

Fluctuating fishing intensities and climate dynamics reorganize the Gulf of Mexico's fisheries resources

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Citation: Kilborn, J. P., M. Drexler, and D. L. Jones. 2018. Fluctuating fishing intensities and climate dynamics reorganize the Gulf of Mexico's fisheries resources. *Ecosphere* 9(11):e02487. 10.1002/ecs2.2487

Abstract. Integrated ecosystem assessment provides a practical framework for implementing ecosystem-based fisheries management (EBFM) while also balancing socioeconomic and ecological objectives. However, significant challenges remain, including (1) the identification of relevant ecosystem-level fisheries management indicators; (2) quantitatively describing the historical qualitative changes to fisheries ecosystem resource organization; (3) elucidating dynamic system regimes and their trade-offs related to variability in both natural and anthropogenic drivers; and (4) distilling and communicating the results to stakeholders and managers. Here, we describe the Ecosystem-Level, Management-Indicator Selection Tool (EL-MIST), which was developed to address these EBFM challenges. We also present a case study from the Gulf of Mexico large marine ecosystem (Gulf LME) where EL-MIST was applied to 79 time series indicators from the Gulf's 2013 ecosystem status report for the period 1980–2011. Results from Gulf LME's EL-MIST model indicated that the functional response of the Gulf's fisheries resources underwent significant reorganizations during the study period, primarily driven by basin-scale climate variability and shifting fishing fleets' targets, effort, and associated regulatory environments, over time. Using EL-MIST, we identified four unique organizational regimes, and we were able to describe the prominent differences in the underlying resources' structure and function between those dynamic regimes. We also detail three pertinent ecological regime shifts over the 30-yr study period and present evidence for the dominating effects of commercial and recreational fishing activities, along with the Atlantic Multidecadal Oscillation and its teleconnected processes, on the organization of fisheries resources. Support for the hypothesis that fishing intensity can affect the relative resilience of a fishery ecosystem that is undergoing climatic and physical–chemical environmental changes is also presented here, as are results implicating a slowing trend in the rates of change across many relevant ecosystem-level fisheries-management indicators. When implementing EBFM, the EL-MIST protocol is useful for distilling the large amounts of information gathered by large-scale monitoring efforts and assessments. This new framework is transferable across management systems, is ideal for use with current indices and metrics, has the flexibility to address a wide range of inquiries, and can help disentangle complex fisheries ecosystem dynamics to help better inform management recommendations.

Key words: decision support tool; ecological indicators; fisheries ecosystems; multivariate statistical modeling; redundancy analysis; regime shift.

Received 6 August 2018; accepted 17 August 2018; final version received 28 September 2018. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Ecosystem-based management for marine fisheries

Ecosystem-based fisheries management (EBFM) is a flexible process that considers the associations among species inhabiting an ecosystem and their responses to the diverse suite of varying environmental and anthropogenic influences that limit and control their populations. In marine systems, EBFM was initially defined by a set of three essential goals: (1) sustainable yield of products for human consumption and animal foods, (2) maintenance of biodiversity, and (3) protection from the effects of pollution and habitat degradation (Larkin 1996). However, the Ecological Society of America viewed ecosystem-based management (EBM) in broader terms, and they advocated for the inclusion of (1) measurable goals to achieve sustainability, (2) ecological models to improve understanding of the system, (3) emphasis on connectivity among constituents of the ecosystem, (4) recognition of the dynamic nature of the system, (5) consideration of context and scale when applying management needs to a specific system, (6) humans as components of the ecosystem, (7) management adaptability over time, and (8) accountability to ensure progress (Christensen et al. 1996). In U.S. fisheries, the incorporation of EBFM into decision-making is strongly advocated for, with the aim of improving the ability to protect, restore, and sustain living marine resources while balancing the competing interests of multiple stakeholders (Link 2016). With the more inclusive working definition for EBFM, and with invigorated focus by government and regulatory agencies, researchers', managers', and stakeholders' efforts have shifted toward implementation (Link 2005).

Integrated ecosystem assessment and ecosystem status reports

Integrated ecosystem assessment (IEA) provides a practical framework for implementing EBFM while balancing socioeconomic and ecological management objectives (Levin et al. 2009). Significant challenges remain, however, including: (1) identification of ecosystem-level leading indicators for monitoring and management (Link 2005, Link et al. 2012), (2) describing chronological system states and shifts in ecosystem response states (Mollmann and Diekmann 2012, Levin and

Mollmann 2015), (3) quantitatively defining historical fishery ecosystem state changes related to dynamic environmental and human use patterns (Hilborn 2011, 2012, Mollmann and Diekmann 2012, Levin and Mollmann 2015), and (4) assessing trade-offs within ecosystems to inform the evaluation of various management strategies. An advantage of the IEA framework is that the scope of an ecosystem assessment is defined relative to the needs of the particular system and its management focus (Levin et al. 2009). When scoping management challenges, it is important to define the goals of the program, and to obtain the best available data and indices that pertain to the particular set of challenges being considered—importantly, these data and indices must be relevant to the scale of the marine ecosystem of interest (Levin 1992). An ecosystem status report (ESR) serves as a critical piece of the IEA framework for a large marine ecosystem (LME) during both the scoping and implementation processes. To produce an ESR, full sets of indicators are developed such that each is representative of a relevant component of the target LME (NOAA 2009, Karnauskas et al. 2013, Andrews et al. 2014). Each indicator time series collected should chronicle the status of a LME's living marine resource(s), physical–chemical environment, and/or associated natural and anthropogenic factors that may affect them (Bowen and Riley 2003, Tscherning et al. 2012, Kelble et al. 2013).

Constrained analysis in EBM

When compiling long-term monitoring datasets and/or conducting EBFM studies, indicators are often parsed into independent subsets using a conceptual model representing drivers, pressures, states, ecosystem services/impacts, and responses for the system (DPSEI; Bowen and Riley 2003, Tscherning et al. 2012, Kelble et al. 2013). However, this framework imposes a hierarchical structure among DPSEI categories that (1) may not actually exist in the LME or (2) fails to consider complex interrelationships that occur among indicators (Tscherning et al. 2012). In many cases, these subsets are analyzed independently using exploratory analyses (e.g., cluster analysis, dimension reduction techniques) to search for potential patterns, and then, inferences across subsets are sometimes drawn between the results of those analyses (NOAA 2009, Diekmann and Mollmann

2010, Andrews et al. 2014, Karnauskas et al. 2015). In the EBM context, a more appropriate analytical approach would employ functional sets of response and predictor indicators to utilize in constrained analyses (e.g., constrained cluster analysis, canonical redundancy analysis[RDA]) to reveal (1) evidence for/against any effect of the set of predictors on the set of responses and (2) assess which potential cause-and-effect relationships are most relevant within the sets of ecosystem indicators considered (Niemeijer and de Groot 2008, Tscherning et al. 2012). Simplification from DPSEr to the response-predictor, constrained-analysis framework allows greater flexibility to frame the scope of management inquiries, and it allows for direct testing of hypotheses concerning relationships between subsets of management-relevant indicators.

Temporal organization of LME management indicators

The full set of indicators supplied in a typical ESR provides a vast wealth of information describing complex interdependencies among key biotic, abiotic, and anthropogenic elements of a LME. However, interpreting the dynamic interactions between multiple indicators of ecosystem status, which themselves vary over time in response to internal driving mechanisms and external influences, can be an overwhelming challenge. Temporal patterns in predictors and responses can be used to identify relatively stable organizational states for a LME, called dynamic regimes (DR; Scheffer and Carpenter 2003), and the suites of indicators that differentiate them. No known system state has been observed to persist indefinitely, and changes from one DR to another, in an EBFM context, can be thought of as changes in food web and ecosystem dynamics across an entire study area. These changes are often represented by changing community compositions and trophic structures (Mollmann and Diekmann 2012, Pershing et al. 2015). Rapid and/or persistent changes from one DR to another, called ecological regime shifts, can have large-scale effects on both the natural ecology of an ecosystem, and the human economies that rely on it (Mollmann and Diekmann 2012, Levin and Mollmann 2015, Wernberg et al. 2016).

It is becoming increasingly important to account for and describe potential regime shifts

and alternate stable states when implementing fisheries management policy (Levin et al. 2009, Mollmann and Diekmann 2012, Levin and Mollmann 2015), but the endeavor is not without its challenges. First, the most basic assumptions of regime shift theory assert that ecosystems are, by their nature, dynamic, ever-changing entities, and the larger a LME is, the more complex the relationships between the components are (deYoung et al. 2008). Furthermore, until it is observed, it is essentially impossible to know whether or not the system will (1) gradually trend toward a new DR over time; (2) abruptly change from one relatively stable condition to another, at some bifurcation point, along a monotonic ecosystem trajectory; or (3) transition to a wholly new DR on a multimodal ecosystem trajectory (Scheffer and Carpenter 2003). Finally, if the existence of alternative, relatively persistent DRs (termed alternate stable states) is confirmed, it is still difficult to determine whether it is possible to return the LME to a previous DR simply by releasing whatever pressure(s) may have precipitated the state change in the first place. Where this is impossible, *hysteresis* is evoked (i.e., more than one relatively stable regime may result from the same set of LME conditions), and in those cases, to return to a more desirable DR may take considerably more differentiation in current LME conditions than what instigated the regime shift to begin with (Conversi et al. 2015).

Hysteresis is particularly problematic to ecosystem-level resource management, due to the desire to manage systems' components such that anthropogenic priorities are met for the long term. This may result in attempts to (1) prolong a DR past its natural life span, based on dynamic LME conditions, or (2) return it to a more desirable DR only to find out—after significant effort—that this is impossible (or highly improbable). If it is desirable to take a holistic approach toward EBFM to gain a more complete understanding of a LME's components (i.e., IEA and ESRs), then it should also be desirable to approach ecological regime shifts similarly. Conversi et al. (2015) advocate for exactly this, and they present a generalized framework for regime shift investigation based on endogenous and exogenous factors, and which is analogous the predictor-response framework advocated here. In both cases, however, the emphasis is twofold: first, to assess the

relationships between food web/trophic dynamics (endogenous/responses) and external abiotic and/or anthropogenic stressors (exogenous/predictors); second, to determine the strength and direction of those relationships.

Study aims

This study presents a new Ecosystem-Level, Management-Indicator Selection Tool (EL-MIST; Fig. 1) that leverages the scientific method in order to perform hypothesis-based tests by

applying state-of-the-art statistical methods specifically designed to model multivariate ecological datasets. Canonical analysis methods (ter Braak 1994, Legendre and Legendre 2012) were used to directly test null hypotheses (H_0) concerning the functional relationships among sets of response and predictor indicators that describe the resources, pressures, and status of any LME where data are available. By employing a holistic approach, EL-MIST will not only characterize the complex dynamics among sets

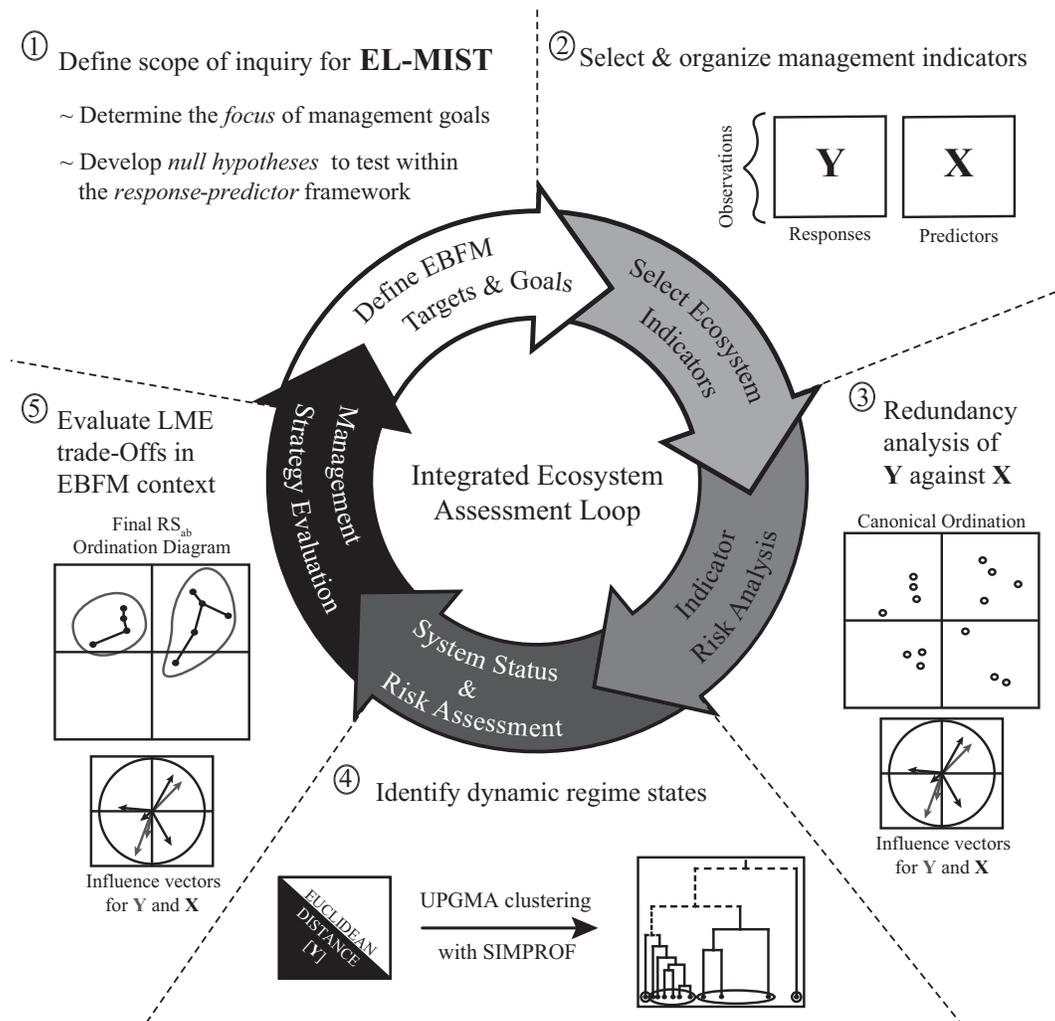


Fig. 1. Conceptual framework for Ecosystem-Level, Management-Indicator Selection Tool (EL-MIST). The inner loop represents the Integrated Ecosystem Assessment (IEA) protocol (Levin et al. 2009) and its five steps (marked by dashed lines and increasing grayscale gradient). The numbered text outside of the IEA loop marks Steps 1–5 for the complementary EL-MIST protocol and indicates how the IEA steps can be enhanced by employing the listed techniques.

of management indicators, but it also uses the relationships uncovered to identify any unique DRs present in the system, while quantitatively estimating which indicators were most important during transitions between those organizational states. A case study from the Gulf of Mexico large marine ecosystem (Gulf LME) is presented, utilizing a subset of ESR data previously explored by Karnauskas et al. (2015). EL-MIST was used in the Gulf LME to (1) test H_0 and determine statistical significance for any effect of the predictor indicators on the variability in the observed response, (2) identify unique DRs and characterize the differences between DR pairs, (3) highlight the most influential predictor indicators affecting the organization of DRs observed, (4) determine the magnitude and direction of the gradients-of-influence on, and within, the observed ecosystem response, and (5) identify indicator trade-offs and patterns that should be targeted for long-term monitoring, further study, and/or management action/policy updates.

