FEATURE ARTICLE

Critical points in ecosystem responses to fishing and environmental pressures

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ABSTRACT: Ecosystem dynamics are often influenced by both environmental and anthropogenic pressures. Increased demand for living marine resources has resulted in global declines of targeted species, which are often managed under a single-species paradigm that does not fully incorporate ecosystem considerations such as ecological interactions or environmental factors. Ecosystem-based fisheries management (EBFM) is a more holistic approach that concurrently addresses human, ecological, and environmental factors influencing living marine resources and evaluates these considerations collectively on a system level. For EBFM, reference points associated with management action need to be quantified. Methods have been developed to assign decision criteria to ecological indicators' response to human-use pressures, yet few efforts have established decision criteria in response to the combined influence of human-use and environmental pressures. We translated ecological indicator response into a surface dependent on both fishing and environmental pressures. Using generalized additive models, we empirically determined critical points at which a small change in fishing and environmental pressure results in an abrupt change in ecosystem status. For the Northeast United States Shelf Large Marine Ecosystem, we identified critical points in ecological indicators that represent system production, size distribution, community structure, and ecosystem functioning. Our findings highlight the need to include both anthropogenic and environmental pressures for delineation of ecosystem decision criteria.

KEY WORDS: Reference points · Ecosystem-based fisheries management · EBFM · Thresholds · GAM · Dynamic factor analysis · DynFA

Critical points (gray polygons) quantified on a surface of ecosystem response dependent upon fishing and environmental pressures.

Image: S. I. Large

INTRODUCTION

In applied ecology, a suite of factors influence ecosystem dynamics, including environmental and anthropogenic stressors, which can alter the structure and functioning of ecosystems and ultimately have direct implications on management actions designed to conserve these systems (Christensen et al. 1996). Ecosystem-based management (EBM) is a living-resource management approach that is holistic in nature and incorporates multiple human uses and ecosystem processes (Christensen et al. 1996). Implementing EBM is not trivial, and like any complex system of decision making, it requires the development of goals, relevant ecosystem assessments, and deci-

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sion criteria for management action (Lackey 1998). EBM has been successfully implemented in terrestrial and aquatic (including marine) ecosystems with varied management goals. Examples where both environmental and anthropogenic factors influence the goods and services provided by their ecosystem include forests altered by fire suppression and logging (Allen et al. 2002) and lotic ecosystems altered by natural variability in flow regimes and obstructed flow caused by dams (Richter et al. 2003). Marine ecosystems are also influenced by natural environmental variability (Beaugrand et al. 2008) and multiple human uses, such as coastal-zone development and the harvest of living marine resources (LMRs; Pauly et al. 1998, Hsieh et al. 2006); however, innate difficulties associated with environmental and ecological sampling create special challenges for implementing marine EBM.

Increased demand for LMRs has resulted in global declines in targeted species' abundance (Hsieh et al. 2006), shifts in biotic processes (Bianchi et al. 2000), and deteriorated fisheries status, impacts that are often exacerbated in a changing environment (Shin & Shannon 2010, Shackell et al. 2012). Traditional single- and multiple-species management approaches often do not fully incorporate ecosystem considerations such as ecological interactions and environmental processes, nor account for the cumulative impacts on LMRs as an interconnected system (Link 2002, Pikitch et al. 2004). Ecosystem-based fisheries management (EBFM) attempts to simultaneously address the effects of human, ecological, and environmental factors that influence LMRs and evaluate these considerations systemically (Larkin 1996).

Implementing EBFM follows the same steps as EBM: pre-defined management goals, an assessment of ecosystem status, and decision criteria to achieve management objectives (Sainsbury et al. 2000). Single-species fisheries management approaches often use decision criteria based on the response of population-level attributes to human-induced pressures (Hilborn & Walters 1992). Analogous to traditional decision criteria, ecological indicators are synthetic and quantifiable attributes that represent ecosystem status and can also be translated into decision criteria for EBFM (Murawski 2000, Rice 2000, Trenkel & Rochet 2003, Jennings 2005, Link 2005). Many ecological indicators have been suggested, and representative indicators have been vetted for routine monitoring of ecosystem status (Link & Brodziak 2002, Link et al. 2002, Link 2005, Methratta & Link 2006, Shin et al. 2010, Shackell et al. 2012).

Translating ecological indicators into decision cri-

teria requires an understanding of ecological thresholds, which occur when a small change in a pressure results in either a large response or an abrupt change in ecosystem state or function (Groffman et al. 2006, Rice 2009). Mathematically, pressure-response thresholds occur (1) when the second derivative of a function is equal to 0 and the first derivative is non-0 or (2) when the second derivative of a function crosses 0, denoting a change in the magnitude or direction (e.g. from concave-up to concave-down) of the function, respectively. Both types of thresholds can be calculated from known functional forms such as piecewise regression models (Samhouri et al. 2010), or estimated from generalized additive models using finite differences (Fewster et al. 2000, Large et al. 2013).

Ecological thresholds have been theoretically and empirically evaluated in response to fishing and environmental pressure (Link 2005, Samhouri et al. 2010, Large et al. 2013). These simple pressure-response relationships may be useful for establishing decision criteria; however, they do not fully account for the combined effect of multiple pressures that concurrently influence ecosystem state (Jennings 2005, Fay et al. 2013, Large et al. 2013). Pressure-response thresholds can be extended into multivariate space by translating ecological indicator response into a surface dependent on both fishing and environmental pressures. The Northeast United States Shelf Large Marine Ecosystem (NES LME) is an ideal ecosystem to evaluate 2 covariate ecological thresholds because both human and environmental pressures have been linked to changes in ecosystem status (Shackell et al. 2012) and ecological and environmental sampling has been conducted regularly throughout the NES LME, resulting in long-term data (e.g. >40 yr) for ecological indicators and both fishing and environmental pressures (NEFC 1988, NEFSC 1998, Methratta & Link 2006, EcoAP 2009, 2012).

