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Modeling dynamic interactions and coherence between marine zooplankton and fishes linked to environmental variability

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ABSTRACT

The dynamics of marine fishes are closely related to lower trophic levels and the environment. Quantitatively understanding ecosystem dynamics linking environmental variability and prey resources to exploited fishes is crucial for ecosystem-based management of marine living resources. However, standard statistical models typically grounded in the concept of linear system may fail to capture the complexity of ecological processes. We have attempted to model ecosystem dynamics using a flexible, nonparametric class of nonlinear forecasting models. We analyzed annual time series of four environmental indices, 22 marine copepod taxa, and four ecologically and commercially important fish species during 1977 to 2009 on Georges Bank, a highly productive and intensively studied area of the northeast U.S. continental shelf ecosystem. We examined the underlying dynamic features of environmental indices and copepods, quantified the dynamic interactions and coherence with fishes, and explored the potential control mechanisms of ecosystem dynamics from a nonlinear perspective. We found: (1) the dynamics of marine copepods and environmental indices exhibiting clear nonlinearity; (2) little evidence of complex dynamics across taxonomic levels of copepods; (3) strong dynamic interactions and coherence between copepods and fishes; and (4) the bottom-up forcing of fishes and top-down control of copepods coexisting as target trophic levels vary. These findings highlight the nonlinear interactions among ecosystem components and the importance of marine zooplankton to fish populations which point to two forcing mechanisms likely interactively regulating the ecosystem dynamics on Georges Bank under a changing environment.

1. Introduction

Marine zooplankton link primary producers to higher-level consumers and can be particularly sensitive indicators of climate variability. Monitoring abundance, species composition and distribution of marine zooplankton provides a way of detecting ecological shifts in marine ecosystems. Moreover, the dynamics of zooplankton have been linked to the variability of fisheries production (Beaugrand et al., 2003; Frank et al., 2005). Climate variability on inter-annual and inter-decadal scales affects overall ecological processes in the ocean. Climate-driven processes have shifted the marine copepod community in the North Atlantic (Beaugrand et al., 2002; Greene and Pershing, 2007; Richardson and Schoeman, 2004), with subsequent influences on fisheries production (Beaugrand et al., 2003; Mountain and Kane, 2010; Pershing et al., 2005). Modeling the dynamics of zooplankton with parallel series of environmental variables and fish abundance allows us to explore the response of biological populations to climate variability and linkages among adjacent trophic levels, and examine potential mechanisms regulating ecosystem dynamics.

Most standard models typically grounded in the concept of linear system may fail to capture the underlying complexity of ecological processes (Boyd, 2012). Although correlative approaches commonly are used, since biological populations can exhibit nonlinear dynamics, subtle changes in climate phenomena can be amplified in marine food webs (Hsieh et al., 2005; Taylor et al., 2002). Even in the absence of external disturbances, plankton communities can exhibit complex dynamical behavior, including chaos, relating to species interactions in food webs (Beninca et al., 2008). Correlation-based approaches to identifying ecological linkages will fail in such a case. In nonlinear systems, forcing and response variables may show no correlation despite clear deterministic and mechanistic relationships among them (Sugihara et al., 2012). From a nonlinear perspective, lack of linear correlation does not necessarily rule out causation. Therefore, examining ecological responses involving

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nonlinear interacting components requires new analytical tools beyond the correlative foundation.

We model the system dynamics of the environment, zooplankton, and fishes in a framework of nonlinear time series models by applying nonparametric nonlinear forecasting models originally developed for a wide variety of problems in natural and social sciences (Sugihara, 1994; Sugihara and May, 1990). These methods have been applied to a number of marine ecosystems (Anderson et al., 2008; Dixon et al., 1999; Glaser et al., 2011, 2013; Hsieh et al., 2005; Liu et al., 2012). We exploit the concept of co-predictability (Engle and Granger, 1987) within a nonlinear context, to examine potential dynamic interactions between ecosystem components (i.e., environment variables, zooplankton, and fishes). Specifically, we apply these nonlinear models to annual time series of four environmental indices, abundance estimates of 22 copepod taxa, and four ecologically and commercially important fish species on Georges Bank, a highly productive region in the northeast U.S. continental shelf Large Marine Ecosystem.

