

Evidence of climate-driven ecosystem reorganization in the Gulf of Mexico

MANDY KARNAUSKAS¹, MICHAEL J. SCHIRRIPA¹, J. K. CRAIG², GEOFFREY S. COOK^{3,4}, CHRISTOPHER R. KELBLE³, JUAN J. AGAR¹, BRYAN A. BLACK⁵, DAVID B. ENFIELD^{3,4}, DAVID LINDO-ATICHATI⁴, BARBARA A. MUHLING^{1,4}, KEVIN M. PURCELL², PAUL M. RICHARDS¹ and CHUNZAI WANG³

¹*Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, FL 33149, USA,*

²*Southeast Fisheries Science Center, National Marine Fisheries Service, 101 Pivers Island Road, Beaufort, NC 28516, USA,*

³*Atlantic Meteorological and Oceanographic Laboratory, Office of Oceanic and Atmospheric Research, 4301 Rickenbacker Causeway, Miami, FL 33149, USA,* ⁴*Rosenstiel School of Marine and Atmospheric Science, Cooperative Institute for Marine and Atmospheric Studies, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA,* ⁵*Marine Science Institute, University of Texas, 750 Channel View Drive, Port Aransas, TX 78373, USA*

Abstract

The Gulf of Mexico is one of the most ecologically and economically valuable marine ecosystems in the world and is affected by a variety of natural and anthropogenic phenomena including climate, hurricanes, coastal development, agricultural runoff, oil spills, and fishing. These complex and interacting stressors, together with the highly dynamic nature of this ecosystem, present challenges for the effective management of its resources. We analyze a compilation of over 100 indicators representing physical, biological, and economic aspects of the Gulf of Mexico and find that an ecosystem-wide reorganization occurred in the mid-1990s. Further analysis of fishery landings composition data indicates a major shift in the late 1970s coincident with the advent of US national fisheries management policy, as well as significant shifts in the mid-1960s and the mid-1990s. These latter shifts are aligned temporally with changes in a major climate mode in the Atlantic Ocean: the Atlantic Multidecadal Oscillation (AMO). We provide an explanation for how the AMO may drive physical changes in the Gulf of Mexico, thus altering higher-level ecosystem dynamics. The hypotheses presented here should provide focus for further targeted studies, particularly in regard to whether and how management should adjust to different climate regimes or states of nature. Our study highlights the challenges in understanding the effects of climatic drivers against a background of multiple anthropogenic pressures, particularly in a system where these forces interact in complex and nonlinear ways.

Keywords: Atlantic Multidecadal Oscillation, fisheries management, human dimension, indicator, large marine ecosystem, regime shift

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Introduction

The concepts of ecosystem stability, thresholds, and successional change have been well-studied over the past century, and the influence of climate on these ecosystem changes has long been recognized (e.g. Elton, 1927; Tansley, 1935; Clements, 1936). For example, climate effects on sardine populations along the west coast of the United States, and their linkages to the economy of California in the 1930s, were made famous in Steinbeck's *Cannery Row*. However, our understanding of regime shifts, multiple stable states, and critical ecosystem transitions remained relatively undeveloped until the mid-1970s (Holling, 1973). In part, this was due to the paucity of long-term time series data

necessary for understanding large spatial and temporal scale processes (May, 1977; McGowan *et al.*, 1998; Bograd *et al.*, 2003). Initial studies of regime shifts were conducted in terrestrial and lacustrine ecosystems, but eventually broadscale synoptic studies were initiated in the marine environment (McGowan *et al.*, 2003). Climate-driven ecosystem shifts have now been described in the northeastern Pacific, North Atlantic, and Baltic Sea (Mantua *et al.*, 1997; Anderson & Piatt, 1999; Hare & Mantua, 2000; Alheit *et al.*, 2005; Edwards *et al.*, 2013), among other regions.

Typically, such studies of climate-driven regime shifts have been limited to biological communities, although we should expect their impacts to ripple through to the human communities that depend on ecosystems as well. This may be due to direct effects of climate on human behavior and resource acquisition activities (e.g. Carter & Letson, 2009; Haynie &

Correspondence: Mandy Karnauskas, tel. 305 361 4592, fax 305 361 4499, e-mail: mandy.karnauskas@noaa.gov

Pfeiffer, 2013) or due to indirect effects of climate on the distribution and availability of resources, which then alter human behavior (e.g. Pinsky & Fogarty, 2012; Pinsky *et al.*, 2013). However, human activities not only respond to ecosystems, but also they are important drivers of change – fundamentally altering the structure, function, and dynamics of natural ecosystems (Vitousek *et al.*, 1997). Thus, anthropogenic and climatic factors may interact and do so antagonistically or synergistically, making it challenging to disentangle or attribute specific drivers on ecosystem processes (Mollmann *et al.*, 2011). Identifying and understanding the full complexity and scale of shifts, and their impacts on the natural and human components of ecosystems, has important ramifications for the management of marine resources.

The Gulf of Mexico (GoM) is the ninth largest body of water in the world and encompasses one of the most ecologically and economically productive ecosystems in North America. Yet, relative to other ecosystems in the United States, the GoM has received little attention in regard to primary drivers and pressures, ecosystem function, and the interaction between climate and human influences. Given the economic and biological importance of the region, this represents a critical knowledge gap. In this study, we explore how the physical, biological, and socioeconomic properties of the GoM have changed since the 1950s, and attempt to identify some of the major climatic or anthropogenic drivers of these changes. To do so, we analyze a suite of indicators capturing the physical, biological, and socioeconomic dimensions of the GoM large marine ecosystem. In the absence of long-term monitoring data for the region, we also consider trends in landings composition data from 1950 to the present. We identify major shifts in both the suite of indicators and landings data and explore links between these shifts and global climate drivers. In the discussion that follows, we describe how both biological and socioeconomic dimensions of the GoM may be altered in response to climate shifts, against a background of complex management activities.

Materials and methods

Indicator selection process

The indicator selection process was initiated with the goal of reaching scientific consensus about a relevant set of measurable indicators spanning the DPSIR (Drivers, Pressures, States, Impacts, Responses) framework. The DPSIR framework has been applied around the globe for more than a decade to describe the key components and linkages between socioeconomic and environmental indicators in a manner that can

inform resource management decision-making (Bowen & Riley, 2003; Tscherning *et al.*, 2012). We chose to apply the DPSIR framework for organizing indicators, because we were interested in investigating climate-driven regime shifts in both the biophysical and socioeconomic components of the GoM ecosystem. To achieve this goal, we first solicited extensive input from a variety of different scientific disciplines to generate a list of indicators. From this initial list of potential candidates, indicators were grouped into six categories: climate drivers, physical pressures, lower trophic level ecosystem states, upper trophic level ecosystem states, fishing impacts, and socioeconomic responses (Karnauskas *et al.*, 2013). To refine this extensive list, a selection process was conducted using a predetermined list of criteria relating to three desirable indicator attributes: responsiveness, degree of representation across the broad ecosystem, and understandability. The link to an online poll was sent via individual emails, list serves, and institutional group email addresses throughout the region. Responses were anonymous, but respondents were asked to include their area of expertise and affiliation. Sixty responses were received, including affiliations with NOAA Fisheries (21), other NOAA laboratories (13), academic institutions (12), and other institutions such as state laboratories or conservation organizations (14). Based on these responses, the top ten scoring indicators from each category were included in subsequent analyses. Details of selected indicators and their data sources and calculations can be found in Karnauskas *et al.* (2013) and in Table 1. Note that indicators were calculated based on raw data sources to the extent possible – for example, stock assessment data were extracted directly from U.S. and Mexican stock assessment reports, rather than relying on synthesis databases. Indicators based on published literature were obtained by communicating directly with authors to ensure that the most accurate and current values were used in the analysis.