Here, we propose a method to identify thresholds in past realized pressure–environment–state space that can be used to identify levels of multiple pressures where abrupt changes in the direction of ecosystem status likely happened. Critical points, or 2-covariate thresholds, occur when the slopes of both pressure variables cross 0 and can be used to identify regions where the direction of indicator response changed as a result of both pressure variables. In a management context, critical points from multiple facets of ecosystem response to important sources of pressure can be integrated to provide advice and support towards delineating salient ecosystem reference points.

MATERIALS AND METHODS

Ecological indicators

Data used in this study were compiled from the Northeast Fisheries Science Center surveys that monitor trends in abundance and distribution of important LMRs, as well as provide information regarding the ecology and oceanography of the NES LME region (Azarovitz 1981, NEFC 1988, NEFSC 1998). Since 1963, this scientific monitoring program has sampled 350 to 400 stations twice per year from Cape Hatteras (North Carolina, USA) to Nova Scotia (Canada) using a random stratified design. Stations within each depth-region stratum were randomly sampled, and surveyed fish or invertebrates were sorted by species, weighed, and their length was measured. Survey data were aggregated spatially and averaged across season to create a single time series for each indicator from 1964 to 2010 (Link et al. 2002). A suite of ecological indicators has been suggested and vetted as useful indicators for assessing ecosystem status for the NES LME (Link 2005, Methratta & Link 2006, EcoAP 2009, 2012). These indicators represent key ecosystem processes such as energy flow, trophic dynamics, community structure, and size distribution (Table 1).

Environmental pressures

Environmental pressures influence circulation patterns, primary production, vertical mixing, and available nutrients across multiple geographic and temporal scales. Within the NES LME, we chose environmental pressures that influence ecosystem status and LMRs across the Atlantic basin, the NES LME, and regional portions of the

Table 1. Ecological indicators used in generalized additive model (GAM) analysis. All indicators were calculated for the Northeast United States Shelf Large Marine Ecosystem (NES LME) from National Marine Fisheries Service (NMFS) fall and spring trawl survey data. Species list used for each indicator can be found in the Supplement at www.int-res.com/articles/suppl/m521p001_supp.pdf. BTS: bottom trawl survey

Indicator	Definition	Data source	Indicator rationale	Rationale source
Length (mean)	Mean length (cm) of individual fish for all spp. from BTS	Azarovitz (1981), NEFC (1988), Link & Brodziak (2002)	Size distribution	Bianchi et al. (2000), Link (2005), Methratta & Link (2006)
Biomass (total)	Total biomass of all surveyed spp. from the BTS ($\times 10^3$ t)	Azarovitz (1981), NEFC (1988), Link & Brodziak (2002)	Allometric and growth dynamics, system production	Fogarty & Murawski (1998), Pauly et al. (1998), Link et al. (2002), Trenkel & Rochet (2003), Jennings (2005), Link (2005), Methratta & Link (2006)
Planktivores and benthivores to piscivores and shrimp-fish feeders ratio	Ratio of abundance of lower trophic level guilds to upper trophic level guilds from BTS	Azarovitz (1981)	Trophic dynamics, energy flow, community structure	Link (2005), Methratta & Link (2006)
Pelagic to demersal ratio	Ratio of pelagic and demersal fishes from BTS (index)	Azarovitz (1981)	Energy flow, community structure	Link (2005), Methratta & Link (2006)
Species richness (frequency)	Number of surveyed spp. from the BTS	Azarovitz (1981), NEFC (1988), Link & Brodziak (2002)	Aggregate community status	Rice (2000), Jennings (2005), Link (2005), Methratta & Link (2006)
Longhorn sculpin biomass (total)	Total biomass of longhorn sculpin from BTS (mt)	Azarovitz (1981), NEFC (1988), Link & Brodziak (2002)	Sensitive species, index of disturbance	Link (2005), Methratta & Link (2006)
Trophic level (TL, mean)	Mean trophic level (as calculated from NMFS diet sampling) of surveyed spp. weighted by abundance (biomass)	Azarovitz (1981), NEFC (1988), Link & Brodziak (2002)	Size distribution, energy flow	Pauly et al. (1998)
Ctenophore abundance	Frequency of Ctenophora found within surveyed spiny dogfish stomachs	Link & Ford (2006)	Ecosystem structure and function, index of environmental change	Link & Ford (2006)

ecosystem. To facilitate analyses with ecological indicators, we averaged intra-annual measures to create a single annual time series for each pressure variable.

The Atlantic multidecadal oscillation (AMO) represents variance in thermohaline circulation patterns and was derived from sea surface temperature (SST; Enfield et al. 2001). The AMO index measures basin-scale warm and cold phases in Atlantic SST, and has been related to hurricane activity and precipitation (1964–2010; data available at www.esrl.noaa.gov/psd/data/correlation/amon.us.data) The North Atlantic oscillation (NAO) is also a basin-scale index that represents teleconnection patterns in the northern hemisphere and influences temperature, precipitation, and wind fields, which have been linked to key ecological processes in the North Atlantic (Stenseth et al. 2002). The NAO was calculated as the difference between the surface pressure of the subtropical (Azores) high and the Subpolar (Iceland) low (1964–2010; data available at https://climate.dataguide.ucar.edu/sites/default/files/climate_index_files/nao_pc_annual.ascii; Hurrell 1995). The majority of NAO variance occurs during the winter months, so we also calculated the mean winter (December to February) NAO index (1964–2010; data available at https://climatedataguide.ucar.edu/sites/default/files/climate_index_files/nao_pc_djf.ascii). SST influences species' distribution, growth, and many other ecological and biological processes. Monthly extended-record SSTs (°C; ERSST v3b; Smith et al. 2008) were averaged across the NES LME into a single annual measurement from 1964 to 2010. Wind stress is a non-thermal regional physical pressure, which influences vertical mixing and horizontal currents. We calculated wind stress (N m^{-2} ; data obtained from NOAA's Environmental Research Division's Data Access Program) as the annual average of monthly mean wind stress for the NES LME from 1967 to 2010 (EcoAP 2012). Stratification influences the vertical distribution of nutrients and oxygen, and was measured as the vertical stacking of layers of water having different densities due to changes in temperature and salinity for the upper 50 m of the water column from 1977 to 2010 ($\text{kg m}^{-3} \text{ m}^{-1}$; EcoAP 2012). Gulf Stream north wall (GSNW) is the index of Gulf Stream position based on principal component analysis (PCA) of the latitude of the north wall at 6 longitudes (79°, 75°, 72°, 70°, 67° and 65° W) and influences vertical circulation and heat transport from tropics to higher latitudes (1966–2010; data available at www.pml-gulfstream.org.uk/data.htm; Taylor 1995).

