Title: Evaluating the influence of press and pulse disturbances on community dynamics of the Northeast US Large Marine Ecosystem

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Running Head: The nature of pulse and press disturbances

Abstract: As climate change intensifies, there is a pressing concern as to how ecological communities respond to disturbances occurring at different intensities and time scales. We explored how the type of disturbance influences the dynamics of a marine community. A pulse disturbance is an abrupt, high magnitude shift in conditions that can cause immediate and significant impacts to an ecological community. Alternatively, press disturbances are long term, multi-generational pressures acting on communities over time. The Northeast US Continental

Shelf Large Marine Ecosystem (NES LME) is one of the fastest warming regions in the world and has experienced historic overfishing. Assemblage shifts in the NES LME have previously been characterized, however, these were prior to an unprecedented pulse disturbance marine heatwave event (MHW) in 2012 followed by punctuated MHWs over the last decade. We quantified community change across the NES LME using a community trajectory analysis, a multivariate tool that utilizes geometric analyses and comparisons of community trajectories, to quantify shifts in dynamic beta diversity. We hypothesized the pulse MHWs would strongly influence ecosystem structure, however, no significant impact was detected. Our analysis indicates that the NES LME continues to tropicalize. However, it was not the pulse marine heatwave events that seemed to drive change, but rather ecosystem overfishing and rising temperatures. Here, we quantified beta diversity over time in marine communities undergoing abrupt environmental changes and press disturbances. When expanded globally, this analysis can compare how variable disturbance pressures may result in different manifestations of beta diversity change within marine assemblages.

Key words: large marine ecosystem, community trajectory analysis, ecosystem overfishing, pulse disturbance, press disturbance

1. INTRODUCTION

One of ecology's central aims is to understand how the nature of disturbances affect community assemblages. Regular small disturbances can maintain diversity (sensu Hutchinson 1961, Connell 1978) while larger and more sudden disturbances can completely reorganize food webs (Filbee-Dexter & Scheibling 2014, Gårdmark et al. 2015). Long-term, multi-generational pressures on communities, such as rising ocean temperatures and fishing pressures, are defined as press disturbances (Bender et al. 1984, Harris 2014). Alternatively, short-term or pulse disturbances, such as marine heat waves (MHWs), disease outbreaks, and storms can have a significant influence on the dynamics and interactions within communities as well (Jentsch & White 2019, Raymond et al. 2022). Pulse events are abrupt, as defined by their magnitude in relation to their duration and have demonstrated significant immediate ramifications for marine communities and negative effects on commercially important species (Jones et al. 2018, Smale et al. 2019, Von Biela et al. 2019, Diamond et al. 2020, Hillebrand & Kunze 2020). However, MHWs do not always disrupt fish biomass and accelerate tropicalization, and these disturbance pressures require additional research to understand (Fredston et al. 2023). Furthermore, an increase in both the spatial extent and potency of press and pulse disturbances in marine ecosystems has been observed across the globe as a result of increasing anthropogenic stressors and climate change (Herring et al. 2015).

These disturbance events have pronounced impacts on the social and economic well-being of fisheries-dependent people around the world (Hamilton & Haedrich 1999, He & Silliman 2019, Mendenhall et al. 2020). Ecological communities provide valuable ecosystem services, support global economic markets, ensure food security across the globe, and capture stunning levels of biodiversity (Costanza et al. 2014, Costello et al. 2020, Trew & Maclean

2021). The loss of such services and the stability of a system to provide them is a legitimate concern due to increasing, unprecedented rates of climate change (Amaya et al. 2023). For example, in 2012 a MHW caused by a combination of atmospheric warming and oceanographic change in the Gulf of Maine initiated earlier onshore migration of lobster and an increase in longfin squid (Mills et al. 2013, Pershing et al. 2018). This shift proved detrimental to the lobster fishery due to the market surplus and subsequent plummet in prices within the US and Canada, however, some fishers took advantage of the expanded squid fishery (Mills et al. 2013). This pulse event caused major disruptions to the socioeconomic systems in the Gulf of Maine, but how it altered the species assemblage at both short- and long-term scales is unclear.

Disturbances and deviations from ideal ecological conditions are often approached through a single or multi-species lens, however assemblage level assessments may capture the dynamics of the whole system where higher scales of biological organization may behave differently than individual components (Levin 1992, Schindler et al. 2015). Biological assemblages are valuable response indicators of changes in the environment as they integrate multiple drivers across trophic levels such that temporal changes in community assemblages suggest system-wide ecosystem change (Legendre & Gauthier 2014, Sturbois et al. 2021). Beta diversity metrics quantify compositional and abundance changes in community members (Dornelas et al. 2013), inform spatial and temporal patterns of community change (Legendre & De Cáceres 2013), and can be used to compare different communities to one another or the same community over time (Sturbois et al. 2021). Here, we quantify changes in beta diversity, community composition over time, in the marine nekton assemblages along the eastern coast of the United States in the Northeast United States Continental Shelf Large Marine Ecosystem (NES LME) using multivariate methods (De Cáceres et al. 2019, Sturbois et al. 2021).

The NES LME is an ocean warming hotspot (Pershing et al. 2015) boasting extensive oceanographic and fisheries data coverage, productive fisheries impacted by intense fishing (Fogarty & Murawski 1998), and unprecedented warming (Pershing et al. 2015, Le Bris et al. 2018). Recently there has been an increase in pulse MHW events (Mills et al. 2013, Chen et al. 2015, Gawarkiewicz et al. 2019) providing a unique opportunity to explore how the region has responded to disturbance pressures of different time scales.

Within the NES LME, the exploitation of commercially and economically relevant species by humans can be traced back centuries (Rosenberg et al. 2005, Grasso 2008, Boudreau et al. 2017). Ecosystem overfishing occurs when the total harvest exceeds what the ecosystem can support and is indicated by a decline in the total ecosystem catch, a decline in the total catch per unit effort of the entire ecosystem, and/or the ratio of total landings to primary production in the system surpassing established thresholds (Link & Watson 2019). Forty to fifty percent of temperate and tropical large marine ecosystems exceed ecosystem overfishing thresholds (Link & Watson 2019). Even with sustainable harvest, ecosystem overfishing can occur if there are declines in primary productivity due to disturbances. Combining these variables captures the important interaction between long term fishing pressures and shifts in primary productivity that may contribute to shifts in community composition.

Multi-decadal warming and shifts in oceanographic conditions play an important role within the NES LME where many of the ecological changes observed in the last 60 years can be explained by climate variability (Lucey & Nye 2010, Nye et al. 2011, Nye et al. 2014, Pershing et al. 2015). Long-term warming has been expressed in species range shifts in response to shifting temperature conditions (Nye et al. 2009, Pinsky et al. 2013, Mills et al. 2024). For example, species rarely seen in the Gulf of Maine such as longfin squid, black sea bass, and blue crab were commonly sighted in 2012 (Johnson 2015). This region is greatly affected by basin-scale climate variability due to the convergence of the Gulf Stream and Labrador Current systems (Greene et al. 2013, Lotze et al. 2022). Recent oceanographic alterations, such as the increased occurrence of warm core rings since 2000 (Gangopadhyay et al. 2019) and shifts in the Gulf Stream in 2008 (Gonçalves Neto et al. 2021), raise concerns about their impact on species assemblages. Increasing water column stratification and changes in nutrient concentrations (e.g. silicate) (Pershing et al. 2005, Ouellet-Bernier & de Vernal 2018) have also facilitated shifts in phytoplankton and zooplankton communities of the NES LME (Morse et al. 2017, Pershing et al. 2021, Lotze et al. 2022, Pershing & Kemberling 2024). It is unclear how these recent changes in oceanographic conditions have impacted the species assemblage; however, implications for the recruitment of commercially important species (Perretti et al. 2017) and range compression with changes in prey quality and availability have already been documented (e.g. the North Atlantic right whale, Record et al. 2019, Meyer-Gutbrod et al. 2021). These alterations in zooplankton populations may disrupt food web pathways (Pershing et al. 2021), with their size ratio potentially signaling broader community-level responses under disturbance pressures.

