DR. MARK A STRATTON (Orcid ID : 0000-0002-8424-8681)

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

MARK A. STRATTON[1] (stratton.ma@gmail.com) (Corresponding author)
GENEVIÈVE M. NESSLAGE[2] (nesslage@umces.edu)
ROBERT J. LATOUR[1] (latour@vims.edu)

[1]*Virginia Institute of Marine Science, College of William & Mary, Gloucester Point, VA, 23062, U.S.A.*
[2]*University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, 146 Williams Street // 0038, Solomons, MD, 20688, U.S.A.*

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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; 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 (i.e., non-internal population processes such as density-dependence) that influence living marine resources. Link *et al.* (2010) describe a 'triad' of 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 and bycatch mortality, 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 one 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 weak. 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 weak or failed recruitment if eggs and larvae are advected to unfavorable habitat (Hjort, 1914). For some species, especially those with protracted spawning strategies, more subtle changes in growth and mortality of early life stages due to an interaction of biophysical conditions (e.g., environmental conditions, food availability) and density-dependence may be more influential to year-class strength than dramatic episodic events (Houde, 1989). Anomalous environmental conditions can influence adult survival as well, for instance mortality events associated with severe temperature conditions (Hurst, 2007). Such variability in local or regional ocean environmental conditions are often linked to atmospheric climate oscillations at much broader scales 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; Morley *et al.*, 2018). 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. Fishery 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. 1). 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 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 (Team, 2015) (see Supporting Information 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 commonly resulting in zero-inflated data (Kuhnert *et al.*, 2005). Zero-inflated models account for false zeros unexpected in reference to the specified underlying probability distribution. Within both GLM and ZIGLM frameworks, we considered Poisson and negative binomial probability distributions (Fig. S1, Table S1; see Supporting Material 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 the trawl sample, effort (as an offset), and if the catch was subsampled (Table S2). We fitted main effects models 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 variances generated for 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 hypotheses

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 1; Fig. S2). Cold-season covariates included the North Atlantic Oscillation (NAO), the Pacific Decadal Oscillation (PDO), the Pacific North American Pattern in winter (PNA$_\mathrm{W}$), 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 impacted 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 ($\mathrm{PNA_S}$), the Western Bermuda High Index (WBHI), 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 S3). We lagged SBT 0 years to account for temperature-driven changes in availability resulting from interannual differences in migration phenology (see Supporting Material, Fig. S3).

Fishing covariates included annual shrimp fishery effort (all species), landings (35 of 71 species), and estimated instantaneous fishing mortality (9 species) (see Supporting Material, 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) because empirical bycatch mortality estimates for all species were unavailable for the study period. 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 S3 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

$$y_t = \mathbf{F}_t{}^{\mathrm{T}}\boldsymbol{\theta}_t + \boldsymbol{v}_t \qquad (1)$$

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

$$\boldsymbol{\theta}_t = \boldsymbol{\theta}_{t-1} + \mathbf{w}_t \qquad (2)$$

where $\mathbf{w}_t$ are process errors with $\mathbf{w}_t \sim \mathrm{MVN}(\mathbf{0}, \mathbf{Q})$ (Holmes *et al.*, 2014). The DLM framework assumes a locally non-linear relationship between a given response and predictor variable. This assumption allowed us flexibility to explore numerous response/predictor combinations, relationships for many of which may not be linear.

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 multi-collinearity, 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 2). 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 $\mathbf{Q}$ 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 ΔAIC_c values ≤ 10, where $\Delta \text{AIC}_c = \text{AIC}_c - \min(\text{AIC}_c)$. 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 S3).

