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Distinct zooplankton regime shift patterns across ecoregions of the U.S. Northeast continental shelf Large Marine Ecosystem

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ABSTRACT

We investigated regime shifts in seasonal zooplankton communities of the Northeast continental shelf Large Marine Ecosystem (NES) and its subcomponent ecoregions over a multi-decadal period (1977–2013). Our cross ecoregion analysis shows that regime shifts in different ecoregions often exhibited very distinct characteristics, emphasizing more granular fluctuations in NES plankton communities relative to previous work. Shifts early in the time series generally reflected an increase in abundance levels. The response of zooplankton abundance within fall communities was more similar among ecoregions than for spring communities. The Gulf of Maine exhibited highly distinct patterns from other ecoregions, with regime shifts identified in the early 1980s, early 2000s, and mid-2000s for spring communities. Regime shifts were identified in the early to mid-1990s for the NES, Georges Bank, and the Mid-Atlantic Bight ecoregions, while the fall communities experienced shifts in the early 1990s and late 1980s for the NES and Georges Bank, but in the late 1990s in the Mid-Atlantic Bight. A constrained correspondence analysis of zooplankton community against local and basin-scale climatological indices suggests that water temperature, stratification, and the Atlantic multidecadal oscillation (AMO) were the predominant factors in driving the zooplankton community composition.

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1. Introduction

Zooplankton, by acting as grazers on primary producers and functioning as a link between microbial communities, phytoplankton, and heterotrophs, are critical in food web pathways that produce upper trophic level production. Indeed, on a global scale, the amount of primary productivity that is channeled through mesozooplankton is more highly correlated with fishery yields than primary productivity itself (Friedland et al., 2012b). Because of their sensitivity to environmental change and their integrative role as a link between trophic levels, zooplankton are often used as ecosystem indicators of both trophic structure and physical ocean conditions (Peterson, 2009). Time series of both copepod species richness and biomass anomalies have been used as ecosystem indicators in the Northern California Current (Hooff and Peterson, 2006; Peterson and Schwing, 2003) and zooplankton are effective ecosystem indicators of fisheries productivity in the California Current Large Marine Ecosystem and the Northeast Atlantic Ocean (Beaugrand et al., 2003; Burke et al., 2013; Peterson, 2009). In the Gulf of Maine and Georges Bank regions, the linkage between climate and cod and haddock recruitment is related to zooplankton community structure and species specific abundances (Friedland et al., 2013; Friedland et al., 2015; Mountain and Kane, 2010). Changes in zooplankton productivity may be one of the most important pathways for climate to impact fish resources in the NES, but zooplankton ecosystem indicators have yet to be developed for this region.

As a result of their critical importance in the ecosystem, regime shifts in zooplankton community composition, defined as abrupt changes between contrasting states of a system that persist through time (deYoung et al., 2008), can have a large ecological impact (Greene et al., 2013; Möllmann et al., 2015; Rocha et al., 2015). Such ecological regime shifts have been identified in North Pacific (Hare and Mantua, 2000), the NW Atlantic (Greene et al., 2013), the North Sea (Beaugrand, 2004), the Eastern Scotian Shelf (Choi et al., 2005), the Mediterranean (Conversi et al., 2010), and the Baltic Sea (Mollmann et al., 2009). These regime shifts may be the result of shifts in climate forcing, the influence of altered habitat and fishing pressures on marine ecosystems, or more likely, a combination of both (Conversi et al., 2015; deYoung et al., 2004; Mollmann et al., 2008). Regime shifts may also be the result of non-linear biotic responses to stochastic changes in physical drivers (Hsieh et al., 2005).

Decadal scale shifts in zooplankton abundance and community structure have been previously documented for segments of the Northeast Continental Shelf Large Marine Ecosystem (NES) (Kane, 2007, 2009; Kane and Prezioso, 2008; Pershing et al., 2005; Pershing et al., 2010). These shifts have been associated with size specific responses

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of large bodied zooplankton taxa such as *Calanus finmarchicus*, which declined in abundance from the early 1990s to the early 2000s, while smaller species such as *Oithona* spp. and *Centropages typicus* increased in abundance (Kane, 2007; Pershing et al., 2005; Pershing et al., 2010). The mechanisms driving the observed changes in zooplankton are not yet fully understood (Hare and Kane, 2012; Pershing et al., 2010). While these studies were vital in demonstrating historical changes in zooplankton community composition, most were specific to particular NES regions such as Georges Bank and the Gulf of Maine. The only two large scale zooplankton studies in the NES focused solely on one species (Kane and Prezioso, 2008) or on annual abundance anomalies (Pershing et al., 2010), rather than holistically assessing variability in zooplankton dynamics during specific seasonal windows. However, because of the distinct seasonal differences in zooplankton communities, a seasonal scale characterization of zooplankton anomalies is necessary to investigate potential drivers of the observed changes in community composition (Pershing et al., 2010), and to inform fisheries management (Friedland et al., 2013).