Human-use pressure

Fishing pressure is influenced by both fishing effort and resource potential, such as the proportion of the community production available to harvest (Jennings 2005, Bundy et al. 2010). From an ecosystem perspective, fishing pressure is challenging to estimate, and the scientific community has yet to reach a consensus on the best practices to calculate ecosystem fishing pressure. One suggested measure of ecosystem fishing pressure is total reported landings over surveyed biomass (Shin et al. 2010); however, in our study, ecological indicators were also formulated with survey data, and including surveyed biomass in our estimate of fishing pressure could have been confounding. Therefore, we quantified fishing pressure as the total live weight of commercial species landings in the NES LME, calculated by aggregating data reported to the National Marine Fisheries Service (NMFS) by dealers at weigh-out, logbooks, and vessel trip reports (NEFSC 1998, Link et al. 2002). By aggregating these data across the full range of targeted species in the NES LME, we contend that total landings is a measure of fishing pressure that is reasonably robust against variation in resource potential. These data cover the entire NES LME, span the years 1964 to 2010, and cover the full range of targeted species in the NES LME.

Common environmental trends

Many environmental pressures influence the structure of the NES LME. While a mechanistic understanding of how each pressure influences ecosystem structure is warranted and has been discussed elsewhere (Link et al. 2002, Methratta & Link 2006, Shackell et al. 2012), our goal here was to identify how ecological indicators respond to the combined influence of fishing and environmental pressure. We used dynamic factor analysis (DynFA) to concentrate the variance from a broad range of important environmental pressure variables into a smaller number of interpretable patterns. Similar in concept to PCA, DynFA restricts axes by the temporal structure of the data and is commonly used to characterize ecological and environmental time series (Zuur et al. 2003, Friedland & Hare 2007). Unlike PCA, however, DynFA trends are not ranked in order of importance. DynFA models time series as linear combinations of common trends, a level parameter, and noise, with models formulated as:

$$Y_{i,t} = Z_{i,1}\alpha_{1,t} + Z_{i,2}\alpha_{2,t} + \dots + Z_{i,m}\alpha_{m,t} + \mu + e_{i,t} \quad (1)$$

Fig. 1. Hypothetical relationship between an indicator, (a) fishing (dashed line), and (b) environmental (solid line) pressures can be viewed as 2 bivariate responses, or as a single surface described as a (c) 3-dimensional perspective plot or (d) a topographic plot, which both contain the relationships described as the dashed and solid lines in (a) and (b). Two-covariate thresholds are present when the first derivative (i.e. slope) of the relationships between indicator response and both (e) fishing and (g) environmental pressures are 0. The 95 % confidence interval of the first derivative of (f) fishing and (h) environmental pressures (dark gray shading around line) are used to identify regions where the slope is not significantly different from 0 (light gray vertical boxes). When the (i) relationship between the indicator and both fishing and environmental pressures crosses 0, a dark polygon denotes a 2-covariate threshold. The second partial derivative test of this region can further describe it as local minima, maxima, or as a saddle point

where y_t is the value of the i^{th} environmental time series at time t , $z_{i,m}$ is the factor loading for the i^{th} time series and the m^{th} common trend, $\alpha_{m,t}$ is the m^{th} common trend at time t , μ is a constant level parameter, and $e_{i,t}$ is noise. Here, we specified the noise component $e_{i,t}$ as normally distributed with mean 0 and covariance matrix $\mathbf{R}$ (Zuur et al. 2003).

We standardized each environmental time series by subtracting the mean and scaling by the standard deviation. Next, we evaluated DynFA models of the environment with the number of common trends varying from 1 to 6. We considered 2 structures for the error covariance matrix $\mathbf{R}$: (1) diagonal and equal and (2) diagonal and unequal, both of which imply no covariance between trends. Diagonal and equal covariance matrices consider the same process variance across all time series, whereas diagonal and unequal covariance matrices consider unique variance values for each time series. DynFA was implemented with the multivariate autoregressive state-space (MARSS) package for R (modeling version 3.4; Holmes et al. 2013). Model selection for DynFA models with differing error covariance structures and the number of common trends was based on the lowest value of Akaike's information criterion corrected for small sample sizes (AICc; Hurvich & Tsai 1989). The estimated common trends from the models selected by AICc were then used as representative of the composite environment pressure in subsequent analysis.

Generalized additive model (GAM) analysis

GAMs were used to create surfaces of ecological indicator responses to fishing and environmental pressures. We used finite differences to calculate partial derivatives of the surface to identify critical points and thresholds in indicator response to multiple pressures (Fig. 1). We fitted separate GAMs for each combination of ecological indicator and DynFA trend, along with fishing pressure (see 'Results: Critical points in 2-covariate GAMs', $n = 24$ models). Including DynFA trends in the GAM allowed us to account for multiple environmental variables in a single model. We fitted GAMs with the formula:

$$I_j = \mu_j + s_j^F(F_j) + s_j^E(a_{j,m}) + \varepsilon_j \quad (2)$$

where I is the j^{th} observation for the indicator, F is fishing pressure, a is the m^{th} DynFA environmental trend, $s^F()$ and $s^E()$ are smoothing functions, and ε is residual error. We reduced the likelihood of overfitting models by estimating the smoothing parameters with a generalized cross validation (GCV; Wood

2004) criterion as implemented in the R package 'mgcv' (Wood 2004). We included an additional ridge penalty enabling the smoothing term to be minimized to 0 through an eigenvalue optimization process (Wood 2003), which effectively allowed the model to eliminate smoothing terms into linear components. We also used typical model diagnostic procedures to check for evidence of autocorrelation and other violations of regression assumptions. After fitting each indicator to Eq. (2), we selected the most suitable model for each combination of predictors using the smallest AICc value.