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 (termed “innovations”) 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):

$$\text{RMSE} = \sqrt{\sum_{t=1}^{n} (Y_t - f_t)^2 / n} \quad (3)$$

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 an age-structured 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

$$\varphi_i = \sum_{j=1}^{J} \left(\frac{c_{ij}}{m}\right) w_j \quad (4)$$

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 (AIC_w; Burnham and Anderson 2002) for non-truncated model j. The parameter φ is a proportion 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

$$\Phi_i = \frac{\sum \varphi_i}{\sum \varphi} \quad (5)$$

where $\sum \varphi_i$ is the sum of persistence 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 ‘magnitude of effect’ for time-dynamic regression parameter estimates as

$$\Gamma_{i,\alpha} = \sum_{j=1}^{J}\left(\frac{(pos-neg)_{ij,\alpha}}{T_j}\right) w_j \qquad (6)$$

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 α, T is the length of time series (always 24 years), and w_j is defined as in Eq. 4. Lag identities were removed from covariates prior to calculating Γ, which is bounded by -1 and 1. Magnitude of effect also implicitly incorporates covariate persistence; 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 diminished magnitude of effect values (i.e., closer to 0). 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 mean marginal predictions 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 years were excluded in DLMs for these species.

RESULTS

Linear modeling

Of the 101 coastal fish and invertebrate species modeled using GLMs (Table S4), we investigated climat and fishing effects for 71 species that had acceptable CVs for ¾ of the 24 year time series (Table 3). Shrimp fishery effort was the most prevalent covariate in dynamic linear models for all broad taxonomic groups, indicating this was the most common covariate in time series models (Table 4). This proxy for bycatch mortality was much more prevalent than any climate effect. Shrimp fishery effort prevalence (Φ) 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 in time-truncated models for 12 and 15 species, respectively, indicating that this covariate was retained in the most supported 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 magnitude of effect 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. 2). For species with direct harvest data, a 'landings' covariate was also relatively prevalent (22%) in models among bony fishes (Table 4). For three species (*Centropristis striata*, *Chaetodipterus faber*, and *Menticirrhus littoralis*) landings had a magnitude of effect of at least 0.7 (Fig. 2). However, the relationship between landings and *C. striata* and *M. littoralis* was positive, indicating possible spurious effects. Strong persistence or magnitude of effect for a covariate does not verify a mechanistic relationship, but does provide evidence of a possible linkage between the exogenous factor and stock 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. Among warm-season climate covariates the Western Bermuda High Index (WBHI) was the most common in DLMs, with 10% overall prevalence (Table 4), persistence greater than 50% for three species, and moderate magnitude of effect ($|\Gamma| \geq 0.5$) for four species (Fig. 2). The Pacific North American Pattern in summer (PNA_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. PNA_S was persistent in more than 50% of weighted models for three species (Table 4). 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 magnitude of effect (Fig. 2) for the PDO: *Callinectes similis*, *Portunus spinimanus*, and *Centropristis striata*.

Five crustacean species had negative and counterintuitive associations with shrimp fishery effort (these species are also vulnerable to bycatch), suggesting possible indirect effects from increased predation from *S. tiburo* (Fig. 2, Fig. 3). 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 ($\Delta\mathrm{AIC}_c = 0$), results from which are depicted in Fig. S6. Forecast bias, measured as 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 S5).

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. 4). 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. 5). Based on biplot species groupings, DLM forecasts and regression coefficient estimates for *S. tiburo* and the five aforementioned crustaceans are compared in Fig. 3 (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 strong magnitude of effect (Fig. 2): *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) 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.

An 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. 3A), and shrimp fishery effort was a moderately persistent ($\varphi \geq 50\%$) negative predictor with moderate magnitude of effect ($|\Gamma| = 0.7$) 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. 3), 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 lowered bycatch risk for the assemblage.

One additional 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 (*Chaetodipterus faber*) had a moderate and negative magnitude of effect for the covariate 'Landings' (Fig. 2). 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. 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 species combined these two regions based on precedent from previous benchmark assessments (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 magnitude of effect for fourteen species – nine bony fish, four elasmobranch, and one invertebrate species (Fig. 2). 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 assumed overall bycatch were lower compared to 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 Φ of 44% for shrimp fishery effort, overall negative associations with 'Effort' in all cases (Fig. S6), and documented bycatch impacts to small coastal sharks (SEDAR, 2013b,a).

