | 0.7 | 0 | fixed | 0.434 |
| | 2 | PDO (0), Landings (2) | 0.27 | 0.099 | 0.67 | 0 | fixed | 0.434 |
| *Paralichthys dentatus* | | | | | | | | |
| | 1 | Effort (1) | 0 | 0.112 | 0.33 | 0.0461 | est. | 0.0332 |
| | 2 | AMO (0) | 0.39 | 0.091 | 0.33 | 0.0259 | est. | 0.05 |
| | 3 | | 0.58 | 0.083 | 0.32 | 0.0519 | est. | 0.0306 |
| *Paralichthys lethostigma* | | | | | | | | |
| | 1 | Effort (1) | 0 | 0.071 | 0.52 | 0.115 | est. | 0.0974 |
| | 2 | PDO (1), Landings (2) | 0.57 | 0.054 | 0.47 | 0 | est. | 0.219 |
| | 3 | SOI (1), Landings (2) | 1.23 | 0.039 | 0.47 | 0 | est. | 0.225 |
| | 4 | Landings (2) | 1.92 | 0.028 | 0.51 | 0 | est. | 0.264 |
| | 5 | PDO (0), Landings (2) | 1.97 | 0.027 | 0.48 | 0 | est. | 0.232 |
| *Peprilus paru* | | | | | | | | |
| | 1 | PDO (0) | 0 | 0.134 | 0.38 | 0 | est. | 0.147 |
| | 2 | PDO (0) | 1.87 | 0.053 | 0.38 | 0 | fixed | 0.297 |
| *Peprilus triacanthus* | | | | | | | | |

| Species | Model | Covariates (lags) | $\Delta AIC_c$ | $AIC_w$ | RMSE | $Q_{est}$ | $r$ | $r_{est}$ |
|---|---|---|---|---|---|---|---|---|
| | 1 | PNAw (0), Effort (3) | 0 | 0.211 | 0.78 | 0.0413 | fixed | 0.309 |
| | 2 | PNAw (0), Effort (3) | 0.77 | 0.144 | 0.8 | 0.112 | fixed | 0.309 |
| *Pomatomus saltatrix* | | | | | | | | |
| | 1 | WBHI (1) | 0 | 0.133 | 0.66 | 0 | fixed | 0.413 |
| | 2 | WBHI (1), Landings (1) | 1.92 | 0.051 | 0.65 | 0 | fixed | 0.413 |
| *Prionotus carolinus* | | | | | | | | |
| | 1 | SOI (1), Effort (2) | 0 | 0.290 | 0.72 | 0.114 | est. | 0.0241 |
| *Prionotus evolans* | | | | | | | | |
| | 1 | Effort (3), SBT (0) | 0 | 0.263 | 0.58 | 0 | fixed | 0.254 |
| | 2 | WBHI (1), Effort (3) | 0.23 | 0.233 | 0.49 | 0 | fixed | 0.254 |
| *Prionotus tribulus* | | | | | | | | |
| | 1 | PNAs (1) | 0 | 0.087 | 0.51 | 0 | fixed | 0.336 |
| | 2 | | 0.62 | 0.064 | 0.56 | 0 | fixed | 0.336 |
| | 3 | AMO (1) | 0.73 | 0.060 | 0.52 | 0 | fixed | 0.336 |
| | 4 | Effort (3) | 1.91 | 0.034 | 0.54 | 0 | fixed | 0.336 |
| *Sardinella aurita* | | | | | | | | |
| | 1 | PNAs (0) | 0 | 0.086 | 1.81 | 1.08 | fixed | 0.59 |
| | 2 | SOI (1) | 0.01 | 0.086 | 1.24 | 0.0784 | est. | 1.14 |
| | 3 | SOI (1) | 1.52 | 0.040 | 1.23 | 0.159 | fixed | 0.59 |
| | 4 | | 1.7 | 0.037 | 1.31 | 0 | est. | 1.73 |
| *Scomberomorus cavalla* | | | | | | | | |
| | 1 | SOI (0), Landings (3) | 0 | 0.144 | 0.89 | 0.0606 | fixed | 0.351 |
| *Scomberomorus maculatus* | | | | | | | | |
| | 1 | Effort (3) | 0 | 0.215 | 0.38 | 0.0544 | est. | 0.0563 |
| *Scophthalmus aquosus* | | | | | | | | |
| | 1 | WBHI (1), Landings (1) | 0 | 0.085 | 0.46 | 0 | fixed | 0.17 |
| | 2 | SOI (0), Landings (1) | 0.18 | 0.078 | 0.48 | 0.00505 | fixed | 0.17 |
| | 3 | Landings (1) | 1.37 | 0.043 | 0.5 | 0.00521 | fixed | 0.17 |
| | 4 | PDO (0), Landings (1) | 1.6 | 0.039 | 0.48 | 0.00602 | fixed | 0.17 |
| *Selene setapinnis* | | | | | | | | |
| | 1 | WBHI (1), Effort (2) | 0 | 0.132 | 0.69 | 0.0341 | fixed | 0.261 |
| | 2 | PNAs (1), Effort (2) | 0.59 | 0.098 | 0.79 | 0.0387 | fixed | 0.261 |
| | 3 | PNAs (1), Effort (2) | 0.61 | 0.097 | 0.69 | 0.0747 | fixed | 0.261 |
| | 4 | Effort (2) | 0.91 | 0.084 | 0.73 | 0.101 | fixed | 0.261 |
| | 5 | WBHI (1), Effort (2) | 1.15 | 0.074 | 0.66 | 0.0642 | fixed | 0.261 |
| *Sphyraena guachancho* | | | | | | | | |
| | 1 | SOI (1) | 0 | 0.327 | 0.86 | 0.0517 | fixed | 0.419 |
| *Stellifer lanceolatus* | | | | | | | | |
| | 1 | AMO (1) | 0 | 0.260 | 0.38 | 0 | est. | 0.144 |
| | 2 | AMO (1) | 1.42 | 0.128 | 0.38 | 0 | fixed | 0.28 |
| *Stenotomus* spp. | | | | | | | | |
| | 1 | | 0 | 0.049 | 0.89 | 0 | est. | 0.796 |
| | 2 | PNAw (0) | 0.54 | 0.037 | 0.85 | 0 | est. | 0.721 |

| Species | Model | Covariates (lags) | $\Delta AIC_c$ | $AIC_w$ | RMSE | $Q_{est}$ | $r$ | $r_{est}$ |
|---|---|---|---|---|---|---|---|---|
| | 3 | PDO (0) | 1.04 | 0.029 | 0.86 | 0 | est. | 0.736 |
| | 4 | NAO (1) | 1.26 | 0.026 | 0.86 | 0 | est. | 0.743 |
| | 5 | NAO (0) | 1.27 | 0.026 | 0.86 | 0 | est. | 0.744 |
| | 6 | PNAw (1) | 1.77 | 0.020 | 0.87 | 0 | est. | 0.759 |
| | 7 | PNAs (1) | 1.84 | 0.019 | 0.91 | 0.378 | fixed | 0.259 |
| | 8 | WBHI (0) | 1.98 | 0.018 | 0.87 | 0.0241 | est. | 0.655 |
| | 9 | SOI (0) | 1.98 | 0.018 | 0.88 | 0 | est. | 0.766 |
| *Stephanolepis hispida* | | | | | | | | |
| | 1 | SOI (1) | 0 | 0.065 | 0.61 | 0.0332 | est. | 0.204 |
| | 2 | AMO (0) | 0.21 | 0.059 | 0.64 | 0.109 | est. | 0.145 |
| | 3 | PNAs (1), Effort (3) | 0.41 | 0.053 | 0.51 | 0 | est. | 0.258 |
| | 4 | SOI (1), Effort (3) | 1.08 | 0.038 | 0.52 | 0 | est. | 0.266 |
| | 5 | Effort (3) | 1.2 | 0.036 | 0.55 | 0 | est. | 0.305 |
| | 6 | SOI (1), Effort (2) | 1.58 | 0.030 | 0.52 | 0 | est. | 0.271 |
| | 7 | PNAs (1), Effort (2) | 1.66 | 0.028 | 0.52 | 0 | est. | 0.272 |
| | 8 | Effort (2) | 1.82 | 0.026 | 0.56 | 0 | est. | 0.313 |
| | 9 | SOI (1) | 1.83 | 0.026 | 0.54 | 0 | fixed | 0.585 |
| | 10 | AMO (1) | 1.93 | 0.025 | 0.57 | 0.0688 | est. | 0.187 |
| *Syacium papillosum* | | | | | | | | |
| | 1 | NAO (1) | 0 | 0.248 | 1.29 | 0.102 | fixed | 0.659 |
| | 2 | WBHI (0) | 0.39 | 0.204 | 1.16 | 0.16 | fixed | 0.659 |
| | 3 | AMO (1) | 1.23 | 0.135 | 1.08 | 0.131 | fixed | 0.659 |
| *Symphurus plagiusa* | | | | | | | | |
| | 1 | NAO (1) | 0 | 0.077 | 1.03 | 0.202 | fixed | 0.444 |
| | 2 | | 0.17 | 0.071 | 0.9 | 0.0862 | fixed | 0.444 |
| | 3 | PNAw (0), Effort (1) | 0.78 | 0.053 | 0.78 | 0 | fixed | 0.444 |
| | 4 | PNAw (1), Effort (2) | 1.03 | 0.046 | 0.84 | 0.023 | fixed | 0.444 |
| | 5 | Effort (2) | 1.52 | 0.036 | 0.85 | 0.0421 | fixed | 0.444 |
| | 6 | Effort (3) | 1.72 | 0.033 | 0.84 | 0.0645 | fixed | 0.444 |
| *Synodus foetens* | | | | | | | | |
| | 1 | | 0 | 0.049 | 0.41 | 0 | fixed | 0.204 |
| | 2 | AMO (1) | 0.26 | 0.043 | 0.38 | 0 | fixed | 0.204 |
| | 3 | AMO (1), Landings (2) | 1.54 | 0.023 | 0.36 | 0 | fixed | 0.204 |
| | 4 | Landings (3) | 1.75 | 0.020 | 0.4 | 0 | fixed | 0.204 |
| | 5 | PNAs (0) | 1.81 | 0.020 | 0.4 | 0 | fixed | 0.204 |
| | 6 | NAO (1) | 1.86 | 0.019 | 0.4 | 0 | fixed | 0.204 |
| | 7 | AMO (1) | 1.95 | 0.018 | 0.38 | 0 | est. | 0.146 |
| | 8 | Landings (1) | 1.96 | 0.018 | 0.4 | 0 | fixed | 0.204 |
| | 9 | SBT (0) | 1.98 | 0.018 | 0.41 | 0 | fixed | 0.204 |
| *Trachinotus carolinus* | | | | | | | | |
| | 1 | Effort (1) | 0 | 0.046 | 0.5 | 0 | fixed | 0.417 |
| | 2 | Effort (3) | 0.11 | 0.043 | 0.51 | 0 | fixed | 0.417 |
| | 3 | Effort (1) | 0.57 | 0.035 | 0.5 | 0 | est. | 0.255 |