METHODS

The EL-MIST framework

The EL-MIST protocol is defined by five steps that can be used to inform all phases of the IEA loop (Fig. 1), and it can complement long-term monitoring programs by providing a comprehensive assessment of the historical dynamics of all management indicators undertaken by the monitoring effort. The analyses described here were conducted using the Fathom (Jones 2017) and Darkside (Kilborn 2018) Toolboxes for MATLAB and were implemented in version R2014b (MATLAB R2014). The steps of EL-MIST are described in detail here, and it is transferrable to any collection of continuous, time series monitoring data. The Gulf LME case study is presented to demonstrate the utility and flexibility of the EL-MIST framework.

Step 1: Define the scope of inquiry.—When exploring ecosystem dynamics, understanding changes in the organization, structure, and functionality of resources, due to changes in anthropogenic pressures and natural ecosystem variability, can help to refine the decision framework used to set and achieve management goals (Jennings 2005, Link 2005, Levin et al. 2009,

Mollmann and Diekmann 2012). The EL-MIST approach allows great flexibility when parameterizing models, but it always relies on the scientifically valid response-predictor paradigm. This allows for hypothesis tests for organizational effects of the predictors on the responses, but the scope of the management inquiry will dictate which null hypothesis (H_{01}) is assessed. Of course, the data on hand are the true limiting factor when deciding the scope, or hypotheses, of interest, and multiple hypotheses can be tested using various data configurations.

Step 2: Select and organize indicators to inform inquiry objectives.—Time series indicators were arranged into two separate multivariate data matrices—one for *response* variables (Y) and one for *predictors* (X). In both cases, the matrices were arranged such that each row corresponded with one observation, and each column represented a variable. Y and X should have a one-to-one relationship with respect to observations, and in the event that a complete observation is missing from one dataset, the matching observation must be removed from the other. In general, EL-MIST tests hypotheses pertaining to whether or not the predictors affected the responses, and the indicators on hand were divided appropriately in order to address the stated goals of the inquiry. As a rule-of-thumb, Y was comprised of indicators that describe the resources/system of interest in abundance, structure, function, and health, and X contained metrics of natural or anthropogenic factors that are hypothesized to impact the particular multivariate arrangement, or organization, of the responses.

Step 3: Conduct canonical analysis of the response-predictor model.—To assess H_{01} , canonical RDA (Rao 1964) was conducted; RDA is widely used in ecology and employs a matrix of predictor indicators (X) to account for the variation in a matrix of response indicators (Y). Multivariate multiple regression of Y against X was performed, and m linear combinations of the indicators in X , called *canonical axes* (CA_m), were generated; their corresponding eigenvalues represent the variance in Y accounted for by each CA_m . The canonical coefficient of determination (R^2 ; Miller and Farr 1971) measured the success that the predictors had in explaining the responses, while the adjusted form of this measure (R^2_{adj} ; Ezekiel 1930) provided an unbiased

estimate of the fraction of variation in Y explained by X (Ohtani 2000). Statistical significance in RDA was determined using distribution free tests, based on 1000 permutations of the residuals of the model (Anderson 2001, Manly 2006), and all P -value interpretations were based on $\alpha = 0.05$. Reduced-space ordination diagrams of Y constrained by X were produced via RDA scaling type-1, allowing objects (years) and the associated indicators underlying both X and Y to be visualized in the multivariate space defined by the two most important CA_m (Legendre and Legendre 2012).

Step 4: Identify and describe ecosystem dynamic regimes.—The EL-MIST procedure identifies LME DRs by determining if multivariate structure existed among years, with respect to the underlying response indicators in Y . A constrained clustering exercise was undertaken by coupling the unweighted pair group method with arithmetic mean (UPGMA; Rohlf 1963) with resemblance profiles as decision criterion (SIMPROF; Clarke et al. 2008, Kilborn et al. 2017). This form of clustering, referred to as SIMPROF clustering hereafter, assesses $H_{o2} =$ “there is no multivariate structure among objects (years) with respect to the set of descriptors (Y).” The method was developed as a form of hypothesis testing-based clustering (Clarke et al. 2008) and is well suited for high-dimensional, continuous datasets with relatively large sample sizes (Kilborn et al. 2017). The assessment of H_{o2} was made at all possible levels of resemblance identified by an UPGMA clustering solution produced from a Euclidean resemblance matrix (Y_{Eucl} ; Legendre and Legendre 2012). To account for multiple tests of significance within a single dendrogram, the progressive Bonferroni P -value correction method (Clarke et al. 2008, Legendre and Legendre 2012) was employed (1000 iterations; $\alpha = 0.05$). Final DR assignments for each year were made such that (1) all years were retained in the solution, and (2) multiple unique clusters of years were combined only if both the UPGMA dendrogram and the SIMPROF algorithm supported their similarity (i.e., supersetting; Clarke et al. 2008).

After identifying distinct DRs, qualitative descriptions of the indicators best accounting for the difference between DR pairs were developed by revisiting the RDA model. Note that the point

of intersection between the orthogonal vector projection from any DR's centroid to any indicator response gradient in Y (Fig. 2) represents an approximation of that DR's modeled value along the gradient projected upon (Legendre and Legendre 2012). To determine the prominence of each individual response indicator for each DR, the distance from the origin to the intersection point was calculated along each gradient. The sign given to that distance was used to represent either the relatively high (positive) or relatively low (negative) end of an indicator's gradient, and assignment was based on the location of the vector's head (positive end). The difference between any DR's signed, centroid-projection value and that of the previous DR along the same indicator gradient [$\Delta_{a,b}(y_i)$, where a and b denote the DRs whose centroids are being compared along gradient y_i] was calculated. The sign and magnitude of $\Delta_{a,b}(y_i)$ values were interpreted as being reflective of the relative change in the i th predictor indicator over the time period between the two DRs selected (i.e., positive values reflect positive changes over time, and vice versa). However, also note that, prior to centroid projection, all m sets of canonical axes' coordinates, for the response's objects and indicator biplot vectors, were multiplicatively weighted by the proportion of the variability in Y explained their respective CA_m .

Next, for pairwise comparisons of DRs a and b , the list of relevant response indicators was reduced by interpreting the proportional contribution to the total dissimilarity between centroids a and b , for each y_i with respect to all Y [$\lambda_{a,b}(y_i)$]. The value $\lambda_{a,b}(y_i)$ is the Euclidean distance between two centroids' projections onto the same gradient (y_i), divided by the total dissimilarity obtained by summing the distances between all pairs of centroid-projection coordinates for a and b , along all indicators in Y . Here, only indicators whose $\lambda_{a,b}(y_i) \geq$ the lower bound of the 75th percentile of all indicators' proportions were retained. These indicators were interpreted as being sufficiently indicative of the factors underlying the difference between any two response states considered. The choice of threshold value is left to the discretion of the researcher and could be replaced by other equally defensible techniques [e.g., the inclusion of the fewest indicators whose $\lambda_{a,b}(y_i)$ sums to a predetermined threshold].

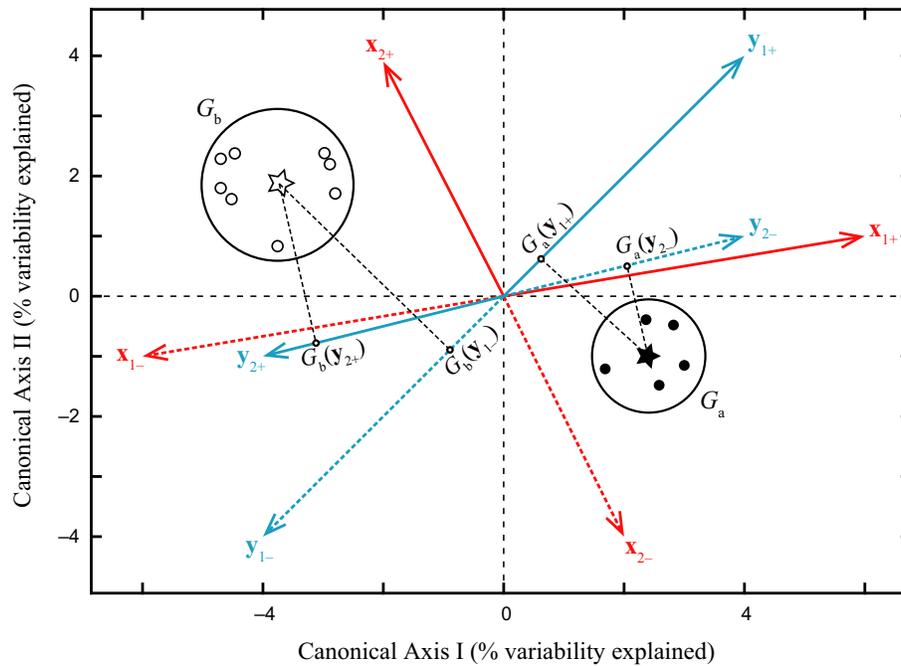


Fig. 2. Redundancy analysis (RDA) scaling type-1 primer. Cartoon depicting the major components of a RDA distance triplot (scaling type-1). The first two canonical axes are drawn, and the proportion of explained variability represented by each CA_m is displayed along each axis. Medium-sized circles represent objects; the colors black and white represent groups a and b , respectively, and like-colored stars represent each group's multivariate centroid. Each object's coordinates are representative of their pairwise dissimilarities, and two objects drawn in close proximity are considered to have low dissimilarity (i.e., are more alike with respect to the underlying gradients of Y). Both Y and X gradients (cyan and red vectors, respectively) are typically only visualized for their positive ends (+; solid vectors), and the negative ends are only implied (-; dotted vectors). Orthogonal projections from each group centroid are drawn and noted with group and vector identifiers. For example, the projection from group a (G_a) onto y_1 is marked with a perpendicular line mapped to the positive end of vector y_i at point $G_a(y_{1+})$ [small white circle]. The Euclidean distance from this point to the origin represents the fitted value for group a onto vector y_1 . The difference in two projections represents the relative difference between the two groups, with respect to the chosen indicator, and is defined by $\Delta_{a,b}(y_i) = G_b(y_i) - G_a(y_i)$. Gradients for X must be interpreted with respect to the variability explained by each CA_m , and their corresponding axis coordinates are representative of the correlation between the underlying indicators and the set of object coordinates obtained along each canonical axis.

Step 5: Evaluate trade-offs in an EBFM context.— Trade-offs between DRs and the predictors that influence them were elucidated by synthesizing all of the information obtained from the RDA and its ordination diagram, the SIMPROF clustering analysis, and the indicator reduction methods described in Step 4. To determine which of the j predictor indicators in X were most influential to the ordination of DRs obtained, and to reduce the list to a more manageable number, the Pearson correlation coefficient ($r_{j,m}$; Legendre and Legendre 2012) was calculated between each

descriptor in X and all CA_m defined by the RDA model. Significance was assessed for all $r_{j,m}$ using permutation methods (5000 iterations; $\alpha = 0.05$; Holm's adjusted P -values), and only the significantly correlated predictor indicators were retained for CA_m where $m = \{I, II\}$. Each predictor's influence to the final ordination of years was determined by extracting the canonical weighting coefficients ($c_{j,m}$) for all X along CA_I and CA_{II} . Canonical weightings were defined by the formula $C = BU$ and can be interpreted in the same manner as regression coefficients

(Legendre and Legendre 2012, pg. 639). Matrix B represents the ordinary-least-squares approximation of the solution to regression of Y against X and is defined as $B = (X'X)^{-1}X'Y$. Matrix U is the result of Eigenanalysis of the fitted values of Y (i.e., the modeled output) where, $Y_{\text{fit}} = XB$, and U is the projection matrix used to represent the canonical RDA solution in Euclidean space (Legendre and Legendre 2012).

Final ordination diagrams were created that contained (1) the identification of LME's DRs through time, (2) the response indicators in Y that best represented differences between the DRs observed, and (3) the predictor indicators in X that were most likely to influence the organization of prominent Y indicators within DRs. Final, reduced RDA visualizations for chronological pairs of DRs a and b were used to highlight potential ecological regime shifts ($RS_{a,b}$), the response indicators that qualitatively describe differences between them, and the underlying human and natural drivers that influenced which DR qualities ultimately became manifest.