As anthropogenic pressures increase, it is crucial to determine whether pulse MHW events have a significant effect on the ecosystem or if gradual warming or other slow, but persistent drivers are more important. The NES LME, spanning from the Gulf of Maine to Cape Hatteras, is categorized into four ecological production units (EPUs) based on variations in physiographic, oceanographic, and biotic conditions (Lucey & Fogarty 2013). With persistent high mean temperatures prevalent in the NES LME, we anticipate the gradual tropicalization of the region's EPUs demonstrated in previous studies will continue (Lucey & Nye 2010). Herein, tropicalization refers to the current assemblage becoming more similar to the historic species assemblage of the adjacent southern EPU (Lucey & Nye 2010). However, our main goal is to understand drivers of change and magnitude of the community response. First, we predict the pulse MHW events will greatly disrupt community-level dynamics, as has been illustrated for individual species and populations (Mills et al. 2013, Pearce & Feng 2013, Frölicher & Laufkötter 2018, Amaya et al. 2023). Second, we expect that the extreme 2012 MHW and subsequent events in 2016 to 2017 caused a distinct impact on the marine community of the NES LME due to prolonged exposure to anomalous temperatures. Third, we hypothesize that the slow press of long-term warming and fishing pressure in the NES LME have significantly influenced community composition. An increase in fishing effort relative to the amount of productivity, captured by the Fogarty Ecosystem overfishing index, can result in adjusted energy flow patterns within the system because of declines in cumulative production, biomass of apex predators, and mean trophic level which can signal community level change (Pauly et al. 1998, Libralato et al. 2008, Link et al. 2015). Specifically, we anticipate the Fogarty index, as an indicator of both top-down and bottom-up pressures, may explain variation in community structure in the NES LME. Our approach considers community change within the context of short term disturbance events and long term ecosystem change and demonstrates quantitative approaches that can provide novel insights into drivers of ecological change.

2. MATERIALS & METHODS

This study investigates shifts in dynamic beta diversity, changes in community composition over time, within the NES LME regional EPUs over the last 50 years. To test the regional variation in community change during the study period we used a community trajectory analysis (CTA), a multivariate tool that extends the analysis of community dissimilarity matrices commonly used by community ecologist. The CTA calculates distances between assemblages (trajectory segment lengths) and the direction of change (trajectory angles) using geometric analyses of community composition over time (De Cáceres et al. 2019). Next, a redundancy analysis was computed to identify the variables associated with community composition in the NES LME through the study period. Lastly, a cross-correlation analysis was used to explore the community-level implications of the intense pulse MHWs.

2.1 STUDY AREA

The NES LME, defined as the area from the Gulf of Maine to Cape Hatteras, is divided into four EPUs classified by patterns in physiographic, oceanographic, and biotic conditions (Lucey & Fogarty 2013). Starting in the north, these include the Scotian Shelf, Gulf of Maine (GOM), Georges Bank (GB), and the Mid-Atlantic Bight (MAB)(Figure 1A). We analyzed data from the GOM, GB, and MAB over the years 1969-2019; because of gaps in spatial and temporal coverage of surveys in the Scotian Shelf, this region was not included in our analyses.

2.2 SURVEY DATA

In this analysis, the EPUs of the NES LME represent distinct ecological communities. We calculated the mean stratified biomass for species in each EPU from the Northeast Fisheries Science Center’s fall bottom trawl survey (Grosslein 1969, Azarovitz 1981). We used only offshore strata within the distinct EPUs that were sampled annually, for a total of 50 years included in the analysis. The year 2017 was dropped from the MAB due to ship issues leading to low coverage. The survey uses a stratified random design to sample fish and macroinvertebrates (Politis et al. 2014). We used only species that composed at least 0.01% of the total biomass in at least one EPU from 1969 to 2019; e.g., a species that met the threshold in the MAB but not in the GOM was included for all ecoregions. This provided a total of 76 finfish and invertebrate species (Table S1).

We used mean stratified biomass (kg per tow) rather than abundance (numbers per tow) because it is a better measure of energy within the system and considers not only changes in numbers of individuals, but the weight of those individuals. All analyses were performed using R Statistical Software (v4.1.2; R Core Team 2021). Mean stratified biomass observations for each species within the separate EPUs were extracted via the "survdat" R package (v1.0, Lucey & Beet 2015).

2.3 COMMUNITY TRAJECTORY ANALYSIS

We conducted a CTA on the mean stratified biomass of the finfish and macroinvertebrate assemblage comprised of 76 selected species over a period of 50 years to explore variability in community trajectories (De Cáceres et al. 2019) (Table S1). A dissimilarity matrix calculates the dissimilarity between two assemblages in space or time using biomass of all species at each site. Here we quantified this dissimilarity with the Hellinger distance coefficient, which computes the Euclidean distance on square root transformed species relative biomass (Legendre & Gallagher 2001). A Hellinger transformation on these data places little to no emphasis on zeros and rare species, is the recommended transformation for evaluating compositional resemblances over time, and fulfills metric and Euclidean properties (Legendre & Gallagher 2001, Legendre and De Cáceres 2013, Sturbois et al. 2021, Toumi et al. 2023).

Two key geometric properties of the CTA that can be used for comparison are the segment length and direction of the trajectories between community states over time and space. The trajectory segment length is representative of the distance between the two observation endpoints in the multidimensional space of the analysis; it illustrates how dissimilar the two consecutive state observations are (De Cáceres et al. 2019). The traditional trajectory segment length measures interannual differences in year-to-year community state observations (see De

Cáceres et al. 2019 and Sturbois et al. 2021 for detailed formulas). We also computed segment lengths relative to the starting assemblage, which extracts the distance calculated when comparing the current year's community state to the initial community state (Sturbois et al. 2021). Segment lengths relative to the starting assemblage visualize how far away from the reference condition the community becomes over the time series. Here, the reference condition is defined by our community observations in 1969. Comparatively, the traditional trajectory segment lengths quantify the magnitude of year-to-year changes in community state.

The CTA also captures change in community state by its directionality. The value of the angle within the CTA falls in a range of 0 to 180 degrees, which is the measured angle of the vector created between the first and second observation and the second and third. In a hypothetical community of three species, if 0, the angle represents that the community is changing in the same way over time, e.g. in both time step 1 and time step 2 species A increases, species B decreases, species 3 stays the same. If 180, then the orientation of the vectors is the same, but is opposite "in sense", e.g. now in time step 2 we would see species A decrease, species B increase, and species C decrease (see De Cáceres et al. 2019 and Sturbois et al. 2021 for detailed formulas). When there is a high angle between two consecutive segments, that means an abrupt change in direction has been detected.