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). In this era of dramatic climate shifts in more temperate ocean waters, temperature forcing may be inherently less impactful to long-term distribution and abundance trends of natural living resources within subtropical waters of the Southeast U.S. LME (Morley *et al.*, 2017).

Although no species had a strong magnitude of effect 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. Morley *et al.* (2017) also show winter conditions to affect coastal invertebrate distribution and biomass in subsequent spring and summer seasons within the Southeast U.S. LME. The influence of the PDO-associated winter conditions on marine assemblages 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. Given the difficulties of accurately estimating remotely-sensed primary productivity in turbid coastal waters (Siegel *et al.*, 2013), *in situ* plankton sampling concomitant with SEAMAP-SA demersal faunal sampling would provide higher quality data for investigating benthic-pelagic linkages and bottom-up effects.

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 in 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. Future investigations of this dataset could benefit from alternative model frameworks with the goal of reducing uncertainty in indices of abundance by accounting for spatial and temporal random effects (e.g., Shelton *et al.*, 2014; Thorson *et al.*, 2015).

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 magnitude of effect for any species. This null result suggests that the SEAMAP-SA dataset may be largely robust to bias in abundance estimates stemming from timing differences in seasonal weather patterns. For populations with distributions soundly within two or more ecosystems (e.g., Southeast and Northeast U.S. LMEs), coordinating the sampling methods, timing, and coverage of fisheries surveys that are spatial neighbors should be further emphasized (Blanchard *et al.*, 2008).

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. 5), 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 LME (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 for several species, 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; Rijnsdorp *et al.*, 2009; Megrey *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 in turn produce a detectable population-level effect.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

M.A.S. obtained data, designed project, conducted analyses, and wrote manuscript. G.M.N. and R.J.L. assisted with and supervised project design, analysis, and writing/editing of manuscript.

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(NCAR, 2013)
(Enfield *et al.*, 2001)
(Wang *et al.*, 2008)
(NCAR, 2015)
(Joyce, 2002)
(Bridgman and Oliver, 2006)
(NCDC, 2015)
(Mantua and Hare, 2002)
(SCO, 2015)
(CPC, 2015a)
(CPC, 2015b)
(Henderson and Vega, 1996)
(Leathers *et al.*, 1991)
(Kalnay *et al.*, 1996)
(Diem, 2013)

TABLES

Table 1. Descriptions of climate covariates considered in dynamic linear models. Correlation values (R, + or −) are for the period of 1988–2013. Time series for all climate covariates are depicted in Fig. S2, except for Sea Bottom Temperature which is depicted in Fig. S3.

Covariate	**Calculation**	**Impacts to southeast U.S. Atlantic 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 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 PNA_W (0.50,+) and SOI (0.61,−)
Pacific North-American Pattern, summer (PNA_S) and winter (PNA_W)	Anomalies in the 500mb geopotential height field observed over the western and eastern U.S. (CPC, 2015a); average of monthly summer (PNA_S; May–Sep)	PNA_S: ↑ (↓) warm-season precipitation (Henderson and Vega, 1996); correlated with WBHI (0.34,−) PNA_W: + (−) phase: ↓ (↑) winter temperatures (Leathers et al., 1991; SCO, 2015); correlated with AMO (0.43,+), PDO

	and winter (PNA_W; Dec–Mar) values	(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 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 Supporting Information)	+ (−) phase: ↑ (↓) summer precipitation, similar to the better known Bermuda High Index (BHI) (Henderson and Vega, 1996; Diem, 2013); correlated with 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 Supporting Information)	Proxy for temporal changes in availability of species due to variation in temperature-induced seasonal or extreme event migration patterns

6

Table 2. Variance parameterizations for each unique combination of covariates. Process error variances for covariates were specified on the diagonal of the **Q** matrix (see Eq. 2). Observation error variance r (see Eq. 1) 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 **Q** estimated	1) estimated, 2) fixed	2
One (1 climate or 1 fishing)	1) Covariate **Q** estimated	1) estimated, 2) fixed	3
Two (1 climate and 1 fishing)	1) Covariate **Q**'s estimated, assumed equal 2) Covariate **Q**'s estimated, assumed unequal	1) estimated, 2) fixed	4