GAMs are very flexible, and to ensure that thresholds are identified on suitable models, we further eliminated models based on the following criteria for both fishing and environmental pressure variables: (1) if the p-value of smoothing terms was greater than 0.05, (2) if the estimated degrees of freedom (EDF) were close to their lower limit (i.e. models with $\text{EDF} \leq 1$ are effectively linear), and (3) if the GCV score for the model decreased once the smoothing term was removed from the model (Wood & Augustin 2002). These criteria ensured that smoothed models were not selected when outperformed by linear terms and significant smoothers were present for both fishing and environmental pressure variables.

We measured uncertainty surrounding each GAM by using a maximum entropy bootstrap (MEboot) regimen as implemented in the R package 'meboot' version 1.1 (Vinod & López-de-Lacalle 2009). MEboot differs from naïve bootstrap because it does not randomly sample with replacement all available data; rather, MEboot preserves the structure and properties of non-stationary and heteroscedastic data. Since our raw data were collected as time series, maintaining the innate data structure ensured models were fit to representative samples. Bootstrap replicates ($br = i \dots 1000$) for ecological indicators and pressure variables were selected from the raw data, and each bootstrapped dataset was fit using a GAM as above. These GAM results were then evaluated for threshold criteria.

Analysis of derivatives

The shape of the relationship between an indicator and 2 pressure variables was captured as a surface composed of a function f . Here, we specified this surface f as a GAM smoother, i.e. $s^F()$ and $s^E()$ for additive models. For a point (a,b) on this surface, the slope was defined by 2 partial derivatives for each direction; the change in x in the x direction and the change in x in the y direction and vice versa (i.e. $f_x(x)$

and $f_x(y)$; $f_y(y)$ and $f_y(x)$). If these partial derivatives passed beyond 0, they indicated regions in each direction x and y where an indicator had a negative ($f_x(x) < 0$; $f_x(y) < 0$) or positive ($f_x(x) > 0$; $f_x(y) > 0$) slope in response to the pressure variables. Further, higher-order partial derivatives were also calculated, where $f_{xx}(x)$ was the rate of change in x in the x direction and $f_{xy}(x)$ was the rate of change in y in the x direction. Critical points for the function f were found when partial derivatives in the x and y direction both crossed 0 (i.e. $f_x(a,b) = f_y(a,b) = 0$). The second partial derivative test was used to classify a critical point as local maximum, minimum, or as a saddle point (see ‘Partial Derivatives’ in Strang 1991). For the determinant $M(x,y) = \det(H(x,y)) = f_{xx}(x,y) f_{yy}(x,y) - (f_{xy}(x))^2$ if $f_x(a,b) = f_y(a,b) = 0$, it was a critical point of f and the second partial derivative test specifies that:

- (1) if $M(a,b) > 0$ and $f_{xx}(a,b) > 0$, then (a,b) was a local minimum of f
- (2) if $M(a,b) > 0$ and $f_{xx}(a,b) < 0$, then (a,b) was a local maximum of f
- (3) if $M(a,b) < 0$, then (a,b) was a saddle point of f
- (4) if $M(a,b) = 0$, then the second derivative test was inconclusive, and the point (a,b) could be a minimum, maximum, or saddle point.

We used the principles above to identify critical points on the surface of the GAM smoother. We used the fitted GAM to predict a surface according to the original data and estimated the first- and second-order partial derivatives of this surface using finite differences (for a pressure-response example of these methods, see Large et al. 2013). To measure uncertainty surrounding these derivatives, we used the fitted GAM to predict surfaces for all bootstrap replicates and estimated all first- and second-order partial derivatives for each bootstrap replicated surface. Derivatives were sorted into ascending order, and the values of the 2.5 % and 97.5 % quantiles were considered the 95 % CI for the first- and second-order partial derivatives of the GAM smoother. We identified critical points of the GAM smoother when we had 95 % certainty that all partial derivatives contain 0. When we identified a critical point, we used the second derivative test to qualify critical points as local extrema. Local maxima and minima represent a concurrent positive or negative influence by both pressure variables on an ecological indicator, whereas saddle points represent indicators that simultaneously changed in

opposing directions in response to each pressure variable. These local extrema define thresholds in nonlinear responses between ecological indicators and pressures. In an EBFM context, these critical points represent potential ecological thresholds, and can clarify potential relationships between multiple variables. All analyses were conducted using R version 3.01 (R Development Core Team 2010).

RESULTS

Common environmental trends

The most suitable model of the dynamic factor models that we tested included 3 trends and a diagonal and unequal error covariance matrix (Table 2). The DynFA model provided only marginal improvement as a data reduction technique, as each trend represents variables that are positively and negatively correlated with it. However, the model did account for colinearity among environmental variables, which further justified the use of DynFA in subsequent analyses. The most parsimonious DynFA model fit the variability of environmental pressure time series reasonably well, as represented by the error covariance matrix, **R** (Table 3, Fig. 2). Here, low values of **R** indicate good model fit. The DynFA model fit AMO and SST reasonably well, and less than 20 and 35 % of variance was left unexplained for each variable. GSNW, both NAO indices, stratification, and wind stress, however, were not well fit by the model, and >50 % of the variance of these variables was not explained by the model. DynFA trends are unitless; however, they were scaled and centered rel-

Table 2. Dynamic factor analysis (DynFA) model selection process. The trend at the top of the list was selected for further analyses. AICc: Akaike's information criterion corrected for small sample size