| Species | Model | Covariates (lags) | $\Delta AIC_c$ | $AIC_w$ | RMSE | $Q_{est}$ | $r$ | $r_{est}$ |
|---|---|---|---|---|---|---|---|---|
| | 4 | | 1.14 | 0.026 | 0.55 | 0.0642 | est. | 0.161 |
| | 5 | Effort (2) | 1.29 | 0.025 | 0.53 | 0 | fixed | 0.417 |
| | 6 | PNAs (0), Effort (1) | 1.52 | 0.022 | 0.48 | 0 | est. | 0.23 |
| | 7 | PNAs (0), Effort (1) | 1.59 | 0.021 | 0.48 | 0 | fixed | 0.417 |
| | 8 | Effort (3) | 1.67 | 0.020 | 0.52 | 0.0247 | est. | 0.194 |
| | 9 | PNAs (0), Effort (3) | 1.68 | 0.020 | 0.48 | 0 | fixed | 0.417 |
| | 10 | PNAs (0), Effort (3) | 1.68 | 0.020 | 0.48 | 0 | est. | 0.231 |
| *Trichiurus lepturus* | | | | | | | | |
| | 1 | WBHI (0), Effort (3) | 0 | 0.271 | 0.58 | 0 | fixed | 0.394 |
| | 2 | WBHI (0), Landings (2) | 1.81 | 0.110 | 0.61 | 0 | fixed | 0.394 |
| *Trinectes maculatus* | | | | | | | | |
| | 1 | AMO (1) | 0 | 0.439 | 0.56 | 0 | fixed | 0.246 |
| *Urophycis floridana* | | | | | | | | |
| | 1 | WBHI (2), Effort (3) | 0 | 0.070 | 0.87 | 0 | fixed | 0.651 |
| | 2 | PNAs (0), Effort (3) | 0.36 | 0.059 | 1.1 | 0.0804 | fixed | 0.651 |
| | 3 | WBHI (2), Effort (1) | 0.81 | 0.048 | 0.88 | 0 | fixed | 0.651 |
| | 4 | Effort (3) | 0.85 | 0.047 | 0.93 | 0 | fixed | 0.651 |
| | 5 | PNAs (0), Effort (3) | 1.03 | 0.043 | 0.87 | 0.0345 | fixed | 0.651 |
| | 6 | PNAs (0), Effort (1) | 1.37 | 0.036 | 0.88 | 0.0327 | fixed | 0.651 |
| | 7 | PNAs (0), Effort (1) | 1.46 | 0.034 | 1.24 | 0.0785 | fixed | 0.651 |
| | 8 | NAO (1), Effort (3) | 1.5 | 0.034 | 0.89 | 0 | fixed | 0.651 |
| | 9 | Effort (1) | 1.57 | 0.033 | 0.94 | 0 | fixed | 0.651 |
| | 10 | WBHI (2), Effort (2) | 1.94 | 0.027 | 0.9 | 0 | fixed | 0.651 |
| Elasmobranchs | | | | | | | | |
| *Dasyatis sabina* | | | | | | | | |
| | 1 | WBHI (2), Effort (1) | 0 | 0.140 | 0.55 | 0 | fixed | 0.449 |
| | 2 | WBHI (2), Effort (3) | 1.4 | 0.070 | 0.57 | 0 | fixed | 0.449 |
| | 3 | WBHI (2), Effort (1) | 1.49 | 0.067 | 0.55 | 0 | est. | 0.299 |
| | 4 | WBHI (2), Effort (2) | 1.63 | 0.062 | 0.57 | 0 | fixed | 0.449 |
| *Dasyatis say* | | | | | | | | |
| | 1 | AMO (2) | 0 | 0.118 | 0.53 | 0 | fixed | 0.285 |
| | 2 | | 0.96 | 0.073 | 0.57 | 0.0523 | fixed | 0.285 |
| | 3 | | 1.09 | 0.069 | 0.55 | 0.1 | est. | 0.128 |
| *Gymnura micrura* | | | | | | | | |
| | 1 | Effort (1) | 0 | 0.121 | 0.44 | 0 | est. | 0.191 |
| | 2 | PDO (1), Effort (1) | 0.13 | 0.114 | 0.41 | 0 | est. | 0.166 |
| | 3 | Effort (1), SBT (0) | 0.88 | 0.078 | 0.44 | 0 | est. | 0.172 |
| | 4 | PDO (0), Effort (1) | 1.17 | 0.067 | 0.42 | 0 | est. | 0.174 |
| | 5 | WBHI (2), Effort (1) | 1.43 | 0.059 | 0.42 | 0 | est. | 0.176 |
| | 6 | Effort (2) | 1.76 | 0.050 | 0.45 | 0 | est. | 0.206 |
| *Mustelus canis* | | | | | | | | |
| | 1 | Effort (3) | 0 | 0.431 | 1.11 | 0.577 | fixed | 0.536 |
| *Raja eglanteria* | | | | | | | | |

| Species | Model | Covariates (lags) | ΔAIC$_c$ | AIC$_w$ | RMSE | $Q_{est}$ | $r$ | $r_{est}$ |
|---|---|---|---|---|---|---|---|---|
| | 1 | PNAs (0), Effort (1) | 0 | 0.106 | 0.68 | 0.0585 | est. | 0.0469 |
| | 2 | PDO (1), Effort (1) | 0.81 | 0.071 | 0.52 | 0 | fixed | 0.264 |
| | 3 | AMO (1) | 1.5 | 0.050 | 0.56 | 0 | fixed | 0.264 |
| | 4 | Effort (1) | 1.53 | 0.049 | 0.56 | 0 | fixed | 0.264 |
| *Rhinoptera bonasus* | | | | | | | | |
| | 1 | AMO (0) | 0 | 0.294 | 0.95 | 0 | fixed | 0.705 |
| *Rhizoprionodon terraenovae* | | | | | | | | |
| | 1 | Effort (1) | 0 | 0.093 | 0.31 | 0 | est. | 0.0935 |
| | 2 | | 0.24 | 0.083 | 0.33 | 0.0234 | est. | 0.0582 |
| | 3 | AMO (2) | 0.77 | 0.064 | 0.31 | 0 | est. | 0.0965 |
| | 4 | PNAs (2), Effort (1) | 1.31 | 0.049 | 0.29 | 0 | est. | 0.0863 |
| | 5 | Total F (1) | 1.64 | 0.041 | 0.32 | 0 | est. | 0.1 |
| *Sphyrna tiburo* | | | | | | | | |
| | 1 | Effort (1) | 0 | 0.126 | 0.29 | 0.0111 | est. | 0.0599 |
| | 2 | WBHI (0), Effort (1) | 1.16 | 0.071 | 0.28 | 0 | est. | 0.0799 |
| | 3 | Effort (2) | 1.85 | 0.050 | 0.32 | 0.013 | est. | 0.0634 |
| | 4 | PNAw (1), Effort (1) | 1.9 | 0.049 | 0.32 | 0.0247 | est. | 0.00871 |
| Invertebrates | | | | | | | | |
| *Arenaeus cribrarius* | | | | | | | | |
| | 1 | PDO (1), Effort (1) | 0 | 0.211 | 0.7 | 0 | fixed | 0.421 |
| | 2 | PNAw (0), Effort (1) | 1.12 | 0.121 | 0.71 | 0 | fixed | 0.421 |
| | 3 | PDO (0), Effort (1) | 1.53 | 0.099 | 0.72 | 0 | fixed | 0.421 |
| *Callinectes ornatus* | | | | | | | | |
| | 1 | PDO (1) | 0 | 0.287 | 0.61 | 0.0777 | est. | 0.147 |
| *Callinectes sapidus* | | | | | | | | |
| | 1 | Effort (2) | 0 | 0.128 | 0.71 | 0 | fixed | 0.427 |
| | 2 | WBHI (1), Effort (2) | 0.15 | 0.119 | 0.67 | 0 | fixed | 0.427 |
| | 3 | PDO (1), Effort (2) | 0.54 | 0.098 | 0.7 | 0.0167 | fixed | 0.427 |
| | 4 | PDO (1), Effort (2) | 0.92 | 0.081 | 0.62 | 0.0345 | fixed | 0.427 |
| | 5 | PNAs (1), Effort (2) | 1.33 | 0.066 | 0.69 | 0 | fixed | 0.427 |
| | 6 | WBHI (2), Effort (2) | 1.84 | 0.051 | 0.7 | 0 | fixed | 0.427 |
| *Callinectes similis* | | | | | | | | |
| | 1 | PDO (1), Effort (2) | 0 | 0.296 | 0.57 | 0 | fixed | 0.239 |
| | 2 | PDO (1), Effort (2) | 1.95 | 0.112 | 0.57 | 0 | est. | 0.326 |
| *Doryteuthis* spp. | | | | | | | | |
| | 1 | SOI (0) | 0 | 0.058 | 0.47 | 0 | fixed | 0.259 |
| | 2 | | 0.38 | 0.048 | 0.51 | 0 | fixed | 0.259 |
| | 3 | PNAs (0) | 0.4 | 0.048 | 0.48 | 0 | fixed | 0.259 |
| | 4 | SOI (0), Landings (2) | 0.75 | 0.040 | 0.45 | 0 | fixed | 0.259 |
| | 5 | Landings (2) | 0.89 | 0.037 | 0.48 | 0 | fixed | 0.259 |
| | 6 | WBHI (1) | 1.6 | 0.026 | 0.49 | 0 | fixed | 0.259 |
| | 7 | Landings (1) | 1.98 | 0.022 | 0.49 | 0 | fixed | 0.259 |
| *Hepatus epheliticus* | | | | | | | | |

| Species | Model | Covariates (lags) | $\Delta\mathrm{AIC}_c$ | $\mathrm{AIC}_w$ | RMSE | $Q_{est}$ | $r$ | $r_{est}$ |
|---|---|---|---|---|---|---|---|---|
| | 1 | PNAs (1) | 0 | 0.210 | 0.59 | 0.0719 | est. | 0.227 |
| | 2 | PNAs (1) | 0.43 | 0.170 | 0.64 | 0.0476 | fixed | 0.454 |
| *Litopenaeus setiferus* | | | | | | | | |
| | 1 | AMO (0) | 0 | 0.218 | 0.56 | 0 | fixed | 0.248 |
| | 2 | SOI (0) | 1.25 | 0.117 | 0.57 | 0 | fixed | 0.248 |
| *Lolliguncula brevis* | | | | | | | | |
| | 1 | SOI (1) | 0 | 0.144 | 0.24 | 0.00307 | est. | 0.0396 |
| | 2 | PDO (1) | 0.96 | 0.089 | 0.23 | 0 | fixed | 0.089 |
| | 3 | PNAw (1) | 1.09 | 0.083 | 0.24 | 0.0032 | est. | 0.0419 |
| | 4 | PDO (1) | 1.11 | 0.082 | 0.23 | 0 | est. | 0.0529 |
| | 5 | SOI (1) | 1.99 | 0.053 | 0.24 | 0.00118 | fixed | 0.089 |
| *Ovalipes ocellatus* | | | | | | | | |
| | 1 | SOI (1) | 0 | 0.139 | 0.68 | 0 | fixed | 0.316 |
| | 2 | SOI (1) | 1.08 | 0.080 | 0.68 | 0 | est. | 0.456 |
| *Ovalipes stephensoni* | | | | | | | | |
| | 1 | | 0 | 0.092 | 0.68 | 0 | fixed | 0.447 |
| | 2 | PDO (0) | 0.63 | 0.067 | 0.64 | 0.0133 | fixed | 0.447 |
| | 3 | WBHI (1) | 0.81 | 0.061 | 0.65 | 0 | fixed | 0.447 |
| | 4 | PNAs (0) | 0.92 | 0.058 | 0.65 | 0 | fixed | 0.447 |
| | 5 | PNAw (1) | 1.4 | 0.045 | 0.66 | 0 | fixed | 0.447 |
| | 6 | WBHI (0) | 1.51 | 0.043 | 0.66 | 0 | fixed | 0.447 |
| | 7 | SOI (0) | 1.88 | 0.036 | 0.67 | 0.012 | fixed | 0.447 |
| *Pagurus pollicaris* | | | | | | | | |
| | 1 | SBT (0) | 0 | 0.233 | 1.22 | 0 | est. | 1.24 |
| | 2 | | 0.81 | 0.156 | 1.29 | 0.528 | fixed | 0.447 |
| | 3 | | 1.08 | 0.136 | 1.24 | 0.249 | est. | 0.89 |
| *Persephona mediterranea* | | | | | | | | |
| | 1 | PNAs (0), Effort (1) | 0 | 0.148 | 0.49 | 0 | fixed | 0.328 |
| | 2 | Effort (1) | 0.24 | 0.132 | 0.54 | 0 | fixed | 0.328 |
| | 3 | PNAw (0), Effort (1) | 1.06 | 0.087 | 0.51 | 0 | fixed | 0.328 |
| | 4 | PDO (0), Effort (1) | 1.3 | 0.077 | 0.51 | 0 | fixed | 0.328 |
| *Portunus gibbesii* | | | | | | | | |
| | 1 | NAO (0) | 0 | 0.205 | 0.73 | 0.159 | fixed | 0.257 |
| | 2 | WBHI (2) | 1.48 | 0.098 | 0.73 | 0.0942 | fixed | 0.257 |
| | 3 | AMO (1) | 1.98 | 0.076 | 0.74 | 0.0851 | fixed | 0.257 |
| *Portunus spinimanus* | | | | | | | | |
| | 1 | PDO (1), Effort (2) | 0 | 0.242 | 0.45 | 0 | est. | 0.199 |
| | 2 | PDO (1), Effort (2) | 0.79 | 0.163 | 0.45 | 0 | fixed | 0.396 |
| *Squilla empusa* | | | | | | | | |
| | 1 | Effort (2) | 0 | 0.095 | 0.56 | 0 | fixed | 0.483 |
| | 2 | Effort (1) | 0.83 | 0.063 | 0.58 | 0 | fixed | 0.483 |
| | 3 | PNAs (1), Effort (2) | 1.75 | 0.040 | 0.59 | 0.0525 | est. | 0.151 |

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# CHAPTER 4

# A shark species and its prey: Relative importance of predation, fishing, and environmental variability to population growth rates

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## ABSTRACT

Multiple processes influence the abundance dynamics of marine fish and shellfish populations, including density-dependence, environmental variability, trophodynamic interactions, and fishing. Because marine food webs are complex and difficult to characterize, determining the relative importance of trophodynamics to a species' population dynamics is challenging. For species that occupy lower trophic positions, accurately explaining and predicting abundance dynamics can be enhanced by accounting for top-down predation pressure. In this study we present food habits of the bonnethead shark (*Sphyrna tiburo*) and results from a multispecies time-series model quantifying the impacts of this predator on population growth rates of five prey species within nearshore coastal Southeast U.S. Atlantic waters: lesser blue crab (*Callinectes similis*), two lady crabs (*Ovalipes ocellatus* and *O. stephensoni*), blotched swimming crab (*Portunus spinimanus*), and a mantis shrimp (*Squilla empusa*). Density-dependence and changes in bycatch mortality were important for explaining *S. tiburo* temporal trends. Population growth rates of multiple prey species were negatively impacted by *S. tiburo* abundance, indicating that predation pressure has a measurable population effect on these prey. Additionally, environmental conditions associated with the Pacific Decadal Oscillation were correlated with the abundance dynamics of multiple prey species. This study highlights advantages of simultaneously accounting for multiple exogenous factors, namely trophodynamic interactions, when modeling abundance trends of lower trophic level fish and shellfish species.