Statistical methods

To explore temporal patterns within the ecosystem, we carried out a principal components analysis (PCA) and chronological clustering for three groups of indicators: (1) drivers and pressures, (2) upper and lower trophic level states, and (3) impacts and responses. Most indicators were distributed normally; where this was not the case, indicators were log-transformed before the ordination was performed. PCA is a statistical matrix operation that reduces a large data set to a smaller number of pseudovariables, or principal components, which explain most of the variation in the data set. Chronological clustering is similar to hierarchical clustering in that it seeks to identify classes of variables based on a distance matrix, but it is constrained by sample order (in this case, years). PCA was carried out on a scaled matrix (time series scaled to mean of zero and standard deviation of one) for the years 1980–2011 for all indicators with at least 25 years of data; any missing values were replaced by the mean value of the time series. Because all variables displayed normal distributions after transformation, and relationships between indicators appeared to be largely linear, PCA was considered the most

Table 1 List of indicators, for which sufficient time series length was available, used in this study. Loading pertain to the first axes of the principal components analyses reported in Fig. 1. For further details on the full suite of indicators considered, data sources and calculations, see Karnauskas *et al.* (2013)

Indicator	Loading	Data source
Drivers and pressures		
Index of fertilizer consumption for Mississippi River watershed	-0.331	U.S. Department of Agriculture
Mean offshore sea surface temperature	-0.320	Advanced Very High Resolution Radiometer (AVHRR)
Offshore sea surface temperature maximum monthly mean	-0.300	Advanced Very High Resolution Radiometer (AVHRR)
Number of oil spills originating from U.S. GoM Atlantic warm pool mean	-0.289	Bureau of Safety and Environmental Enforcement
Area of the northern GoM hypoxic zone	-0.215	Atlantic Oceanographic and Meteorological Laboratory
Hurricane activity (ACE index)	-0.146	Louisiana Universities Marine Consortium
Mean streamflow Mississippi River	-0.117	Wang <i>et al.</i> (2011)
Marsh flooding rate in Barataria Bay, LA	0.066	U.S. Geological Survey
Total suspended sediment discharge Mississippi River	0.074	T. Minello, unpublished data
Total precipitation Mississippi River watershed	0.101	U.S. Army Corps of Engineers
Atlantic warm pool day of year of maximum formation	0.118	Milly and Dunne (2011)
Annual mean dissolved oxygen off TX in summer	0.138	Atlantic Oceanographic and Meteorological Laboratory
Annual mean dissolved oxygen off LA in fall	0.227	Southeast Area Monitoring and Assessment Program
Number of oil rigs installed U.S. GoM	0.264	Southeast Area Monitoring and Assessment Program
Annual mean dissolved oxygen off LA in summer	0.267	Bureau of Ocean Energy Management
Total basin load of nitrogen Mississippi River	0.282	Southeast Area Monitoring and Assessment Program
Annual mean dissolved oxygen off TX in fall	0.303	U.S. Geological Survey
States	0.342	Southeast Area Monitoring and Assessment Program
Abundance index of blacknose shark in northern GoM	-0.302	Southeast Data, Assessment and Review (SEDAR)
Abundance index of yellowedge grouper in northeastern GoM	-0.287	Southeast Data, Assessment and Review (SEDAR)
Abundance index of tilefish in northeastern GoM	-0.284	Southeast Data, Assessment and Review (SEDAR)
Abundance index of blacktip shark in northern GoM	-0.279	Southeast Data, Assessment and Review (SEDAR)
Abundance index of roseate spoonbill 1	-0.215	National Audubon Society Christmas Bird Count
Abundance of <i>Farfantepenaeus brasiliensis</i> in southern GoM	-0.207	Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación
Abundance index of tilefish in northwestern GoM	-0.179	Southeast Data, Assessment and Review (SEDAR)
Species evenness off LA	-0.168	Southeast Area Monitoring and Assessment Program
Species evenness off TX	-0.162	Southeast Area Monitoring and Assessment Program
Abundance of <i>Sicyonia brevirostris</i> in southern GoM	-0.144	Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación
Shannon–Weiner diversity off LA	-0.139	Southeast Area Monitoring and Assessment Program
Abundance index of gray triggerfish in northern GoM	-0.132	Southeast Data, Assessment and Review (SEDAR)
Pelagic to demersal ratio in northern GoM	-0.077	Southeast Area Monitoring and Assessment Program
Abundance index of yellowedge grouper in northwestern GoM	-0.072	Southeast Data, Assessment and Review (SEDAR)
Species richness off TX	-0.054	Southeast Area Monitoring and Assessment Program
Shannon–Weiner diversity off TX	-0.041	Southeast Area Monitoring and Assessment Program
Mammal stranding events in northern GoM	-0.004	NOAA National Marine Mammal Health and Stranding Response Database
Mean biomass of zooplankton, offshore U.S. GoM in spring	0.015	Southeast Area Monitoring and Assessment Program
Species richness off LA	0.035	Southeast Area Monitoring and Assessment Program
Abundance index of Spanish mackerel in northern GoM	0.053	Southeast Data, Assessment and Review (SEDAR)
Abundance index of cobia in northern GoM	0.059	Southeast Data, Assessment and Review (SEDAR)
Abundance of menhaden in northern GoM	0.098	Vaughan <i>et al.</i> , 2011; SEDAR 27
Mean trophic level in northern GoM	0.101	Southeast Area Monitoring and Assessment Program

Table 1 (continued)