To compute the CTA and extract trajectory segment lengths, segment lengths relative to the starting assemblage, trajectory angles, and ordination diagrams we used the "ecotraj" package (v.0.0.1, methods per De Cáceres et al. 2019, Sturbois et al. 2021). The trajectory segment lengths and segment lengths relative to the starting assemblage for each individual EPU were extracted for the entirety of the sampling period to determine the magnitude of change in community state from year to year and relative to the reference state in 1969. Similarly, the trajectory angles for each individual EPU were extracted for the entirety of the sampling period to provide the directional change in community state.

2.4 COVARIATES

We compared a series of covariates to the changes the NES LME finfish and macroinvertebrate assemblage experienced. The selection of covariates set out to provide proxies for pulse disturbances and long-term pressures within the system in three categories: biological, physical, and socio-economic variables. A description of all covariates is displayed in Table 1. These covariates included annual observations of: zooplankton size ratio, the mean Gulf Stream index position, bottom temperature anomalies, MHW cumulative intensity, and the Fogarty ecosystem overfishing index. Ecosystem overfishing represented a major socio-economic driver based upon carrying capacity limits to production (Link 2021). When overfished, the system's catch level results in a decline of catch per unit effort which can result in the systemic depletion of the ecosystem's resources. Oppositely, continued ecosystem underfishing can suggest excess productivity or the possible underutilization of the fishery that can be further explored (Link & Watson 2019). Annual variable observations were extracted via the "Documentation of Ecosystem Indicator Reporting" package "ecodata"(v.0.1.0, Bastille & Hardison 2018) except for the zooplankton size ratio data. Due to constraints in MHW data availability, covariate observations from 1982 to 2019 were used for this study (Table 1).

2.5 CROSS CORRELATION ANALYSIS

Cross correlations were then conducted to detect if pulse marine heatwaves had lagged effects on the magnitude and directionality of change in the NES LME communities. Cross correlations determine the relationship between two time series at time *t and t+k (k = time lag)* and estimate a correlation coefficient for each time lag *k* considered within the analysis. Here, lags in the correlation up to seven years were considered. The threshold of seven years was set to avoid further exploring potentially spurious environmental relationships. A cross correlation is significant when the absolute value of the correlation coefficient exceeds:

$$2 \div \sqrt{(n - |k|)} \text{ (Yoo et al. 2023).}$$

Where *n* is the number of observations and *k* is the time lag. Here, we used a time series of the difference in MHW cumulative intensity as our possible predictor and the trajectory metrics, both segment lengths and angles, as our response variable. A significant cross correlation coefficient here may suggest MHW changes “lead” significant changes in trajectory segment lengths and angles. This analysis was also completed using the “vegan” R package (v.2.5-7, Oksanen et al. 2020) with data from 1982 to 2019 due to MHW data availability.

2.6 REDUNDANCY ANALYSIS

To test the relative importance of pulse and press disturbances on changes to the community assemblage over time we used a redundancy analysis on each EPU to summarize the variation due to the set of explanatory covariates being tested. We modeled relationships between community composition and each of the covariates from 1982 to 2017. A complete time series was required to compute the redundancy analysis so data was limited given the MHW time series began in 1982 and MAB data coverage was disrupted in 2017. The analysis was completed using the “vegan” R package (v.2.5-7, Oksanen et al. 2020). All covariate data were standardized, scaled to zero mean and unit variance, for comparison and inclusion in the redundancy analysis. The species data included in the redundancy analysis were Hellinger transformed as they were in the CTA. Forward stepwise model selection was used to determine the best model to explain community composition through the condition that the AIC of the new model including the additional variables had a lower AIC than the simpler model (Table S2). We defined the best model as the one that had the lowest AIC and if the difference in AIC values of two models was less than two, we choose the most parsimonious model (Burnham & Anderson 2002) (Table S2). We used variable partitioning to account for the possible correlation between covariates and to extract the marginal and conditional effects of each variable included in the final model. An analysis of variance (ANOVA) was conducted on each global, marginal, and conditional model to determine the significance ($p < 0.05$) of variance between models (Table S3).

3. RESULTS

The principal coordinate analysis generated by the CTA displays the temporal shifts in community state observations within the NES LME marine assemblage over the past fifty years (Fig 1B). The axes represent the principal coordinates, linear combinations of the original variables that explain the maximum variance in the data. Axis 1 and Axis 2 represent the two most significant principal coordinates, collectively explaining 67% of the total variation in community state observations over the fifty-year period (Fig. 1B) Samples that cluster closely together indicate similar community compositions, while those farther apart suggest significant shifts in assemblage structure. The trajectory segment lengths, represented by arrows connecting each consecutive point, quantify the magnitude of change the community is experiencing from one year to the next (Fig. 1B). The variance in the MAB was better described by PCoA 1 (x-axis, Fig 1B). The variance in the GOM and GB EPUs was orthogonal to the MAB and better explained by PCoA 2 (y-axis in Fig 1B). Over time, the MAB became more distinct from the other two EPUs and showed a higher degree of dissimilarity from its historic observations earlier in the time series (Fig.2C and Fig. 3).

The ordination of ecoregions over the sampling period revealed a long-term tropicalization across EPUs (Figure 2A-C). In the GOM, the later observations in the time series resemble the historic assemblage of the ecoregion to its south, GB (Fig. 2A). Similarly, within GB the current assemblage more closely resembles the historic MAB assemblage (Fig. 2B). In recent years the more northward ecoregions demonstrate community compositions that are more like the compositions of the southward regions at the beginning of the time series. The MAB did not have a southern neighboring region explored within this analysis; however, we did observe the MAB shifting uniquely over time (Fig. 2C). Over the entire time series, the MAB shifted the furthest from its 1969 reference state (Fig. 3). Segment lengths relative to the starting assemblage are highest in the MAB and lowest in GB (Fig. 3C and 3D). Observations of segment lengths relative to the starting assemblage increase monotonically in the first 20 years of the time series in all three EPUs (Fig. 3A). In the 1990's these relative segment lengths peak and then are relatively smooth with a slight average uptick across all three EPUs after 2010.

A redundancy analysis was conducted on each EPU individually to investigate the variables associated with the variation in beta diversity. The covariates within this study follow similar trends within all three EPUs, apart from the GOM which experienced higher levels of ecosystem overfishing prior to 2000 (Fig. 4). Each of the EPUs is influenced by different covariates (Fig. 5), however, the community-level influence of ecosystem overfishing manifests in all three EPUs. Forward stepwise model selection selected ecosystem overfishing as a significant variable in all three EPUs (Table S2). MHWs in the MAB and the Gulf Stream index in GB were also including in the best fitting models for these regions (Fig. 5B and 5C, Table S2).

Variance in community composition explained by the model selected covariates ranged between 13% in the MAB to 18.6% in GB (Table 2). Within the GOM, the Fogarty ecosystem overfishing index is a significant covariate. 13.43% of the variation in community composition over the sampling period can be attributed to this term. Within GB, the Gulf Stream Index and the Fogarty ecosystem overfishing index explained 18.58% of the variation in community composition over the sampling period. After variable partitioning, the conditional effect of the Gulf Stream Index is approximately 5% and the conditional effect of the Fogarty ecosystem overfishing index is 3%. The shared variance between the two is 5.8%. The effect of both variables is significant. The MAB model selection determined the Fogarty ecosystem overfishing index and MHW cumulative intensity to be significant with 13% of variation over the sampling period explained by these two variables. After variable partitioning, the conditional effect of both the Fogarty index and MHW cumulative intensity is 3.4%, with a shared variation between the two of 1%. Significant global, marginal, and conditional models in our EPUs also suggests that the included variables are significant and distinct thus supporting our conclusions here (Table S3).