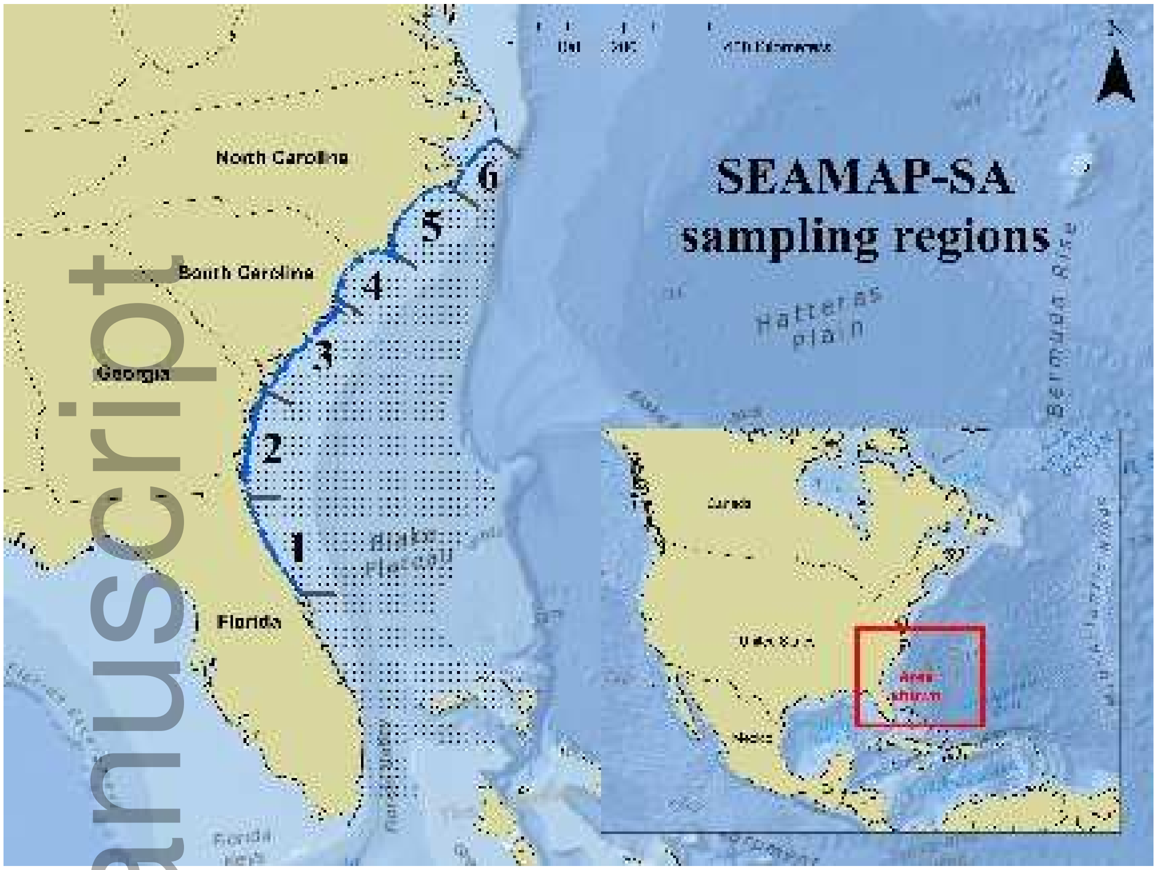
Table 3. Species for which climate and fishing effects were investigated using dynamic linear models. Species for three genera (Eucinostomus, Stenotomus, Doryteuthis) were grouped for analysis due to difficulties of rapid on-board survey taxonomic identification. Species identification numbers are referenced in Table 4.