Indicator	Loading	Data source
Abundance index of brown pelican 1	0.135	National Audubon Society Christmas Bird Count
Abundance of commercial shrimp species in northern GoM	0.145	Southeast Area Monitoring and Assessment Program
Abundance index of mutton snapper in northern GoM	0.211	Southeast Data, Assessment and Review (SEDAR)
Abundance index of king mackerel in northern GoM	0.221	Southeast Data, Assessment and Review (SEDAR)
Abundance index of brown pelican 2	0.223	U.S. Geological Survey Breeding Bird Survey
Abundance index of gag grouper in northern GoM	0.231	Southeast Data, Assessment and Review (SEDAR)
Abundance index of roseate spoonbill 2	0.270	U.S. Geological Survey Breeding Bird Survey
Kemp's Ridley nesting rates in Tamaulipas, Mexico	0.290	P. Richards, unpublished data
Impacts and responses		
U.S. fishing effort for menhaden in vessel-ton-weeks	-0.300	J. Smith, unpublished data
Total landings of menhaden in U.S. GoM	-0.236	National Marine Fisheries Service Commercial Fisheries Statistics
Total landings of finfish excluding menhaden in U.S. GoM	-0.217	National Marine Fisheries Service Commercial Fisheries Statistics
Number of recreational angler days in the United States	-0.187	National Marine Fisheries Service, Headboat Survey
Mean fork length of southern kingfish in U.S. recreational catch	-0.156	National Marine Fisheries Service Recreational Fisheries Statistics
Mean trophic level of U.S. commercial catch	-0.143	National Marine Fisheries Service Commercial Fisheries Statistics
Total Mexican revenues from commercial fishing	-0.056	Comisión Nacional de Acuacultura y Pesca (CONAPESCA)
Growth rate of gray snapper in northern GoM	-0.045	Black <i>et al.</i> (2011)
Number of registered boats in coastal GoM Mexican states	0.003	Comisión Nacional de Acuacultura y Pesca (CONAPESCA)
Proportion of predatory fishes in U.S. commercial catch	0.023	National Marine Fisheries Service Commercial Fisheries Statistics
Total landings of invertebrates in U.S. GoM	0.024	National Marine Fisheries Service Commercial Fisheries Statistics
Mean fork length of Atlantic croaker in U.S. recreational catch	0.041	National Marine Fisheries Service Recreational Fisheries Statistics
Total landings of finfish in Mexican GoM	0.049	Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación
Total recreational landings in U.S. GoM	0.079	National Marine Fisheries Service Recreational Fisheries Statistics
Total U.S. revenues from commercial fishing	0.105	National Marine Fisheries Service Commercial Fisheries Statistics
Mean trophic level of U.S. recreational catch	0.147	National Marine Fisheries Service Recreational Fisheries Statistics
Mean trophic level of U.S. commercial catch excluding menhaden	0.159	National Marine Fisheries Service Commercial Fisheries Statistics
Number of recreational angler trips in the United States	0.172	National Marine Fisheries Service, Marine Recreational Fishery Statistics
Total landings of invertebrates in Mexican GoM	0.192	Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación
Mean fork length of southern flounder in U.S. recreational catch	0.195	National Marine Fisheries Service Recreational Fisheries Statistics
Mean fork length of spanish mackerel in U.S. recreational catch	0.215	National Marine Fisheries Service Recreational Fisheries Statistics
Mean fork length of spotted sea trout in U.S. recreational catch	0.225	National Marine Fisheries Service Recreational Fisheries Statistics
Proportion of predatory fishes in U.S. commercial catch excluding menhaden	0.241	National Marine Fisheries Service Commercial Fisheries Statistics

Table 1 (continued)

Indicator	Loading	Data source
Mean trophic level of Mexican commercial catch	0.244	Food and Agriculture Organization FishStat database
Proportion of predatory fishes in Mexican commercial catch	0.244	Food and Agriculture Organization FishStat database
Mean fork length of sheepshead in U.S. recreational catch	0.249	National Marine Fisheries Service Recreational Fisheries Statistics
Proportion of predatory fishes in U.S. recreational catch	0.261	National Marine Fisheries Service Recreational Fisheries Statistics
Mean fork length of red snapper in U.S. recreational catch	0.265	National Marine Fisheries Service Recreational Fisheries Statistics
Mean fork length of red drum in U.S. recreational catch	0.273	National Marine Fisheries Service Recreational Fisheries Statistics

appropriate ordination technique. Inspection of biplots of indicator loadings and temporal scores confirmed the suitability of the technique for this analysis. Annual scores for the first two principal component axes were plotted in two dimensions; this allowed for visualization of the temporal variations in the progression of the ecosystem state. The first principal component annual scores, which represent a quantitative description of the overall state of the ecosystem, were then evaluated using the STARS algorithm which is used to find significant shifts in a time series (Rodionov & Overland, 2005). Chronological clustering based on a Euclidean distance matrix was carried out on the same data matrix used for the PCA (rioja library; Juggins, 2012; R Development Core Team, 2011).

Unlike other regions of the United States such as the southwest and northeast, where standardized trawl surveys have been carried out since the 1950s and 1960s, major fishery data collection programs were not implemented in the GoM until the 1980s. Monitoring programs for hypoxia, chemical contaminants, and other aspects of the GoM were largely initiated in the 1980s, as were satellite observations. The only comprehensive biological data sources for the GoM that extend to the 1950s are commercial fishery landings data. The use of catch data alone for the purpose of tracking changes in abundance is the subject of substantial debate (Hilborn & Branch, 2013; Pauly, 2013), and landings are expected to be influenced by management regulations and economic factors. However, landings composition data are germane to our study because we are interested in both changes in abundance and the economic drivers and responses related to these changes. Thus, the consideration of landings serves as a complementary analysis, as the catch data are largely independent from the stock-assessment-based fishery indicators used in the indicator analysis. Landings data for the GoM were compiled through the U.S. National Marine Fisheries Service's online Commercial Fishery Statistics queries (<http://www.st.nmfs.noaa.gov/index>). When log-transformed landings data were analyzed with PCA, the ordination produced a 'horseshoe effect' – that is, a distortion of the data along the second axis which can produce misleading results; this artifact precluded the use of PCA for ordination of the landings data. Therefore, nonmetric multidimensional scaling (NMDS) was

conducted on groups with at least 55 years of data (in pounds wet weight, separated by major groups or species); means were imputed for missing values. As for the indicator groups, chronological clustering was also carried out on the landings data. Traffic light plots were produced by color-coding the scaled raw data matrix according to quintile and then ordering the species in sequence according to their loadings on the first and second NMDS axes, respectively. These plots provide a simple visualization of the species-specific trends in landings over time. To further explore any independent effects of climate vs. management drivers, we also distinguished managed species groups vs. unmanaged species groups on these plots. To test for statistical differences in the species groups responsible for driving the observed trends, a *t*-test was carried out on the absolute value of the loadings for managed vs. unmanaged species groups, on both the first and second NMDS axes.

Anderson *et al.* (2009) suggest that conclusions regarding the presence of ecosystem shifts are strengthened when multiple, independent methods confirm the same patterns. Shifts identified via a combination of independent ordination methods employed here (PCA, based on linear combinations of variables into a small set of synthetic variables; chronological clustering, based on a distance matrix with clusters constrained by sample order; NMDS, an iterative technique which seeks to preserve the information in a distance matrix in two dimensions; and the STARS algorithm, based on sequential *t*-tests of a time series) thus provide confidence that observed breaks are not due to a statistical artifact. Note that PCA, chronological clustering, and STARS were used to analyze the suite of indicators, whereas NMDS, chronological clustering, and STARS were used to analyze landings data.