# INTRODUCTION

Food web interactions influence the abundance dynamics of species. During the 20th century this fundamental idea gained prominence in ecology through the seminal works of Elton (1927) and Lindeman (1942), which in turn prompted an acceleration of trophic ecology research beginning in the 1960's (e.g., Connell, 1961; Paine, 1966) that continues presently (Libralato *et al.*, 2014). The importance of food web dynamics has long been recognized within the marine fisheries scientific community (e.g., Baird, 1873), yet the leading paradigm of fisheries science is inherently single-species with a stock or population emphasis (Angelini and Moloney, 2007; Link, 2010). Although single-species methods that do not consider exogenous variables still dominate fisheries assessments globally (Skern-Mauritzen *et al.*, 2016), more holistic approaches that include multispecies considerations have gained importance through the development and implementation of novel and practical analytical methods (Plagányi *et al.*, 2014; Collie *et al.*, 2016).

Quantitative multispecies assessment models in fisheries science take many forms ranging from relatively simple multispecies production models (Collie and Gislason, 2001) to those that model trophic webs of entire ecosystems complete with socioeconomic considerations (Pauly *et al.*, 2000; Fulton *et al.*, 2005). There is utility for every model framework no matter its level of complexity, although there have been recent calls for contextually appropriate models with intermediate levels of complexity that minimize uncertainty (Plagányi *et al.*, 2014; Collie *et al.*, 2016). Within the relatively data-rich Northeast U.S. Atlantic region, multiple forms of multispecies age-structured assessment models with predation components have provided tactical management advice (i.e., quantitative, short-term; Link, 2010) (Plagányi *et al.*, 2014). Mohn and

Bowen (1996) implemented a Leslie matrix approach to model the effects of grey seal (*Halichoerus grypus*) predation on Atlantic cod (*Gadus morhua*), concluding that grey seal predation mortality was not a major contributor to the collapse of this iconic stock. Garrison et al. (2010) applied a refined version of multispecies virtual population analysis (MSVPA) to Atlantic menhaden (*Brevoortia tyrannus*) and several of its primary predators, emphasizing the importance of time-varying predator diet information for effective assessment of menhaden and forage fish generally. Curti et al. (2013) applied a multispecies catch-at-age model functionally related to MSVPA (Jurado-Molina *et al.*, 2005); predicted abundance patterns for three demersal groundfish species differed between single-species and multispecies model formulations due to interplay between natural and fishing mortality. Only with robust predator diet data were these frameworks able to be implemented.

For many marine and aquatic species, an assessment model framework may not be appropriate or necessary because the species is not an actively managed resource. For some managed species, insufficient catch, life history, or trophic data may not permit the use of an assessment model framework that may require many mechanistic assumptions (Hampton *et al.*, 2013). In such cases, hypotheses regarding trophic interactions can be tested via multivariate autoregressive (MAR) models, a class of statistical time series models rooted in the Gompertz equation describing population growth with density-dependence (Ives *et al.*, 2003). MAR state-space (MARSS) models extend the MAR framework by allowing specification of observation error in addition to process error (Hampton *et al.*, 2013). MAR modeling has been implemented within planktonic freshwater systems (Ives *et al.*, 1999; Francis *et al.*, 2014), marine fish communities

(MacNally *et al.*, 2010; Torres *et al.*, 2017), and within terrestrial systems to a lesser extent (Vik *et al.*, 2008; Ruhí *et al.*, 2015) (see Hampton et al., 2013 for a review of applications across system types).

In the Southeast U.S. Atlantic, the marine system in which this study takes place, multispecies trophic modeling has been very limited. Okey and Pugliese (2001) constructed a preliminary Ecopath model (Polovina, 1984) for the region, but inputs were mostly based on expert knowledge and diet characterizations from outside of the ecosystem. Although there are numerous diet studies for Southeast U.S. Atlantic fish predators (reviewed by Marancik and Hare, 2005), the lack of trophic modeling efforts in the region can in part be attributed to a lack of robust food studies programs with spatiotemporal sampling consistency such as those conducted in the Northeast U.S. Atlantic (Garrison and Link, 2000) and North Pacific (Livingston *et al.*, 2017) . To advance the use of multispecies models in Southeast U.S. Atlantic region, we utilized the MARSS modeling framework to quantify predation effects of a specialist marine predator, the bonnethead shark (*Sphyrna tiburo*), on the abundance dynamics of five crustacean prey species:  lesser blue crab (*Callinectes similis*), ocellate lady crab (*Ovalipes ocellatus*), coarsehand lady crab (*Ovalipes stephensoni*), blotched swimming crab (*Portunus spinimanus*), and a mantis shrimp (*Squilla empusa*). Within Southeast U.S. Atlantic waters, Stratton et al. (2017) reported a population decline of these prey species concomitant with a population rebound of the bonnethead following a decline in bycatch mortality (SEDAR, 2013b). Each of these five crustacean species are either documented or likely diet components of *S. tiburo* (Bethea et al., 2007; Cortés et al., 1996; Kroetz et al., 2017; Lessa and Almeida, 1998; this study). Although our focus was on top-down predation effects, the MARSS framework enabled us to concurrently evaluate the effects of fishing, density-dependence, and relevant environmental drivers on population growth rates of these six species. Based on results for this predator-prey system, implications for modeling commercially-important crustacean populations in a multispecies context within the region are discussed.

## METHODS

### Survey description

Bonnethead and crustacean relative abundance data were obtained from the Southeast Area Monitoring and Assessment Program – U.S. South Atlantic (SEAMAP-SA), a fishery-independent bottom trawl survey operated by the South Carolina Department of Natural Resources (SCDNR; Charleston, SC). SEAMAP-SA samples the demersal biological assemblage from Cape Canaveral, FL to Cape Hatteras, NC thrice annually during northern spring, summer, and fall. The survey employs a stratified fixed station design, whereby a pre-determined subsample of fixed stations are chosen for seasonal sampling from a pool of all possible fixed stations distributed across multiple sampling regions. At each sampling station, two tongue trawl nets (13.5-m wingspan) are towed on the bottom for 20 minutes from a double-rigged 23-m St. Augustine shrimp trawler. The catch is brought on-board, sub-sampled (if necessary) and sorted, all individuals are identified to the lowest possible taxon and enumerated, and allometric data are collected for certain priority species. SEAMAP-SA data are publicly available at seamap.org (SEAMAP-SA Data Management Work Group, 2014).

### Shark diet characterization

To characterize bonnethead diet composition within the study area, stomach samples were collected during three sampling seasons:  Fall 2012, Spring 2013, and Fall 2013. Diet samples were not collected in summer for logistical reasons because diet sampling efforts were part of a larger multispecies diet collection effort. At each sampling station, length and weight were measured for all *S. tiburo* individuals captured. Specimens were euthanized and their stomach and contents excised and preserved in a Normalin fixative for later laboratory diet characterization. Euthanization procedures were approved by the College of William & Mary's Institutional Animal Care and Use Committee. In the laboratory, wet stomach contents were sorted and identified to the lowest possible taxon, then weighed to the nearest thousandth of a gram. Percent diet composition of prey groups were calculated gravimetrically using a cluster sampling estimator:

$$\%D_{jk} = \sum_{i=1}^{N} \frac{m_{ijk}}{m_{ij}} \times 100 \qquad (13)$$

where $m_{ijk}$ is the total weight prey group $k$ in the stomachs of all predators in size group $j$ captured at sampling site $i$. Predators were separated into small and large size groups (see next subsection). By pooling all predators from the same size group captured at a given site into one "group stomach", intra-sample correlation in diet is reduced (Bogstad *et al.*, 1995). Other applications of the cluster sampling estimator to diet data have included a proportional sample size weighting coefficient representative of the fraction of individuals subsampled at each location (Buckel *et al.*, 1999; Latour *et al.*, 2008; Buchheister and Latour, 2015). However, inclusion of this term was not necessary here since all *S. tiburo* specimens captured during the three specified seasons were processed for diet characterization.

## Data specification

For input into MARSS models, we generated standardized annual indices of relative abundance using 21 years of SEAMAP-SA relative abundance data from 1994 to 2014 collected within the four southernmost SEAMAP-SA sampling regions from Cape Canaveral, FL to Cape Fear, NC (Fig. 12). SEAMAP-SA also samples within Onslow and Raleigh Bays of North Carolina, but *S. tiburo* is uncommon in those areas during northern summer and largely absent during spring and fall (MAS, unpublished SEAMAP-SA data).

All trawl sampling stations were within the nearshore zone, defined here as coastal ocean waters between 15 and 30-ft water column depth.

For *S. tiburo*, we generated separate indices for small and large animals based on length frequency data. Small animals were separated from large animals by total length cutoffs of 61 and 69-cm for spring and summer data, respectively (Fig. 13); fall data were not used for generating shark relative abundance indices. An abundance of young, small animals appear in SEAMAP-SA catches during fall sampling (October-November), many of which are neonates pupped during late summer parturition (Manire *et al.*, 1995). Based on age-specific length ranges from Frazier et al. (2014), sharks in the small size category correspond to ages 0-3, while those in the large size category are 3+ years old. The bimodal pattern in *S. tiburo* SEAMAP-SA length-frequency data may be due to habitat partitioning of age 2-3 sharks (~60-70 cm total length) outside of the survey range, a faster growth rate for this age range (Frazier *et al.*, 2014) resulting in fewer of those animals being sampled, or a combination of both.

To allow *S. tiburo* predation impacts to be reflected in prey population abundance indices, the year was redefined as between October through September. Bonnethead indices were generated with spring (April-May) and summer (July-August) data during year $t$, while prey indices were generated using fall data from the same calendar year (October-November) but specified in the model as year $t + 1$.

### Abundance indices

Standardized annual indices of relative abundance were generated by modeling numbers of individuals per tow with covariates using generalized linear models (GLMs) (Nelder and Wedderburn, 1972) and zero-inflated generalized linear models (ZIGLMs)

(Lambert, 1992; Hall, 2000). We tested four GLM frameworks: negative binomial GLM (NBGLM), Poisson GLM (PGLM), zero-inflated negative binomial GLM (ZINB), and zero-inflated Poisson GLM (ZIP) (Table S2; McCullagh and Nelder 1989; Zuur *et al.* 2009; Hilbe 2011). A decision tree was implemented to identify the optimal model framework for each species (Fig. 14). Tow-level covariates included at this stage of analysis were year (categorical), season (categorical, two levels for predator models), region (categorical, four levels), and effort (log-transformed $m^2$ area of seafloor swept, input as an offset variable).

To determine if a species dataset was zero-inflated, Akaike's Information Criterion (AIC) (Akaike, 1973) was used to compare a main effects ZINB model with all covariates in the count process and region in the binomial process ('binomial_Y' model) to the same model with no covariates in the binomial process ('binomial_N' model). A season covariate was not included in prey species models given that only fall data were utilized. If $\mathrm{AIC}_{binomial\_Y} - \mathrm{AIC}_{binomial\_N} \leq 2$, strong support was evident for a ZIGLM framework. For zero-inflated datasets, a likelihood ratio test ($\alpha = 0.05$) was conducted to determine if the saturated ZIP was overdispersed compared to the saturated ZINB (Zuur *et al.*, 2012). This test requires nested models and is appropriate here because a ZIP is a special nested case of a ZINB (Hilbe, 2011). For instances where $\mathrm{AIC}_{binomial\_Y} - \mathrm{AIC}_{binomial\_N} > 2$, a regular GLM framework (i.e., non- zero-inflated) was selected. Dispersion was calculated for the PGLM as the ratio of squared and summed Pearson residuals to the residual degrees of freedom (McCullagh and Nelder, 1989); we considered a PGLM unacceptably overdispersed if dispersion $> 2$.

Once an optimal GLM framework was selected for each species, an information-theoretic approach (Burnham and Anderson, 2002) to model selection was adopted with the goal of identifying the most parsimonious combination of tow-level covariates. We fitted main effects models for all combinations of tow-level covariates and retained the model with the lowest $\mathrm{AIC}_c$ value (Sugiura, 1978). The index variable "Year" and the scaler "Effort" were included in every model considered for selection. For each species' most supported GLM, we estimated annual relative abundances by averaging the marginal mean predictions for each year (Searle *et al.*, 1980). Final annual index estimates and variances were estimated via year-stratified bootstrapping (*n* = 5,000) (Efron, 1983).