	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 4. Prevalence Φ (Eq. 5) of climate and fishing covariates in time-truncated dynamic linear models, and species with at least 50% persistence φ (Eq. 4) for a given covariate. Species identification numbers referenced for persistence are specified in Table 3. 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 Φ**				**Species with persistence $\varphi \geq 0.5$**
			All	BF	E	I	**(numbers refer to species in Table 3)**
Warm	WBHI	71	10%	11%	10%	8%	1, 29, 46
	PNA$_S$	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$_W$	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** E: **49**, 50, **51**, **52**, 53, 56 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%	



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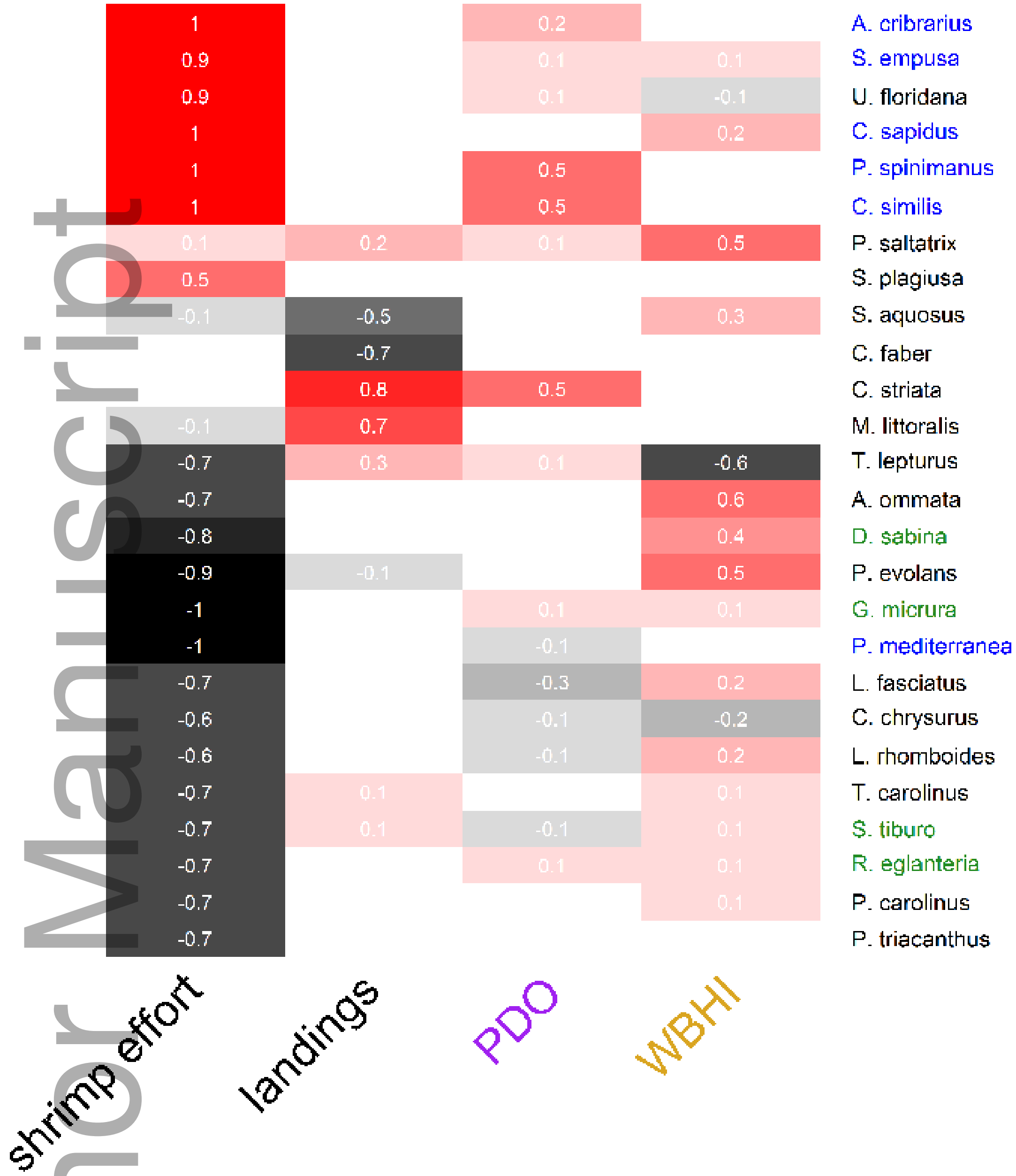