R matrix	Trends	Log likelihood	Δ AICc	AICc weight	Cumulative AICc weight
Diagonal and unequal	3	−380.28	0.00	0.77	0.77
Diagonal and equal	3	−388.82	3.17	0.16	0.93
Diagonal and unequal	2	−388.52	4.84	0.07	1.00
Diagonal and equal	2	−398.84	12.02	0.00	1.00
Diagonal and equal	4	−388.82	12.39	0.00	1.00
Diagonal and unequal	4	−382.66	14.37	0.00	1.00
Diagonal and equal	5	−388.82	19.47	0.00	1.00
Diagonal and unequal	5	−383.36	23.16	0.00	1.00
Diagonal and equal	6	−388.82	24.27	0.00	1.00
Diagonal and unequal	6	−383.36	28.18	0.00	1.00
Diagonal and unequal	1	−412.62	39.59	0.00	1.00
Diagonal and equal	1	−421.70	44.82	0.00	1.00

Table 3. Values of R indicate the portion of variance in the environmental pressure time series that is unexplained by the dynamic factor analysis (DynFA). Low values indicate a good model fit. AMO: Atlantic multidecadal oscillation, NAO: North Atlantic oscillation

Environmental pressure	R
AMO	0.16
Gulf Stream north wall	0.49
NAO (annual)	0.64
NAO (winter)	0.56
Sea surface temperature	0.33
Stratification	0.70
Wind stress	0.54

ative to the standard deviation and mean from environmental time series. Therefore, a DynFA trend's mean was equal to 0 and provided a reference point for interpretation. Interpreting DynFA trends is similar in concept to that of PCA, where DynFA trends are comparable to PCA axes on a biplot that act to concentrate the variance of environmental pressures. DynFA factor loadings are comparable to component vectors (i.e. arrows), where the relative value of factor loadings describes the association between environmental pressure time series and a particular trend, and a cut-off value of 0.2 delimits a strong association between environmental pressures and a DynFA

Fig. 2. Time series of dynamic factor analysis (DynFA) modeled fits (lines) for annual mean values of environmental pressure variables (points) (a) Atlantic multidecadal oscillation (AMO), (b) Gulf Stream north wall, (c) annual North Atlantic oscillation (NAO), (d) winter NAO, (e) sea surface temperature, (f) stratification, and (g) wind stress

trend (Zuur et al. 2003). The first common trend rapidly declined during the late 1960s and gradually increased before leveling off at a high value in the early 2000s (Fig. 3a). AMO and wind stress had strong positive loadings on DynFA Trend 1, and both annual and winter NAO indices had strong negative factor loadings on this trend (Fig. 3b). After an initial decrease in the late 1960s, the second common trend increased between the early 1970s and 1990s and sub-

sequently decreased in the remaining decades (Fig. 3c). GSNW and both annual and winter NAO indices had strong positive factor loadings on DynFA Trend 2, and wind stress had strong negative factor loadings on this trend (Fig. 3d). The third common trend rapidly increased in the first decade of the time series, fluctuated about 0, and continued to increase from the late 1990s until 2010 (Fig. 3e). SST had a strong positive factor loading on DynFA Trend 3 (Fig. 3f).

Fig. 3. (a,c,e) Trends and (b,d,f) factor loadings from the best dynamic factor analysis (DynFA) model. Loadings >0.2 and <-0.2 are considered important in the DynFA model, and these cut-off values are shown as dashed lines

Critical points in 2-covariate GAMs

Of the 24 possible 2-covariate GAMs among ecological indicators, common DynFA trends, and fishing pressure, 22 included at least 1 significant ($p < 0.05$) term. Of these 22 significant models, 11 were reduced to linear models because the EDF ≤ 1.0 or the GCV decreased when the smoothing term was removed. Three models contained only a single significant smoothing term, and the remaining 8 models included smoothing functions for both explanatory variables as smoothing functions (Table 4). Deviance explained by models that included smoothing functions for both covariates was greater than 50%; however, models that did not include smoothing functions explained less than 50% of the deviance. The impetus of this study was to identify 2-covariate thresholds, so we focused on models that included significant nonlinear components for both explanatory variables. Finally, the entire range of pressure values was used to create the surface predicted from GAM smoothing functions. Since we were using this

surface to model past realized combinations of pressure–environment–state space, we limited our interpretation of trends and thresholds to a minimum convex hull with a 10% buffer surrounding the raw data to prevent interpreting results beyond the spread of the raw data.

DynFA Trend 1 (DynFA 1 hereafter) was positively correlated with AMO and wind stress, and negatively correlated with both NAO indices. DynFA 1 and fishing pressure were significant pressure variables for 3 of the 8 ecological indicators: ctenophore abundance, length, and species richness (Table 4). Ctenophore abundance had a dome-shaped response to both DynFA 1 and fishing pressure. Saddle points were present when fishing pressure was approximately 400 000 t and DynFA 1 was slightly higher than average (~ 0.75 ; Fig. 4a). The intersection of these saddle points was also identified as a local maximum where ctenophore abundance was greatest. Length increased in response to both pressure variables, and saddle points (i.e. regions that increase in one direction and decrease in the other direction) were present

Table 4. Generalized additive model (GAM) results for each ecological indicator response to each dynamic factor analysis (DynFA) trend and fishing pressure. **Bold** p-values indicate significant ($p < 0.05$) 2-covariate nonlinear models that were used in sub-sequent critical point analyses. s: smoothing function; NA: parameter not used in the best model