## Multispecies modeling

A multivariate autoregressive state-space (MARSS) modeling framework was utilized to quantify the relative effects of density-dependence, trophic interactions, and exogenous factors on population growth rates for our species of interest. The MARSS model we implemented is represented in matrix notation as follows (Holmes *et al.*, 2014):

$$\mathbf{x}_t = \mathbf{B}\mathbf{x}_{t-1} + \mathbf{u} + \mathbf{C}\mathbf{c}_t + \mathbf{w}\text{, where } \mathbf{w} \sim \mathrm{MVN}(0, \mathbf{Q}) \qquad (14a)$$

$$\mathbf{y}_t = \mathbf{Z}\mathbf{x}_t + \mathbf{a} + \mathbf{D}\mathbf{d}_t + \mathbf{v}_t\text{, where } \mathbf{v}_t \sim \mathrm{MVN}(0, \mathbf{R}_t) \qquad (14b)$$

where the $\mathbf{x}_t$ equation is the state process and the $\mathbf{y}_t$ equation is the observation process. Multivariate response time series data are represented as $\mathbf{y}_t$ and covariate data as $\mathbf{c}_t$ and $\mathbf{d}_t$. The elements of $\mathbf{C}$ are estimated (time-invariant and linear) effects of $\mathbf{c}_t$ on states $\mathbf{x}_t$, and the elements of $\mathbf{D}$ are estimated effects of $\mathbf{d}_t$ on observations $\mathbf{y}_t$. The matrix **B** holds estimated time-invariant community interactions, which were of primary interest for this study. Vectors $\mathbf{u}$ and $\mathbf{a}$ are scaling terms, with $\mathbf{u}$ fixed at zero. Both predator and prey population time series resembled random walks, thus we assumed all populations were at equilibrium and demeaned the input (observed) time series data. Vectors $\mathbf{w}$ and $\mathbf{v}_t$ are process and measurement errors, respectively, with associated variance-covariance matrices $\mathbf{Q}$ and $\mathbf{R}_t$.

The effects of multiple covariates on population trends were considered (Table 7). Two covariates were considered within the state process (Eq. 14a), one fishing-related and the other environmental. Covariate coefficients were estimated separately for each prey species and shark size group. A recent stock assessment for *S. tiburo* indicated bycatch within commercial penaeid shrimp trawl nets was the largest source of mortality for the stock (SEDAR, 2013b), thus we considered a measure of shrimp fleet trawling effort as a proxy for bycatch mortality derived from Walter and Isley (2014) (see Appendix II). Crustacean species are also common bycatch in this fishery (Scott-Denton *et al.*, 2012), so the effect of this covariate on prey species was also examined. Previous research indicated that the Pacific Decadal Oscillation (PDO) was correlated with abundance patterns for multiple crustacean species (Stratton *et al.*, 2017), thus we considered the effect of the PDO on each of the five prey species. In addition to state process covariates, an average annual temperature anomaly for the study region was considered as a covariate within the observation process (Eq. 14b). This covariate was intended to capture potential changes in availability of species sampled by the survey due to interannual differences in temperatures that in part act to govern migration phenology. Annual temperature anomalies were calculated as the normalized average of mean bottom temperature at sample locations within each SEAMAP-SA sampling region and season (spring/summer for predator indices, fall for prey indices).

Several assumptions were made prior to model selection using AIC. We were primarily interested in the effects of predation on crustacean prey species abundances, thus for simplification we did not estimate the effects of prey species abundances on predator species abundance within the **B** matrix. All time series were assumed independent of one another, thus covariances ($\mathbf{R}_t$ and **Q** off-diagonals) were fixed at zero. Time-specific measurement error variances were fixed as those variances estimated from GLM bootstrapping in log space. We assumed all indices shared a process error variance $q$ because estimating more than one process error variance parameter resulted in either model non-convergence or the inability to estimate uncertainty due to confounded parameters. Unbiased parameter coefficients and associated uncertainties were estimated from parametric bootstrapping appropriate for state-space models (*n* = 500) (Stoffer and Wall, 1991; Cavanaugh and Shumway, 1997) and Akaike weighted:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^{R}\exp(-\frac{1}{2}\Delta_r)} \tag{15}$$

where $w_i$ is the Akaike weight of model $i$ in model set $r$, and $\exp(-\frac{1}{2}\Delta_i)$ is proportional to the relative log-likelihood of model $i$ (Burnham and Anderson, 2002). Final weighted parameter estimates were calculated as:

$$\hat{\hat{\beta}} = \frac{\sum_{i=1}^{R} w_i \hat{\beta}_i}{\sum_{i=1}^{R} w_i} \tag{16}$$

where $\hat{\beta}$ is the parameter estimate in model $i$, and $\hat{\hat{\beta}}$ is the weighted parameter estimate (Symonds and Moussalli, 2011). Because our model set did not contain a single model with an Akaike weight greater than 0.9, we used “full-model” averaging as opposed to “natural” averaging (see Symonds and Moussalli, 2011). Bootstrapped CIs and model predicted abundances (‘states’) were also weighted using this method. A shrinkage estimator can be applied for estimating the variance of $\hat{\hat{\beta}}$ and symmetric CIs based on $\hat{\hat{\beta}}$ (Lukacs *et al.*, 2010), however this formulation was inappropriate for our application because bootstrapped CIs were asymmetric for many community interaction coefficients. Bias of model-predicted abundances were assessed by Root Mean Squared Error (RMSE) (Hyndman and Koehler, 2006):

$$\mathrm{RMSE} = \sqrt{\textstyle\sum_{t=1}^{n}(Y_t - S_t)^2/n} \tag{17}$$

where $S_t$ is the time-specific predicted state value for observation $Y_t$ for a time series of length $n$.

## Co-occurrence analysis

As a complement to diet data and multispecies model results, we estimated probabilities of co-occurrence (Veech, 2013) for *S. tiburo* size groups and modeled prey species based on tow-level data from 1994-2014. We also estimated co-occurrence probabilities for commercially-important crustacean prey species that we were unable to include in multispecies modeling due to high uncertainty in their GLM indices. Co-occurrence probabilities were estimated using only tows in which the relevant shark size group was captured. Co-occurrence analysis allowed us to gain a cursory understanding of preferential prey species selection for each shark size group.

## Computing

We conducted all statistical analyses in R (R Core Team, 2016) using the following packages: *MASS* and *pscl* (Jackman, 2015) for generalized linear modeling; *MARSS* (Holmes *et al.*, 2012) for multispecies modeling; *AICcmodavg* (Mazerolle, 2015) and *lmtest* (Zeileis and Hothorn, 2002) for model selection; *boot* (Canty and Ripley, 2015) and *MARSS* for bootstrapping; *cooccur* for co-occurrence analysis (Griffith *et al.*, 2016); *ggplot2* (Wickham, 2009) and *gridExtra* (Auguie, 2016) for plotting; *doBy* (Højsgaard and Halekoh, 2014), *dplyr* (Wickham and Francois, 2016), *foreach* and *doParallel* (Revolution Analytics and Weston, 2015), *formula.tools* (Brown, 2015), *plyr* (Wickham, 2011), and *reshape2* (Wickham, 2007) for data manipulation and programming.

## RESULTS

### Shark diet characterization

During three seasons of diet sampling (Fall 2012, Spring 2013, and Fall 2013), a total of 89 small and 207 large *S. tiburo* specimens were collected from 29 and 44 sampling stations, respectively. The diet composition by weight of both small and large bonnethead sharks was predominated by crustaceans, followed distantly by teleost fishes and other taxa (Table 8). The number of identified prey types within stomachs of large sharks was greater than that in small sharks, indicating a broader potential prey field and dietary breadth for larger animals. Compared to small sharks, large sharks consumed more portunid crabs, mantis shrimps (Stomatopoda), and horseshoe crabs (Limulidae), both in terms of number of species and percent diet by weight. Compared to large sharks, small sharks selected crustacean taxa such as crabs, shrimps and copepods with smaller maximum body sizes (e.g., *Rimapenaeus constrictus*, *Gilvossius setimanus*). A greater number of teleost fish species were identified in the stomachs of large sharks, although the percent weight of fish was similar among size groups.

### Abundance indices

The optimal framework for species indices was either a zero-inflated negative binomial GLM or a negative binomial GLM (Table 9). For all indices where a NBGLM was optimal, the model with the lowest AIC values contained the covariate “Region” along with required covariate “Year” and the scaler log-transformed “Effort” offset. For species indices estimated within a ZINB framework the covariate “Region” was always contained in the model with the lowest AIC value, in both the count and binomial processes. The covariate “Season” was not contained in the lowest AIC model for either predator index. Median annual observation variance, a summary statistic useful for comparing how precisely a species or size group was sampled, was lowest for the large bonnethead index (0.10) and highest for *O. stephensoni* (0.51); most species had median values on the low end of this range (Table 9). GLM-estimated index time series trends for both shark size groups exhibited positive directional change through time (Fig. 15A) concomitant with a decrease in shrimp trawling effort. All prey species exhibited an overall decreasing linear trend in abundance during the study period (Table 9), as well as displayed some level of synchronicity for interannual fluctuations in abundance (Fig. 15B).

### Multispecies modeling

MARSS models with various combinations of covariates were fitted and ranked with AIC. Twenty models for which community interactions (**B** matrix off-diagonals) were estimated (Table 10) had AIC values at least 43 points less than twenty comparable models with only density-dependence estimated (not tabulated). This comparison of model sets indicates that including community interactions improved fits for all models regardless of covariate parameterizations. Community interaction models with the most support always contained parameters estimating the effect of fishing on predator size groups and the effect of the PDO on prey species (Table 10). The effects of fishing on prey species and of temperature anomalies on predator or prey species were not always contained in the highest ranked models, indicating their lesser importance to explaining abundance dynamics. Eleven models with strong to moderate support ($\Delta$AIC < 7) had non-zero AIC weights and were used to obtain final weighted parameter coefficient estimates and confidence intervals (CIs).

Estimated predator-on-prey effects were negative and significant at $\alpha = 0.01$ for large sharks on three of the five prey species – *C. similis*, *O. stephensoni*, and *S. empusa*. A predation effect was not seen for small sharks on any prey species (Table 11, Fig. 16). Density-dependence was indicated for large sharks and all prey species, but not for small sharks. A negative effect of large on small sharks was detected, but not vice versa. Trophic effects of small and large sharks on prey species had consistent positive and negative biases, respectively (Table 11). The level of bias for these parameters was related to the magnitude of time-varying observation errors fixed for each species based on realistic GLM-estimated variances; the magnitude and bias of community interaction estimates, as well as CI asymmetry, all decreased as fixed observation errors were artificially reduced by 50% and 90% (results not shown). Fishing negatively impacted abundances of both shark size groups (Fig. 16), as well as some prey species at $\alpha = 0.05$ (Table 12). Abundances for all prey species except *O. stephensoni* were positively associated with the PDO. *O. ocellatus* was negatively associated with temperature anomalies, likely indicating increased availability to the survey gear when fall water temperatures were below average.

Akaike-weighted process error variance ($q$) shared among all time series was estimated at 0.017 (99% CI: 0.001, 0.028), which was an order of magnitude less than then lowest median annual observation variance (Table 9). The unbiased bootstrap estimate for $q$ was 0.027. For most species and size groups, MARSS model predictions generally tracked observed (i.e., GLM-estimated) abundance estimates (Fig. 17). Model predicted abundances were least biased for large sharks and *C. similis* (RMSE = 0.07) and most biased for *O. stephensoni* (RMSE = 0.54). A comparison of model 7 (see Table

10) fitted with community interactions versus the same model fitted with only density-dependence revealed informative differences in model prediction bias and uncertainty (Table 13). For prey species *C. similis*, *P. spinimanus*, and *S. empusa*, prediction bias was improved (i.e., lower RMSE) by including community interactions. For *Ovalipes* spp. prediction bias worsened when community interactions were included. For *O. stephensoni*, this result conflicts with the strong negative predation effect on this species estimated for large sharks. Prediction bias for large sharks increased substantially when an interaction with small sharks was included, while bias for small sharks was nearly unchanged when a competitive effect of large sharks was included. Although changes in prediction bias between model types varied among species, prediction uncertainty (i.e., median SE across years) was improved for all species when community interactions were included (Table 13).

### Co-occurrence probabilities

Of the five prey species included in multispecies modeling, *C. similis* and *O. stephensoni* had the highest median probability of nearshore co-occurrence in either spring or summer (> 40%) with large bonnetheads (Table 14). These two prey species also had the highest model-estimated predation effects from large sharks (Table 11). *O. ocellatus, P. spinimanus* and *S. empusa* were less likely to co-occur with large sharks in spring and summer (12-28% range in median probability). The commercially-important *Callinectes sapidus* (blue crab) had low co-occurrence probabilities for both shark size groups (Table 14) despite its importance in the diets of both (Table 8). Two commercially-important penaeid shrimps had high probabilities of co-occurrence with both shark size groups: *Farfantepenaeus aztecus* (brown shrimp) in summer and

*Litopenaeus setiferus* (white shrimp) in spring and summer. Both shrimp species were found in shark stomachs (Table 8).