The objective of this study is to provide new ecological insights into the dynamics of marine ecosystems from a nonlinear perspective of exploring the linkages across trophic levels and potential forcing mechanisms. Prior studies have shown that exploited fish populations are more likely to contain nonlinear dynamics than unexploited populations (Anderson et al., 2008; Glaser et al., 2013), that aggregation of variables across scales may obscure nonlinear signals (Sugihara et al., 1999), and that life history is related to the likelihood of nonlinear dynamics (Hsieh and Ohman, 2006). Therefore, we address three priori hypotheses. Our first hypothesis is that the dynamics of marine copepods are less complex (i.e., lower dimensionality and linear dynamics) than that of marine fishes due to relatively less anthropogenic impacts on zooplankton in contrast to exploited fishes. The second hypothesis is that population dynamics of copepods should be more complex at finer taxonomic levels than at high taxonomic scales because aggregating groups might blur the dynamic features evident in species-based analyses. The third hypothesis is that marine copepods would be more dynamically associated with environmental variation (e.g., AMO, NAO, temperature, salinity) rather than with fishes since copepods have a short life cycle and presumably respond quickly and directly to environmental change. To test these hypotheses, we analyze zooplankton time series compiled for a series of taxonomic levels ranging from species to order to examine their dynamic features (i.e., dimensionality and evidence of nonlinearity) of this system. Finally, we quantify dynamic linkages among adjacent trophic levels by measuring co-predictability between ecosystem components (rather than correlation), and explore the potential underlying mechanisms regulating ecosystem dynamics in a changing environment.

2. Material and methods

2.1. Model data

2.1.1. Zooplankton time series

Zooplankton abundance on Georges Bank (Fig. 1) has been measured since 1977 (see Kane, 2007), first, during the Northeast Fisheries Science Center (NEFSC) Marine Resources Monitoring, Assessment, and Prediction Program (MARMAP) and later through the Ecosystem Monitoring (EcoMon) Program on the northeast U.S. continental shelf. In this analysis we focus on 22 copepod taxa (Table 1) during the period 1977 to 2009. Briefly, zooplankton samples were collected using a 61-cm diameter, 0.333 mm mesh size Bongo net with a flowmeter mounted in the center of the frame and towed obliquely at ~1.5 knots from a maximum depth of 200 m or 5 m above the bottom to the surface. Specimens were preserved in 5% formalin. In the laboratory, samples were reduced to approximately 500 organisms by sub-sampling with a modified box splitter. Zooplankton were sorted, counted and identified to the lowest possible taxa at the Polish Plankton Sorting and Identification Center in Szczecin, Poland. Abundance estimates are expressed as number per 10 m^2. Further details concerning the zooplankton sampling protocol are available in Kane (2007).

This zooplankton monitoring program was designed to sample the ecosystem at least six times per year (Sherman, 1980). However, in some cases survey cruises did not cover the region at the same time each year due to weather and operational constraints. To reduce the bias of irregular sampling to comparisons between seasons and years, we compiled the mean abundance estimates for 22 copepod taxa from

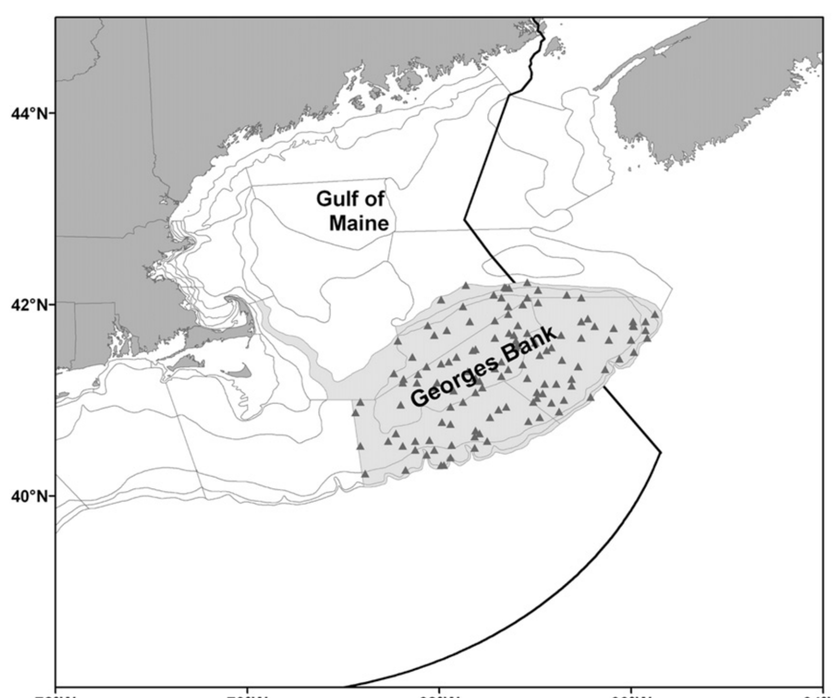

Fig. 1. The Georges Bank ecosystem with dark gray triangles plotted as an example of zooplankton sampling stations in a typical year of 2007 on the EcoMon cruises, light gray shaded area plotted for the NEFSC bottom trawl survey strata and the solid black line indicating the EEZ.