	shrimp effort	landings	PDO	WBHI
A. cribrarius	1		0.2	
S. empusa	0.9		0.1	0.1
U. floridana	0.9		0.1	-0.1
C. sapidus	1			0.2
P. spinimanus	1		0.5	
C. similis	1		0.5	
P. saltatrix	0.1	0.2	0.1	0.5
S. plagiusa	0.5			
S. aquosus	-0.1	-0.5		0.3
C. faber		-0.7		
C. striata		0.8	0.5	
M. littoralis	-0.1	0.7		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

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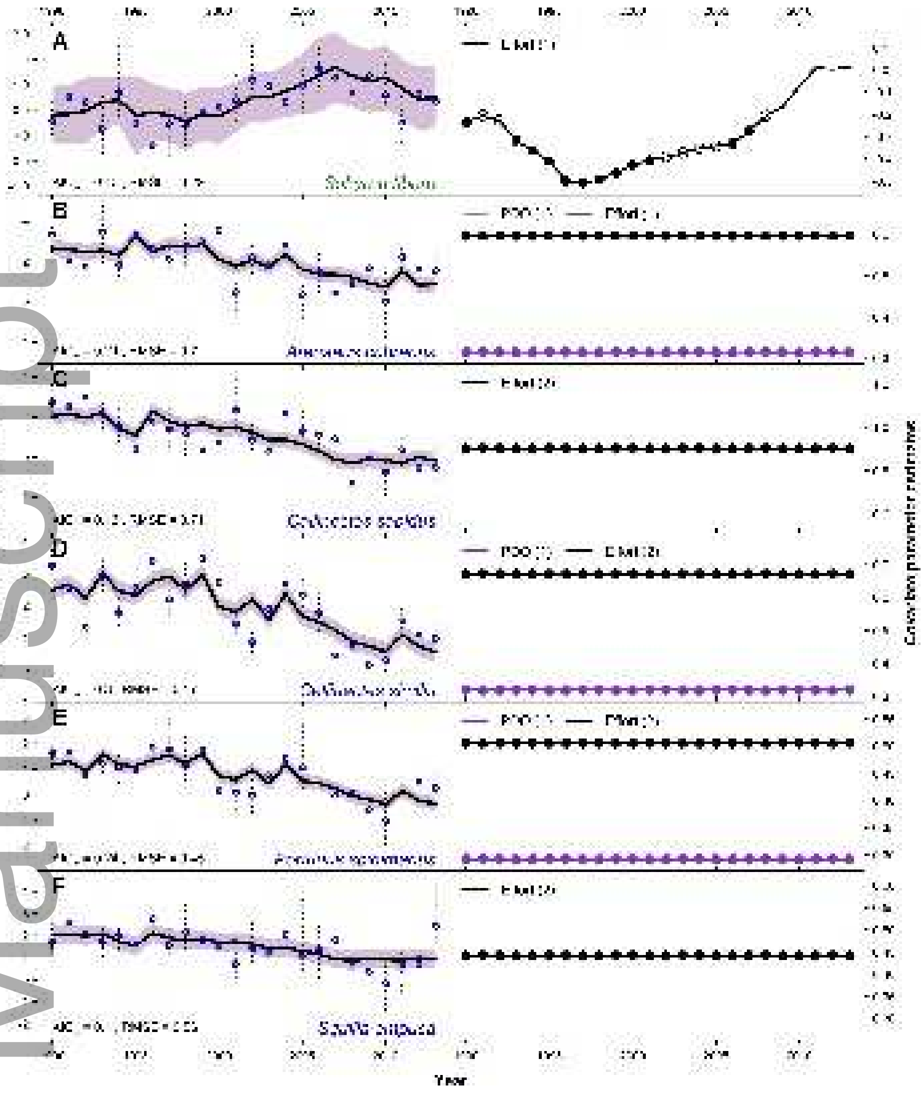