We evaluated a suite of climate indices to elucidate potential relationships between broadscale climate patterns and the observed changes in the GoM. We considered the three most influential and well-known modes of variability in the Atlantic Ocean [Atlantic Multidecadal Oscillation (AMO), Atlantic Meridional Mode, and North Atlantic Oscillation], as well as two modes of variability centered on the Pacific which are well-known to drive fishery dynamics and have a global

footprint [the El Niño Southern Oscillation and the Pacific Decadal Oscillation (PDO)]. Climate indices were obtained from the National Oceanic and Atmospheric Administration's Earth System Research Laboratory page (<http://www.esrl.noaa.gov/psd/data/climateindices/>). The suite of indices was compared via a correlation analysis to each of the principal component yearly scores from the indicator PCAs and the first and second NMDS axes from the landings ordination. For each pair of climate indices and ordination yearly scores, the cross-correlation function was calculated for lags of 0–10 years. The time lag achieving the maximum correlation was reported. Because this analysis required the exploration of a large number of correlations (25 climate-ordination pairs, each for 11 possible lags), we carried out a randomization test to determine the probability that any particular correlation would be spurious. This was achieved by randomizing the order of the time series of yearly ordination scores 1000 times, finding the maximum correlation between each climate index and randomized time series, and reporting the 99th percentile of the 1000 random correlations. Observed correlations higher than this value are those occurring by chance with a probability of 1%. Because one particular climate mode, the AMO, was observed to be highly correlated with temporal changes in the ecosystem, we carried out additional analyses in reference to this index. To elucidate potential effects of the AMO on the physical environment and lower trophic dynamics of the GoM, we carried out *t*-tests to determine whether significant differences in indicator values occurred between warm and cool AMO phases. These tests were carried out on the same indicator data set as above, after log transformation when necessary. Finally, the first principal component yearly scores from the indicator PCAs and the second NMDS axis from the landings analysis were plotted against the AMO. A local polynomial regression line was fit to each scatterplot (using a smoother span of 2/3). All analyses were carried out in R version 2.13.2. (R Development Core Team, 2011).

Results

Ordination analyses on suites of three indicator groups: (1) drivers and pressures, (2) ecosystem states, and (3) impacts and responses provided a characterization of the dominant ecosystem-wide variations over time. Annual scores from the first principal component of each group show a clear and consistent ecosystem-wide shift, with a major break in the mid-1990s (Fig. 1a, c, e). In all three cases, the STARS (sequential *t*-test analysis of regime shifts) algorithm identified the commencement of a new 'regime' in PC1 in either 1995 or 1996. For the group of drivers and pressures, only a single significant break in PC1 was identified for 1995. For the state indicators and indicators of impacts and responses, the most significant shift was identified in 1996. However, for these latter two groups, other significant breaks were also identified in the first principal component score time series (1990 and 2005 for states,

and 1988 and 2005 for impacts and responses). Chronological clustering analyses similarly indicate a single significant shift in ecosystem-wide indicators between 1994 and 1996 (Fig. 1b, d, f). Note that the STARS analysis is based only on PC axis 1, which explains between one-fourth and one-third of the variation in each data set, and thus, the breaks are not expected to align exactly with the chronological clustering. An inspection of the correlation matrix of the suite of indicators indicated no systematic problems with high correlations between certain types of indicators. Most indicators were not correlated to a high degree; only 8% of indicator pairs had an $R > |0.60|$ and only 1% of pairs had an $R > |0.80|$.

Ordination analysis of commercial fishery landings within the GoM revealed a gradual linear change along NMDS fisheries landings axis 1 after the 1960s, whereas axis 2 revealed rapid periods of change in the 1960s and 1990s (Fig. 2a). An NMDS ordination in only two dimensions was shown to produce an excellent fit (stress = 0.06). Both NMDS and chronological clustering confirm a major break in landings composition from 1977 to 1978 (Fig. 2b). The second NMDS axis, along with the secondary breaks in the chronological clustering plot, indicates major shifts in the composition of commercial landings during the mid-1960s and mid-1990s. These breaks correspond with shifts in the AMO between warm and cool phases (Fig. 2a). Along the first NMDS axis, species with the highest loadings (i.e. those contributing the most weight to the observed temporal trends) are largely managed species or species groups (Fig. 2c), although the loadings of managed groups were not significantly higher than those of unmanaged groups ($P = 0.61$). Along the second NMDS axis, unmanaged species groups were largely responsible for driving temporal trends and their loadings were higher than those of managed species ($P = 0.04$, Fig. 2d). The analysis of landings data was largely independent from the analysis of the indicator group, as there were few high correlations between the indicators and landings data sets (only 1% of landings-indicator pairs with $R > |0.80|$).

Of the five major climate modes of variability explored, the AMO appeared to be most closely related to the temporal changes in the suite of indicators and landings composition data. The AMO index was highly correlated with the first principal component of the drivers and pressures, state indicators, and impacts and responses, and also with the second NMDS axis of the landings composition (Fig. 3). The Atlantic Meridional Mode is highly correlated with the AMO ($R = 0.78$) and thus was also found to be correlated with ecosystem dynamics, but to a lesser extent, suggesting the