No significant influence of MHW pulse disturbances on the speed and directionality of community change was detected in this study (Fig. 6, Table S4) (see *Supplemental Methods - 1.1 Cross Correlation Interpretation* for details).

4. DISCUSSION

4.1 TROPICALIZATION IN THE NES LME

The NES LME finfish and macroinvertebrate assemblage continues to tropicalize (Lucey & Nye 2010), but the recent MHW pulse events did not result in an abrupt shift in the assemblage and did not appear to accelerate this change. Rather ecosystem overfishing was the one variable that most described changes in all three NES LME communities. While MHWs in the MAB and Gulf Stream index in GB also added to the explanatory power of our models, their impact was small. However, the fact that individual indicators of enhanced warming in the NES LME did not add explanatory power to our models does not mean that warming is not important. The Fogarty ecosystem overfishing index incorporates both fishing and productivity into one metric. Temperature and stratification can greatly impact productivity (Behrenfeld et al. 2006, Polovina et al. 2008, Van De Poll et al. 2013), such that the combined effect of heavy fishing and a decline in productivity could have a much larger effect on the species assemblage than warming alone. As such, understanding how both fishing and climate impact species assemblages and ecosystem resilience are critical to effectively manage fisheries (Lotze et al. 2019).

We were surprised pulse MHW events did not cause sudden and large changes in species assemblages, but an important distinction to make is that we are investigating these disturbances at the community level. Pulse disturbances can cause significant impacts within marine communities on short time scales (Johnston & Keough 2002, Walker & Schlacher 2011, Wijaya et al. 2022) and to specific taxa (Von Biela et al. 2019, Diamond et al. 2020, Raymond et al. 2022), however, how these impacts could extend to the community and persist at longer time scales is poorly understood. Within the NES LME, we have observed pronounced but smooth tropicalization in the marine assemblage over time compared to the abrupt shifts we anticipated. Climate driven shifts in populous cold and warm water species synergized by fishing have been observed in North Atlantic waters and perhaps a similar dynamic may be at play here (Gushing & Dickson 1977, Sundby & Nakken 2008, Drinkwater & Kristiansen 2018). Compositional changes in the NES LME could be the result of long-term overfishing of commercially important benthic cold water species (e.g. cod, haddock, yellowtail flounder) that allowed warm water species to increase as has been observed in temperate marine ecosystems (Wernberg et al. 2016).

As pulse MHWs become more frequent and water temperatures increase, the incremental shifts in composition may accumulate and lead to tremendous change (Jacquet & Altermatt 2020), but not in the abrupt fashion we expected, as observed here. Both pulse and press events can affect individual species more than the community assemblage on short time scales, and their interactions may not ripple through the entire community immediately but could lead to lower resilience in the future.

4.2 PULSE DISTURBANCES – MARINE HEATWAVES

When explicitly testing metrics from the CTA, we do not see any significant influence of pulse MHWs on the magnitude and directionality of community change in the entire NES LME. This result is contrary to our initial hypothesis, as we anticipated the drastic nature of MHWs would drive a rapid and directional change in the aftermath of the disturbance across all EPUs. While these pulse disturbances create striking environmental contrast for community members to adapt and adjust to, marine systems can demonstrate higher levels of resilience to these pulse disturbances as a function of their high connectivity and functional redundancy where complex food webs provide a wide range of ways for the community to recover successfully (Hillebrand & Kunze 2020). Another factor that may contribute to these results is that species in this study tend to be longer-lived, as opposed to annual species that experience less ability to buffer from intense events. The spatial and temporal scale at which we analyzed the community can mask the effects of pulse events (Heim et al. 2021). Nekton could be changing their distribution within our EPUs to compensate for change without changing the overall community assemblage. This suggests that the NES LME is a highly resilient ecosystem, even though it has changed and tropicalized over the last 50 years (O’Leary et al. 2017).

The NES LME, like many western boundary current systems, is warming and is predicted to warm more quickly with anthropogenic climate change because of the poleward displacement of the western boundary currents (Wu et al. 2012, Saba et al. 2015, Yang et al. 2016). MHWs have been prominent in frequency and intensity in boundary current waters, but the effects have not been reported in western boundary current literature as much as eastern boundary current areas (Holbrook et al. 2019). Perhaps this is because the MHWs tend to be shorter in duration in these systems and/or because the western boundary current communities are adapted to high seasonality and interannual variability (Holbrook et al. 2019). Even so, the expectation of more intense and frequent MHWs begets the question of how these regional dynamics may respond in the future if pulse dynamics become a more consistent environmental condition.

We did find evidence in our redundancy analysis that MHWs impacted the MAB EPU, and that the MAB EPU is changing differently than the GOM and GB. Within the NES LME, there is a significant influence of subregions on community structure (Kleisner et al. 2016, Roberts et al. 2022). Cape Hatteras, North Carolina serves as the boundary between the MAB and the South Atlantic Bight. In this region, the Hatteras Front, and the convergence of cooler, low salinity waters in the MAB meeting the warmer, high salinity waters of the South Atlantic Bight creates a strong physical barrier and highly dynamic region (Savidge 2002). Even mobile species in the area can be restricted in moving beyond this barrier and/or be genetically distinct from northern stocks (e.g., short-finned pilot whales, Thorne et al. 2017 and Atlantic croaker, Schaffler et al. 2009). Species in the MAB can also be more vulnerable at the edge of their optimal thermal and geographic ranges (e.g., Atlantic surfclam, Timbs et al. 2019). Together, these dynamics may drive the different pattern of change that we saw in the MAB to anomalous temperatures and may be the mechanism associating the stronger influence of pulse disturbances like MHWs. Within the GOM and GB EPUs, we did not see a strong impact of MHWs; although individual species may be affected, in a resilient system the community as a whole can remain relatively stable.

4.3 PRESS DISTURBANCES – ECOSYSTEM OVERFISHING

In contrast to pulse disturbances, across all three EPUs, ecosystem overfishing explained a fraction of the observed variation in community composition, as indicated by the significance of the Fogarty ecosystem overfishing index in the redundancy analyses. The Fogarty index is unique in that it in essence captures both environmental change and fishing by relating primary productivity dynamics to the total landings in the system (Link & Watson 2019). The same magnitude of landings in two time periods could result in ecosystem overfishing when productivity declines presumably because of some environmental change (Behrenfeld et al. 2006, Polovina et al. 2008, Van De Poll et al. 2013). Historically we have also observed exhaustive, intense fishing pressure within the NES LME; predatory fish biomass reconstructions suggest biomass declines of greater than 70 to 80% from 1900 to 2000 in the region (Christensen et al. 2003). Using multi-faceted covariates, like the Fogarty index, may prove to be a more auspicious approach to capturing dynamics at the community level by accounting for multiple important factors influencing the system.

For comparison to our findings, a recent ecological assessment of eastern spotted skunk den use patterns with a redundancy analysis observed 19.6% of variation in den type selection attributed to the constrained covariates considered (Thorne & Ford 2022). In another study, a redundancy analysis was deployed to explore the relationship between soil heavy metal concentrations and environmental variables and found a total of 43.3% of variation in heavy metal concentrations, 36.3% and 16.6% respectively, attributed to soil properties and anthropogenic variables (Song et al. 2016). Their assessment considered a single sampling event of 99 sites in Wenling, China. While low, we consider an observed range of 13-18% of variation attributed to our constrained variables within an analysis of 76 species over 35 years to be noteworthy. Assemblage level dynamics are complex, thus finding comparable explained variance to single species studies and research with a narrower temporal scope within a marine assemblage is promising.