## DISCUSSION

In this study, we present evidence that multiple processes govern the abundance dynamics of a coastal marine predator and five of its prey species. Multispecies model results informed by empirical diet data revealed that the inclusion of trophic interactions was important for explaining the abundance dynamics for multiple crustacean species we examined. Model-estimated predation effects were greater in magnitude than endogenous (density-dependence) and other exogenous (fishing, environmental) effects, although each type of factor was informative in explaining population growth patterns for *S. tiburo* and some prey species. Considering all of these processes simultaneously – density-dependence, fishing, trophodynamics, and environmental variability – provided a more complete understanding of population regulating factors and their relative importance.

Our primary focus was to test the hypothesis that *S. tiburo* had measurable population impacts on crustacean species of interest. This ensemble of species was chosen for modeling based on two lines of evidence. First, there is indirect but convincing time series evidence that a population rebound of *S. tiburo*, which followed a reduction in bycatch mortality for this predator species (SEDAR, 2013b), had indirect trophic effects on multiple demersal crustacean populations (Stratton *et al.*, 2017). Second, our diet results are in agreement with studies from other regions characterizing the bonnethead as a specialist predator that feeds primarily on crustaceans, especially crabs (Cortés *et al.*, 1996; Lessa and Almeida, 1998; Bethea *et al.*, 2007; Kroetz *et al.*, 2017). Thus, the five *S. tiburo* prey species that were reliably sampled by SEAMAP-SA were included in multispecies models. *P. spinimanus* was the only prey species we modeled that has not been identified to species in any *S. tiburo* diet study to date. In our study, unidentified *Portunus* sp. comprised 4.2% of *S. tiburo* diet by weight, thus *P. spinimanus* may have been present but not positively identified.

## Trophodynamics

Our work demonstrates the particular utility of investigating trophic interactions for explaining time series trends for marine species potentially subject to high predation rates. In nearly all modern day fishery stock assessments, predation is encapsulated within a natural mortality parameter, which is difficult to estimate and thus typically assumed based on life history characteristics (Vetter, 1988). Natural mortality is commonly fixed at too low a value in single species stock assessments because predation is not explicitly accounted for, potentially resulting in less conservative biological reference points (Tyrrell *et al.*, 2011). For marine species that occupy lower trophic levels such as forage fishes, accounting for predation can be critical for proper management (Tyrrell *et al.*, 2008). Although the currency used in the MARSS model framework is population growth rate (Ives *et al.*, 2003) and not mortality rate, the former directly reflects the combination of mortalities and births within the population. In our case the prey species of interest are not of commercial interest, thus implementing a multispecies time series model was more suitable than an assessment framework.

The MARSS framework has most often been implemented for species or species groups that are of ecological and conservation interest (Francis *et al.*, 2014; Paleczny *et al.*, 2015; Ruhí *et al.*, 2015; Greenville *et al.*, 2016), though some recent efforts have utilized this modeling tool to assess the status of populations that have direct economic value in marine systems (Tolimieri *et al.*, 2017; Torres *et al.*, 2017). Although the prey species we modeled are not commercially-important, this framework could be extended to actively-managed crustacean species in the Southeast U.S. Atlantic region. Diet data from this study and others document the blue crab (*C. sapidus*) as an important prey resource for the bonnethead, especially large females that frequent estuaries where blue crabs are in higher densities (Ulrich et al. 2007, Castro 2011, this study). Although SEAMAP-SA is not a suitable survey for generating a *C. sapidus* index abundance within our study range, Colton et al. (2014) reviewed *C. sapidus* time series trends derived from stock assessments and revealed an overall decline from 1990-2008 in Florida, Georgia, and South Carolina. Assessment-derived *C. sapidus* interannual trends also appear synchronous with trends for the five prey species we modeled, suggesting that these six species are responding to similar exogenous factors despite the estuarine habitat preference of *C. sapidus*. This apparent synchrony indicates that increased predation pressure is likely in part responsible for the overall recent decline of *C. sapidus*, a species that accounted for 25% of all fishery landings revenue (> $46 million) in the U.S. South Atlantic region during 2014 (NMFS, 2016).

We made the simplifying assumption that *S. tiburo* was the only predator affecting prey species population growth trends. Although this assumption is unrealistic, existing diet data does not suggest other predators that would evoke the decreasing prey population growth trends we observed. Cobia (*Rachycentron canadum*) is another well-documented specialist crustaceavore in the region with high prey type overlap to *S. tiburo* (Smith, 1995; Arendt *et al.*, 2001). Red drum (*Sciaenops ocellatus*) is also known to feed on blue crabs and other crustaceans (Scharf *et al.*, 2000), although red drum are more generalist feeders (Peacock, 2014; Kroetz *et al.*, 2017). Comparable abundance trends within the region for cobia and red drum during our study period have been decreasing and unchanged, respectively (SEDAR, 2013a; ASMFC, 2017), thus changes in the abundances of these two predators are unlikely to have contributed to overall decreasing trends in crustacean abundances. An alternative hypothesis is that a recent increase in overall fish community biomass due to reduced bycatch mortality (Stratton *et al.*, 2017) has resulted in higher cumulative predation rates from other yet unidentified predator species in addition to *S. tiburo*. The hypothesis is untestable without additional community trophic information.

Although this predator is fully capable of predating upon other available prey such as fishes, the bonnethead shark has mechanical, sensory and behavioral adaptations especially evolved for detection, capture and processing of hard-shelled crustaceans, especially crabs (Wilga and Motta, 2000). The overall decrease in the bonnethead's preferred prey base in recent decades raises questions about the potential impact of reduced prey availability on individual growth, survival, and reproductive success of this predator, given its specialist feeding tendencies. The slight decreasing trend for both size groups during the latter half of the time series (Fig. 15) may signal that this species has reached a new carrying capacity despite steadily decreasing total fishing mortality. This study was focused on predator-on-prey effects, although prey-on-predator effects could be tested within the MARSS framework at the population level. Doing so would require additional model complexity by distinguishing input indices between males and females as well as mature versus immature individuals.

### Environmental effects

Results from this study revealed dual effects from predation and environmental variability on multiple prey species. Although predation effects were stronger than environmental effects in our case, considering both concurrently is critical for properly characterizing the effects of either on population stochasticity (Kilpatrick and Ives, 2003) and estimating unbiased community interaction terms within the MARSS framework (Holmes *et al.*, 2012). At the population level, the mechanism for predator-on-prey effects is intuitive (mortality) unless there are demonstrated prey behavioral modifications that affect individual vital rates other than survival (e.g., growth; Halpin 2000). In marine species that are broadcast spawners, environmental stochasticity commonly confers variability to recruitment success (e.g., Eggleston et al. 2010, Miller et al. 2016, Wang et al. 2017) and thus the rate of population growth. Extreme meteorological conditions (e.g., extreme winter cold events) may impact adult survival, but young animals are often more susceptible (Hurst, 2007).

We assume that the positive effect of the PDO on prey species is also related to young-of-the-year survival, although a mechanism has not been identified. Fall abundances for all modeled prey species peaked consistently following a winter in which the PDO index spiked upward (Fig. 15; model years 2000, 2005, and 2012). Southeast U.S. winter weather conditions are on average colder and wetter during a positive PDO phase (Mantua and Hare, 2002; SCO, 2015), suggesting that these conditions positively affect vital rates and population growth rates for the five species we modeled. Although all prey species exhibited consistent positive abundance responses during years in which the PDO spiked upward, reproductive timing and strategy varies among them; *Ovalipes* spp. broadcast spawn in cold months while *C. similis* and *P. spinimanus* do so in warm months (Williams, 1984), and *S. empusa* females guard their eggs in burrows during warm months (Wortham, 2009). These reproductive differences yet similar abundance trends suggest that conditions associated with the PDO are affecting winter survival of juveniles and adults perhaps more so than larval recruitment success. Given the greater life history knowledge and economic importance of *C. sapidus* compared to the crustacean species we modeled, we suggest a detailed investigation into PDO conditions and the response of blue crab stocks within our study region.

**Future directions**

Multispecies trophic models presume understanding of food web relationships based on empirical data (Collie *et al.*, 2016). Only with increased investment in scientific data-collecting platforms with spatiotemporal sampling consistency (e.g., Garrison and Link 2000, Buchheister and Latour 2015) will multispecies modeling become a truly viable tool for researchers and managers in the Southeast U.S. Atlantic region. Implementing a multispecies diet data collection program is costly and time-intensive, thus we recommend first establishing on-going sampling of common mid- to upper trophic level predators (e.g., *S. tiburo*, *S. ocellatus*, *R. canadum*, *Rhizoprionodon terraenovae*). These predators feed on or have high co-occurrence probabilities with blue crab and penaeid shrimps, crustacean species that currently support 50% of all fisheries revenue in the region (NMFS, 2016). Despite our focus on discussion of multispecies food web interactions, environmental effects cannot be ignored when attempting to explain population abundance trends and stochasticity of lower trophic level fish and shellfish species. We suggest building upon the work of existing environmental studies of Southeast U.S. Atlantic demersal species (e.g., Hare and Able 2007, Eggleston et al. 2010, Stratton et al. 2017) toward further identification and characterization of how meteorological phenomena affect vital rates of living marine resources in the region.

A key benefit of the state-space approach is the ability to partition variation in the observations from true process variation in the population(s) being modeled. In this study, GLM-estimated observation error variances were a level of magnitude higher (0.10-0.51 range among species) than process error variance (0.017) estimated from multispecies models. A sensitivity analysis with artificially reduced observation error variance (results not reported) revealed in higher process error variance but overall less uncertainty in parameter estimates and abundance predictions. This result demonstrates the utility of the state-space approach to improve practical reality of the modeled system (Fleischman *et al.*, 2013). One feature the MARSS framework would benefit from is the ability to specify uncertainty in covariates. This capability has been demonstrated in other state-space model frameworks (e.g., Miller et al. 2016) and would further improve the flexibility of the MARSS approach.

In conclusion, this application of a multivariate state-space time series approach revealed important ecological interactions for demersal species in the Southeast U.S. Atlantic region. The potential to implement ecosystem-based modeling approaches within the region would increase with the expansion of existing state and federal fisheries data collection programs. In the absence of additional investments in these programs, multispecies models with the appropriate level of complexity should be prioritized above ecosystem modeling approaches not able to be supported by sufficient empirical data (e.g., Okey and Pugliese 2001). Only with a fundamental, data-driven understanding of the environmental, trophodynamic, and anthropogenic characteristics of this marine system can ecosystem-based approaches to fisheries management be successfully implemented on a broad scale.

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## TABLES

Table 7. Covariates considered within MARSS models.

| Covariate | Relevant species | Process | Calculation | Reasoning |
|---|---|---|---|---|
| Penaeid shrimp trawl fishery effort | Predator and prey | State (Eq. 14a) | Total annual commercial trips (log-transformed) | Proxy for bycatch mortality (Scott-Denton *et al.*, 2012; SEDAR, 2013b) |
| Pacific Decadal Oscillation (PDO) | Prey | State | Statistical reconstruction of *in situ* SST in the North Pacific Ocean (NCDC, 2015); average of monthly winter (Dec–Mar) values | Correlation demonstrated in previous research (Stratton *et al.*, 2017) |
| Temperature anomaly | Predator and prey | Observation (Eq. 14b) | Annual average of mean temperature anomalies within four sampling regions; calculated from spring/summer data for *S. tiburo* and fall data for prey species | Potential changes in availability to survey gear due to interannual differences in migration phenology |

Table 8 (table on following two pages). *Sphyrna tiburo* diet characterization in nearshore coastal habitats from Cape Canaveral, FL to Cape Fear, NC during Fall 2012, Spring 2013, and Fall 2013. Diet percentages by weight (Eq. 13) are based on 89 and 207 individual small and large shark specimens, respectively, collected from 29 and 44 sampling stations.