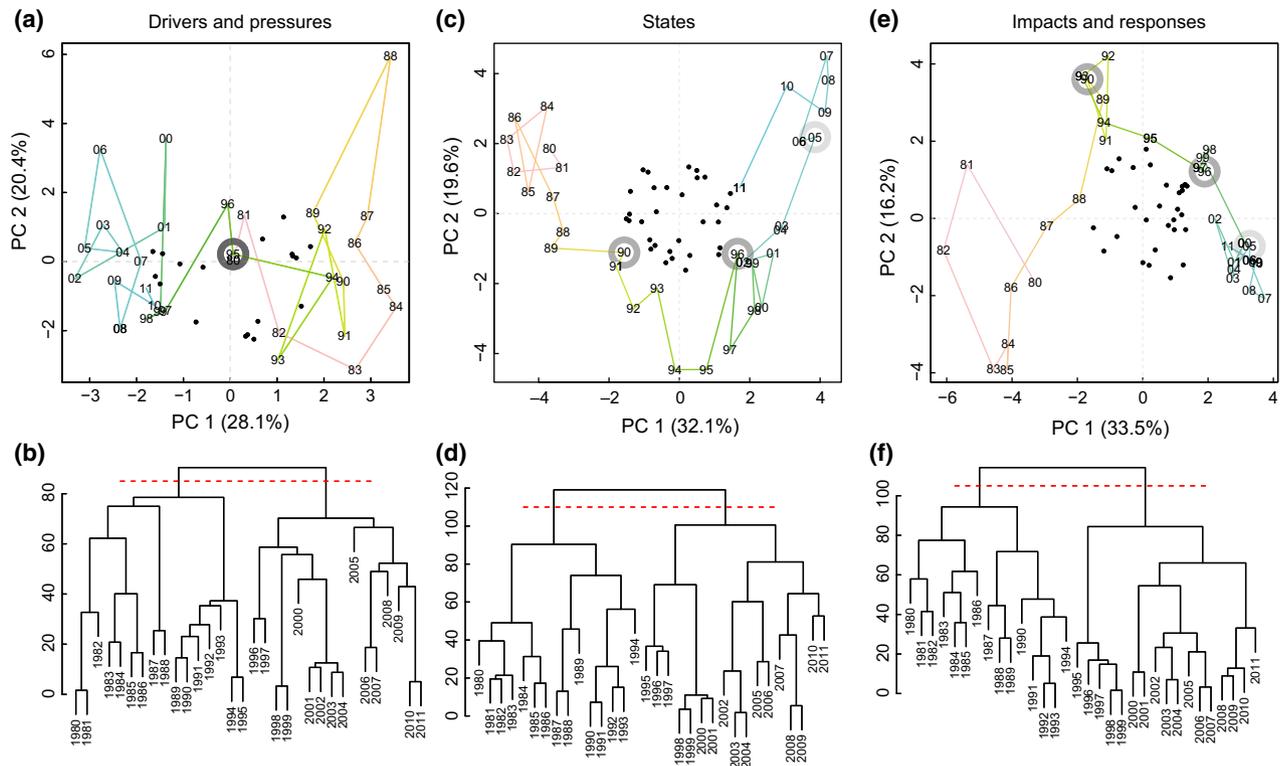


Fig. 1 Multivariate analyses of three groups of ecosystem indicators: drivers and pressures (a, b), states (c, d), and impacts and responses (e, f). Top row (a, c, e): Yearly scores of first two principal components are plotted, based on principal components analysis (PCA) of ecosystem indicator values from 1980 to 2011. Segments are color-coded on a continuous scale to aid reader in the interpretation of change through time. Circles represent breaks in the first principal component (i.e. the first year of a new regime) as identified by the STARS algorithm; significance is denoted by darkness of circle color (darker lines = higher significance; all breaks $P < 0.01$). Small dots denote indicator loading on the first two axes. Bottom row (b, d, f): Chronological clustering analysis of ecosystem indicators from 1980 to 2011. Horizontal dotted lines denote the threshold for significance of breaks.

AMO is a more direct proxy for the important climate drivers. All correlations with the AMO were highest with a lag of zero years, suggesting an immediate rather than lagged ecosystem response. A lagged correlation of 4 years was found between the PDO and the first NMDS axis of the landings composition ordination. Note that the PDO largely mirrors the overall pattern of landings in the GoM (correlation of $R = 0.50$ with total landings). Furthermore, the well-known regime shift of 1977 is temporally aligned with major fisheries legislation (see discussion), and thus, the PDO is confounded by other factors (Fig. 4). Of the five indices, the AMO was clearly the best overall proxy of probable drivers of ecosystem dynamics in the GoM.

Some of the potential impacts of the AMO on physical conditions and lower trophic level states of the Gulf of Mexico are elucidated by considering changes in individual indicators between the most recent cool and warm phases (Fig. 5). During AMO warm phases, surface temperatures in the Gulf of Mexico are also war-

mer (Fig. 5a, b, c). Fertilizer use in the Mississippi River watershed basin increases drastically from the last AMO cool phase to warm phase; however, precipitation in the watershed and total nitrogen load decreased (Fig. 5d, e, f). In the northwestern and northeastern regions of the GoM, concentrations of mercury within oyster tissues are also reduced during the warm phase (Fig. 5g and h). Several measures of hypoxia in the northern Gulf indicate that hypoxia is exacerbated during the warm AMO phase; the area of the hypoxic zone is significantly larger, and dissolved oxygen values off the coasts of Louisiana and Texas are reduced (Fig. 5j, k, l, m, n). The warm phase of the AMO is also associated with a reduction in total biomass of zooplankton in nearshore waters in the fall season (Fig. 5q) but no change in offshore biomass of zooplankton during the spring season (Fig. 5t). The AMO warm phase also corresponds with reduced abundance of ichthyoplankton for two benthic fish families (Fig. 5r and s) but no change in the abundances of mesopelagic ichthyoplankton families (Fig. 5u and v).

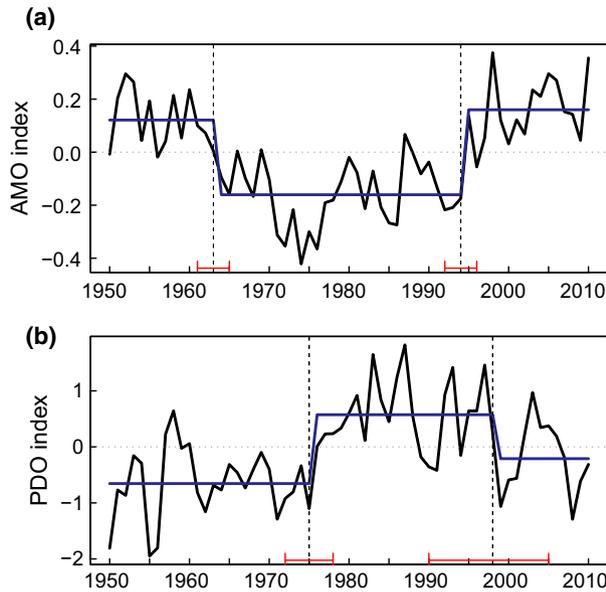


Fig. 4 Time series of the Atlantic Multidecadal Oscillation (a) and Pacific Decadal Oscillation (b), with significant breaks and their confidence intervals identified using a sequential *F*-test algorithm.

identified. This suggests that drivers and pressures are affected more directly by a single factor, while states, impacts and responses, are influenced by multiple factors. Furthermore, the species groups which were most heavily responsible for driving the community shift in the mid-1960s and mid-1990s were unmanaged species, which are less likely to be directly impacted by management regulations. In the discussion below, we first describe a mechanistic hypothesis by which the AMO may influence the physical environment of the GoM, particularly with regard to temperature and hypoxia. We suggest that, via these physical influences, the AMO alters higher-level dynamics and socioeconomic responses. Then, we discuss the observed changes in landings composition over the past 60 years, in light of these climate changes, against a background of significant management regime changes and economic forces.