Ecological indicator	Environmental pressure	Model	p-value		Deviance explained
			Landings	Environment	
Longhorn sculpin biomass	DynFA Trend 1	$y \approx \text{Landings}$	0.001	NA	0.45
	DynFA Trend 2	$y \approx \text{Landings}$	0.001	NA	0.45
	DynFA Trend 3	$y \approx \text{Landings} + \text{Environment}$	0.001	0.013	0.52
Biomass	DynFA Trend 1	$y \approx \text{Environment}$	NA	0.001	0.47
	DynFA Trend 2	$y \approx \text{Landings} + \text{Environment}$	0.090	0.102	0.34
	DynFA Trend 3	$y \approx s(\text{Landings}) + s(\text{Environment})$	0.003	0.001	0.68
Ctenophore abundance	DynFA Trend 1	$y \approx s(\text{Landings}) + s(\text{Environment})$	0.006	0.002	0.57
	DynFA Trend 2	$y \approx s(\text{Landings}) + \text{Environment}$	0.001	0.001	0.65
	DynFA Trend 3	$y \approx \text{Landings} + \text{Environment}$	0.074	0.001	0.44
Length	DynFA Trend 1	$y \approx s(\text{Landings}) + s(\text{Environment})$	0.001	0.001	0.52
	DynFA Trend 2	$y \approx s(\text{Landings}) + s(\text{Environment})$	0.001	0.002	0.53
	DynFA Trend 3	$y \approx s(\text{Landings}) + s(\text{Environment})$	0.019	0.001	0.60
Pelagic to demersal ratio	DynFA Trend 1	$y \approx \text{Landings} + s(\text{Environment})$	0.001	0.001	0.88
	DynFA Trend 2	$y \approx s(\text{Landings}) + s(\text{Environment})$	0.001	0.001	0.92
	DynFA Trend 3	$y \approx s(\text{Landings}) + s(\text{Environment})$	0.001	0.001	0.67
Planktivores and benthivores	DynFA Trend 1	$y \approx \text{Environment}$	NA	0.001	0.42
	DynFA Trend 2	$y \approx \text{Environment}$	NA	0.001	0.41
	DynFA Trend 3	$y \approx \text{Landings} + \text{Environment}$	0.001	0.129	0.26
Species richness	DynFA Trend 1	$y \approx s(\text{Landings}) + s(\text{Environment})$	0.001	0.001	0.78
	DynFA Trend 2	$y \approx s(\text{Landings})$	0.001	NA	0.39
	DynFA Trend 3	$y \approx \text{Landings} + \text{Environment}$	0.003	0.001	0.70
Trophic level	DynFA Trend 1	$y \approx s(\text{Environment})$	0.066	NA	0.07
	DynFA Trend 2	$y \approx \text{Environment}$	NA	0.027	0.10
	DynFA Trend 3	$y \approx \text{Landings} + \text{Environment}$	0.020	0.140	0.12

when DynFA 1 values were slightly below average (approx. -1.0 ; Fig. 4b). Species richness decreased in response to fishing pressure and when DynFA 1 was near 0; however, this relationship did not have any significant critical points (Fig. 4c).

DynFA Trend 2 (hereafter DynFA 2) represented positive loadings for both NAO indices and GSNW, and negative loadings for AMO and wind stress. DynFA 2 and fishing pressure were significant pressure variables for 2 of the 8 ecological indicators: length and pelagic to demersal ratio (Table 4). Length increased with fishing pressure and was greatest when DynFA 2 was slightly below the mean. Saddle points were present when DynFA 2 was approximately 0, and length was much lower when DynFA 2 was above or below 0 (Fig. 5a). Pelagic to demersal ratio increased in response to DynFA 2 and decreased in response to fishing pressure. Saddle points were present when fishing pressure was approximately 400 000 t (Fig. 5b) and DynFA 2 was negative. Below 400 000 t, the relationship between pelagic to demersal ratio and fishing pressure was positive, and the relationship turned negative above 400 000 t.

DynFA Trend 3 (hereafter DynFA 3) had strong positive loadings for SST. DynFA 3 and fishing pressure were significant pressure variables for 3 of the 8 ecological indicators: biomass, length, and pelagic to demersal ratio. Biomass was variable in response to DynFA 3 and decreased in response to fishing pressure. A local minimum was present when fishing pressure was 800 000 t and DynFA 3 was slightly below the mean (Fig. 6a). Length decreased in response to DynFA 3 and marginally increased in response to fishing pressure; however, this relationship did not have any significant critical points (Fig. 6b). Pelagic to demersal ratio decreased in response to fishing pressure and was greatest corresponding to saddle points when DynFA 3 was slightly below the mean (approx. -1 ; Fig. 6c).

Fig. 4. Topographic surfaces represent the pressure–environment–state fit of 2 covariate generalized additive models. A minimum convex hull with a 10% buffer surrounding the raw data (dashed polygon) and rug plots along the top and right margins provide an estimate of data distribution across each model fit. Shaded polygons are significant critical points that fall within 95% CI of 0 for partial derivatives in both directions, indicating no significant difference from 0. The second partial derivative test (described in the ‘Materials and methods: Analysis of derivatives’) was used to define each polygon as local maximum (dark gray), saddle points (gray), or local minimum (light gray). (a) Ctenophora abundance, (b) mean length, and (c) species richness response to fishing pressure and dynamic factor analysis (DynFA) 1

Fig. 5. (a) Mean length and (b) pelagic to demersal ratio response to fishing pressure and dynamic factor analysis (DynFA) 2. Details as in Fig. 4

DISCUSSION

In this study, we applied the concept of pressure-response thresholds (Large et al. 2013) to 2-covariate relationships by translating ecological indicator response into a surface dependent on both fishing and environmental pressures. Our approach used concepts borrowed from calculus and bolstered with a time-series appropriate bootstrap regimen (Vinod & López-de-Lacalle 2009) to identify critical points in ecosystem response to multiple pressures. Critical points were identified when the rate of change of an indicator with respect to both pressure variables crossed 0, which represented levels of pressure where ecosystems had an abrupt nonlinear change in direc-

Fig. 6. (a) Biomass, (b) mean length, and (c) pelagic to demersal ratio response to fishing pressure and dynamic factor analysis (DynFA) 3. Details as in Fig. 4

tion, and as such may represent ecological thresholds. These ecological thresholds can be used to examine past realized combinations in the pressure–environment–state space to further understand how anthropogenic pressure may influence ecosystem structure and function while concurrently accounting for environmental variation.