EL-MIST case study for the Gulf of Mexico LME

The Gulf of Mexico qualifies as a LME with an areal extent of just over 1.5 million km^2 and an average depth of ~ 1600 m (Kumpf et al. 1999). Living marine resources within the Gulf LME support valuable commercial and recreational fisheries, and in 2012, the Gulf's commercial fisheries landings contributed \$763 million in revenue to the economies of the five Gulf States (Texas, Louisiana, Mississippi, Alabama, and Florida). Additional estimated sales impacts ranged from a low of \$17 million in Florida to \$2.5 billion in Texas, with a total sales impact of \$5.26 billion in 2012. Also in 2012, approximately 3.1 million recreational anglers took an estimated 23 million fishing trips into Gulf waters. These recreational fishing activities contributed, either directly or indirectly, \$10 billion to their respective regional economies (NMFS 2014). However, recent studies indicate that many exploited species are currently experiencing overfishing, due in part to changing fishing patterns during recent decades (SEDAR 2015, 2016, 2018). Overfishing of exploited stocks may manifest in a variety of population-level responses, including declining abundances, reduced sizes, and skewed sex ratios (Coleman et al. 1996, Ault et al. 2005a, b).

Gulf EL-MIST scope of inquiry.—This particular study was framed to answer the specific question: “What influence do human activity, climate dynamics, and environmental forcing (predictors) have on the overall status, structure, and function of the Gulf LME's associated fishery resources (responses)?” As stated in EL-MIST Step 1, by defining the scope of the management inquiry in this way, a statistical H_o was generated, and a useful logical framework for parameterizing the ecosystem model and organizing the selected indicators presented itself. For this case study, H_{o1} = “The variability in predictor indicator time series' of anthropogenic and environmental pressures cannot be used to explain the variability in indicators of ecosystem resources and socioeconomic responses over the same time period.” Using EL-MIST in this way allowed for the exposition of underlying fisheries DRs and the description of the indicators that describe and organize them over time.

Gulf EL-MIST management indicator organization.—An ESR for the Gulf LME was published in 2013, providing full details of more than 100 indicators that were developed to reflect the dynamic nature of the Gulf of Mexico's marine ecosystem, its associated resources, and its dependent coastal communities for the period 1950–2011 (Karnauskas et al. 2013). In many cases, consistent annual records were not available until the 1960s or 1980s, while other indicators were reliably recorded or modeled throughout the entire period of the ESR. Following the DPSEER approach, Karnauskas et al. (2013) arranged the indicators as: (1) *drivers* (Fig. 3) describing climate and physical measures of the environment; (2) *states* (Fig. 4) providing abundance measures of living marine resources at both upper and lower trophic levels (UT and LT, respectively), along with corresponding diversity indices; and (3) *responses* (Fig. 5) capturing impacts relevant to fishery resource structure and socioeconomic change (e.g., fishery revenues). During the application of Step 2 in the Gulf EL-MIST case study, time series from all of the DPSEER categories were reconfigured into a single pair of data matrices—composed of response and predictor indicators—such that the resultant ecosystem model was directly related to the scope in the inquiry, and the testable hypothesis (H_{o1}), defined in above.

A subset of 79 indicators from the 2013 Gulf ESR were used. The $i = 49$ response (Table 1) and

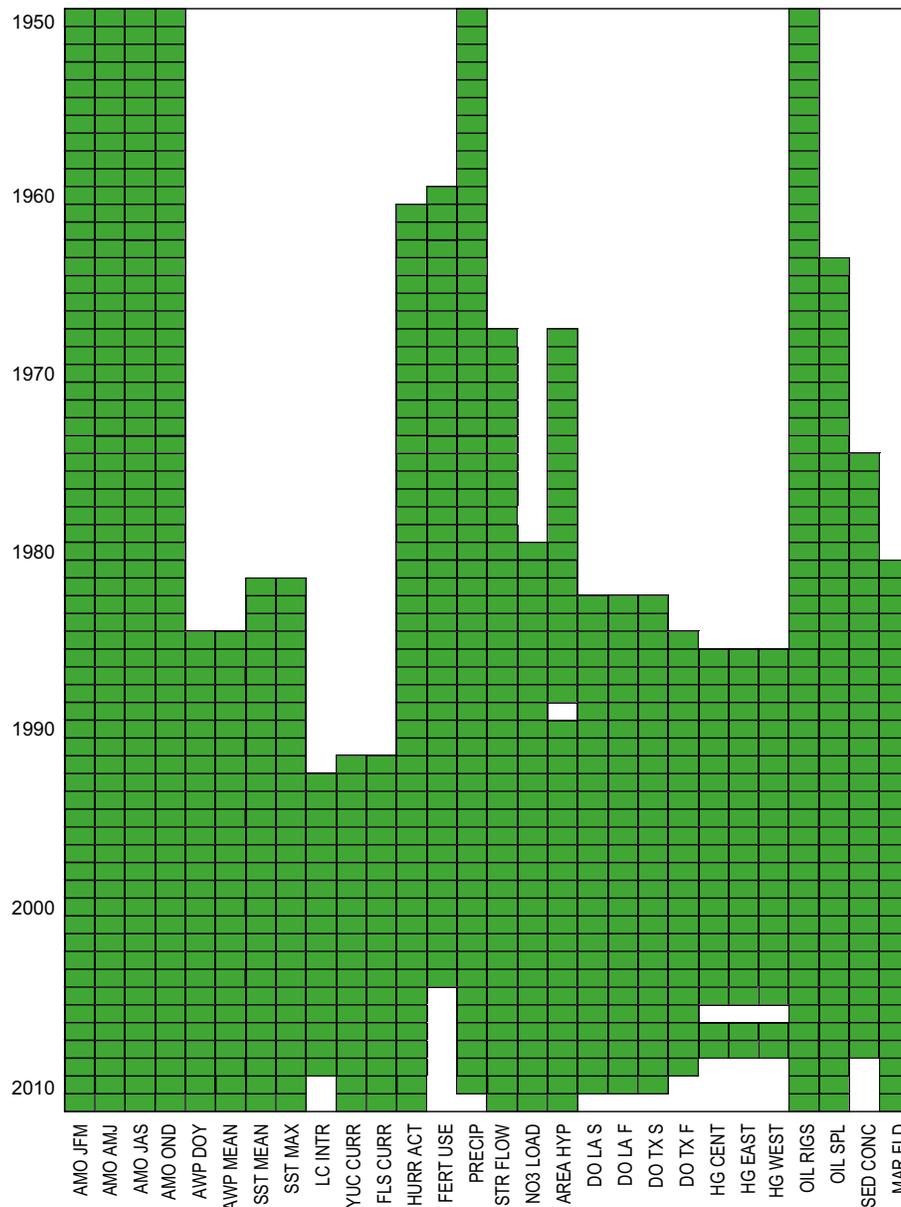


Fig. 3. Gulf of Mexico large marine ecosystem (LME) 2013 ecosystem status report (ESR) *drivers*. Visualization of the driver time series indicators, for the period 1950–2011, contained in the 2013 ESR for the Gulf LME (Karnauskas et al. 2013). Driver indicators represent the climate and physical factors of the LME. Solid squares signify years where data were available, and whitespace indicates missing values. Indicators were categorized using the original authors' DPSE framework categories.

$j = 30$ predictor (Table 2) indicators were compiled into continuous time series data matrices (Y and X , respectively) for the period 1980–2011. In cases where an indicator's observation was missing for any year, the time series' mean value was imputed (Karnauskas et al. 2015). Both matrices

were standardized via z-score translation due to differences in units of measure between indicators (Legendre and Legendre 2012). The response indicators in Y were chosen as the set of descriptors that accounted for (1) the population status of relevant UT and LT species, (2) the structure and

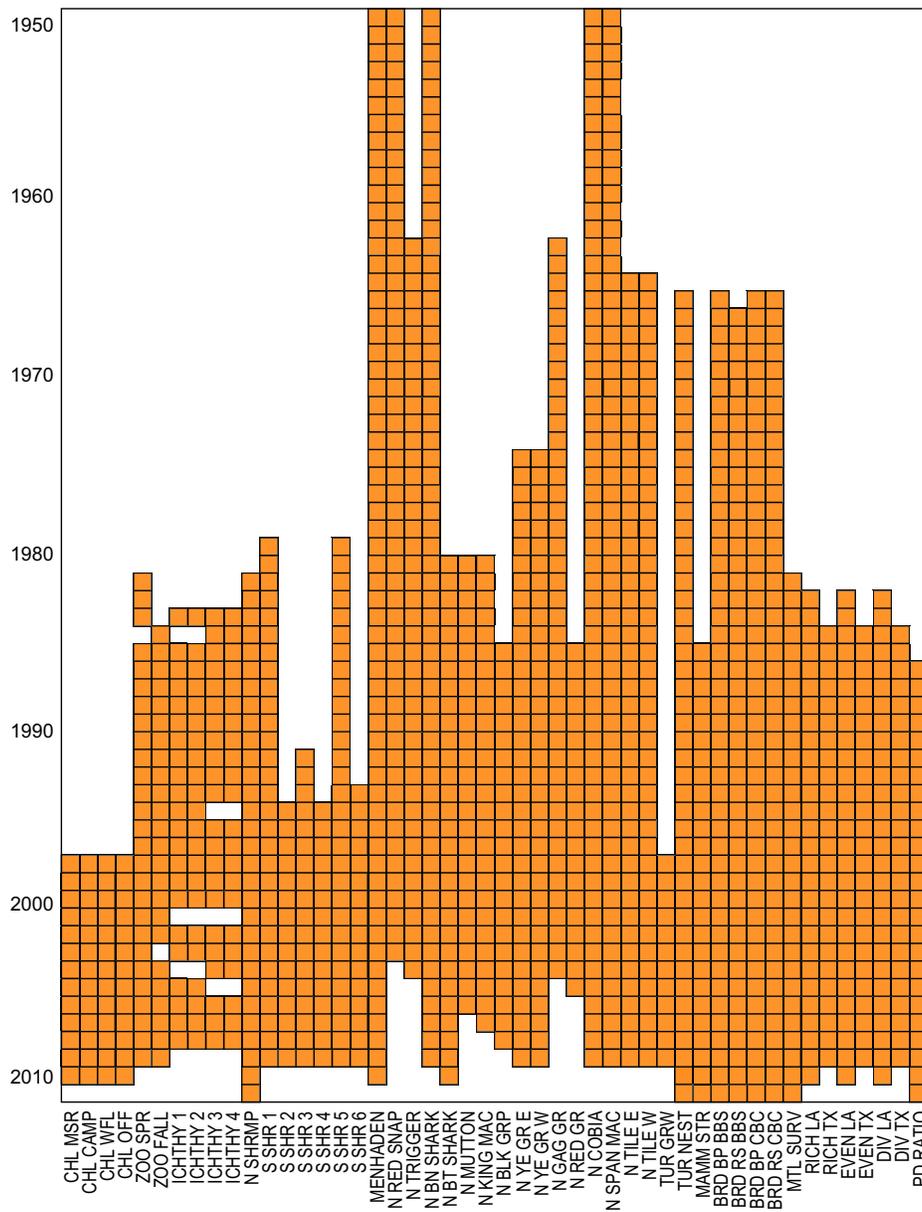


Fig. 4. Gulf of Mexico large marine ecosystem (LME) 2013 ecosystem status report (ESR) *states*. Visualization of the state time series indicators, for the period 1950–2011, contained in the 2013 ESR for the Gulf LME (Karnauskas et al. 2013). State indicators represent the estimated stock sizes for various resource pools within the Gulf. Solid squares signify years where data were available, and whitespace indicates missing values. Indicators were categorized using the original authors’ DPSE framework categories.

function of the Gulf LME’s commercial and recreational fisheries resource complexes and stocks, and (3) the socioeconomic value of both the U.S. and Mexican commercial fishing fleet returns (Table 1). Predictor indicators in X included

descriptors of: (1) large-scale climatological features, fisheries (2) extractions and (3) effort, both commercial and recreational, (4) the natural physical–chemical environment, and (5) oil industry activity (Table 2).