Physical effects of the AMO on the Gulf of Mexico

The AMO is a measure of basinwide sea surface temperature variation in the North Atlantic, adjusted to

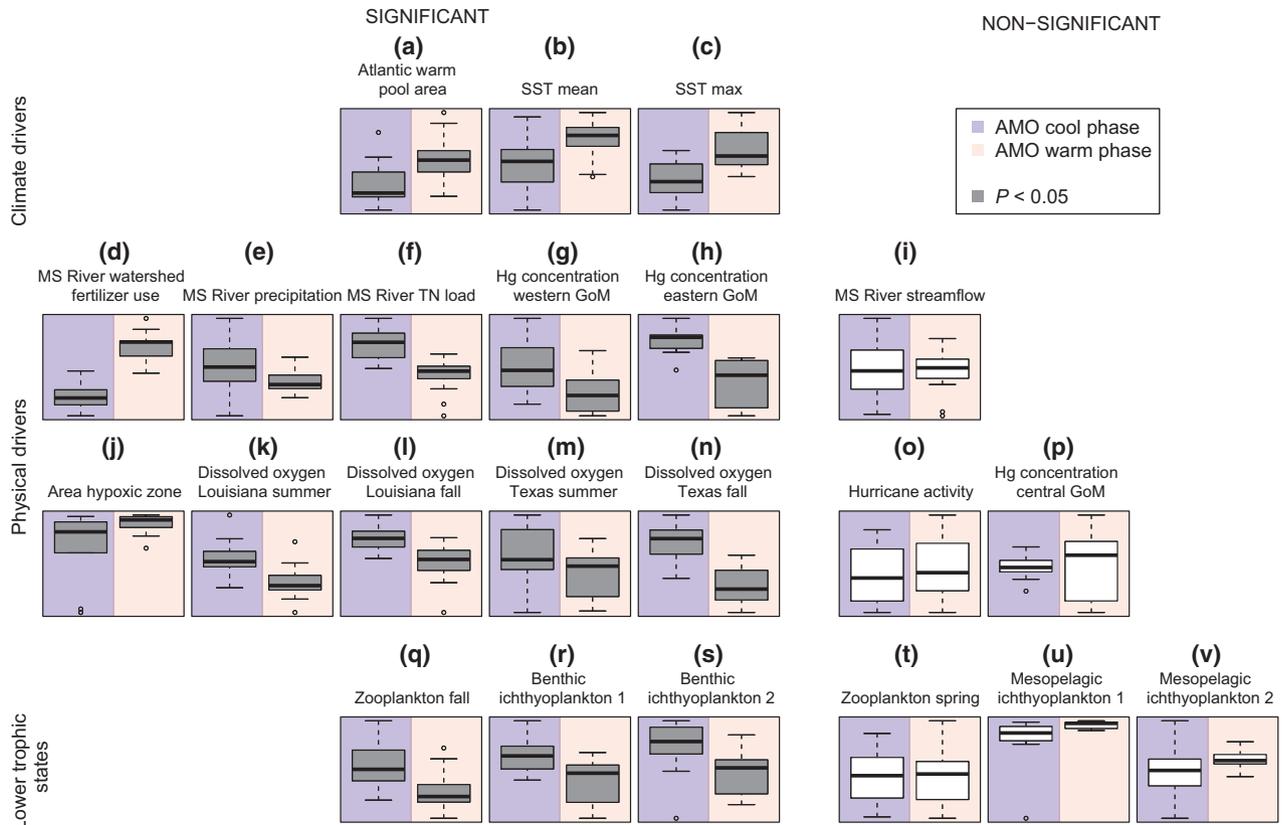


Fig. 5 Boxplots showing differences in indicator values during Atlantic Multidecadal Oscillation (AMO) cool (1970–1995) vs. warm (1996–2011) phases. Indicators with significantly different means between phases ($P < 0.05$) appear with shaded boxes.

remove trends in anthropogenically forced warming (Enfield *et al.*, 2001; McCabe *et al.*, 2004). It is calculated from the Kaplan 5.0 degree latitude by 5.0 degree longitude data set by taking an area-weighted average over Atlantic sea surface temperature from 0 to 70 degrees North. The AMO was in a warm phase from approximately 1927 to 1965, switched to a cool phase from 1965 to 1995, and once again switched to a warm phase where it remains at present (Fig. 4a). The AMO has been invoked as the explanatory factor for a number of biological phenomena in the Atlantic Ocean (Shackell *et al.*, 2012; Edwards *et al.*, 2013; Nye *et al.*, 2014). It has been shown to have an influence on North Atlantic fisheries since the early 1900s (Edwards *et al.*, 2013) and is correlated with community-wide fishery responses in seven northwestern Atlantic ecosystems (Shackell *et al.*, 2012). However, the AMO is rarely invoked as the causal mechanism for biological changes in the GoM (but see Sanchez-Rubio *et al.*, 2011).

The GoM is characterized by an intense and highly variable mesoscale circulation dominated by three main features: the Yucatan Current, the Loop Current, and eddies shed by the Loop Current. These oceanic features are responsible for driving many of the physical, biological, and chemical properties of the region. The Yucatan Current and Loop Current influence the GoM on multidecadal timescales, and they fluctuate with both the AMO and the Atlantic meridional overturning circulation (AMOC; Liu *et al.*, 2012). The AMOC is the branch of global thermohaline circulation which carries warm upper waters into high latitudes and returns cold deep waters southward into the South Atlantic. In the absence of long-term measurements of the AMOC, modeling studies generally show that North Atlantic sea surface temperature is positively correlated with the AMOC on decadal to multidecadal timescales, with the AMOC leading temperatures by a fraction of a cycle (Knight *et al.*, 2005; Zhang & Wang, 2013). Using a high-resolution ocean model of the GoM embedded in an ensemble of global models, Liu *et al.* (2012) found that the Yucatan Current and Loop Current are synchronized with the AMOC, and when strong, they advectively warm the GoM. Therefore, the AMO can influence oceanic features and physical properties in the GoM via its indirect influence on the Yucatan Current and Loop Current, such that when the AMO is in its warm phase and the AMOC is strong, the GoM is expected to be warmer. Note that the AMOC itself has only been measured directly since 2004 (Smeded *et al.*, 2014) and thus we cannot test whether it has a more direct influence on the GoM than the AMO.

The AMO may influence other physical and biogeochemical aspects of the GoM via teleconnections with atmospheric dynamics (Enfield *et al.*, 2001). The Missis-

issippi–Atchafalaya River system, which drains the largest watershed in North America, has a major influence on the physical and biological dynamics of the northwestern GoM through its role in freshwater and nutrient inputs. Runoff from the Mississippi River declines 10% during a warm AMO phase due to associated reductions in rainfall (Enfield *et al.*, 2001; Fig. 5e). Such changes in freshwater input may be associated with changes in sediment and nutrient fluxes, affecting coastal marine productivity. Because the mixed layer depth in the tropical oceans tends to be driven largely by temperature, increases in surface temperatures associated with an AMO warm phase result in a decrease in the depth of the mixed layer (Zhang *et al.*, 2012). Changes in temperature and freshwater input have implications for stratification, surface plankton productivity, and the development of hypoxia.