Strengths and weaknesses of the method

Generalized additive modeling is a robust statistical framework commonly used to identify nonlinear relationships (Hastie & Tibshirani 1990). One criticism of GAMs is the propensity to over-fit the model to the data. Parameterizing models to be selective against overly curvaceous models, yet sensitive to appropriate nonlinear models can prove challenging. As such, reconciling trade-offs between model selectivity and sensitivity is important in defining decision criteria. We specified our models to prevent over-fitting and to be conservative against nonlinear relationships by using penalized regression splines and *a priori* model selection criteria (Wood & Augustin 2002, Wood 2003), and we identified significant 2-covariate nonlinear relationships in one-third of our models. With more lenient selection criteria, we may have identified more significant nonlinear 2-covariate pressure-response relationships; however, these relationships may not have been suitably robust. Since a suite of ecological indicators is necessary to capture ecosystem response to pressures (Rice & Rochet 2005), we propose that strong signals from a few indicators may be more advantageous than weak signals from many indicators.

Ecosystems are inherently complex, and multivariate techniques are often used to characterize environmental processes into general patterns that describe ecosystem processes and facilitate comprehension and comparison (Shackell et al. 2012). We used DynFA to simplify the main environmental pressure variables for the NES LME into a selection of common trends that represent ecosystem responses and concentrate the variance such that each DynFA trend might conceptually represent a different dimension of this variance. By using DynFA common trends as explanatory variables, we also reduced the number of models necessary to characterize the relationships of interest and were not constrained by collinearity between environmental variables. For example, if we had fit GAMs for each combination of ecological indicator and fishing and environmental pressure, we would have had 64 unique 2-covariate

models. The DynFA approach concentrated environmental variance into 3 common trends, and the number of models was reduced to 24, decreasing the likelihood of false correlations. The ability to identify critical points between ecological indicators, fishing, and specific environmental pressures was diminished (although the latter could be inferred from factor weightings); however, DynFA provided a suitable balance between explanatory power and dimension reduction.

Critical points and ecological thresholds

Converting ecological indicators into suitable decision criteria is necessary to operationalize EBFM (Link 2005, Samhouri et al. 2010). In this study, we examined thresholds that represent the level of an indicator at which a small increase in a pressure variable results in an abrupt change in the direction of indicator response, which can be used to maximize ecosystem return on investment for a management decision (Groffman et al. 2006). Thresholds are advantageous from a management perspective because a small change in a pressure can result in a substantial improvement in system, or ecosystem, status (Samhouri et al. 2010). These approaches are nascent but growing in a wide range of ecological applications (Andersen et al. 2009, Clements et al. 2010, Fay et al. 2013, Large et al. 2013). In single-species fisheries management parlance, the concept of thresholds are captured in reference points such as B_{msy} or F_{msy} , where crossing beyond a certain population attribute may result in decreased stock status or fisheries' yield (Hilborn & Walters 1992). We identified critical points, or 2-covariate thresholds, in ecological indicators that represent system production (total biomass), size distribution (mean length), community structure (pelagic to demersal ratio), and ecosystem functioning (ctenophore abundance). Abrupt changes in the direction of these fundamental ecosystem features in response to multiple pressures highlight the importance of integrating multiple dimensions of information to better understand ecosystem level responses to complex relationships between multiple pressures. Yet not all critical points are the same. Saddle points were the most common type of critical point identified in our study and represent situations where the environment could have a positive influence on indicator status while fishing pressure has a negative influence. For example, the response of mean length to fishing and DynFA 2 contained saddle points when the value of DynFA 2, primarily

representative of positive NAO indices and negative wind stress, was slightly less than 0. Mean length increased with fishing pressure, but was greatest when the value of DynFA 2 was slightly below the mean. Counterintuitively, the ecological indicator was positively linked to fishing pressure, and the magnitude of the indicator value was negatively linked to the environmental pressure. This implies that environmental factors can mitigate or offset known effects from fishing pressures, and vice versa (Link et al. 2012). Ecosystems respond to opposing signals from a variety of pressures, and ecological indicators may be negatively influenced by fishing or the environment, while simultaneously being positively influenced by another pressure.

Critical points representing local extrema were also identified in our study. For example, ctenophore abundance was greatest when fishing pressure was approximately 400 000 t and DynFA 1, representative of positive AMO and wind stress and negative NAO indices, was approximately 1.0. Ctenophore abundance rapidly decreased when both pressure values were above or below these critical points. Similarly, total survey biomass was lowest when fishing pressure was 800 000 t and DynFA 3, representative of positive SST loadings, was approximately 0. Total survey biomass was much higher away from high pressure values. Therefore, ecosystem status might be influenced by additive or multiplicative signals from multiple pressures, and ecological indicator response may be much more (or less) than otherwise expected.

We used an additive approach to parameterize our models, and our findings describe the combined ecological indicator response to fishing and environmental pressures. Preliminary analyses investigated interactions between fishing and environmental pressures; however, these relationships did not fundamentally change the pressure–environment–state surface or associated critical points. Further, including interactions added an additional layer of complexity to an already highly dimensional analysis. Recent studies and reviews highlight the prevalence of non-additive (i.e. synergistic or antagonistic) interactions between multiple stressors in marine ecosystems (e.g. Crain et al. 2008). Modeling exercises for the NES LME, however, have found additive effects more prevalent (Nye et al. 2013). Identifying non-additive interactions between multiple pressures could be an important consideration for EBFM because cumulative effects could be much greater than expected and may require stricter management (Nye et al. 2013). We suggest that future studies exploring the prevalence and potential outcomes of

non-additive interactions on ecological thresholds should include ensemble methods such as the gradient forest method (Large et al. unpubl.).