| Hierarchical prey taxonomic categories | | | Bonnethead % diet by weight | |
|---|---|---|---|---|
| General group | Family level or higher | Genus species | Small | Large |
| **Crustacea TOTAL** | | | **87.9** | **76.8** |
| | Crustacea unid. | | 17.9 | 2.0 |
| | Decapoda unid. | | 28.3 | 25.8 |
| | **Portunidae TOTAL** | | **14.3** | **28.8** |
| | Portunidae | | 6.2 | 3.4 |
| | | *Arenaeus cribrarius* | - | 1.5 |
| | | *Callinectes* sp. | - | 3.6 |
| | | *Callinectes sapidus* | 1.7 | 7.9 |
| | | *Callinectes similis* | 6.3 | 2.0 |
| | | *Ovalipes* sp. | - | 1.3 |
| | | *Ovalipes ocellatus* | - | 2.4 |
| | | *Ovalipes stephensoni* | - | 1.9 |
| | | *Portunus* sp. | - | 4.2 |
| | | *Portunus gibbesii* | - | 0.3 |
| | | *Portunus sayi* | - | 0.2 |
| | **Pisidae TOTAL** | | **-** | **2.9** |
| | | *Libinia* sp. | - | 0.3 |
| | | *Libinia dubia* | - | 1.7 |
| | | *Libinia emarginata* | - | 0.9 |
| | **Anomura TOTAL** | | **1.3** | **0.3** |
| | Anomura unid. | | 1.0 | 0.2 |
| | Albuneidae unid. | | 0.2 | - |
| | | *Albunea catherinae* | - | <0.1 |
| | | *Albunea paretii* | - | <0.1 |
| | | *Pagurus pollicaris* | <0.1 | <0.1 |
| | Cancridae | *Cancer* sp. | - | 1.8 |
| | Cancridae | *Cancer irroratus* | 0.2 | - |
| | Panopeidae | *Panopeus herbstii* | 0.4 | - |
| | Pinnotheridae | | 1.6 | - |
| | **Stomatopoda TOTAL** | | **5.1** | **11.7** |
| | Nannosquillidae | *Platysquilloides enodis* | - | 1.3 |
| | Squillidae unid. | | 1.9 | 0.9 |
| | | *Squilla empusa* | 3.1 | 9.5 |
| | **Penaeidae TOTAL** | | **12.9** | **3.6** |
| | Penaeidae unid. | | 4.2 | - |
| | | *Farfantepenaeus aztecus* | - | 1.0 |
| | | *Litopenaeus setiferus* | 1.1 | 2.3 |
| | | *Rimapenaeus constrictus* | 7.2 | 0.2 |
| | | *Xiphopenaeus kroyeri* | 0.4 | - |
| | Sergestidae | *Acetes* sp. | <0.1 | - |
| | Callianassidae | *Gilvossius setimanus* | 3.6 | - |
| | Upogebiidae | Upogebiidae | <0.1 | - |

| Hierarchical prey taxonomic categories | | | Bonnethead % diet by weight | |
|---|---|---|---|---|
| General group | Family level or higher | Genus species | Small | Large |
| | Mysidae | *Neomysis americana* | 0.1 | - |
| | Pennellidae | *Lernaeenicus* sp. | 2.1 | - |
| **Teleostei TOTAL** | | | **5.5** | **6.2** |
| | Teleostei unid. | | 5.1 | 3.1 |
| | Clupeiformes unid. | | - | 1.5 |
| | | *Anchoa mitchilli* | 0.4 | - |
| | Ephippidae | *Chaetodipterus faber* | - | 0.4 |
| | **Sciaenidae TOTAL** | | **-** | **0.6** |
| | | *Menticirrhus* sp. | - | 0.2 |
| | | *Micropogonias undulatus* | - | 0.4 |
| | Stromateidae | *Peprilus triacanthus* | - | 0.6 |
| **Chelicerata** | Limulidae | *Limulus polyphemus* | - | 3.4 |
| **Polychaeta TOTAL** | | | **-** | **0.7** |
| | Polychaeta unid. | | - | 0.5 |
| | Nereididae | *Nereis* sp. | - | <0.1 |
| | Opheliidae | *Ophelia denticulata* | - | 0.1 |
| **Mollusca TOTAL** | | | **1.2** | **0.4** |
| | Mollusca unid. | | 1.1 | 0.1 |
| | Gastropoda unid. | | 0.1 | <0.1 |
| | Loliginidae | *Loligo pealeii* | - | 0.2 |
| **Other TOTAL** | | | **5.4** | **12.6** |
| | Unidentified | | 5.3 | 10.6 |
| | Abiotic | | <0.1 | 1.7 |
| | Plantae | | <0.1 | 0.1 |
| | Cnidaria | | - | 0.2 |

Table 9. Generalized linear modeling results. The optimal GLM framework was either a negative binomial GLM or zero-inflated negative binomial GLM. Variate and covariate letter abbreviations in model formulae are N ("Number"), Y ("Year"), R ("Region"), and E ("Effort"). For indices where a ZINB was optimal, the lowest AIC model always contained the covariate "Region" in the binomial process. Dispersion was calculated at the ratio of squared and summed Pearson residuals to the residual degrees of freedom. Annual observations variances were estimated from bootstrapping in log space.

| Species type | Species | GLM framework | Formula for model with lowest AIC | GLM dispersion | Median annual observation variance | Linear time series trend |
|---|---|---|---|---|---|---|
| Predator | *Sphyrna tiburo*, Sm. | ZINB | N ~ Y + R + E \| R | 1.23 | 0.16 | +0.03 |
| | *Sphyrna tiburo*, Lg. | NBGLM | N ~ Y + R + E | 1.14 | 0.10 | +0.05 |
| Prey | *Callinectes similis* | ZINB | N ~ Y + R + E \| R | 1.35 | 0.12 | -0.09 |
| | *Ovalipes ocellatus* | NBGLM | N ~ Y + R + E | 1.37 | 0.15 | -0.08 |
| | *Ovalipes stephensoni* | ZINB | N ~ Y + R + E \| R | 0.89 | 0.51 | -0.06 |
| | *Portunus spinimanus* | NBGLM | N ~ Y + R + E | 1.63 | 0.27 | -0.11 |
| | *Squilla empusa* | NBGLM | N ~ Y + R + E | 1.27 | 0.18 | -0.13 |

Table 10. Multispecies model selection results for the twenty covariate combinations. An “X” indicates that a covariate effect was estimated; effects were estimated separately for each species or size group. ‘K’ is the total number of parameters estimated, ‘logLik’ is the log-likelihood, ΔAIC is the difference in AIC for a given model and the AIC for the most-supported, and $w_i$ is the Akaike model weight (Eq. 15).

| Model rank | Covariate effect included? | | | | | Model weighting | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Fishing | | PDO | Temperature anomaly | | K | logLik | ΔAIC | $w_i$ |
| | Predator | Prey | Prey | Predator | Prey | | | | |
| 1 | X | X | X | | | 39 | -114.5 | 0 | 0.217 |
| 2 | X | X | X | | X | 44 | -109.7 | 0.3 | 0.183 |
| 3 | X | | X | | | 34 | -119.7 | 0.4 | 0.178 |
| 4 | X | X | X | X | | 41 | -112.7 | 0.5 | 0.17 |
| 5 | X | | X | | X | 39 | -115.5 | 2.0 | 0.079 |
| 6 | X | | X | X | X | 41 | -113.9 | 2.8 | 0.052 |
| 7 | X | X | X | X | X | 46 | -109.0 | 3.0 | 0.049 |
| 8 | X | | X | X | | 36 | -119.5 | 4.1 | 0.028 |
| 9 | X | | | X | | 31 | -124.9 | 4.8 | 0.02 |
| 10 | X | X | | X | | 36 | -120.0 | 5.1 | 0.017 |
| 11 | X | X | | | | 34 | -122.9 | 6.8 | 0.007 |
| 12 | X | | | | | 29 | -128.2 | 7.5 | 0 |
| 13 | | | | X | | 29 | -129.3 | 9.6 | 0 |
| 14 | X | | | X | X | 36 | -123.1 | 11.3 | 0 |
| 15 | X | X | | X | X | 41 | -118.4 | 11.7 | 0 |
| 16 | X | | | | X | 34 | -125.4 | 11.8 | 0 |
| 17 | X | X | | | X | 39 | -120.7 | 12.5 | 0 |
| 18 | | | | X | X | 34 | -127.1 | 15.3 | 0 |
| 19 | | | | | | 27 | -134.6 | 16.2 | 0 |
| 20 | | | | | X | 32 | -131.9 | 20.8 | 0 |

Table 11. Community interaction (**B**) matrix of Akaike-weighted estimates (Eq. 16), bias-corrected estimates [in square brackets], weighted 99% confidence intervals (in parentheses), and the number of models with non-zero weights (see Table 10) in which the parameter estimate was significant at $\alpha = 0.01$ {in curly brackets}. With columns and rows denoted as $j$ and $i$, respectively, coefficient $\mathbf{B}_{i,j}$ should be interpreted as the trophic effect of species $j$ on species $i$. Asterisked and bolded estimates are significant $\alpha = 0.05$ and $\alpha = 0.01$, respectively. Density-dependence (diagonals) and community interaction (off-diagonals) estimates are significant if different from 1 and 0, respectively.

| Species | *S. tiburo*, Sm. | *S. tiburo*, Lg. | *C. similis* | *O. ocellatus* | *O. stephensoni* | *P. spinimanus* | *S. empusa* |
|---|---|---|---|---|---|---|---|
| *S. tiburo*, Sm. | 1.03 [0.71]<br>(-0.24, 4.44)<br>{0 of 11} | **-4.22** [-2.63]<br>(-14.66, -1.86)<br>{11 of 11} | - | - | - | - | - |
| *S. tiburo*, Lg. | 0.18 [0.02]<br>(-0.09, 1.86)<br>{0 of 11} | **-0.75** [-0.38]<br>(-4.4, 0.47)<br>{11 of 11} | - | - | - | - | - |
| *C. similis* | -0.17 [-0.43]<br>(-1.6, 2.73)<br>{0 of 11} | **-3.67** [-2.48]<br>(-12.17, -1)<br>{10 of 11} | **-0.29** [-0.28]<br>(-0.65, 0.13)<br>{11 of 11} | - | - | - | - |
| *O. ocellatus* | -0.39 [-0.5]<br>(-1.42, 1.38)<br>{1 of 11} | -1.78* [-1.26]<br>(-7.02, 0.44)<br>{6 of 11} | - | **-0.03** [-0.02]<br>(-0.53, 0.41)<br>{11 of 11} | - | - | - |
| *O. stephensoni* | 0.72 [0.48]<br>(-0.88, 4.32)<br>{0 of 11} | **-4.06** [-2.82]<br>(-15.08, -0.52)<br>{9 of 11} | - | - | **-0.4** [-0.42]<br>(-0.9, 0.47)<br>{11 of 11} | - | - |
| *P. spinimanus* | -0.79 [-0.96]<br>(-2.22, 1.55)<br>{1 of 11} | -2.51* [-1.76]<br>(-9.81, 0.85)<br>{5 of 11} | - | - | - | **0.1** [0.12]<br>(-0.42, 0.53)<br>{11 of 11} | - |
| *S. empusa* | -0.11 [-0.28]<br>(-1.17, 2.17)<br>{0 of 11} | **-2.49** [-1.72]<br>(-8.62, -0.16)<br>{9 of 11} | - | - | - | - | **-0.24** [-0.23]<br>(-0.77, 0.4)<br>{11 of 11} |

Table 12. Akaike-weighted covariate coefficient estimates, weighted 99% confidence intervals (in parentheses), and the number of models with non-zero weights (see Table 10) in which the parameter estimate was significant at $\alpha = 0.01$ (in curly brackets). Asterisked and bolded estimates have weighted confidence bounds that do not contain zero and are significant at $\alpha = 0.05$ and $\alpha = 0.01$, respectively. In contrast to community interactions (Table 11), bootstrapping revealed minimal bias in covariate estimates, thus bias-corrected estimates are not reported.

| Species | Covariate | | |
|---|---|---|---|
| | Fishing | PDO | Temperature |
| *S. tiburo*, Sm. | **-0.86** | - | 0.07 |
| | (-1.89, -0.25) | | (-0.04, 0.15) |
| | {8 of 11} | | {0 of 6} |
| *S. tiburo*, Lg. | **-0.44** | - | -0.03 |
| | (-0.81, -0.08) | | (-0.09, 0.05) |
| | {10 of 11} | | {0 of 6} |
| *C. similis* | -0.45* | **0.7** | -0.08* |
| | (-1.19, 0.08) | (0.31, 1.08) | (-0.2, 0.03) |
| | {0 of 6} | {8 of 8} | {1 of 4} |
| *O. ocellatus* | -0.33* | **0.39** | **-0.12** |
| | (-0.82, 0.09) | (0.09, 0.69) | (-0.21, -0.01) |
| | {0 of 6} | {7 of 8} | {3 of 4} |
| *O. stephensoni* | -0.45 | 0.14 | 0.01 |
| | (-1.36, 0.41) | (-0.41, 0.65) | (-0.18, 0.2) |
| | {0 of 6} | {0 of 8} | {0 of 4} |
| *P. spinimanus* | -0.44* | **0.52** | -0.12* |
| | (-1.18, 0.15) | (0.09, 1) | (-0.28, 0.02) |
| | {0 of 6} | {7 of 8} | {1 of 4} |
| *S. empusa* | 0.13 | **0.38** | -0.08 |
| | (-0.5, 0.63) | (0.05, 0.7) | (-0.2, 0.03) |
| | {0 of 6} | {6 of 8} | {0 of 4} |

Table 13. Comparison of bias and uncertainty of model predictions for a model (model 7 in Table 10, all covariates included) with density-dependence (DD) estimated versus the same model with both DD and community interactions estimated. RMSE is Root Mean Square Error (Eq. 17). "Improvement" is the difference between the model with community interactions and the model with DD only.

| | Prediction bias (RMSE) | | | Prediction uncertainty (median SE across years) | | |
|---|---|---|---|---|---|---|
| Species | DD only | DD + Interactions | Improvement | DD only | DD + Interactions | Improvement |
| *Sphyrna tiburo*, Sm. | 0.27 | 0.265 | +0.005 | 0.324 | 0.189 | +0.135 |
| *Sphyrna tiburo*, Lg. | 0.004 | 0.064 | -0.059 | 0.279 | 0.05 | +0.229 |
| *Callinectes similis* | 0.277 | 0.105 | +0.172 | 0.306 | 0.203 | +0.102 |
| *Ovalipes ocellatus* | 0.185 | 0.281 | -0.096 | 0.303 | 0.153 | +0.15 |
| *Ovalipes stephensoni* | 0.336 | 0.546 | -0.21 | 0.444 | 0.214 | +0.23 |
| *Portunus spinimanus* | 0.372 | 0.236 | +0.135 | 0.389 | 0.23 | +0.159 |
| *Squilla empusa* | 0.208 | 0.166 | +0.042 | 0.345 | 0.16 | +0.185 |