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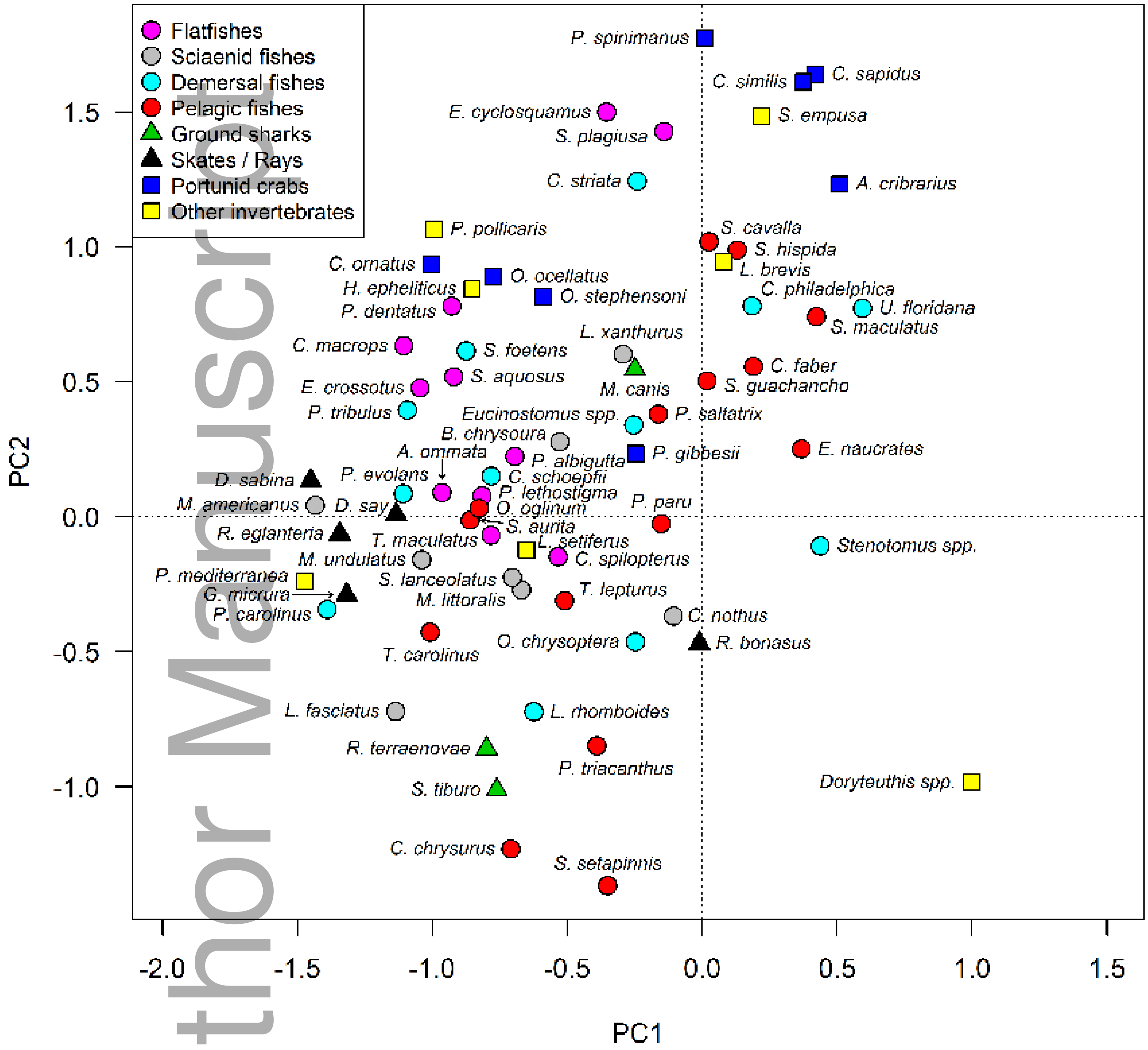