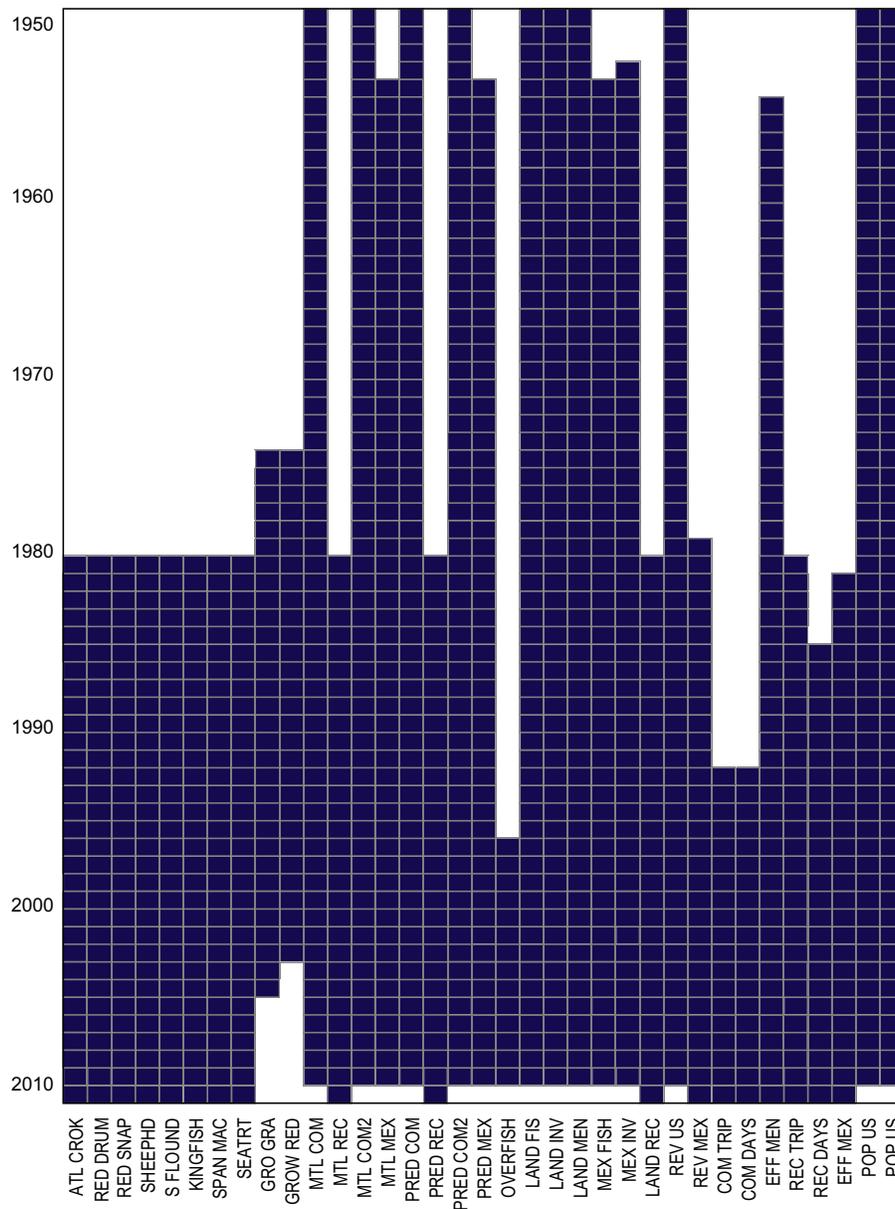


Fig. 5. Gulf of Mexico large marine ecosystem (LME) 2013 ecosystem status report *responses*. Visualization of the response time series indicators, for the period 1950–2011, contained in the 2013 ecosystem status report for the Gulf LME (Karnauskas et al. 2013). Response indicators are representative of the structure and function of various important resource pools within the Gulf. Solid squares signify years where data were available, and whitespace indicates missing values. Indicators were categorized using the original authors’ DPSE framework categories.

RESULTS

Constrained canonical analysis

Gulf EL-MIST response-predictor RDA model.— The RDA analysis in Step 3 yielded statistically significant results ($F = 3.780$, $R^2 = 0.991$, $R^2_{adj} = 0.729$,

$df_{model} = 30$, $df_{error} = 1$, $P\text{-value} < 0.01$); therefore, the H_{01} of no explanatory power of the predictor indicators for the observed fisheries ecosystem response was rejected. Of the total variability in Y explained by the model, ~48% of that variability was described by the first two canonical axes

Table 1. Response indicator list for Gulf of Mexico Ecosystem-Level, Management-Indicator Selection Tool (EL-MIST).

<i>i</i>	Y	Description	EL-MIST category	DPSER
1	MENHADEN	Abundance of Menhaden (<i>Brevoortia patronus</i>) in N Gulf	Population state—LT	State—LT
2	N SHRMP	Abundance of all commercial Shrimp spp. in N Gulf	Population state—LT	State—LT
3	S SHR 1	Abundance of Redspotted Shrimp (<i>Farfantepenaeus brasiliensis</i>) in S Gulf	Population state—LT	State—LT
4	S SHR 5	Abundance of Crystal Shrimp (<i>Sicyonia brevirostris</i>) in S Gulf	Population state—LT	State—LT
5	BRD BP BBS	Abundance of Brown Pelican (<i>Pelecanus occidentalis carolinensis</i>) BBS survey	Population state—UT	State—UT
6	BRD BP CBC	Abundance of Brown Pelican (<i>Pelecanus occidentalis carolinensis</i>) CBC survey	Population state—UT	State—UT
7	BRD RS BBS	Abundance of Roseate Spoonbill (<i>Platalea ajaja</i>) BBS survey	Population state—UT	State—UT
8	BRD RS CBC	Abundance of Roseate Spoonbill (<i>Platalea ajaja</i>) CBC survey	Population state—UT	State—UT
9	N BN SHARK	Abundance of Blacknose Shark (<i>Carcharhinus acronotus</i>) in N Gulf	Population state—UT	State—UT
10	N BT SHARK	Abundance of Blacktip Shark (<i>Carcharhinus limbatus</i>) in N Gulf	Population state—UT	State—UT
11	N COBIA	Abundance of Cobia (<i>Rachycentron canadum</i>) in N Gulf	Population state—UT	State—UT
12	N GAG GR	Abundance of Gag (<i>Mycteroperca microlepis</i>) in N Gulf	Population state—UT	State—UT
13	N KING MAC	Abundance of King Mackerel (<i>Scomberomorus cavalla</i>) in N Gulf	Population state—UT	State—UT
14	N MUTTON	Abundance of Mutton Snapper (<i>Lutjanus analis</i>) in N Gulf	Population state—UT	State—UT
15	N SPAN MAC	Abundance of Spanish Mackerel (<i>Scomberomorus maculatus</i>) in N Gulf	Population state—UT	State—UT
16	N TILE E	Abundance of Tilefish (<i>Caulolatilus</i> spp. and <i>Lopholatilus chamaeleonticeps</i>) in NE Gulf	Population state—UT	State—UT
17	N TILE W	Abundance of Tilefish (<i>Caulolatilus</i> spp. and <i>Lopholatilus chamaeleonticeps</i>) in NW Gulf	Population state—UT	State—UT
18	N TRIGGER	Abundance of Gray Triggerfish (<i>Balistes capricus</i>) in N Gulf	Population state—UT	State—UT
19	N YE GR E	Abundance of Yellowedge Grouper (<i>Epinephelus flavolimbatus</i>) in NE Gulf	Population state—UT	State—UT
20	N YE GR W	Abundance of Yellowedge Grouper (<i>Epinephelus flavolimbatus</i>) in NW Gulf	Population state—UT	State—UT
21	REV MEX	Total revenue for Mexican commercial fishing	Revenue—Commercial fishing	Socioeconomic
22	REV US	Total revenue for U.S. commercial fishing	Revenue—Commercial fishing	Socioeconomic
23	DIV LA	Shannon-Weiner diversity off Louisiana in fall	Structure/Function—All fishes	Impact
24	DIV TX	Shannon-Weiner diversity off Texas in fall	Structure/Function—All fishes	Impact
25	EVEN LA	Species evenness off Louisiana in fall	Structure/Function—All fishes	Impact
26	EVEN TX	Species evenness off Texas in fall	Structure/Function—All fishes	Impact
33	MTL SURV	Mean trophic level in N Gulf	Structure/Function—All fishes	Impact
27	PD RATIO	Ratio of pelagic to demersal fish in catches in N Gulf	Structure/Function—All fishes	Impact
28	RICH LA	Species richness off Louisiana in fall	Structure/Function—All fishes	Impact
29	RICH TX	Species richness off Texas in fall	Structure/Function—All fishes	Impact
30	MTL COM	Mean trophic level of U.S. commercial catch	Structure/Function—Commercial fishes	Impact
31	MTL COM2	Mean trophic level of U.S. commercial catch (excl. Menhaden)	Structure/Function—Commercial fishes	Impact
32	MTL MEX	Mean trophic level of Mexican commercial catch	Structure/Function—Commercial fishes	Impact
34	PRED COM	Proportion of predatory fishes in U.S. commercial catch	Structure/Function—Commercial fishes	Impact

(Table 1. Continued.)

<i>i</i>	Y	Description	EL-MIST category	DPSER
35	PRED COM2	Proportion of predatory fishes in U.S. commercial catch (excl. Menhaden)	Structure/Function—Commercial fishes	Impact
36	PRED MEX	Proportion of predatory fishes in Mexican commercial catch	Structure/Function—Commercial fishes	Impact
37	MTL REC	Mean trophic level of U.S. recreational catch	Structure/Function—Recreational fishes	Impact
38	PRED REC	Proportion of predatory fishes in U.S. recreational catch	Structure/Function—Recreational fishes	Impact
39	ATL CROK	Mean fork length of Atlantic Croaker (<i>Micropogonias undulatus</i>) in U.S. recreational catch	Structure/Function—Stock specific	Impact
40	GROW GRA	Growth rate of Gray Snapper (<i>Lutjanus griseus</i>) in N Gulf	Structure/Function—Stock specific	Impact
41	KINGFSH	Mean fork length of Southern Kingfish (<i>Menticirrhus americanus</i>) in U.S. recreational catch	Structure/Function—Stock specific	Impact
42	RED DRUM	Mean fork length of Red Drum (<i>Sciaenops ocellatus</i>) in U.S. recreational catch	Structure/Function—Stock specific	Impact
43	RED SNAP	Mean fork length of Red Snapper (<i>Lutjanus campechanus</i>) in U.S. recreational catch	Structure/Function—Stock specific	Impact
44	S FLOUND	Mean fork length of Southern Flounder (<i>Paralichthys lethostigma</i>) in U.S. recreational catch	Structure/Function—Stock specific	Impact
45	SEATRT	Mean fork length of Spotted Seatrout (<i>Cynoscion nebulosus</i>) in U.S. recreational catch	Structure/Function—Stock specific	Impact
46	SHEEPHD	Mean fork length of Sheepshead (<i>Archosargus probatocephalus</i>) in U.S. recreational catch	Structure/Function—Stock specific	Impact
47	SPAN MAC	Mean fork length of Spanish Mackerel (<i>Scomberomorus maculatus</i>) in U.S. recreational catch	Structure/Function—Stock specific	Impact
48	MAMM STR	Mammal stranding events in N Gulf	Structure/Function—Stock specific	State—UT
49	TUR NEST	Nesting rates for Kemp's Ridley Turtle (<i>Lepidochelys kempii</i>) in Tamaulipas, Mexico	Structure/Function—Stock specific	State—UT

Notes: Full details for all $i = 49$ response (Y) indicators used for the EL-MIST analysis of the Gulf of Mexico. All data were drawn from the 2013 Gulf ecosystem status report (Karnauskas et al. 2013, 2015). Descriptor categories, as assigned for this study (EL-MIST) and by the original authors (DPSER), are included here.

($CA_I = 31.96\%$, $CA_{II} = 16.18\%$). The other 28 orthogonal axes (CA_m where $m = \{III-XXX\}$) accounted for 50.96% of the remaining explained variability, with only the $m = \{III, IV, V\}$ axes individually accounting for more than 5–8% (see Kilborn 2017, Appendix D, Table D.1 for complete RDA table outputs). The full RDA ordination diagram (Fig. 6) was used as a two-dimensional representation of the final 30-dimensional RDA solution and visualized the variability in Y explained by X only along the first two canonical axes. The annual coordinates on the plot were drawn with respect to the values in Y_{Euc} and any two years placed close to one another were considered more alike than those that were relatively far apart. Vector biplots for all y_i and x_j were used to represent the indicators' gradients that underlie (1)

the ordination of years based on Y_{Euc} (Fig. 6a), and (2) the predictors' (X) capacity to explain the organization of Y (Fig. 6b).

Constrained clustering and management-indicator selection

Gulf EL-MIST identification and description of dynamic regimes.—The results of the SIMPROF clustering of Y_{Euc} (Appendix S1: Table S1) identified eight statistically significant groups of years in multivariate space (Fig. 7). Each unique group represented a set of years whose response indicator organization was numerically distinct when compared to all other sets of years' arrangements. Of the eight groups identified, four were composed of no more than three years {1987–1989}, {1995, 1997}, {1996}, and {2010}, and

Table 2. Predictor indicator list for Gulf of Mexico Ecosystem-Level, Management-Indicator Selection Tool (EL-MIST).