Table 14. Percent probabilities of co-occurrence for shark size groups and prey species in nearshore waters during 1994-2014. Probabilities were calculated using only tows (*n* = sample size) in which the relevant shark size group was captured (*n* = the number of tows with *S. tiburo*). Numbered regions correspond to those shown in Fig. 12: 1) Florida (FL), 2) Georgia (GA), 3) South Carolina (SC), and 4) Long Bay (SC).

| **Season** | **Spring** | | | | | **Summer** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Region** | **1** (FL) | **2** (GA) | **3** (SC) | **4** (LB) | **Median** | **1** (FL) | **2** (GA) | **3** (SC) | **4** (LB) | **Median** |
| ***Sphyrna tiburo*, Small** | *n* = 201 | *n* = 32 | *n* = 4 | *n* = 3 | | *n* = 160 | *n* = 95 | *n* = 35 | *n* = 7 | |
| *Callinectes similis* | 41 | 31 | 25 | 33 | **32%** | 13 | 42 | 60 | 43 | **43%** |
| *Ovalipes ocellatus* | 10 | 34 | | 67 | **34** | 3 | 22 | 20 | | **20** |
| *Ovalipes stephensoni* | 21 | 44 | 75 | 67 | **55** | 3 | 21 | 26 | 43 | **23** |
| *Portunus spinimanus* | 10 | 16 | | 67 | **16** | 9 | 15 | 23 | 71 | **19** |
| *Squilla empusa* | 5 | 38 | 50 | | **38** | 11 | 27 | 29 | 29 | **28** |
| Non-modeled commercially-important species | | | | | | | | | | |
| *Callinectes sapidus* | 4 | 3 | | | **3** | 3 | 8 | 3 | 14 | **6** |
| *Farfantepenaeus aztecus* | 38 | 9 | | | **24** | 57 | 75 | 74 | 29 | **66** |
| *Litopenaeus setiferus* | 55 | 66 | 50 | 33 | **52** | 84 | 46 | 43 | 14 | **45** |
| ***Sphyrna tiburo*, Large** | *n* = 150 | *n* = 205 | *n* = 129 | *n* = 66 | | *n* = 151 | *n* = 191 | *n* = 191 | *n* = 139 | |
| *Callinectes similis* | 35 | 32 | 21 | 2 | **27%** | 12 | 43 | 61 | 37 | **40%** |
| *Ovalipes ocellatus* | 16 | 39 | 36 | 20 | **28** | 5 | 24 | 20 | 29 | **22** |
| *Ovalipes stephensoni* | 19 | 63 | 61 | 50 | **56** | 4 | 15 | 27 | 42 | **21** |
| *Portunus spinimanus* | 8 | 23 | 19 | 33 | **21** | 5 | 6 | 17 | 44 | **12** |
| *Squilla empusa* | 5 | 31 | 30 | 3 | **18** | 7 | 25 | 25 | 17 | **21** |
| Non-modeled commercially-important species | | | | | | | | | | |
| *Callinectes sapidus* | 2 | 2 | 8 | 3 | **3** | 4 | 6 | 9 | 9 | **7** |
| *Farfantepenaeus aztecus* | 39 | 9 | 9 | | **9** | 52 | 73 | 82 | 48 | **63** |
| *Litopenaeus setiferus* | 49 | 63 | 62 | 18 | **56** | 76 | 44 | 52 | 21 | **48** |

## FIGURES

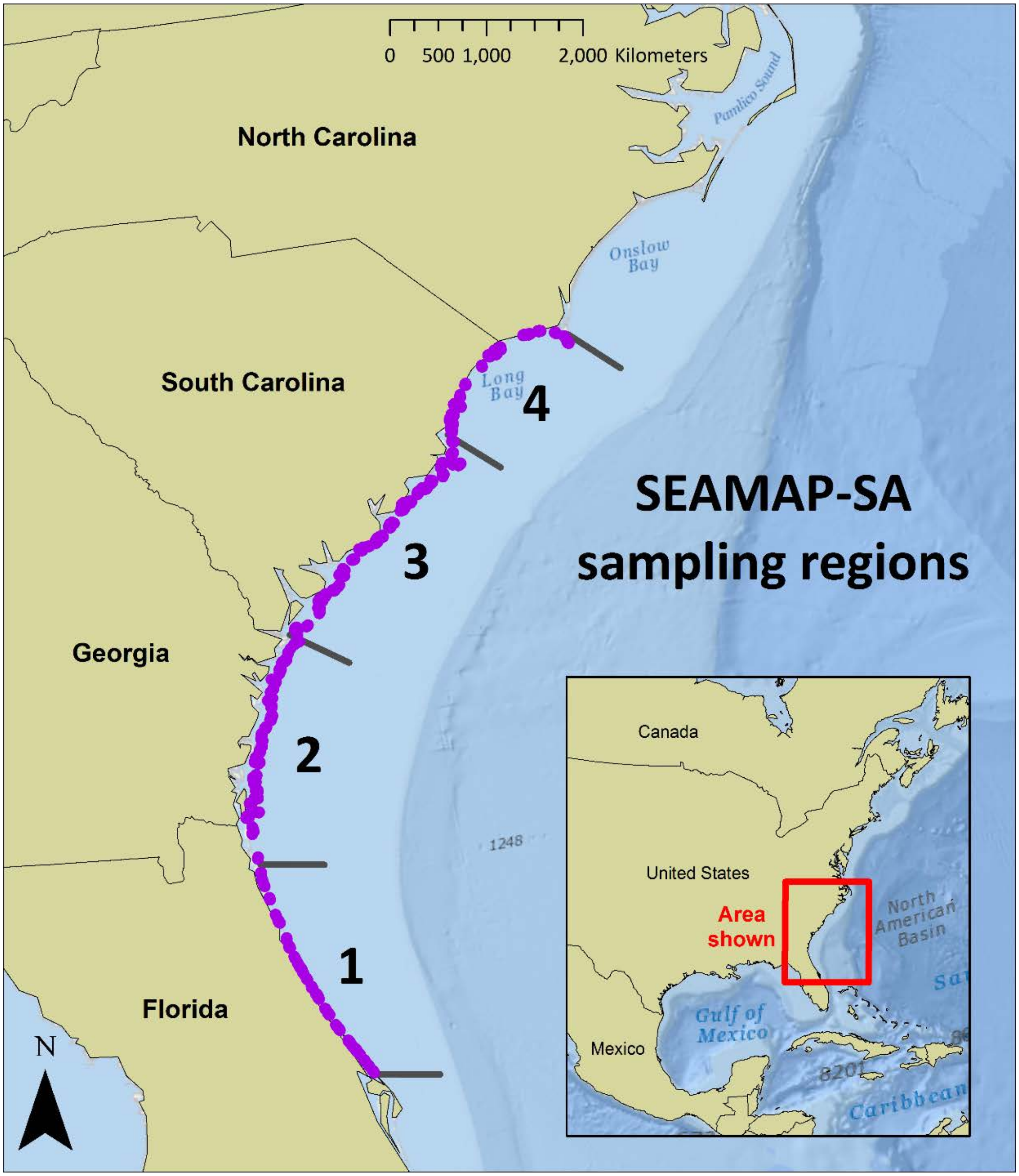


Figure 12. The study area within coastal Southeast U.S. Atlantic waters. Overlapping purple points indicate SEAMAP-SA fixed stations sampled during 1994-2014. Numbered regions are 1) Florida, 2) Georgia, 3) South Carolina, and 4) Long Bay.

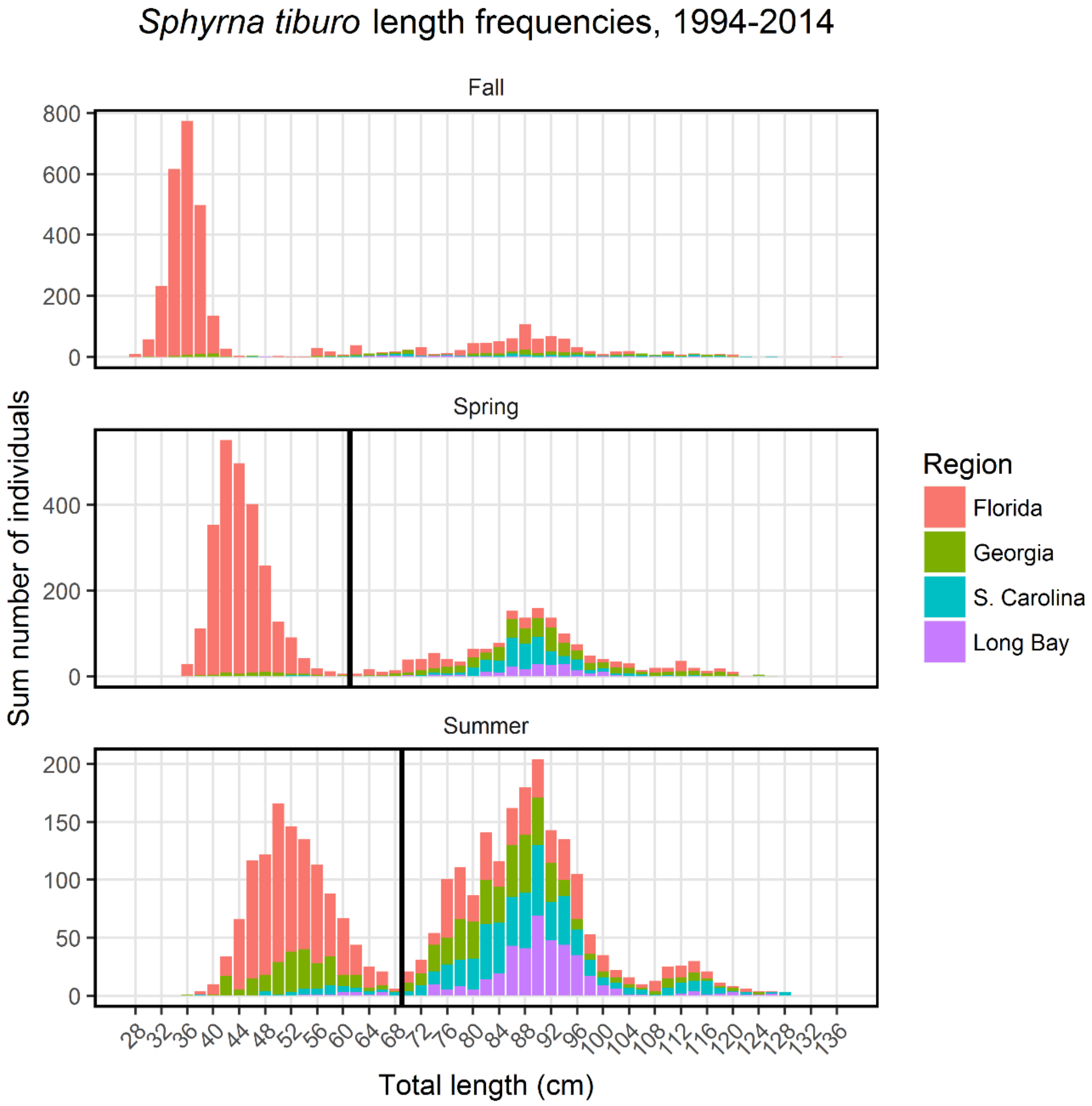


Figure 13. Length frequencies for the bonnethead shark (*Sphyrna tiburo*). Vertical black lines indicate the season-specific division imposed for assigning individuals to size groups (Small or Large). Note different y-axis scales among panels. Regions correspond to those shown in Fig. 12: 1) Florida, 2) Georgia, 3) South Carolina, and 4) Long Bay.