It is clear that zooplankton are important indicators of environmental variability, and an assessment of variability in zooplankton assemblages and drivers of such changes is essential to understanding the ecology of NES LME. As no coast-wide analysis of zooplankton variability has been conducted in the NES at ecologically relevant seasonal scales, here we holistically investigate regime shifts in seasonal zooplankton communities in the NES LME and in its subcomponent ecological production units.

2. Methods

2.1. Zooplankton community data

The Northeast Continental Shelf Large Marine Ecosystem can be divided into four ecological productivity units (EPUs) – the Gulf of Maine (GOM), Georges Bank (GBK), the Mid-Atlantic Bight (MAB), and the Scotian Shelf (Lucey and Fogarty, 2013) (Fig. 1); the Scotian Shelf unit was not included in this analysis due to poor temporal and spatial sample coverage throughout the time series. Zooplankton abundance data were obtained from the EcoMon and MARMAP data sets, which cover the period from 1977 through 2013 (Kane, 2007). Briefly, zooplankton samples were collected throughout the NES primarily during spring and fall cruises using oblique tows of bongo nets with a mesh size of 333 μm. Because of inconsistent sampling effort and the random stratified sampling design used for the EcoMon program, the spatial coverage between years was not uniform over the time series. The samples were post-stratified to one-degree bins and sensitivity analysis was performed using a one-at-a-time approach in order to determine which years and samples to include that would minimize spatial bias while excluding years that had poor coverage. To be included in the analysis, any given year had to have at least 35% spatial coverage for a given EPU, and any spatial bin had to have been sampled in at least 30 out of the possible 37 years. The data set was limited to only those taxa that occurred during at least 20% of the time series, which limited the analysis to 28 taxa (Table 1). For each taxa, a seasonally stratified area-weighted

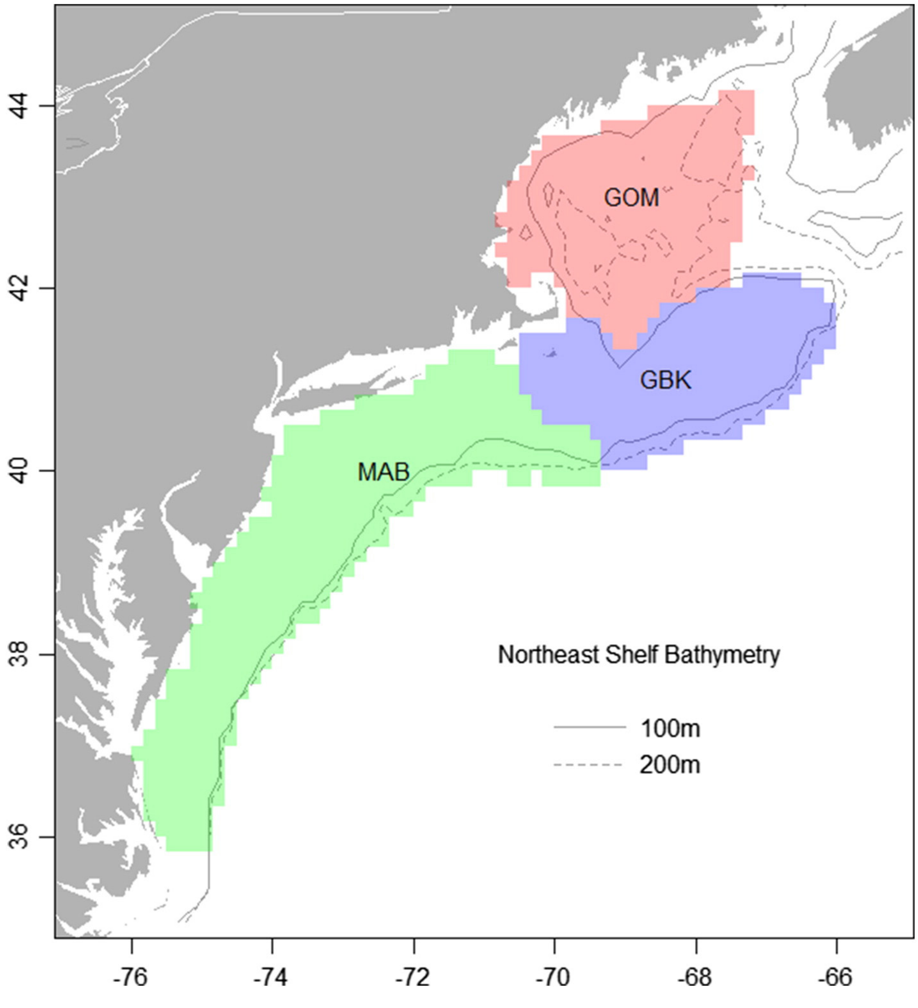

Fig. 1. The ecological productivity units which collectively comprise the Northeast Continental Shelf Large Marine Ecosystem (NES): the Gulf of Maine (GOM, in *red*), Georges Bank (GBK, in *blue*), and the Mid-Atlantic Bight (MAB, in *green*). The Scotian Shelf (east of the GOM, not shown) is not included in this analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)