<i>j</i>	X	Description	EL-MIST category	DPSER
1	AMO MEAN	Annual mean value of Atlantic Multidecadal Oscillation	Climatology—Basin	Climate
2	AWP DOY	Atlantic Warm Pool maximum, day of year	Climatology—Basin	Climate
3	AWP MEAN	Atlantic Warm Pool annual mean	Climatology—Basin	Climate
4	MAR FLD	Marsh flooding rate in Barataria Bay, LA	Climatology—Local	Physical
5	HURR ACT	ACE index of hurricane activity	Climatology—Regional	Physical
6	PRECIP	Total precipitation for Mississippi River watershed	Climatology—Regional	Physical
7	LAND FIS	Total landings U.S., finfish (excluding Menhaden)	Fisheries extraction—Commercial	Climate
8	LAND INV	Total landings U.S., invertebrates	Fisheries extraction—Commercial	Climate
9	MEX FISH	Total landings Mexico, all finfish	Fisheries extraction—Commercial	Impact
10	MEX INV	Total landings Mexico, invertebrates	Fisheries extraction—Commercial	Impact
11	LAND MEN	Total landings U.S., Menhaden (<i>Brevoortia patronus</i>)	Fisheries extraction—Commercial	State—LT
12	LAND REC	Total landings U.S., recreational fishes	Fisheries extraction—Recreational	Impact
13	EFF MEN	U.S. Menhaden (<i>Brevoortia patronus</i>) fishing effort	Fishing effort—Commercial	Impact
14	EFF MEX	Number of Mexican registered fishing boats	Fishing effort—Commercial	Socioeconomic
15	REC DAYS	Number of U.S. recreational fishing days	Fishing effort—Recreational	Impact
16	REC TRIP	Number of U.S. recreational angler trips	Fishing effort—Recreational	Impact
17	DO LA F	Annual mean dissolved O ₂ off Louisiana in fall	Physical environment—Local	Physical
18	DO LA S	Annual mean dissolved O ₂ off Louisiana in summer	Physical environment—Local	Physical
19	DO TX F	Annual mean dissolved O ₂ off Texas in fall	Physical environment—Local	Physical
20	DO TX S	Annual mean dissolved O ₂ off Texas in summer	Physical environment—Local	Physical
21	SED CONC	Total suspended sediment discharge for the Mississippi River	Physical environment—Local	Physical
22	STR FLOW	Mean streamflow for Mississippi River	Physical environment—Local	Physical
23	SST MAX	Max monthly mean sea surface temperature	Physical environment—Regional	Climate
24	SST MEAN	Mean offshore sea surface temperature	Physical environment—Regional	Climate
25	ZOO SPR	Mean biomass of zooplankton offshore U.S. in spring	Physical environment—Regional	Climate
26	AREA HYP	Area of hypoxic zone in N GoMex	Physical environment—Regional	Physical
27	FERT USE	Index of fertilizer consumption for Mississippi River watershed	Physical environment—Regional	Physical
28	NO3 LOAD	Mississippi River total basin load of NO ₃	Physical environment—Regional	Physical
29	OIL RIGS	Number of U.S. GoMex oil rigs installed	Resource extraction—Commercial	Physical
30	OIL SPL	Number of U.S. GoMex oil spills	Resource extraction—Commercial	Physical

Notes: Full details for all $j = 30$ response (X) indicators used for the EL-MIST analysis of the Gulf of Mexico. All data were drawn from the 2013 Gulf ecosystem status report (Karnauskas et al. 2013, 2015). Descriptor categories, as assigned for this study (EL-MIST) and by the original authors (DPSER), are included here.

most were combined with the four larger sets to form supersets. However, to retain a relatively high-resolution clustering solution, 2010 was allowed to persist as its own group. What remained was four sets of years, and one singleton year, that were uniquely arranged with respect to the structure and function of the Gulf LME's fisheries resources (Fig. 7), hereafter referred to as DRs. The examination of the chronological transitions between adjacent DR pairs is important because it represents the natural progression of fisheries resources over time (Fig. 6b), but also because these could be considered analogous to ecological regime shifts.

Therefore, even though it is notoriously difficult to determine, based only on management indices, if a true regime shift has transpired (Schaffer 2009), we refer to the comparison of DR_a to DR_b as the ecological shift from regime a to regime b —or, $RS_{a,b}$. Additional consideration beyond the adjacent DR pairs was also given to $RS_{1,A}$ as this pair represented the first and last DRs in the time series, and this relationship could inform on the dynamics of persistent changes over the entire study period.

The minimum proportional contribution to the difference between all $RS_{a,b}$ for any response indicator was $\lambda_{a,b}(y_i) = 0.02\%$ and the maximum

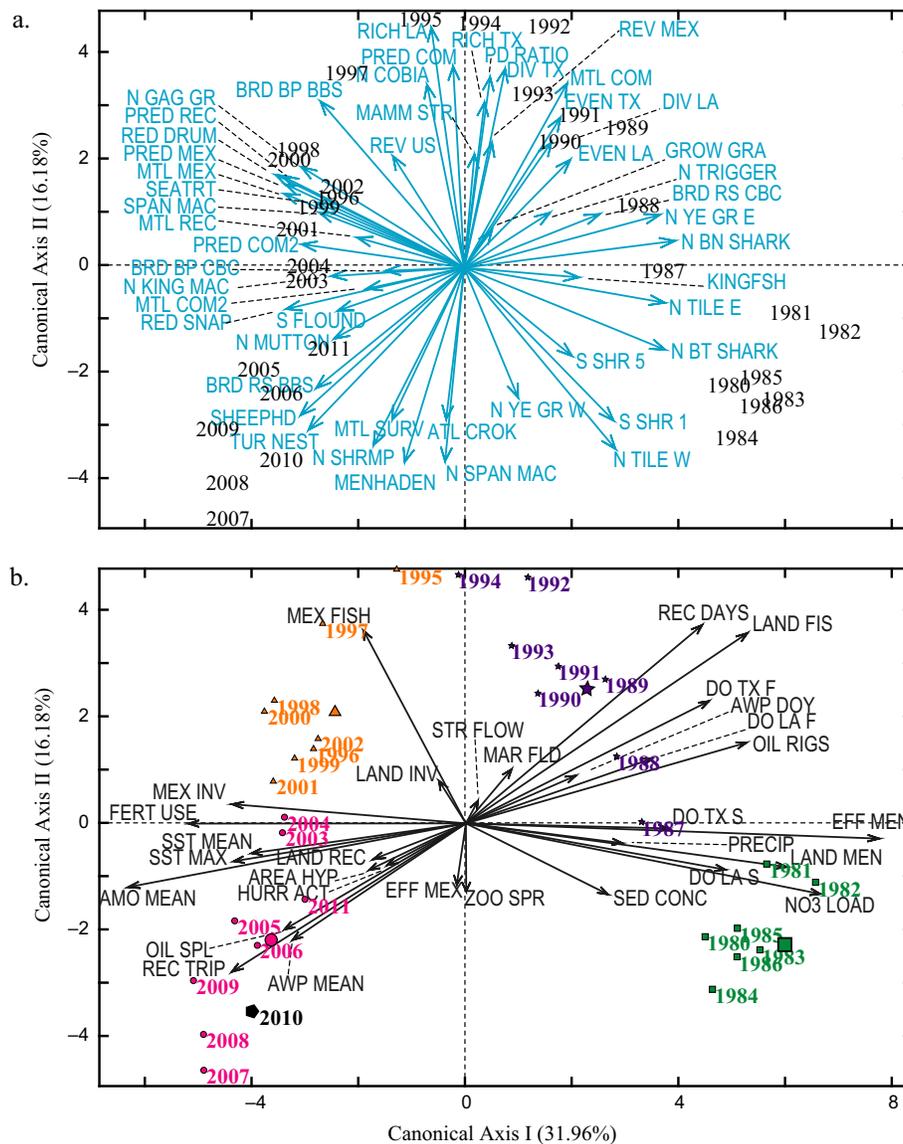


Fig. 6. Gulf Ecosystem-Level, Management-Indicator Selection Tool (EL-MIST) full response-predictor redundancy analysis (RDA) model visualization. Redundancy analysis ordination diagram of the first two CA_m of the Gulf large marine ecosystem response-predictor RDA model's solution for 1980–2011. CA_I (31.96%) is depicted on the abscissa with CA_{II} (16.18%) along the ordinate axis. (a) The distance biplot ordination of years (objects) and the underlying Y gradients (cyan vectors) comprising the dissimilarities (proximity) between each object. (b) The same distance biplot of years alongside the underlying X gradients (gray vectors) describing the dynamic ecosystem pressures. The ordination of years in both panels is identical, but the objects' colors and symbols in panel (b) depict the final dynamic regime (DR) assignments from EL-MIST (see Fig. 7). Each set of filled symbols is unique to each DR and matches the large symbol representing the DR's centroid. Both sets of biplot vectors have been scaled by a factor of 15 for interpretability. See Fig. 2 for additional details of RDA scaling type-1 distance triplots.

abundances of Spanish Mackerel (*Scomberomorus maculatus*) in the UT food web. Changes to commercial fish stocks were evidenced by decreasing MTL (incl. Gulf menhaden) in the U.S. catches and by declining Mexican fisheries' revenues. Fisheries-independent indicators of species richness, evenness, and diversity also exhibited declining values offshore TX (fall only). Also evident in the northern Gulf were community demographic shifts favoring demersal species over pelagics in the northern Gulf and increasing MTL in independent-monitoring survey catches Gulf-wide. Other indicators of positive change during RS_{3,4} included less frequent mammal stranding events and increasing mean fork lengths for Atlantic Croaker (*Micropogonias undulatus*).

Gulf EL-MIST evaluation and selection of predictors.—The ordination of years (i.e., the DRs) was produced by projecting the standardized Y data into the canonical space defined by the RDA of Y against X. As noted previously (Fig. 2), interpretations of the Y and X biplot vectors, along with the objects that are composed and influenced by them, must be made with strict consideration of the canonical axes defined by the RDA process. This is primarily due to the fact that RDA, unlike traditional exploratory analysis (e.g., principal components analysis), seeks to define what percentage of the total variability in Y can be explained by the variability in X, and the resultant CA_m are the weighted, linear combinations of the predictors in X that accomplish that most successfully. The DR shifts RS_{1,4} and RS_{2,3} were separated in canonical space primarily along CA_I, and CA_{II} best accounted the differences between RS_{1,2} and RS_{3,4} (Fig. 6b). In all four cases, the DRs being compared (1) varied mostly along one CA_m and (2) had one DR plotted on the positive end of the axis and the other on the negative end.

The post-hoc check for predictors' correlations ($r_{j,m}$) with each CA_m revealed significant correlations between 13 of 30 indicators from X with CA_I, and three with CA_{II} (Table 4). Only one predictor identified for CA_{II} was not also retained for CA_I (Mexican finfish landings); all other CA_{II} indicators were significantly correlated with CA_I. The canonical regression coefficients for the predictor indicators from C ranged from $c_{j,m} = -0.97$ (number of U.S. recreational fishing days) to $c_{j,m} = 2.74$ (total U.S. finfish landings excluding

Gulf menhaden, *Brevoortia patronus*) along CA_I, and ranged from $c_{j,m} = \{-1.47$ to $3.21\}$ along CA_{II} (number of U.S. recreational fishing days and total U.S. finfish landings excluding Gulf menhaden, respectively). The minimum absolute value for all significant CA_I coefficients (i.e., the lowest magnitude of influence) was $c_{j,m} = -0.09$ (number of oil drilling rigs installed), and $c_{j,m} = 1.20$ (total Mexican finfish landings) for CA_{II}.

The top five numerical influences ($|c_{j,m}| > \sim 1$) along CA_I were (1) the total U.S. commercial finfish landings (excluding Gulf menhaden), (2) the total basin load of dissolved inorganic nitrate (NO₃) from the Mississippi river outflow, (3) the U.S. Gulf menhaden fishing effort, (4) the annual mean value of the Atlantic Multidecadal Oscillation index (AMO), and (5) the number of U.S. recreational fishing days. Along CA_{II}, the $|c_{j,m}|$ for U.S. finfish landings (excl. Gulf menhaden) was more than double the next ranked weighting, and all three significant indicators had $|c_{j,m}| > 1$: (1) total U.S. commercial finfish landings (excl. Gulf menhaden), (2) the number of U.S. recreational fishing days, and (3) total Mexican finfish landings (Table 4).

After identifying the RS_{a,b} pairs of interest, refining the list of response indicators that describe the differences between them, and reducing the list of predictors to those that are significantly correlated to CA_I and CA_{II}, the final EL-MIST ordination diagrams were created. For this case study, we created three visualizations to illustrate the Gulf LME's reorganization of fisheries resources between 1980 and 2011 (Fig. 8a–c), with an additional diagram displaying the relationships between all of the retained predictors and responses for all DRs noted (Fig. 8d).

DISCUSSION

The utility of EL-MIST is the distillation of large amounts of interconnected data in a way that can be useful for informing fisheries managers and stakeholders who are undertaking resource management at the ecosystem scale. Specifically, EL-MIST was designed to fit within the IEA process (Fig. 1) and to utilize time series data compiled into regional ESRs (or any other long-term monitoring database). It is critical that the arrangement of the model's indicator sets is consistent with the scope of the particular