The drainage basin of the Mississippi–Atchafalaya River system annually produces the largest hypoxic zone in the Western Hemisphere. Generally, hypoxia in this region is understood to be caused primarily by nutrient-driven excesses in springtime algal production, which increases organic material to the lower water column and thereby increases respiration. Strengthening stratification in the summer months then prevents oxygen from diffusing below the pycnocline (Scavia *et al.*, 2003). However, a variety of factors are involved in driving interannual variations in the magnitude and extent of hypoxia, including seasonal changes in wind stress, the passages of fronts and hurricanes, atmospheric warming, freshwater discharge, offshore circulation, and aerobic and anaerobic sediment respiration (Bianchi *et al.*, 2010 and references within). Likely, the AMO has some indirect influence on the timing, severity, and extent of hypoxia via its effects on riverine output, stratification, and broad circulation. Indeed, the warm phase of the AMO is associated with increased extent and levels of hypoxia (Fig. 5j–n). Additionally, in the warm phase of the AMO, there are significantly lower levels of zooplankton biomass in the nearshore waters during the fall season (but not offshore during the spring) and lower abundances of benthic ichthyoplankton indicator species (but not mesopelagic ichthyoplankton). Determining whether these patterns in lower trophic levels are driven by hypoxia or other climate-related drivers, and in turn how the changes in lower trophic levels drive upper trophic dynamics, requires further study.

Socioeconomic responses

Since the 1950s, the human population in the coastal GoM has increased steadily, along with anthropogenic pressures such as coastal development, energy

exploitation, and tourism (Fleming *et al.*, 2014). The region suffers from an overall paucity of socioeconomic data with sufficient spatial and temporal resolution to adequately resolve human responses to changes in the ecosystem (Karnauskas *et al.*, 2013). Regardless, our analyses identified an apparent shift in the mid-1990s within the limited group of socioeconomic response indicators considered, including marked declines in U.S. commercial finfish and menhaden landings, inflation-adjusted revenues, and fishing effort. In contrast, invertebrate landings (primarily composed of penaeid shrimp), while variable, have remained relatively constant during this period. Inflation-adjusted invertebrate revenues declined, likely in response to a growing supply of imported shrimp (Keithly & Poudel, 2008). In Mexico, landings of invertebrates increased; however, there was no difference in finfish landings or revenues. Recreational effort in the United States also decreased coincident with the shift in the AMO, while recreational landings showed no change. Recreational fishing effort may be influenced by management as well as by climate; for example, Carter & Letson (2009) found that fishing effort increased during El Niño periods, which are associated with cooler and wetter winters in the southeastern United States as well as a reduction in landfalling hurricanes. The reasons for these shifts are not immediately apparent as they are likely driven by some combination of climate effects (or factors correlated with climate effects), management regulations, and the interactions between these forces.

Variations in landings data

Landings data can serve as a very coarse measure of the abundance of harvested species, but also reflect changes in management regulations and economic conditions. Thus, it is expected that landings data will be heavily influenced by management effects, against a background of potentially changing abundances, or changing patterns of availability to the fishery due to climatic factors. The late 1970s break in landings composition, identified by the two ordination analyses, corresponds with a number of significant management and economic changes. Firstly, U.S. Congress passed the Fishery Conservation and Management Act of 1976 (now known as the Magnuson-Stevens FCMA), which established management authority over an exclusive economic zone (EEZ) from the coast to 200 miles offshore. The immediate effect of this Act was a number of treaties between Mexico and the United States, which specifically granted each country a quota of any surplus beyond the harvesting capacity of the home country (Rosendahl, 1984). These treaties thus spurred steps by both Mexico and the United States to augment

fishing industries and increase harvesting, which was further aided by legislation such as the American Fisheries Promotion Act of 1980. In addition, there were several federal programs that fostered the development of fishing capacity, including vessel construction loans, tax-deferred vessel repair and construction programs, fuel-tax relief, and gear replacement funds (Hanna *et al.*, 2000). Rapid expansion of commercial fisheries in the United States was observed as domestic fleets took the place of foreign fleets; for example, in 1981, foreign fishing accounted for 61% of the total EEZ commercial catch, and by 1991, this had been reduced to 1% (National Research Council, 1994).

The implementation of major fisheries legislation is confounded with a number of significant economic changes, which climaxed in a severe recession in the early 1980s. Notably, U.S. prime interest rates reached an all-time high in 1980, inflation-adjusted U.S. fuel prices reached an all-time high in 1981 (with the exception of 2008), and the U.S. unemployment rate reached an all-time high in 1982. Such economic forces certainly had the capacity to restructure fishing practices or increase overall fishing capacity in a period when other forms of employment became increasingly scarce. A number of fisheries were also driven by changes in market demand. For example, the increase in landings of sharks, which have the highest loading on the first NMDS axis, was driven by a major expansion in shark fisheries in the late 1970s due to the increased demand for their fins and cartilage (SEDAR, 2012; Fig. 2c).

Finally, at the same time as these management and economic drivers were likely reshaping fisheries in the region, alterations were occurring in the forage base of the GoM. In particular, fishing effort for menhaden increased rapidly in the late 1970s. Menhaden abundance steadily declined from the 1950s to the 1970s and then quickly increased until the mid-1980s (Vaughan *et al.*, 2011). Such an increase in forage abundance may have facilitated the expansion of fisheries on some of the major predator species; however, menhaden abundance reached an all-time low in the 1990s, while landings of many predators remained constant.

The second axis of the NMDS landings analysis correlates with the AMO, and secondary breaks in its chronological clustering are aligned with two major shifts in this climate mode (Fig. 2a and b). Such a pattern in ordination analyses might also be produced by fisheries that initially underwent a post-WWII expansion, followed by several decades of unsustainably high catch rates, and then a period of depletion throughout the 1990s when the management regulations began to be enacted. However, the species groups driving the trends on the second axis are dominated by unmanaged species (e.g. barracudas, bonitos, blue runner),

supporting the notion that this axis largely represents processes unrelated to management (Fig. 2d). Furthermore, inspection of trends in landings for the GoM shows that major eras of fisheries expansion occurred for many species groups from the late 1970s to early 1980s and that declines of many groups occurred starting in the late 1980s (Fig. 2c). Thus, the secondary breaks in landings composition appear to be more strongly correlated with large climate drivers rather than management activity. This finding is largely independent of the shift identified in the analysis of indicators, as the majority of indicators with high loadings were not related to landings (Table 1), and observed high correlations between indicators and landings were minimal.