Decision criteria

Fisheries production and ecosystem status have been linked to multiple drivers including fishing, trophodynamics, and the environment (Gaichas et al. 2012, Link et al. 2012). In a management context, establishing limits for multiple pressures quickly becomes complex. Exploring the past realized pressure–environment–state surfaces can be helpful in identifying patterns where multiple pressures may have contributed to altered ecosystem states, and can also be used to inform future management choices. The NES LME has experienced substantial variation in fleet size, targeted species, and allowable catch limits since the middle of the 20th century. During the early 1960s, distant water fleets rapidly overexploited multiple species including haddock, silver hake, herring, and mackerel, but important groundfish such as cod were not overexploited (Fogarty & Murawski 1998). Fishing pressure was greatest during this time and our analyses identified the NES LME as a pelagic depleted system (i.e. low pelagic to demersal ratio) dominated by larger fish (i.e. longer mean length), which has been noted elsewhere (EcoAP 2009). Our critical point analysis identified a significant threshold at ~400 000 t landings, suggesting that above this level of exploitation there was a change in the direction of ecosystem structure (i.e. pelagic to demersal ratio) and functioning (i.e. ctenophore abundance) in the NES LME. Furthermore, environmental pressures also influenced the NES LME ecosystem status. DynFA 3 had strong positive factor loadings from SST, and when temperatures were cooler than average, the NES LME was a pelagic-dominated system (i.e. high pelagic to demersal ratio), which has been shown in other studies (e.g. Rose 2005). When temperatures departed from this level, the NES LME rapidly changed in biomass and community composition. Therefore, we can use the past realized pressure–environment–state surfaces for the NES LME to help describe patterns in ecosystem response and identify thresholds that signify an abrupt change in ecosystem structure.

We evaluated ecological indicator response to multiple pressure variables and found that each ecological indicator response differed according to both fishing and the environmental pressure. Combining univariate ecological thresholds into synthetic, multi-

variate decision criteria might better represent ecological status. Future studies should evaluate ecological thresholds as a suite of ecological indicators using ensemble or multivariate approaches, which will develop an understanding of ecosystem thresholds (cf. Link et al. 2002). Additionally, simulation modeling and model validation using a management strategy evaluation framework might be used to evaluate potential ecosystem responses to decision criteria derived from ecological thresholds (Fay et al. 2013, 2014). Understanding how to combine multiple thresholds (e.g. ecological, socio-economic) to create ecosystem thresholds will facilitate decision criteria to support management action.

How would one use these thresholds to act in a management setting? For example, the pelagic to demersal ratio is a common ecological indicator used to describe energy transfer and food-web structure (de Leiva Moreno et al. 2000, Methratta & Link 2006, Nye et al. 2013). If our management objective was to maintain an ecosystem with the pelagic to demersal ratio between 1.2 and 1.4, a region of the response surface known to correspond to desirable ecosystem conditions (Fogarty & Murawski 1998), we could maintain fishing pressure at or below the 400 000 t threshold and still maintain our desired ecological indicator value. However, the value of the ecological indicator is also highly dependent upon environmental state. In response to DynFA Trend 2 (characterized largely by positive NAO and negative wind stress) and fishing pressure, the pelagic to demersal ratio between 1.2 and 1.4 only occurred when DynFA Trend 2 was greater than ~ 1.0 . When DynFA Trend 2 was less than 1.0, the pelagic to demersal ratio was never within the observed range, thereby obviating our ability to achieve our management objective. We conclude that multiple pressures can be important and that the magnitude of indicator response and ecological thresholds are highly conditioned upon multiple pressure variables. Including both anthropogenic and environmental pressures is essential when setting these ecosystem-level decision criteria.

Conclusions

Natural environmental variability (Beaugrand et al. 2008) and human exploitation (Myers et al. 1997, Pauly et al. 1998, Link et al. 2012) both influence marine ecosystem structure and function. As scientists, managers, and policy makers move towards the implementation of ecosystem-based approaches to management, reference points for management

action need to be developed. Our results indicate that ecosystem attributes may have either linear or abrupt and non-linear responses to both fishing and environmental pressures for the NES LME. Both linear and non-linear responses are important and useful to inform management decision. Linear relationships indicate that related ecosystem decisions fall strictly in the realm of policy, and science cannot clearly distinguish between states, whereas non-linear relationships may contain distinct critical points where ecosystem status can be maximized (Samhouri et al. 2012). We suggest that the values of these critical points can be used to identify magnitudes of pressures that might result in abrupt ecosystem change. Further, these critical points can be included in simulation modeling exercises to more fully understand ecosystem dynamics and potential tradeoffs as we develop decision criteria to support ecosystem-based approaches to management.

The approach we present here has broad applications beyond fisheries management. Threshold analyses have been used to explore changes in ecological response time series to prioritize conservation efforts (Fewster et al. 2000) and to assess recovery in degraded ecosystems (Clements et al. 2010). Similarly, threshold analyses have also looked at changes in an attribute's response to a single pressure, such as coral reef health to fishing pressure (Bellwood et al. 2004) or ecosystem responses to lake eutrophication (Carpenter et al. 1999). However, each of these examples likely has multiple pressures acting on the system simultaneously, and exploring the surface of response over time or multiple pressure space could improve the ability to formulate meaningful decision criteria. The method we present here holds promise for informing decision criteria to multiple pressures because (1) it describes ecosystem patterns via robust ecological indicators, (2) it is flexible to implement since it is only reliant on a suitable GAM surface to identify patterns and critical points, and (3) it is extendible to multiple pressures with the application of DynFA.

The need to implement a more holistic management framework, such as EBM, is apparent because living resources and the ecosystems that they function within are affected by a range of perturbations including effects from anthropogenic sources and those associated with natural environmental variability. To facilitate the implementation of EBM, a practical method to address all potential stressors and cumulative impacts simultaneously on a variety of ecosystem attributes is to use ecological indicator thresholds to inform decision criteria for manage-

ment action. As Andrewartha & Birch (1954) noted so long ago, we often see the most striking ecosystem response when competing forces interact, and we note the potential for complex relationships (e.g. synergistic and antagonistic) between multiple pressure variables. As the application of ecological thresholds continues to develop, these relationships should be explored further. The approach we present here will provide yet another step towards facilitating the implementation of EBM by clarifying how multiple pressures influence ecosystem status, and how these responses can be applied to formulate decision criteria for management action.

Acknowledgements. This work was supported by a NOAA NMFS Fisheries and the Environment (FATE) grant. We thank all those who participated in the NEFSC bottom trawl survey and have maintained this database. We thank B. Wells, J. Samhour, and 2 anonymous reviewers for their thoughtful comments on earlier versions of this work.

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