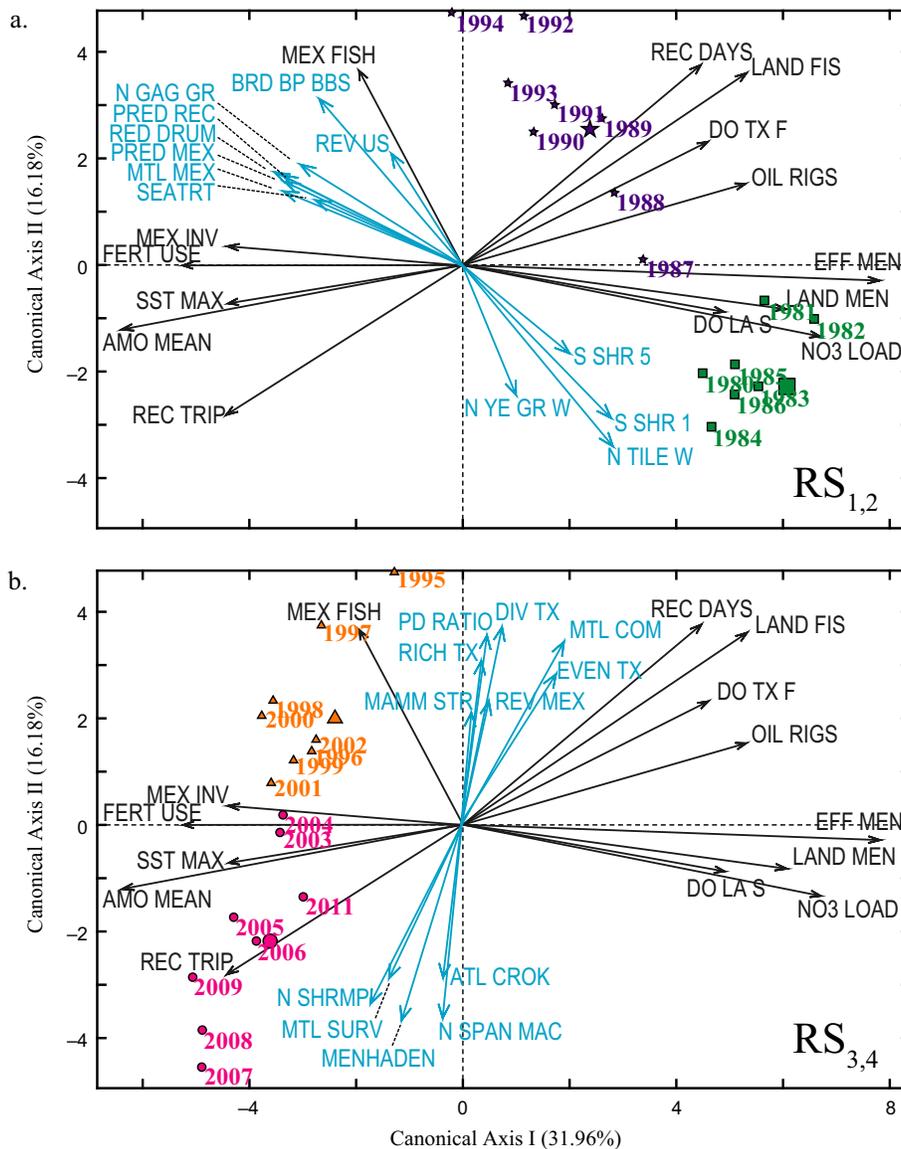
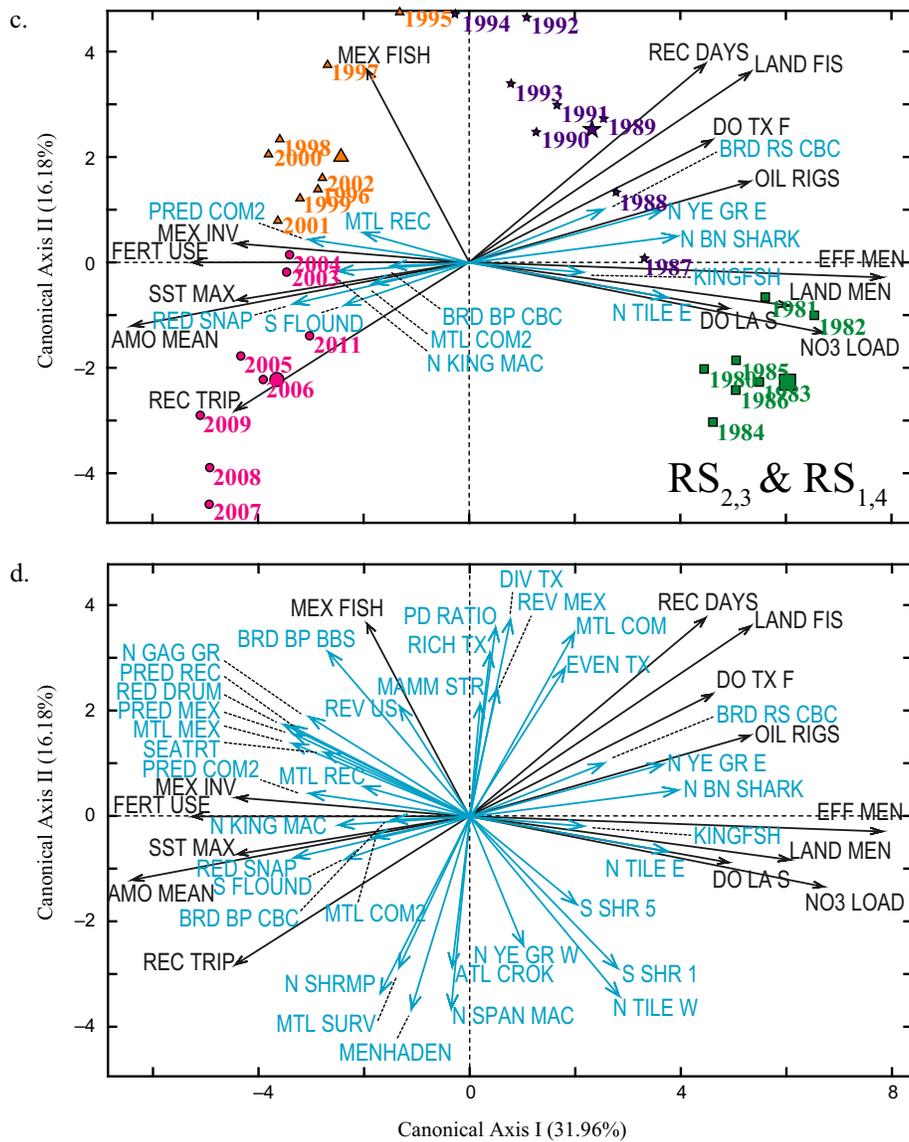


Fig. 8. Final Ecosystem-Level, Management-Indicator Selection Tool (EL-MIST) visualizations for notable $RS_{a,b}$ in the Gulf large marine ecosystem (LME). Redundancy analysis (RDA) distance triplots combining all relevant EL-MIST results, in reduced formats, specific to describing the differences between the response state pairs *a* and *b* noted in the bottom right-hand corner. Three panels describe the following notable regime shifts in the Gulf LME's fisheries resources: (a) $RS_{1,2}$: transition from DR_1 to DR_2 , (b) $RS_{3,4}$: DR_3 to DR_4 , (c) $RS_{2,3}$: DR_2 to DR_3 and $RS_{1,4}$: DR_1 to DR_4 . The final panel (d) shows all of the Y and X management indicators (cyan and dark gray, respectively) that were retained by EL-MIST using its indicator selection methods (i.e., y_i whose $\lambda_{a,b} \geq 75$ th percentile, and all x_j that were significantly correlated with CA_I or CA_{II}). In panels (a–c), only the years contained in the $RS_{a,b}$ of interest were plotted; all other years were removed for clarity. Figure symbols, colors, and scaling factor are identical to Fig. 6; see Fig. 2 for additional details of RDA scaling type-1, distance triplots.



(Fig. 8. Continued)

management concern and follows the response-predictor framework, if it is to be an effective tool.

The Gulf of Mexico LME example shown here indicated that human fishing activities and environmental variability significantly affected the overall structure, function, and productivity of the LME's fisheries resources. The RDA results indicated the majority of the explained variability in the EL-MIST model was described by CA_I (31.96%), with a lesser amount described by CA_{II}

(16.18%). When considering the separation between the DRs during any notable RS_{a,b}, ideal separation between DRs' centroids, for interpretive purposes, would be plotted perfectly along only one canonical axis. Recall, that (1) each CA_m can be represented by, essentially, a multiple regression equation describing the location for the LME along that one-dimensional axis, and (2) the spatial proximity among points on an axis represents similarity with respect to the underlying indicators used to make that axis's equation. Since

Table 3. Table of $\Delta_{a,b}(Y)$.

Response category	Indicator	RS _{1,2}	RS _{2,3}	RS _{3,4}	RS _{1,4}	
Lower trophic level	MENHADEN	-0.06	0.86	0.82	1.62	
	N SHRMP	0.29	1.14	0.79	2.22	
	S SHR 1	-1.42	-1.32	0.00	-2.74	
	S SHR 5	-1.41	-1.38	-0.07	-2.85	
Upper trophic level	BRD BP BBS	1.43	1.28	-0.04	2.66	
	BRD BP CBC	1.18	1.53	0.40	3.10	
	BRD RS BBS	0.80	1.44	0.63	2.88	
	BRD RS CBC	-1.01	-1.51	-0.52	-3.04	
	N BN SHARK	-1.14	-1.53	-0.43	-3.10	
	N BT SHARK	-1.33	-1.48	-0.22	-3.03	
	N COBIA	1.18	0.49	-0.54	1.13	
	N GAG GR	1.38	1.43	0.14	2.95	
	N KING MAC	1.17	1.53	0.40	3.10	
	N MUTTON	0.94	1.49	0.56	2.99	
	N SPAN MAC	-0.55	0.37	0.79	0.62	
	N TILE E	-1.26	-1.51	-0.31	-3.09	
	N TILE W	-1.43	-1.26	0.06	-2.64	
	N TRIGGER	-0.89	-1.48	-0.59	-2.96	
	N YE GR E	-1.07	-1.52	-0.48	-3.07	
	N YE GR W	-1.37	-0.90	0.33	-1.95	
	Revenues	REV US	1.43	1.14	-0.16	2.41
		REV MEX	0.25	-0.69	-0.82	-1.27
	Structure and function	ATL CROK	-0.50	0.43	0.80	0.73
DIV LA		-0.50	-1.28	-0.74	-2.52	
DIV TX		0.49	-0.44	-0.80	-0.75	
EVEN LA		-0.70	-1.40	-0.67	-2.77	
EVEN TX		-0.44	-1.25	-0.75	-2.45	
GROW GRA		-0.54	-1.31	-0.73	-2.57	
KINGFSH		-1.23	-1.52	-0.35	-3.10	
MAMM STR		0.57	-0.35	-0.79	-0.57	
MTL COM		-0.35	-1.19	-0.77	-2.31	
MTL COM2		1.10	1.53	0.46	3.08	
MTL MEX		1.33	1.48	0.22	3.03	
MTL REC		1.29	1.50	0.27	3.07	
MTL SURV		0.24	1.10	0.80	2.13	
PD RATIO		0.29	-0.65	-0.82	-1.19	
PRED COM		0.92	0.08	-0.69	0.31	
PRED COM2		1.25	1.52	0.33	3.09	
PRED MEX		1.34	1.47	0.20	3.01	
PRED REC		1.35	1.46	0.19	3.00	
RED DRUM		1.35	1.46	0.19	3.00	
RED SNAP		1.09	1.53	0.46	3.08	
RICH LA		1.08	0.32	-0.61	0.79	
RICH TX		0.46	-0.48	-0.81	-0.82	
S FLOUND		1.04	1.52	0.50	3.06	
SEATRT	1.34	1.47	0.21	3.02		
SHEEPHD	0.76	1.42	0.65	2.83		
SPAN MAC	1.32	1.48	0.23	3.04		
TUR NEST	0.68	1.39	0.68	2.75		

Notes: Differences between centroid projections, representing the magnitude and direction of change for each response indicator in Y (rows), for notable RS_{a,b} (columns). Any y_i that met the threshold requirements set in Step 4 of EL-MIST are presented in boldface.

Table 4. Correlated predictors and canonical axis weights.

Axis	Predictor	$c_{j,m}$	P -value	EL-MIST category
CA _I	LAND FIS	2.74	<0.01	Fisheries extraction—Commercial
	NO3 LOAD	2.06	<0.01	Physical environment—Regional
	EFF MEN	1.46	<0.01	Fishing effort—Commercial
	AMO MEAN	1.11	<0.01	Climatology—Basin
	REC DAYS	−0.97	<0.05	Fishing effort—Recreational
	MEX INV	−0.86	<0.05	Fisheries extraction—Commercial
	FERT USE	−0.82	<0.01	Physical environment—Regional
	SST MAX	−0.60	<0.05	Physical environment—Regional
	LAND MEN	−0.56	<0.01	Fisheries extraction—Commercial
	DO LA S	0.30	<0.01	Physical environment—Local
	DO TX F	−0.26	<0.05	Physical environment—Local
	REC TRIP	0.10	<0.05	Fishing effort—Recreational
	OIL RIGS	−0.09	<0.01	Resource extraction—Commercial
	CA _{II}	LAND FIS	3.21	<0.05
REC DAYS		−1.47	<0.05	Fishing effort—Recreational
MEX FISH		1.20	<0.01	Fisheries extraction—Commercial

Notes: Table of EL-MIST predictor indicators (x_j) that were significantly correlated with the first two canonical axes (5000 iterations; $\alpha = 0.05$). Canonical axis weights ($c_{j,m}$) are sorted by descending $|c_{j,m}|$; P -values and predictor subcategory assignments are also given.

we identified the major determinants along the Gulf EL-MIST axes (Table 4), we can now describe which predictors most influenced the separation of DRs along each axis, and by extension, which predictors are the most valuable for continued monitoring and management purposes. It should also be noted that any relationships uncovered along CA_I should be interpreted as the primary response (due to the greater percentage of the variability in Y explained), with secondary responses along CA_{II}, and so on for all m .

Predictor influences in the Gulf LME (1980–2011)

While it is notable that both CA_I and CA_{II} were most strongly influenced by U.S. commercial fishing pressure in the Gulf (excluding menhaden), the indicators influencing the primary axis were generally from three overarching categories of predictors: (1) fishing extraction and effort, (2) large-scale climatological forcing, and (3) physical–chemical environmental changes (e.g., NO₃ loading). Fisheries pressures accounted for 46.2% of all significant CA_I indicators, with an additional 7.7% being representative of oil extraction, highlighting the impact of anthropogenic influences (53.8%) on the primary fisheries response in the Gulf LME. The remaining 46.2% of influential predictors were indicative of (1) climate dynamics

and (2) changes to the Gulf's physical–chemical environment that can largely be attributed to the complex teleconnections between the LME's regional/local dynamics, and basin-scale climatological changes (Enfield et al. 2001, Ting et al. 2011, Zhang et al. 2012, Nye et al. 2014, Karnauskas et al. 2015).