Prolonged pressures from fishing and shifts in productivity regimes within the NES LME act over the course of multiple generations and cause shifts in the reproductive success, species-level interactions, and health of marine community members through incremental, but persistent change (Carozza et al. 2018). The Fogarty index was consistently highest in the GOM, and this system experienced the most directional change. We observed a shared variance between the Fogarty index and mean Gulf Stream Index supporting the strong link between oceanographic processes and productivity dynamics in this ecoregion (Lee et al. 1991, Boyce et al. 2017). Ocean circulation and transport play critical roles in the nutrient transport and water column conditions necessary for increased primary productivity (Dai et al. 2023). Altered nutrient ratios and oceanographic regime shifts within the GOM are well-documented (Smith et al. 2012). In particular, the Fogarty index peaked in 1990-2000, and this leads to the period when we see marked change in the assemblage of zooplankton and GOM nekton. In all three EPUs the Fogarty index peaks prior to 2005, and the monotonic increase in segment lengths relative to the starting assemblage across all regions in this period may result in part from the press of ecosystem overfishing on assemblage conditions. The changes in composition we observed here could be indicative of the community repartitioning interactions to maintain system-level functionality even as individual species have varied over time (Hautier et al. 2014, Hoover et al. 2014**)**, especially due to the large-scale tropicalization of the region.

5. CONCLUSION

Climate and fishing not only drive shifts in interactions and species success, but the two pressures interact with one another to further degrade historic community conditions (Planque et al. 2010, Free et al. 2019). Discerning the difference between these pressures and the influence of humans and climate is difficult. The Fogarty ecosystem overfishing index encompasses both social-ecological interactions within the system as well as biological changes. No single variable could explain the change in community assemblage. We suggest more nuanced variables that address both anthropogenic and biological interactions may demonstrate a higher impact than any one environmental variable, even those with strong signals such as MHWs. One mechanism for further improving this work is to explore long-term pressures in the broader temporal context of marine ecosystems. Exploration of the paleo oceanographic and archaeological records to establish premodern baselines would provide conditions for a more comprehensive understanding of both climate and human impacts, well modeled recently in the GOM and Scotian Shelf (Lotze et al. 2022).

The amount of variability explained in the region-specific redundancy analyses was very low. Since the redundancy analysis is a constrained multivariate analysis, this suggests that some environmental variability or variables that we did not include in the redundancy analysis might be able to explain the changes in community assemblage that we observed in the unconstrained CTA analysis. We chose environmental variables that represented the dominant physical, biological, and socio-economic drivers in the region. We did not explicitly consider trophic interactions even though the nature of trophic interactions is critical in the resilience of ecosystems (Berlow 1999, McCann 2000). Trophic interactions likely moderate community dynamics within the NES LME and we suggest they be evaluated in future endeavors. While these mechanisms and pressures are more difficult to quantify over multiple generations, they represent important forces in how marine communities operate now and in the future.

Even though we did not see the impact of MHW dynamics we anticipated, this analysis was a successful collaboration of multiple techniques to explore disturbance dynamics. We believe the NES LME to be a resilient system, and this analysis is the beginning of further research to quantify beta diversity metrics through time and explore their utility as ecological indicators. The methods applied here should be applied to other assemblages to compare the apparent resiliency of different ecosystems; mechanisms described in this study may drive the NES LME's lack of dynamic response to severe, short-term events and serve as a launching point for supplemental research endeavors. Notably, methods to detrend MHW events to account for prolonged heat stress and water column location are emerging and represent another facet of pulse perturbation stress that we recommend be applied to this system in future study (Wang et al. 2022).

As climate change continues to alter marine ecosystems and impact fisheries, directing management actions to buffer the impacts of climate change or enhance the ability of people to respond to disturbance events is critical. Reducing fishing pressure, ameliorating eutrophication, and restoring habitats may yield more immediate benefits for ecosystem management than attempting to manage or predict nature's stochasticity (Scheffer 2009). As we determine appropriate management actions for stressed ecological systems, being attentive to how changes in fishing pressure can be compounded by abiotic factors and climate cycles will help align harvest levels and fishing strategies with stock productivity and biomass (Rogers & Dougherty

2018, Cline et al. 2019, Beaugrand et al. 2022). Our application of this emerging method in a large marine ecosystem creates an opportunity to explore how these metrics can serve as ecological indicators in response to disturbance pressures. While recent advancements in modeling and predictive research within marine fisheries have made significant strides, there remains a notable gap in community-level assessments encompassing both abiotic and biotic environmental conditions and interactions, which this study aims to advance.

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7. DATA AVAILABILITY

The data and the code used for data analysis, visualization, and modeling is openly accessible on GitHub at [https://github.com/IleanaF/MEPS_pulse_press]. Researchers are encouraged to refer to the provided references for further exploration and validation.

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9. TABLES

Variable	Variable Category	Disturbance Type	Description	Location and Time Series Length
Small to large zooplankton ratio	Biological	press	The ratio of abundance of small zooplankton (*Pseudocalanus spp*, *Centropoges typicus*, *Centropages hamatus*, and *Temora longicornis*) to large zooplankton (*Calanus finmarchicus*). Abundance is recorded as number of individuals per 10 m^2, extracted from the Northeast Fisheries Science Center Ecosystem Monitoring program observations (Bucklin et al. 2019).	Measured within each individual EPU 1977-2019
Gulf Stream index position	Physical	press	Annual time series of the relative position of the north wall of the Gulf Stream index (Joyce et al. 2019). The Gulf Stream is a warm ocean current flowing northward along the eastern United States that has a long-term increasing trend with decadal variability in its position. A positive index indicates that the Gulf Stream is in a more poleward position which is positively correlated with temperature on the NES shelf (Nye et al. 2011).	One value for all regions within the NES LME. 1954 - 2021
Bottom temperature anomalies	Physical	press	The anomaly time series depicts the variance between regional mean temperatures and predicted reference temperatures derived from historical regional averages (1981-2010) for the same time of year using a multiple linear regression model (Mountain 1991).	Measured within each individual EPU 1977 - 2021
Ecosystem overfishing - the Fogarty index	Socio-Economic	press	The ratio of total catches to total primary productivity in an ecosystem measured in parts per thousand (Link & Watson 2019).	Measured within each individual EPU 1960 - 2019
Marine heatwave cumulative intensity	Physical	pulse	A measure of the severity of marine heatwaves calculated by multiplying marine heatwave intensity (temperature anomaly in Celsius) and duration (cumulative degree days) using satellite sea surface temperature measurements. Marine heatwaves are defined as five or more days when sea surface temperatures are warmer than the 90th percentile based on a 30-year historical baseline period (Hobday et al. 2016).	Measured within each individual EPU 1982 - 2019

Table 1. Key variables examined for influence on community structure within the Northeast US Continental Shelf Large Marine Ecosystem (NES LME). Annual observations of each variable from 1982 to 2017 were considered within the redundancy analysis. Here we pulled observations from the three ecological production units (EPUs) within the NES LME used in this

study.