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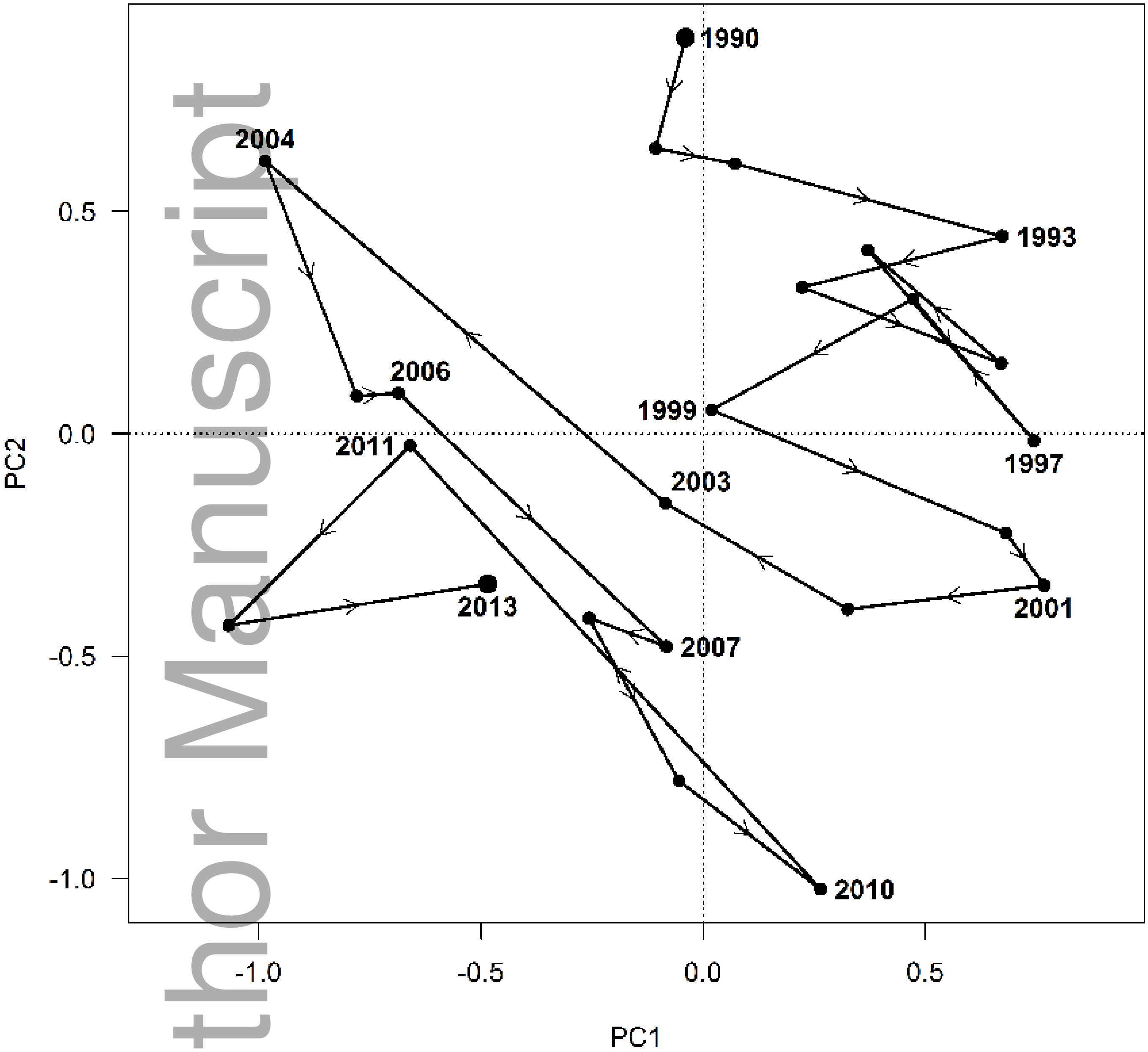

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