The EL-MIST model identified only one basin-scale climatic factor as a major organizing factor for Gulf LME fisheries resources, the AMO, and the model also captured the generally agreed upon AMO phase shift from a cold (negative) to warm (positive) regime between 1994 and 1995 (Nye et al. 2014). The AMO index is primarily a measure of sea surface temperature (SST) across the North Atlantic basin and is hypothesized to have far-reaching teleconnections, including those related to ocean circulation (Nye et al. 2014) and stratification (Zhang et al. 2012), precipitation patterns (Enfield et al. 2001), and cyclone activity (Vimont and Kossin 2007). Since the phenomenon was first described around the time of the 1994/1995 phase shift (Schlesinger and Ramankutty 1994), only the dynamics of the cold-to-warm change have been directly observed; the frequency of the AMO is currently unknown. The effects attributed to the AMO vary by locale (Nye et al. 2014), and our contention here is that the following environmental changes in the Gulf LME

were coincident with the 1994/1995 transition of the AMO (in descending order of influence to the Gulf's fisheries): (1) decreasing NO_3 loading from the Mississippi watershed, (2) increasing input of terrestrial fertilizers, (3) increasing Gulf-wide SST maximum values, and (4) decreasing dissolved O_2 concentrations in continental-shelf waters off LA and TX (spring and fall, respectively).

It would be incorrect to characterize CA_I as only the axis of climate forcing and ecosystem change, especially given the fact that over half of the predictors correlated with CA_I were from anthropogenic influences. Furthermore, biomass extractions and fishing effort underwent great shifts during the period of this study, for a multitude of reasons, not the least of which being legislative actions and evolutions in resource management foci and methods (Adams et al. 2000, Smith et al. 2003, Coleman et al. 2004, Karnauskas et al. 2015). The size of the commercial fishing fleet increased throughout the 1980s as a result of federal development programs and the American Fisheries Promotion Act of 1980 (National Research NRC 1994, Hsu and Wilen 1997, Karnauskas et al. 2015), and these increases coincided with peaks in landings of all finfish and for fishing effort on Gulf menhaden. Also notable, the Sustainable Fisheries Act was implemented in 1996, resulting in more science-based and direct management of Gulf fisheries resources (Hsu and Wilen 1997) by the Gulf's Fisheries Management Council.

Menhaden dominated fish catches in the Gulf throughout the period of this study (Karnauskas et al. 2013), and they continue to be the largest component of modern commercial catches in the Gulf LME (NMFS 2014). While decreasing U.S. commercial extractions of shrimp species over time were not negligible, the steadily rising Mexican invertebrate extractions had a significant explanatory influence on CA_I (Fig. 6b). Recreational fishing also played an organizing role in the Gulf LME (Coleman et al. 2004, Karnauskas et al. 2015), but to what extent is still somewhat unclear. The 1980s and early- to mid-1990s were indicative of higher numbers of fishing days but lower individual angler trips, while the late 1990s through the 2010s displayed the opposite trends. Interpretation of the dynamics at play is difficult to untangle in light of the many scenarios that could potentially explain them, including increasing numbers of anglers, changes in

seasonal closures, variable operating costs for fishing, fluctuating customer demand, increasing international competition, and weather-related concerns (Adams et al. 2004, McCluskey and Lewison 2008, Carter and Letson 2009).

Given the unique combination of predictors that were significantly correlated with CA_I , the primary control axes produced by EL-MIST were best described as the axis of climate change and fishing pressures. To summarize CA_I , it was characterized by relatively high commercial fishing effort and extractions, and a physical environment dominated by the AMO cold regime in the 1980s (positive end), and then changed with relatively reduced commercial effort and landings, increased recreational effort, a more stringent regulatory environment, and an AMO warm regime, beginning around 1995, and which continued through the end of the study period. For CA_{II} , all three significant predictors were explicitly related to either commercial or recreational fishing activities (Table 4). The dominance of fishing indicators for CA_{II} implies that the vertical variability between DRs was best explained by the secondary canonical axis and was exclusively driven by changes in fisheries resource extractions.

Fisheries-response regime shifts in the Gulf LME (1980–2011)

Four distinct DRs, with durations of at least seven years, were identified by the EL-MIST model, and they were accompanied by three chronological ecological regime shifts ($\text{RS}_{a,b}$) that were explained by the canonical axes described above. The congruent manifestations of the short- and long-term responses, displayed by the shifts $\text{RS}_{2,3}$ and $\text{RS}_{1,4}$, respectively, implied that this was the dominant reorganization of the Gulf LME's fisheries resources over the period of this study. Additional weight was added to this claim by the fact that the centroid pairs for $\text{RS}_{2,3}$ and $\text{RS}_{1,4}$ were separated only along the primary canonical axis in our EL-MIST model (CA_I). It should also be noted that CA_I changes from a positive to negative phase between the years 1994 and 1995, the same bifurcation point implied by the interpretation of our Gulf EL-MIST clustering results above, the AMO regime shift, and high fisheries management uptake.

Karnauskas et al. (2015) described one ecosystem-wide regime shift in the Gulf's fisheries

resources from 1980 to 2011 during the mid-1990s, and they argued that the AMO was a fundamental factor in that shift. The same study also explored changing fishing activities throughout the LME (which they claim also notably change in the mid-1990s); unfortunately, the authors were only able to infer dynamic relationships between independent DPSE datasets, given that they primarily employed exploratory methods (Karnauskas et al. 2015) and not constrained analyses between coupled datasets (i.e., hypothesis testing). Fortunately, the results produced by our Gulf EL-MIST model agree with their assessment that the AMO and its indirect effects were major reorganizing factors for the Gulf's fisheries resources; therefore, we are providing additional evidence to support their claim here. Additionally, the EL-MIST model also pointed to direct connections between the fisheries resources' stability and, not only large-scale climate factors, but also for human fishing patterns and extractions. In fact, the results indicated that the effects of fishing dominated the explanatory signal on both of the first two canonical axes. However, due to (1) the number of climate-related variables selected to represent CA_I , (2) the fact that CA_I explained ~32% of the modeled response, and (3) the high axis-weighting values for both AMO and NO_3 loading, the effects of AMO on fisheries resources should not be ignored.

The Gulf ecosystem's response to these pressures was estimated with respect to $i = 49$ different indicators, but by using the EL-MIST framework, we can see that the most prominent qualitative differences between the pre- and post-1994 DRs were primarily expressed in the UT species' abundances, and in metrics for multi- and single-species stock structure and function. Of the five UT fish species' abundance indices noted by EL-MIST, the only one to show increases over time was King Mackerel, all others (from deep water tilefish to coastal sharks) declined. Over the same period, however, some recreational fork lengths increased while other decreased, and MTLs of commercial and recreational catches (U.S.), along with the proportion of predators in commercial catches, went up—all potential signs of stock rebuilding or strengthening.

When compared to others' analyses, further divergence in our assessment of the Gulf LME is the fact that EL-MIST identified the presence of

at least two more ecosystem-wide, ecological regime shifts during the period 1980–2011— $RS_{1,2}$ and $RS_{3,4}$. Even though these two transitions occurred primarily along CA_{II} , which was best described by human fishing activity, the observed responses for the two shifts were totally different. These differential responses to changing fishing efforts and extractions highlighted the dramatic effect that human activity, particularly in the northern Gulf, had on specific stocks and resources across the whole LME. $RS_{1,2}$ was characterized by declining abundances in the LT, whereas during $RS_{3,4}$ the LT species selected were increasing in abundance. During $RS_{1,2}$, there were also mixed responses in the UT abundance indices, but the indicators of multi- and single-species structure and function were all increasing. This is very much in contrast to $RS_{3,4}$, where eight of the 12 indicators selected to characterize the changes in this period were drawn from the structure and function category, and, of those eight, all but two were in decline. Furthermore, the magnitude of these effects was much lower during $RS_{3,4}$ than for any other $RS_{a,b}$ identified by EL-MIST.

EL-MIST in the Gulf of Mexico LME: putting it all together

The relatively orderly chronological progression of the LME's DRs lead to the discussion of ecological regime shifts above. However, it is important to note that the order of the DR manifestations may or may not be relevant to managers, since it is theoretically possible for an ecosystem to change from one DR to another, while only progressing through new organizational states not previously considered (or observed). Furthermore, should true alternative stable states exist, it may not be possible to manage the LME's trajectory to a preferred historical response state at all, due to a hysteretic effect (Beisner et al. 2003, deYoung et al. 2008, Scheffer 2009). Nevertheless, whether or not the DRs noted in this exercise were true alternative stable states or not is inconsequential. Functionally, the organization of fisheries resources in the Gulf LME was numerically distinct over the 30-year study period; so much so, that no less than four DR states should be considered during that period. In fact, there were eight unique numerical signatures in the multivariate organization of

indicators, but for interpretive purposes that number was consolidated here.

When examined in chronological order, the trajectory of the Gulf LME fisheries resources (Fig. 8) began transitioning in the mid-1980s, mostly induced by fishing pressures, before the onset of a major climate-regime shift marked by the 1994/1995 AMO phase-change. The timing of this climate shift was coincident with drastic fishing regulatory changes, such as, the Florida net ban initiated in 1995 (Adams et al. 2000) and the Sustainable Fisheries Act in 1996 (Hsu and Wilen 1997). After $RS_{2,3}$, another intermediate shift in fisheries responses was noted in the early 2000s, which was once again exacerbated by changing fishing activities. If only $RS_{1,4}$ were examined, it would appear as though great gains had been made in the overall state of the Gulf LME's fisheries composition and structure, and this result is consistent with others' findings as well (Karnauskas et al. 2013, 2015). However, by utilizing EL-MIST, we can see that there are differential responses for all Y , in both the magnitude and direction, when examining the three chronological RSs from 1980 to 2011 (Table 3).

Close examination of the $\Delta_{a,b}(y_i)$ values in Table 3 showed that the pace of change across the noted $RS_{a,b}$ followed three general patterns. The most prevalent pattern was displayed by 33 of the 49 Y indicators and manifest as changes that, regardless of sign, speed up between $RS_{2,3}$ when compared to $RS_{1,2}$, and then slow down during $RS_{3,4}$ [$\Delta_{1,2}(y_i) < \Delta_{2,3}(y_i) > \Delta_{3,4}(y_i)$]. The slowing-over-time of the gains in the structure and function of the LME (i.e., rising MTL and number of predators in catches) is consistent with analyses of the Gulf fisheries with menhaden and shrimp trends removed (de Mutsert et al. 2008), and it was also noted in the size spectrums of many recreational fishes. This first-order pattern in the rates of change across all regime shifts suggests that there is a stabilizing of resources underway (for better or worse) and could be construed as evidence for true alternative stable states in the Gulf LME (Beisner et al. 2003), which, to our knowledge, has not been formally identified previously. The remaining 16 indicators were either always increasing or always decreasing relative to the $RS_{a,b}$ examined over time. Generally, the $\Delta_{3,4}(y_i)$ values displayed far reduced magnitudes (positive or negative) of

change when compared to those from either of the other two $RS_{a,b}$, and, once again, these slowing rates can be interpreted as stability being conferred to the resource pool as time from the 1994/1995 bifurcation point increases.

IMPLICATIONS AND FUTURE WORK

Employing the EL-MIST framework allowed the distillation of the voluminous information contained in the 2013 Gulf of Mexico LME's ESR, and it allowed for testing of the hypothesis (H_{o1}) pertaining to fisheries resources' structure, function, and status in the Gulf being affected by anthropogenic pressures and natural physical-chemical variability. The interpretation of the EL-MIST results has shown (1) that this relationship does exist in the Gulf LME, (2) that the differential responses in the marine resources can be characterized as DRs, and (3) that ecological regime shifts between DRs have characteristic relationships that can be used to describe the trade-offs between ecosystem predictors and fisheries resource responses.

The Gulf LME's fisheries resources are sensitive to the basin-scale warming of the North Atlantic Ocean and to the teleconnected processes associated with it. These changes induced a long-term shift in the living marine resources, but these were not the only factors driving the patterns observed. Recreational and commercial fishing activity played very large roles in all of the regime shifts described here and could potentially be construed as the primary organizing forces for this complex system. Perhaps, the changing pressure from significant fisheries expansions in the 1980s tested the limits of the resources' resilience, conferred by a previous equilibrium period's stability (or reduced exploitation rates), and eventually pushed the system past a threshold point. Another proposition is that the environment of increasing regulatory restrictions on fishing activity might have changed the dynamics and structure of the resources by virtue of affecting human usage-patterns—either directly, or indirectly—via the introduction of new legislative measures or management actions. There is no question that fishing regulatory changes had profound effects on the function and stability of fisheries resources in the Gulf LME; however, there is much to be learned regarding the effects of individual management decisions. Focused testing

and evidence are required to say with certainty that any management action had a quantifiable and direct effect on the outcome of any marine resource, and the use of empirical simulation studies or management strategy evaluations (Sainsbury et al. 2000, Levin et al. 2009, Wayte 2009) to examine any trade-offs uncovered by EL-MIST is strongly encouraged.

The causal implications elucidated by EL-MIST between predictor gradients (and their axes weightings), and the dynamics of any $RS_{a,b}$ should be interpreted as justification for more detailed studies, or as support for continued long-term monitoring efforts and research. Several important commercial and recreational Gulf species noted above displayed marked changes over the period of this study, and potential improvements to predictive and/or assessment models could be made immediately by adding considerations of (1) basin-scale climate effects and teleconnected processes selected for by EL-MIST, (2) non-target species with analogous or cascading responses, or (3) trends in rates of change for specific subsets of indicators at well-defined intervals.

Finally, among the greatest advantages of the IEA assessment loop are its iterative and adaptive qualities. EL-MIST fits into the IEA loop at all five critical components, and it can be used to narrow the focus during complex management evaluations, while taking competing pressures and responses into account. This is especially useful in management systems covering large areal extents, containing many management stakeholders and interest groups, or having diverse aquatic resources and/or coastal communities reliant upon them. Even within the context of this Gulf of Mexico LME's case study, additional configurations of the 100+ indicators contained within the ESR could be used to investigate other management inquiries. The EL-MIST protocol is a transferrable and powerful tool that can be used to distill large and complex, ecosystem-level management-indicator datasets, and to provide subsets of relevant indicators for future consideration or implementation in EBFM efforts.