Ecological Production Unit	Partition	Inertia	Proportion	Overall Explained Variance	Adjusted R^2
Gulf of Maine	Total	0.12379	1		
Gulf of Maine	Constrained	0.01662	0.1343	13.43%*	0.10882*
Gulf of Maine	Unconstrained	0.10717	0.8657		
Georges Bank	Total	0.09926	1		
Georges Bank	Constrained	0.01845	0.1858	18.58%*	0.13651*
Georges Bank	Unconstrained	0.08081	0.8142		
Mid Atlantic Bight	Total	0.11563	1		
Mid Atlantic Bight	Constrained	0.01505	0.1301	13.01%*	0.07740*
Mid Atlantic Bight	Unconstrained	0.10059	0.8699		

Table 2. Variance partitioning results for three Ecological Production Units (EPUs): Gulf of Maine, Georges Bank, and Mid-Atlantic Bight. The table presents the total inertia, constrained inertia, and unconstrained inertia for each EPU, along with the proportion of variance explained, adjusted R squared, and whether the ANOVA determined the results to be significant ($p < 0.05$, here all values are $p < 0.001$), designated by a *. Model selection and ANOVA reporting are found in Tables S2 and S3, respectively.

10. FIGURES

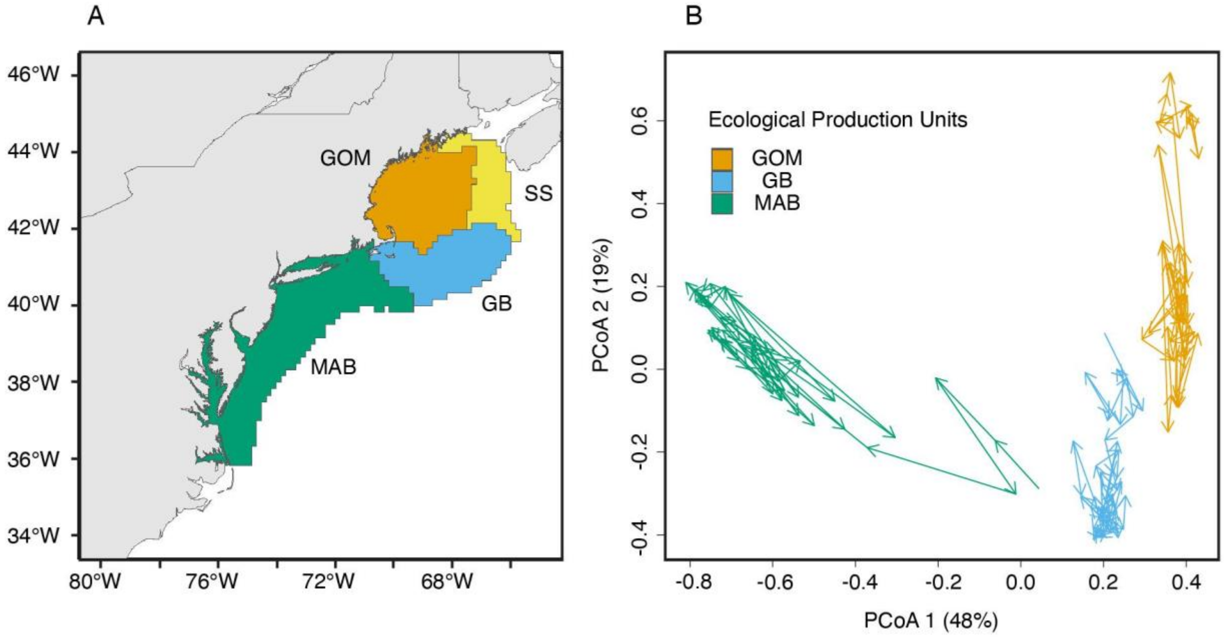

Figure 1. (A) The Northeast US Continental Shelf Large Marine Ecosystem (NES LME) is broken into four ecological production units: the Scotian Shelf (SS), Gulf of Maine (GOM), Georges Bank (GB), and the Mid Atlantic Bight (MAB). (B) The community trajectory analysis for the NES LME (excluding SS due to data limitations) where the arrows between points visualize the different states of the community from year to year. PCoA Axis 1 captures 48% of variation and PCoA Axis 2 captures 19% for a total of 67%.

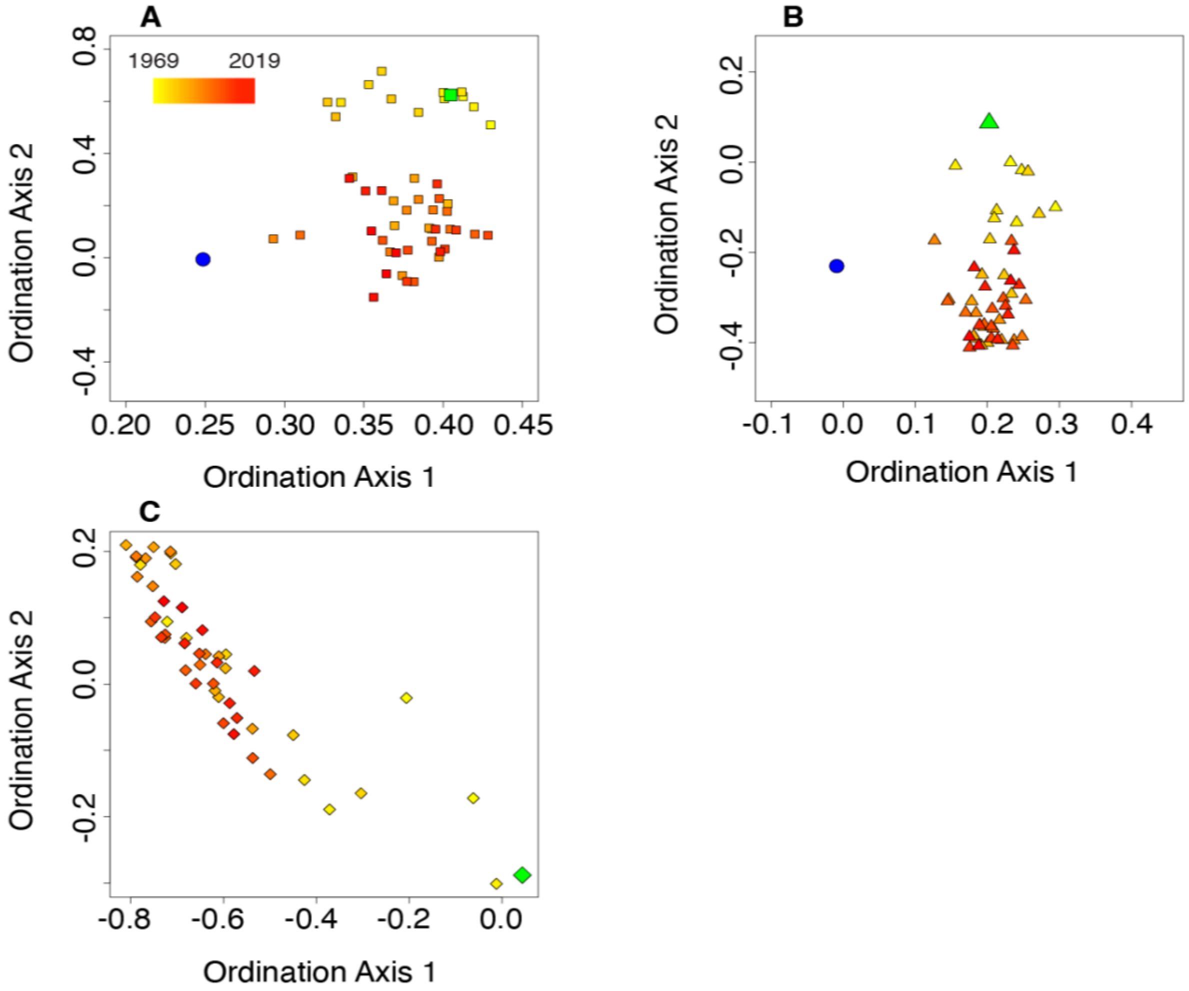

Figure 2. The ordination diagram for each of the three ecological production units examined; (A) Gulf of Maine, (B) Georges Bank, and (C) Mid Atlantic Bight. There are two reference points within each ordination. The blue circular point represents the average location of community observations from the 1960s of the ecoregion to its south, such that the blue point in (A) the Gulf of Maine references the average Georges Bank assemblage of the 1960s, (B) Georges Bank references the average Mid Atlantic Bight of the 1960s and (C) The Mid Atlantic Bight does not have a southern ecoregion included in this analysis so is excluded. The green diamond denotes the first community state observation used in the trajectory analysis in 1969. Segment lengths relative to the starting assemblage are calculated from this point.