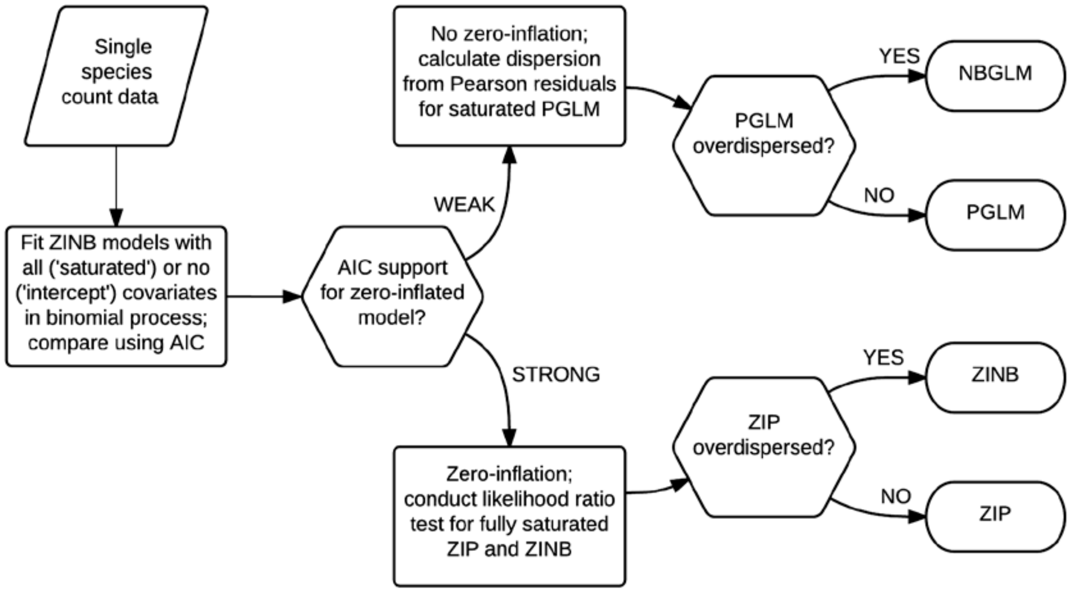
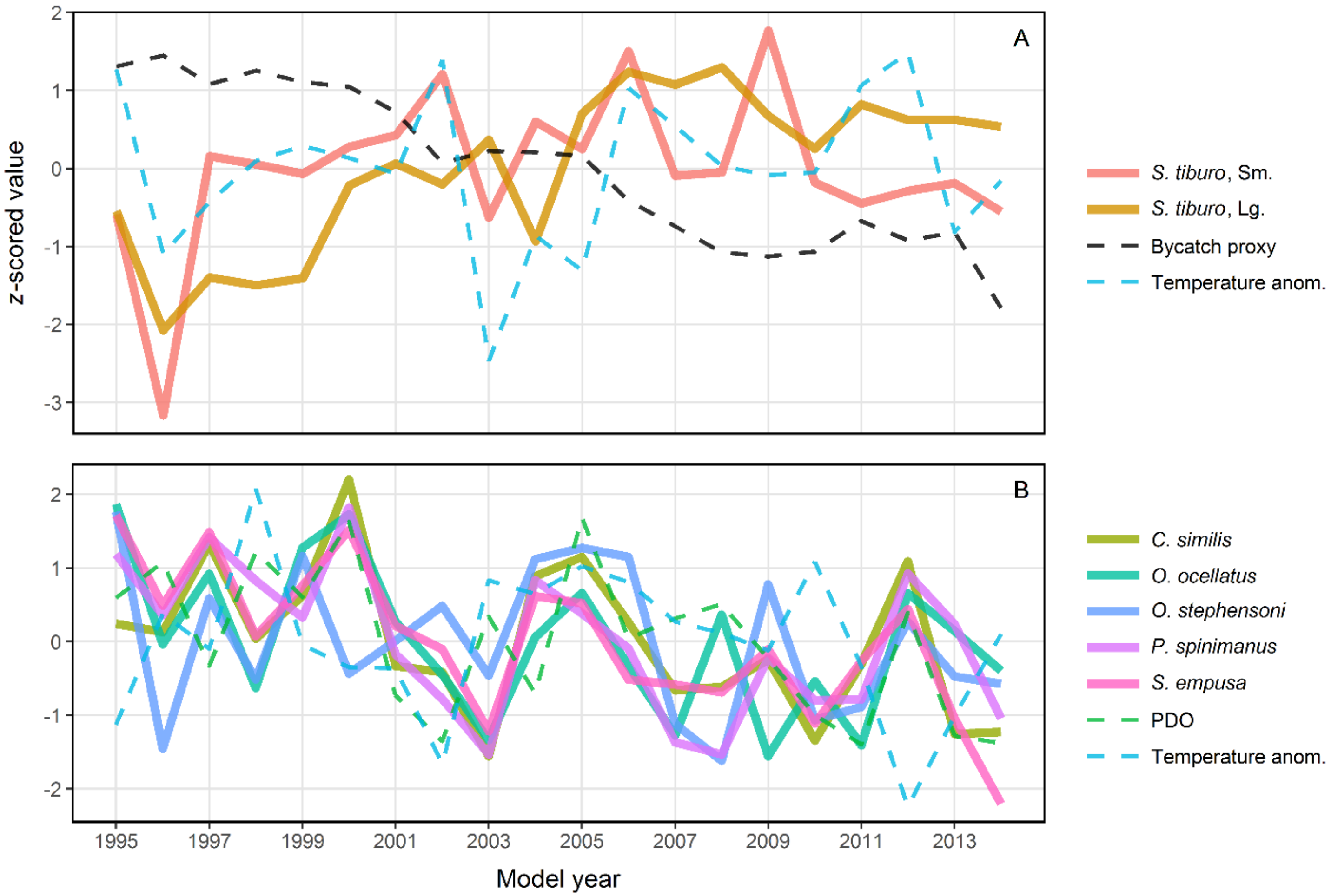


Figure 14. Decision tree for identifying the optimal generalized linear framework for each species and index. Four GLM frameworks were considered: Poisson (PGLM), negative binomial (NBGLM), zero-inflated Poisson (ZIP), and zero-inflated negative binomial (ZINB). Mathematics for these frameworks are reported in Table 7.

Figure 15. Observed index trends for predator size groups (A), prey species (B), and covariates (see Table 7 for descriptions) included in multispecies modeling. *z*-scored time series are depicted for proper scale visualization, although predator and prey time series were demeaned and not *z*-scored for multispecies modeling. “Model year” indicates how the time series were specified in MARSS models, not the calendar year in which the data were collected or calculated (see Methods subsection “Data specification”).



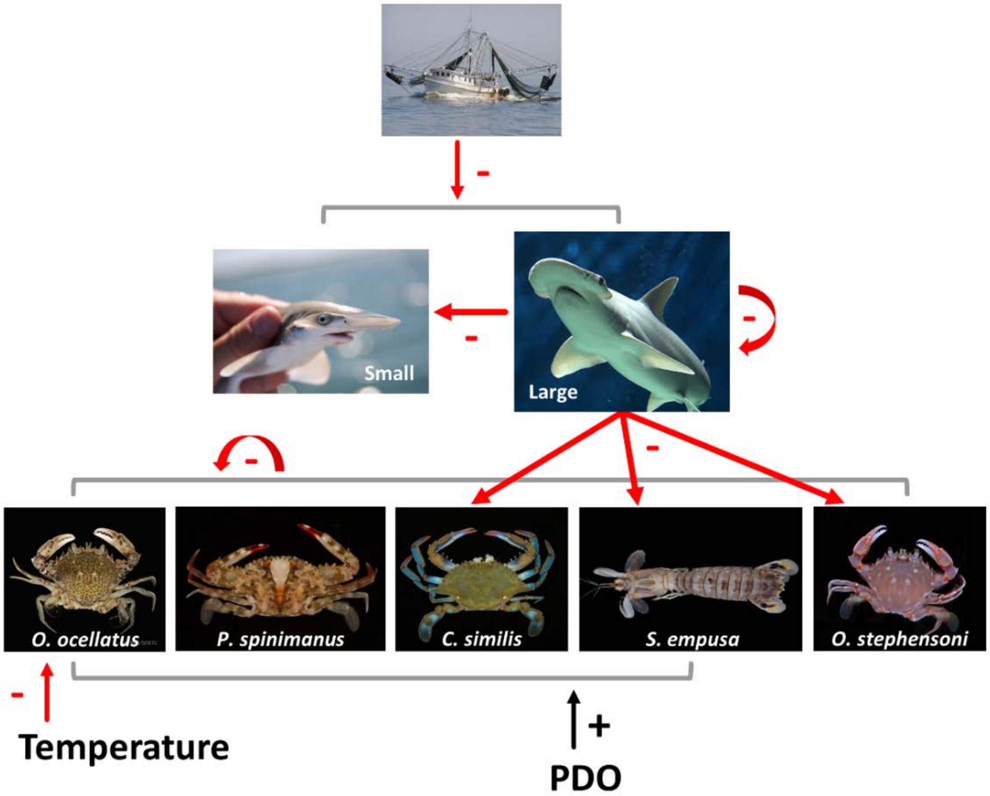


Figure 16. Significant ($\alpha = 0.01$) community interactions and covariate effects from MARSS model outputs. Covariates included bycatch from fishing, annual temperature anomalies, and the Pacific Decadal Oscillation (PDO) index. Black and red lines indicate positive and negative interactions, respectively. Gray brackets indicate groups of species or shark size groups with the same sign for an interaction or effect. Large sharks and all prey species exhibited some level of density-dependence (red half-circle arrows). Community interaction and covariate coefficients are reported in Tables 11 and 12, respectively.

Figure 17 (figure on following page). Multispecies model abundance inputs and weighted predictions. GLM-estimated index values (black circles) are depicted with bootstrapped 95% confidence intervals (vertical lines). AIC-weighted MARSS predictions (color-coded lines consistent with Figure 15) are depicted with bootstrapped 95% CIs (gray polygons). Root mean squared error (RMSE, Eq. 17) is a measure of prediction bias (RMSE = 0 is no bias). “Model year” indicates how time series were specified in MARSS models, not the calendar year in which the data were collected (see Methods subsection “Data specification”). For clarity, two *P. spinimanus* values with anomalously low lower CI bounds are depicted as open black circles without error bars.

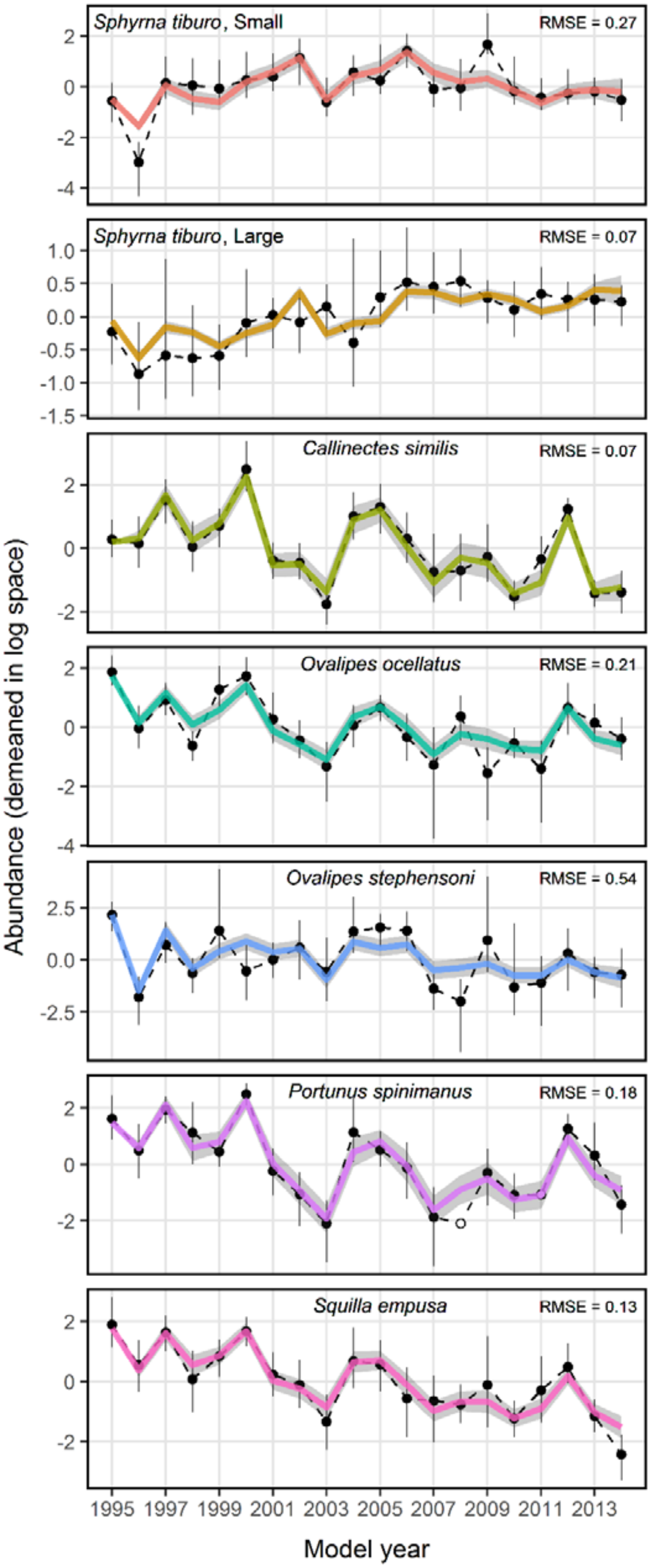


Figure 17 (caption on previous page).

# VITA

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Born in Atlanta, Georgia in 1983, Mark graduated from Lakeside High School in Decatur, Georgia in 2002. He earned a B.S. in Biology from Rhodes College in Memphis, Tennessee in 2006. Following employment with the Bureau of Land Management and South Carolina Department of Natural Resources, Mark enrolled in the Graduate Program in Marine Biology at the College of Charleston in Charleston, South Carolina. After earning his M.S. in Marine Biology in 2011, he matriculated to the doctoral program at the School of Marine Science, College of William & Mary.