ACKNOWLEDGMENTS

The original conception of this work was made by J. Kilborn and expanded into the management context

with input from M. Drexler. D. Jones provided in-depth advice to J. Kilborn for the development of the EL-MIST statistical analysis and its MATLAB implementation. All analyses were produced by J. Kilborn using MATLAB code developed by both J. Kilborn and D. Jones. J. Kilborn wrote and edited the original manuscript and compiled the tables, figures, and supplemental information. All authors commented on the manuscript throughout the draft preparation process.

This work was completed in partial fulfillment of the requirements for J. Kilborn's doctoral degree. J. Kilborn was supported by NOAA-National Marine Fisheries Service grants NA10NMF4550468 and NA17NMF4330318. This work was also partially supported by the Ocean Conservancy under direction from M. Drexler. We would also like to thank Dr. M. Karnauskas for providing datasets from the Gulf of Mexico Ecosystem Status Report (2013) and for feedback on preliminary results. All associated MATLAB code and data files are included in Data S1 and S2.

LITERATURE CITED

- Adams, C. M., E. Hernandez, and J. C. Cato. 2004. The economic significance of the Gulf of Mexico related to population, income, employment, minerals, fisheries and shipping. *Ocean & Coastal Management* 47:565–580.
- Adams, C., S. Jacob, and S. Smith. 2000. What happened after the net ban? FE-123. Institute of Food and Agricultural Science, University of Florida, Gainesville, Florida, USA.
- Anderson, M. J. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* 58:626–639.
- Andrews, K. S., G. D. Williams, and V. V. Gertseva. 2014. California current integrated ecosystem assessment, phase III report: anthropogenic drivers and pressures. NOAA, Northwest Fisheries Science Center, Seattle, Washington, USA.
- Ault, J. S., J. A. Bohnsack, S. G. Smith, and J. G. Luo. 2005a. Towards sustainable multispecies fisheries in the Florida, USA, coral reef ecosystem. *Bulletin of Marine Science* 76:595–622.
- Ault, J. S., S. G. Smith, and J. A. Bohnsack. 2005b. Evaluation of average length as an estimator of exploitation status for the Florida coral-reef fish community. *Ices Journal of Marine Science* 62:417–423.
- Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1:376–382.
- Bowen, R. E., and C. Riley. 2003. Socio-economic indicators and integrated coastal management. *Ocean & Coastal Management* 46:299–312.

- Carter, D. W., and D. Letson. 2009. Structural vector error correction modeling of integrated sportfishery data. *Marine Resource Economics* 24:19–41.
- Christensen, N. L., et al. 1996. The report of the ecological society of America committee on the scientific basis for ecosystem management. *Ecological Applications* 6:665–691.
- Clarke, K. R., P. J. Somerfield, and R. N. Gorley. 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology* 366:56–69.
- Coleman, F. C., W. F. Figueira, J. S. Ueland, and L. B. Crowder. 2004. The impact of United States recreational fisheries on marine fish populations. *Science* 305:1958–1960.
- Coleman, F. C., C. C. Koenig, and L. A. Collins. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environmental Biology of Fishes* 47:129–141.
- Conversi, A., et al. 2015. A holistic view of marine regime shifts. *Royal Society Philosophical Transactions Biological Sciences* 370:20130279.
- de Mutsert, K., J. H. Cowan, T. E. Essington, and R. Hilborn. 2008. Reanalyses of Gulf of Mexico fisheries data: Landings can be misleading in assessments of fisheries and fisheries ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 105:2740–2744.
- deYoung, B., M. Barange, G. Beaugrand, R. Harris, R. I. Perry, M. Scheffer, and F. Werner. 2008. Regime shifts in marine ecosystems: detection, prediction and management. *Trends in Ecology & Evolution* 23:402–409.
- Diekmann, R., and C. Mollmann. 2010. Integrated ecosystem assessments of seven Baltic Sea areas covering the last three decades. *ICES Cooperative Research Report* 302:1–90.
- Enfield, D. B., A. M. Mestas-Nunez, and P. J. Trimble. 2001. The Atlantic multidecadal oscillation and its relation to rainfall and river flows in the continental US. *Geophysical Research Letters* 28:2077–2080.
- Ezekiel, M. 1930. *Methods of correlation analysis*. John Wiley and Sons, New York, New York, USA.
- Hilborn, R. 2011. Future directions in ecosystem based fisheries management: a personal perspective. *Fisheries Research* 108:235–239.
- Hilborn, R. 2012. The evolution of quantitative marine fisheries management 1985–2010. *Natural Resource Modeling* 25:122–144.
- Hsu, S. L., and J. E. Wilen. 1997. Ecosystem management and the 1996 Sustainable Fisheries Act. *Ecology Law Quarterly* 24:799–811.
- Jennings, S. 2005. Indicators to support an ecosystem approach to fisheries. *Fish and Fisheries* 6:212–232.
- Jones, D. L. 2017. *The Fathom Toolbox for MATLAB: software for multivariate ecological and oceanographic analysis*. University of South Florida, College of Marine Science, St. Petersburg, Florida, USA. <https://www.marine.usf.edu/research/matlab-resources/>
- Karnauskas, M., M. J. Schirripa, C. R. Kelble, G. S. Cook, and J. K. Craig. 2013. *Ecosystem status report for the Gulf of Mexico*. Technical Memorandum NMFS-SEFSC-653, NOAA, Southeast Fisheries Science Center, Miami, Florida, USA.
- Karnauskas, M., et al. 2015. Evidence of climate-driven ecosystem reorganization in the Gulf of Mexico. *Global Change Biology* 21:2554–2568.
- Kelble, C. R., D. K. Loomis, S. Lovelace, W. K. Nuttle, P. B. Ortner, P. Fletcher, G. S. Cook, J. J. Lorenz, and J. N. Boyer. 2013. The EBM-DPSER conceptual model: integrating ecosystem services into the DPSIR framework. *PLoS ONE* 8:e70766.
- Kilborn, J. P. 2017. *Investigating marine resources in the Gulf of Mexico at multiple spatial and temporal scales of inquiry*. Dissertation. University of South Florida, Ann Arbor, Michigan, USA.
- Kilborn, J. P. 2018. *The Darkside Toolbox for MATLAB*. University of South Florida, College of Marine Science, St. Petersburg, Florida, USA.
- Kilborn, J. P., D. L. Jones, E. B. Peebles, and D. F. Naar. 2017. Resemblance profiles as clustering decision criteria: estimating statistical power, error, and correspondence for a hypothesis test for multivariate structure. *Ecology and Evolution* 7:2039–2057.
- Kumpf, H., K. A. Steidinger, and K. Sherman. 1999. *The Gulf of Mexico large marine ecosystem: assessment, sustainability, and management*. Blackwell Science, Malden, Massachusetts, USA.
- Larkin, P. A. 1996. Concepts and issues in marine ecosystem management. *Reviews in Fish Biology and Fisheries* 6:139–164.
- Legendre, P., and L. Legendre. 2012. *Numerical ecology*. Third English edition. Elsevier, Amsterdam, The Netherlands.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Levin, P. S., M. J. Fogarty, S. A. Murawski, and D. Fluharty. 2009. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. *PLoS Biology* 7:e1000014.
- Levin, P. S., and C. Mollmann. 2015. Marine ecosystem regime shifts: challenges and opportunities for ecosystem-based management. *Philosophical Transactions of the Royal Society B-Biological Sciences* 370:20130275.

- Link, J. S. 2005. Translating ecosystem indicators into decision criteria. *Ices Journal of Marine Science* 62:569–576.
- Link, J. 2016. Ecosystem-based fisheries management policy. NMFSPD 01-120, U.S. Department of Commerce, NOAA, National Marine Fisheries Service, Washington, D.C., USA.
- Link, J. S., S. Gaichas, T. J. Miller, T. Essington, A. Bundy, J. Boldt, K. F. Drinkwater, and E. Moksness. 2012. Synthesizing lessons learned from comparing fisheries production in 13 northern hemisphere ecosystems: emergent fundamental features. *Marine Ecology Progress Series* 459:293–302.
- Manly, B. F. 2006. Randomization, bootstrap and Monte Carlo methods in biology. Chapman & Hall/CRC Press, Boca Raton, Florida, USA.
- MATLAB. R2014. The MathWorks, Natick, Massachusetts, USA.
- McCluskey, S. M., and R. L. Lewison. 2008. Quantifying fishing effort: a synthesis of current methods and their applications. *Fish and Fisheries* 9:188–200.
- Miller, J. K., and S. D. Farr. 1971. Bimultivariate redundancy: a comprehensive measure of interbattery relationship. *Multivariate Behavioral Research* 6:313–324.
- Mollmann, C., and R. Diekmann. 2012. Marine ecosystem regime shifts induced by climate and overfishing: a review for the northern hemisphere. Pages 303–347 in G. Woodward, U. Jacob, and E. J. Ogorman, editors. *Advances in ecological research*, Vol 47: global change in multispecies systems, Pt 2. Elsevier Academic Press, San Diego, California, USA.
- Niemeijer, D., and R. S. de Groot. 2008. Framing environmental indicators: moving from causal chains to causal networks. *Environment, Development and Sustainability* 10:89–106.
- NMFS. 2014. Fisheries economics of the United States, 2012. NMFS-F/SPO-137, NOAA, U.S. Department of Commerce, Washington, D.C., USA.
- NOAA. 2009. Ecosystem Assessment Report for the Northeast U.S. Continental Shelf Large Marine Ecosystem. Ref Doc. 09-11, U.S. Department of Commerce, NOAA, Northeast Fisheries Science Center, Woods Hole, Massachusetts, USA.
- NRC. 1994. Improving the management of US marine fisheries. National Academies Press, National Research Council, Washington, D.C., USA.
- Nye, J. A., M. R. Baker, R. Bell, A. Kenny, K. H. Kilbourne, K. D. Friedland, E. Martino, M. M. Stachura, K. S. Van Houtan, and R. Wood. 2014. Ecosystem effects of the Atlantic Multidecadal Oscillation. *Journal of Marine Systems* 133:103–116.
- Ohtani, K. 2000. Bootstrapping R-2 and adjusted R-2 in regression analysis. *Economic Modelling* 17:473–483.
- Pershing, A. J., K. E. Mills, N. R. Record, K. Stamieszkin, K. V. Wurtzell, C. J. Byron, D. Fitzpatrick, W. J. Golet, and E. Koob. 2015. Evaluating trophic cascades as drivers of regime shifts in different ocean ecosystems. *Philosophical Transactions of the Royal Society B-Biological Sciences* 370:20130265.
- Rao, C. R. 1964. The use and interpretation of principal component analysis in applied research. *Sankhya: The Indian Journal of Statistics, Series A(1961–2002)* 26:329–358.
- Rohlf, F. J. 1963. Classification of *Aedes* by numerical taxonomic methods (Diptera: Culicidae). *Annals of the Entomological Society of America* 56:798–804.
- Sainsbury, K. J., A. E. Punt, and A. D. M. Smith. 2000. Design of operational management strategies for achieving fishery ecosystem objectives. *Ices Journal of Marine Science* 57:731–741.
- Scheffer, M. 2009. Alternative stable states and regime shifts in ecosystems. Page 809 in S. A. Levin, editor. *The Princeton guide to ecology*. Princeton University Press, Princeton, New Jersey, USA.
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* 18:648–656.
- Schlesinger, M. E., and N. Ramankutty. 1994. An oscillation in the global climate system of period 65–70 years. *Nature* 367:723–726.
- SEDAR. 2015. SEDAR 43, Stock Assessment Report: Gulf of Mexico Gray Triggerfish. U.S. Department of Commerce, NOAA, National Marine Fisheries Service, Southeast Fisheries Science Center, North Charleston, South Carolina, USA.
- SEDAR. 2016. SEDAR 33, Stock Assessment Update Report: Gulf of Mexico Greater Amberjack. U.S. Department of Commerce, NOAA, National Marine Fisheries Service, Southeast Fisheries Science Center, North Charleston, South Carolina, USA.
- SEDAR. 2018. SEDAR 51, Stock Assessment Report: Gulf of Mexico Gray Snapper. U.S. Department of Commerce, NOAA, National Marine Fisheries Service, Southeast Fisheries Science Center, North Charleston, South Carolina, USA.
- Smith, S., S. Jacob, M. Jepson, and G. Israel. 2003. After the Florida net ban: the impacts on commercial fishing families. *Society & Natural Resources* 16:39–59.
- ter Braak, C. J. F. 1994. Canonical community ordination. Part I: basic theory and linear methods. *Écoscience* 1:127–140.
- Ting, M. F., Y. Kushnir, R. Seager, and C. H. Li. 2011. Robust features of Atlantic multi-decadal variability and its climate impacts. *Geophysical Research Letters* 38:L17705.

- Tscherning, K., K. Helming, B. Krippner, S. Sieber, and S. G. Y. Paloma. 2012. Does research applying the DPSIR framework support decision making? *Land Use Policy* 29:102–110.
- Vimont, D. J., and J. P. Kossin. 2007. The Atlantic Meridional Mode and hurricane activity. *Geophysical Research Letters* 34:L07709.
- Wayte, S. E. 2009. Evaluation of new harvest strategies for SESSF species. CSIRO Marine and Atmospheric Research, Hobart and Australian Fisheries Management Authority, Canberra, Australian Capital Territory, Australia.
- Wernberg, T., et al. 2016. Climate-driven regime shift of a temperate marine ecosystem. *Science* 353:169–172.
- Zhang, L. P., C. Z. Wang, and L. X. Wu. 2012. Low-frequency modulation of the Atlantic warm pool by the Atlantic multidecadal oscillation. *Climate Dynamics* 39:1661–1671.

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