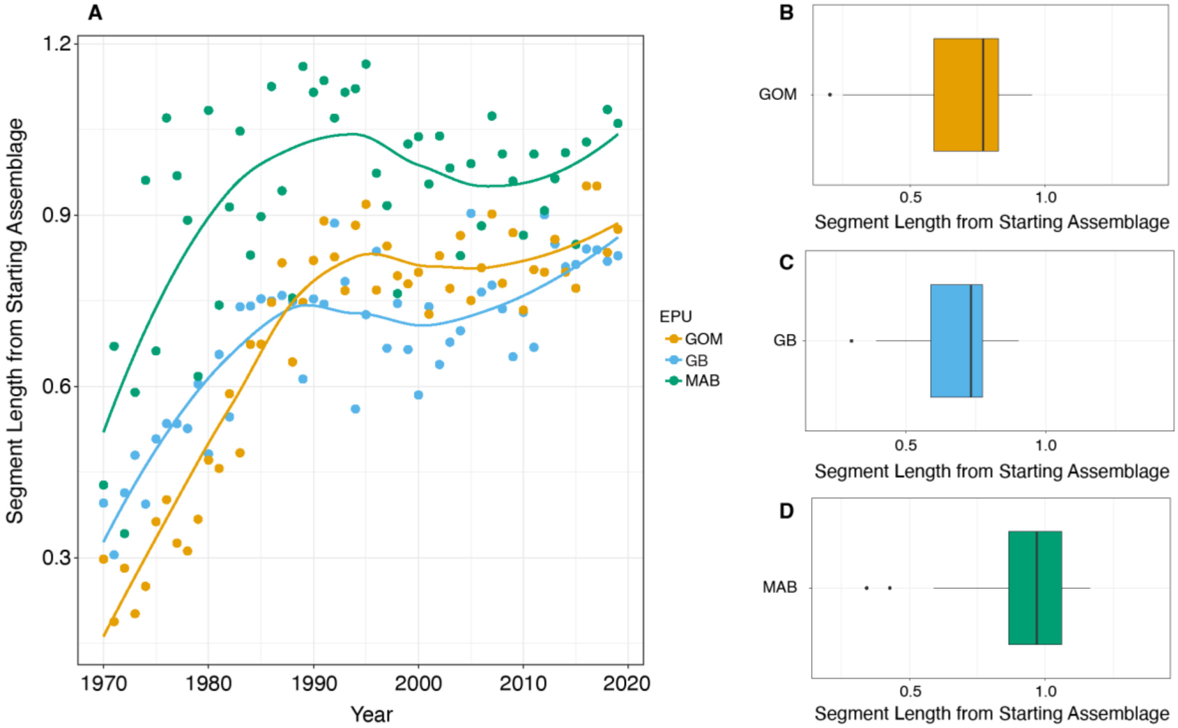

Figure 3. (A) Scatter plot displaying distribution of segment lengths relative to the starting assemblage in 1969 within each ecological production unit (EPU). The larger the value the further from the reference condition the community state in the given year is. A locally weighted scatterplot smoothing (LOESS) curve is overlaid. (B) Boxplot displaying the distribution of segment lengths from the starting assemblage in the Gulf of Maine (GOM), (C) Georges Bank (GB), and (D) the Mid Atlantic Bight (MAB). Each box represents the interquartile range within the respective category, with the median indicated by the horizontal line within the box. The whiskers extend to the minimum and maximum values within 1.5 times the interquartile range, while outliers are plotted individually.