Identifying specific, consistent patterns of species and population-level effects of given environmental disturbances, especially in highly variable and ecologically diverse regions like the GoM, can be exceedingly difficult (Rose, 2000). However, the influence of temperature on the distribution and physiology of marine organisms has been well-documented in the GoM (Li & Clarke, 2005; Manzano-Sarabia *et al.*, 2008; Fodrie *et al.*, 2010). Also, coastal hypoxia may act alone or in concert with other variables to induce spatial shifts in the abundance of upper trophic level species (Craig *et al.*, 2005; Zhang *et al.*, 2009; Craig, 2012), alter pelagic and benthic community assemblages (Craig & Bosman, 2013), and affect habitat availability, selection, and quality (Craig & Crowder, 2005; Switzer *et al.*, 2009; Zhang *et al.*, 2014). However, existing work suggests that hypoxia does not affect overall fisheries productivity or trophic structure of the ecosystem (Chesney *et al.*, 2000; Cowan, 2009; Bianchi *et al.*, 2010). The absence of a lag between AMO shifts and landings shifts suggests that species with short life histories were affected by processes relating to the AMO or that direct mechanisms were responsible, such as temperature-driven spatial reorganization. Indeed, mobile pelagic species such as bonito, permit, and other jacks have high loadings on the second NMDS axis and show responses to both the mid-1960s and mid-1990s shift; such species can easily shift distributions in response to temperature. The absence of a lag between the AMO and ecosystem dynamics does not exclude the possibility of lagged effects on certain ecosystem components, but merely indicates that the strongest effects of the AMO on the ecosystem as a whole are those direct in nature. Along the second NMDS axis, species with positive loadings are largely pelagic species while those with negative loadings are largely demersal or estuarine species, suggesting some commonality in community responses to climate. Note, however, that changes in the landings of these species are not synchronous, likely because cli-

mate affects different species via different mechanisms and on different timescales. The absence of clear species-level responses to climate drivers is perhaps a reason why this shift has not been previously documented in the literature, which has largely focused on species-level studies; these shifts are only apparent when considering simultaneously the observed changes in a broad suite of organisms. Also, the GoM has high species diversity and life-history diversity relative to other ecosystems which have been the focus of such studies, and thus, there is greater potential for climate effects to act via a wide variety of mechanisms. The complexity in linkages between drivers, pressures, and lower and upper trophic levels – all in addition to the many regulatory changes implemented in the GoM over the past decades – produces the complex patterns in landings composition that we observe.

Management implications

Other studies have suggested the AMO acts as a proxy for a number of complex processes that may simultaneously affect the biology of ecosystems (Alheit *et al.*, 2014). We suspect that this is the case for the GoM – likely, the AMO exerts its influence through a combination of factors. These may include the following: changes in temperature, current patterns, mixed layer depth, and biogeochemical cycling patterns, as well as the indirect effects of these changes on various trophic levels and the human communities dependent on the system. Examining the first principal component annual scores and the first NMDS scores against the AMO indicates a threshold-like response of the ecosystem (Fig. 6). Ecosystem state (represented by the quantity on each *y*-axis) appears to display a more rapid rate of change as the AMO approaches zero, suggesting the presence of nonlinear effects of the climate driver on ecosystem state. The absence of data points in the upper right and lower left quadrats of all four scatterplots indicates that the physical, biological, and socioeconomic attributes of the GoM differ between the warm and cool phases of the AMO, signifying the presence of multiple ecosystem states.

The correlation of decadal-timescale indices, such as the AMO, to ecological data sets has great potential to improve our understanding of key ecological processes. However, a consistent difficulty with this approach is the lack of reliable and unbiased long-term time series of biological measurements (Hare & Mantua, 2000; deYoung *et al.*, 2004). This problem is particularly pertinent to fisheries-dependent information, such as the commercial landings data used in this study. Fishermen's harvesting decisions are driven by interdependent biological, economic, technological, and

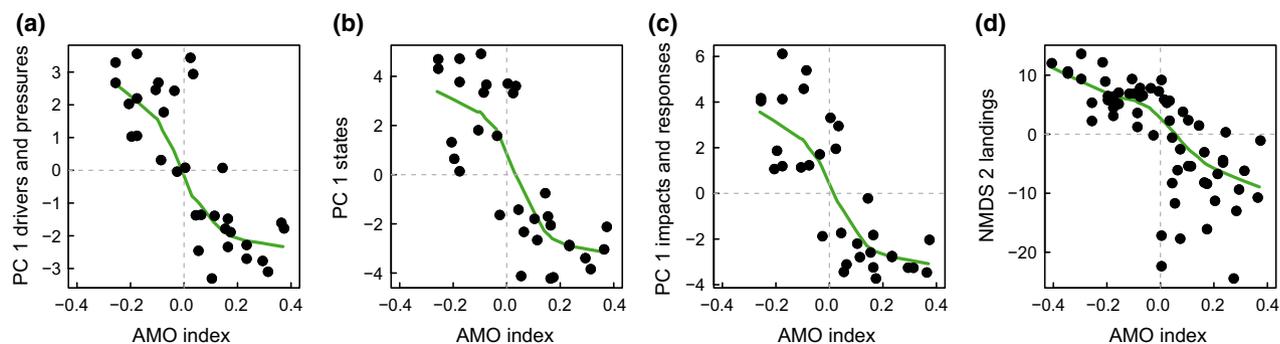


Fig. 6 The Atlantic Multidecadal Oscillation (AMO) index plotted against the first principal component scores for three indicator groups (a–c) and the second nonmetric multidimensional scaling score for the landings data analysis (d). Lines are local polynomial regression fits.

regulatory considerations (Bishop, 2006). Fishing activity may also indirectly influence nontarget components of the ecosystem. For example, the sharp reduction in shrimp trawling effort in the GoM from the mid-2000s onwards is well correlated with recent increases in adult landings of red drum and Atlantic croaker, as well as the abundance of sciaenid larvae (Muhling *et al.*, 2012) which are a major component of shrimp trawl bycatch (Diamond *et al.*, 2000). Additionally, while bottom-up effects such as those described above are important, potential top-down effects should not be dismissed. The biomass of some large pelagics, such as bluefin tuna and blue marlin, has decreased substantially over the past several decades (ICCAT, 2012). Although these species are not present in the GoM year-round, their potential effects on ecosystem structure remain unknown. Finally, there are unknown time lags in ecosystem responses to potential drivers, and the present analysis mixes ‘fast’ (e.g. plankton) and ‘slow’ (e.g. sea turtles) variables that may respond on very different timescales (Carpenter & Turner, 2001).

Regardless of these difficulties, our analyses strongly suggest that a major ecosystem-wide shift occurred in the GoM in the mid-1990s. We suggest that, given the available evidence, a climate-driven shift related to the AMO is the most parsimonious explanation. However, further research is needed to provide a more complete understanding and to address some of the alternative hypotheses discussed above. There are obvious management ramifications in understanding the specific nature of the mid-1990s shift, but documenting its existence enables us to more effectively manage our natural resources. For example, despite the implementation of rebuilding plans, a number of fish stocks remain overfished (Sewell, 2013), and managers may be advised to consider whether environmental causes play a role. Such considerations are particularly important in light of recent research suggesting that the environment

plays a significant role in fishery dynamics – perhaps even greater than the role of management actions (Vertpre *et al.*, 2013; Szuwalski *et al.*, 2014). Future research should focus on identifying the specific mechanisms responsible for the ecosystem shifts documented here, and in understanding how our knowledge of these mechanisms can be integrated into existing management of the GoM large marine ecosystem.

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