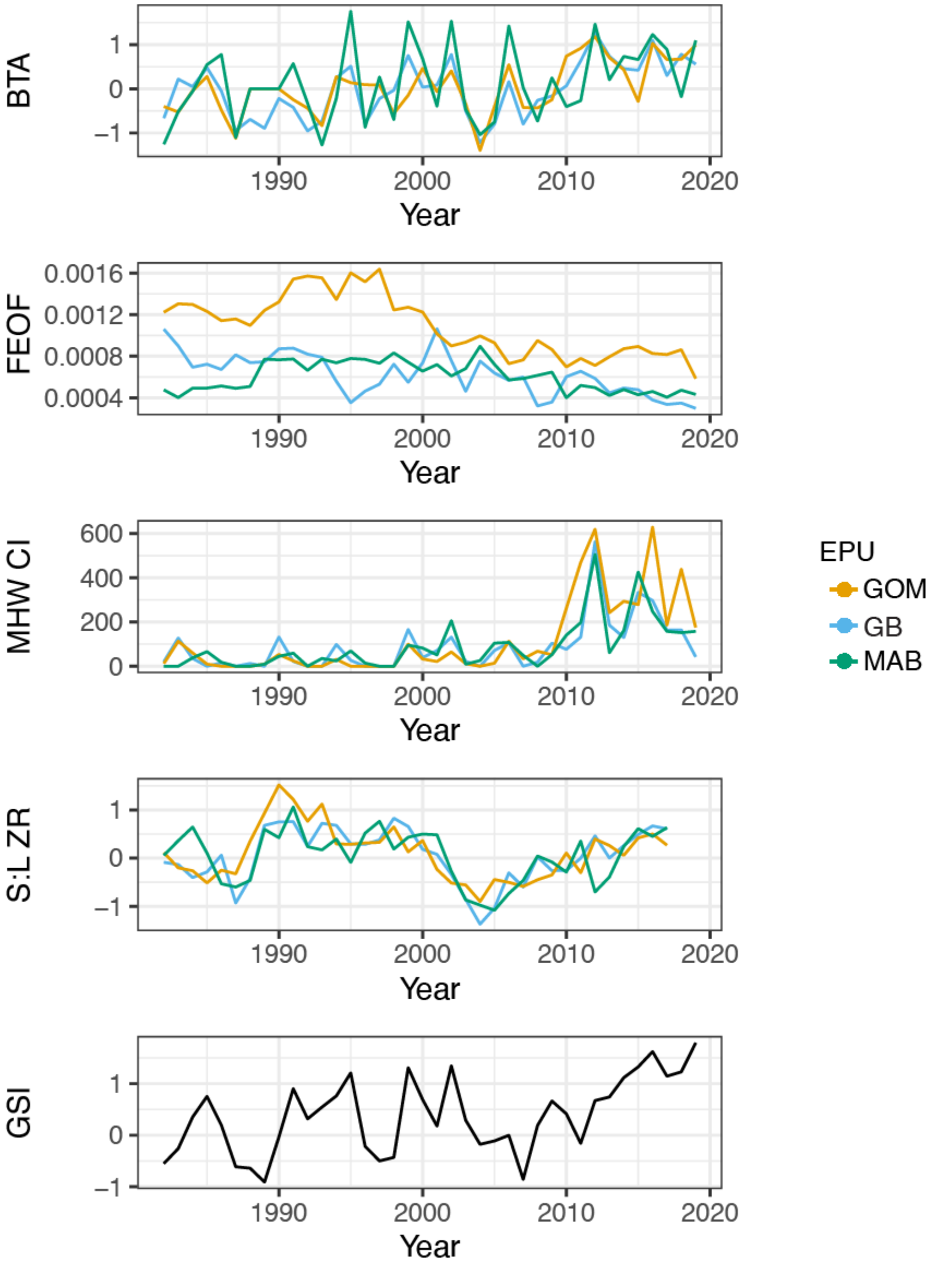

Figure 4. The time series of annual observations for bottom temperature anomalies (BTA), the Fogarty ecosystem overfishing index (FEOF), marine heatwave cumulative intensity (MHW CI), the small to large zooplankton ratio (S:L ZR), and mean Gulf Stream index position (GSI) limited by years with full data availability (starting in 1982 for MHW CI). A full description of these variables is in Table 1.

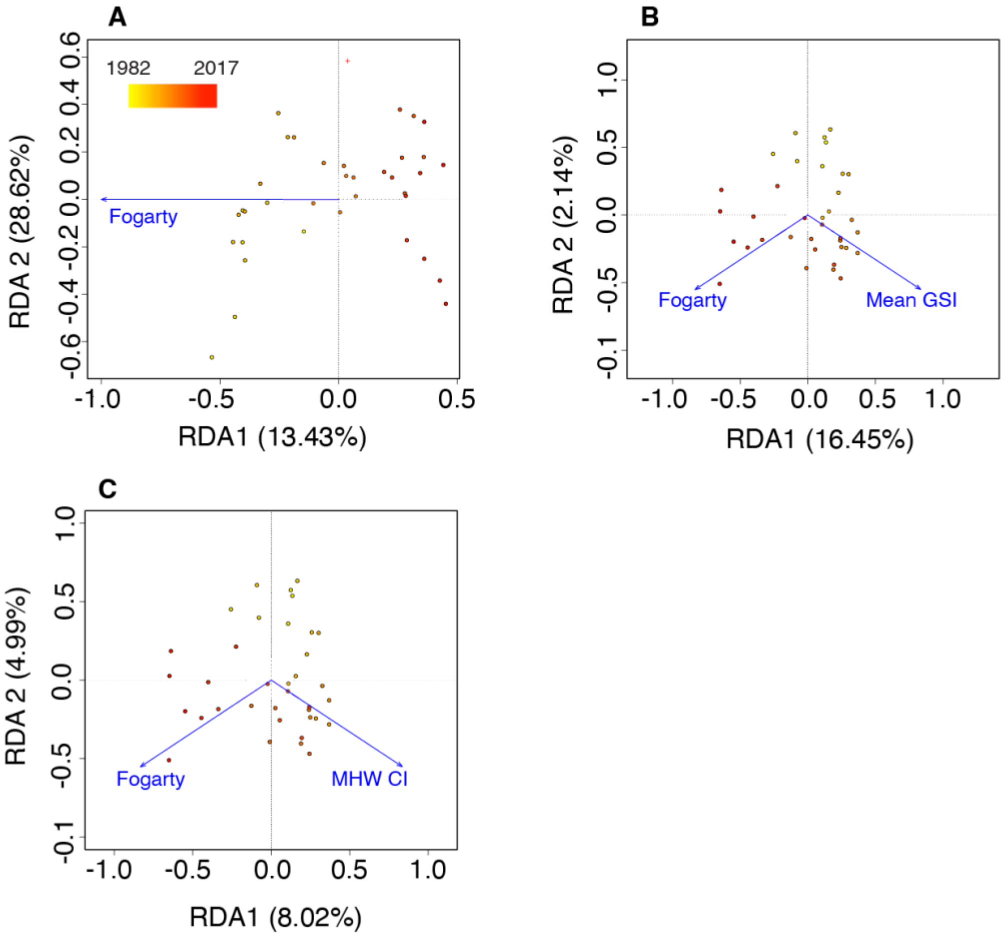

Figure 5. Redundancy analysis (RDA) of covariate influence on community structure and composition over the study period for all three ecological production units (A) the Gulf of Maine, (B) Georges Bank, and (C) the Mid Atlantic Bight with data from 1982 to 2017. Circles are the RDA scores for each sampling year with time represented in the gradient of colors from yellow (earliest years) to red (latest). MHW CI is the annual marine heatwave cumulative intensity and Mean GSI is the mean Gulf Stream index position (Table 1).

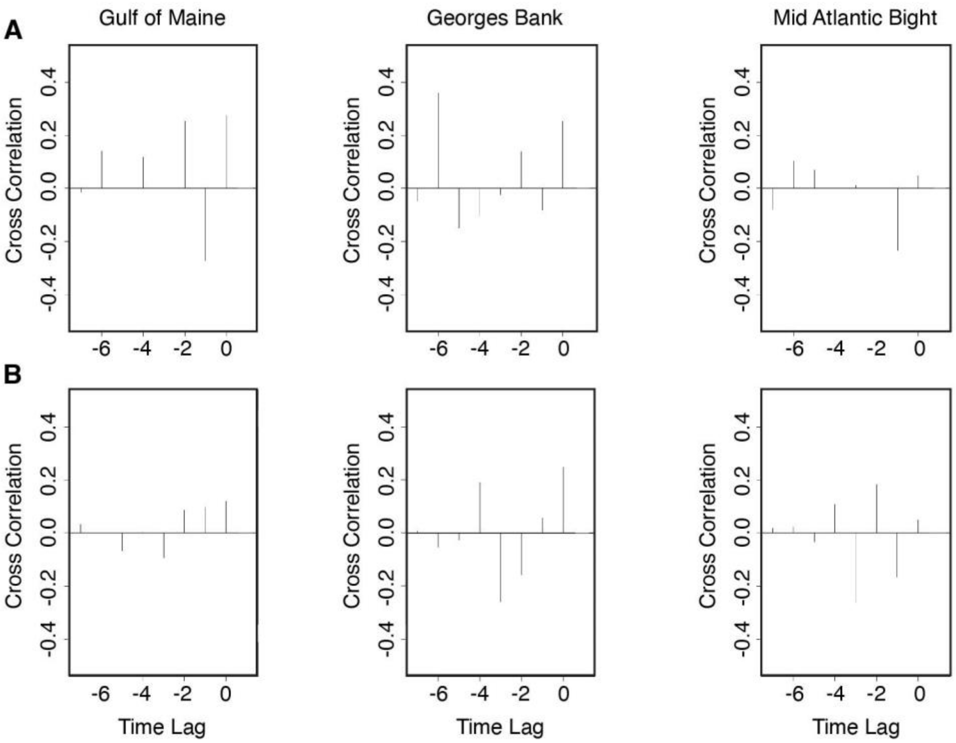

Figure 6. Cross correlation relationships between marine heatwave cumulative intensity and (A) the magnitude of community change (community trajectory analysis segment lengths), and (B) the directionality of change (community trajectory analysis angles) on a lag of 7 years. Within all three ecological production units no cross correlation exceeds calculated thresholds for significance.