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Bloom or bust: synchrony in jellyfish abundance, fish consumption, benthic scavenger abundance, and environmental drivers across a continental shelf

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ABSTRACT

Increases in gelatinous zooplankton (GZ) populations, their dominance of some ecosystems, their impacts to other taxa, and their questionable trophic value remain global concerns, but they are difficult to quantify. We compared trends in GZ abundance from direct sampling for the northeast U.S. continental shelf and tested their association with GZ consumption by spiny dogfish (*Squalus acanthias*); the abundance of two benthic scavengers: Atlantic hagfish (*Myxine glutinosa*) and grenadiers (Family: Macrouridae); and four environmental indices: Atlantic Multidecadal Oscillation, North Atlantic Oscillation, and sea surface and bottom temperatures. Defined as scyphozoans, siphonophores, ctenophores, and salps, the abundance of GZ on the shelf has oscillated with blooms approximately every 10 to 15 years. Conservative estimates of annual removal of GZ by spiny dogfish ranged from approximately 0.3 g individual^{-1} to 298 g individual^{-1} with spiny dogfish being the primary GZ feeder sampled on the shelf. The examination of three abundance series for GZ identified one shelf-wide trend and strong relationships with 2-year lagged consumption and scavenger abundance (namely hagfish), and sea surface temperature. With multimodel inference, these covariates led to an optimal model of GZ abundance. Blooms of GZ abundance on this shelf were influenced by environmental change, provide surges of food for spiny dogfish, and may offer "food falls" for scavenging fishes. The bioenergetic tradeoffs of consuming greater amounts of GZ compared to other major prey (e.g. fishes) remain unknown; however, these surges of food in the northwest Atlantic appear to be important for fishes, including support for benthic scavenger productivity.

Keywords: gelatinous zooplankton bloom, trophic ecology, northwest Atlantic, climate change, scavenging, time series analysis.

INTRODUCTION

Resilience of marine ecosystems amid overfishing and climate change is a global concern (e.g. Nye *et al.*, 2013; Litzow *et al.*, 2014; Blenckner *et al.*, 2015). Particularly, regime shifts can lead to communities dominated by species with reduced or minimal economic value and lower functional diversity (e.g. Frank *et al.*, 2005; Möllmann *et al.*, 2009; Howarth *et al.*, 2014). One group of taxa with this reputation is gelatinous zooplankton (GZ) or “jellyfish.” The presence of these taxa has received some attention with regard to anthropogenic pressure, climate change (Richardson *et al.*, 2009; Utne-Palm *et al.*, 2010; Purcell, 2012), and fisheries interactions (Möller, 1984; Purcell and Arai, 2001; Conley and Sutherland, 2015). Monitoring GZ abundance and predicting blooms is especially important as their negative effects are felt throughout ecosystems, including the disruption of human activities reliant on marine environments (Schrope, 2012; Graham *et al.*, 2014; Qiu, 2014). One topic that has received limited attention in direct response to GZ abundance and more specifically bloom periods is fish feeding behavior (Milisenda *et al.*, 2014). To our knowledge no studies have addressed this topic considering long time series (decades) of GZ abundance, fish diets, benthic scavenger abundance, and environmental indices on a shelf-wide scale.

Blooms of marine and freshwater organisms come in many forms such as dinoflagellates, diatoms, cyanobacteria, seaweed, and GZ (considered here) with varying ecological and economic consequences (see Burkholder *et al.*, 1992; Paerl and Huisman, 2008; Smetacek and Zingone, 2013). A recurrence of GZ blooms and increases in their abundance for the world's oceans have been documented (Richardson *et al.*, 2009; Brotz *et al.*, 2012). However, their global dominance of ecosystems is uncertain (Condon *et al.*, 2012), and their pulses are believed to be fundamental to marine ecology (Boero *et al.*, 2008). Although ecosystem responses to GZ invasions (e.g. Black Sea; Kideys, 2002) and GZ-egg/larval fish interactions (e.g. Purcell and Arai, 2001) have received some attention, understanding how marine communities, namely adult fishes, respond to pulses of GZ over long time periods for continental shelves remains unknown. At a much smaller spatial scale (1 m^2 plots), increases in GZ abundance have been shown to modify the behavior of parrotfishes (Family Scaridae) by limiting their grazing frequency in addition to reducing seagrass abundance and habitat complexity under an experimental design (Stoner *et al.*, 2014). Similarly, in the Strait of Messina between Italy and Sicily, the seasonal diet of the Mediterranean bogue (*Boops boops*) on the mauve stinger jellyfish (*Pelagia noctiluca*) was examined and related to the energy reward gained from actively preying on gonadic tissue (Milisenda *et al.*, 2014). Thus, with the uncertainty of global GZ dynamics and their utility in ecosystems (Richardson *et al.*, 2009; Utne-Palm *et al.*, 2010; Condon *et al.*, 2012), the relationship between GZ blooms and the fish community has received minimal if any attention at the large spatio-temporal scale of a continental shelf (hundreds of thousands of square kilometers) and multiple decades of sampling.

The northeast US continental shelf fish community has had a long history of anthropogenic influence, including overfishing (Sherman *et al.*, 1996; Fogarty and Murawski, 1998), and effects of climate change (Nye *et al.*, 2009). The status of GZ for this shelf has been explored in several capacities from fishes as samplers of GZ (Link and Ford, 2006; Ford and Link, 2014) to full ecosystem models incorporating GZ as a major taxa group given their notable presence (Link *et al.*, 2010). However, these works highlight both the challenges of sampling and modeling GZ, and emphasize its inclusion in models for better ecosystem understanding particularly with documented increases in GZ abundance for this shelf. With the uncertainty surrounding future GZ abundance and the negative consequences reported for many shelf-ecosystems (Richardson *et al.*, 2009; Condon *et al.*, 2013; Brodeur *et al.*, *In review*), an analysis of fish community responses to GZ blooms is warranted here.

The episodic events of benthic scavenging by fishes and other fauna in response to "jelly falls" following blooms has been recently documented (e.g. Sweetman and Chapman, 2011; Sweetman *et al.*, 2014). These events provide localized surges of energy and transport carbon to benthic systems (Lebrato *et al.*, 2013a; Lebrato *et al.*, 2013b) with rates of removal akin to other carrion falls (e.g. fishes; Sweetman *et al.*, 2014). Scavenging is an important ecosystem process whereby energy can be recycled in the food web by upper trophic levels – a fundamental response to sudden, dramatic increases in faunal abundance such as with GZ. In marine ecology, the more notable types of carrion falls are from whales and large fishes (Haag, 2005; Higgs *et al.*, 2014). These events provide major food sources for deep-sea fauna, particularly for scavenging fishes. Two fish taxa of the north Atlantic that are well-known benthic scavengers include Atlantic hagfish (*Myxine glutinosa*; Martini, 1998) and grenadiers (Family: Macrouridae; Armstrong *et al.*, 1992). Considering these taxa, Atlantic hagfish are known to scavenge GZ experimentally (Sweetman *et al.*, 2014), and grenadiers have been observed in association with large-carrion falls (Higgs *et al.*, 2014).

Here we identify common trends in GZ abundance for three continental shelf regions of the northeast U.S., and document important relationships among fishes, GZ abundance, and the environment. We hypothesize that increases in GZ abundance are coupled with environmental oscillations, provide increased prey resources for a known GZ predator: spiny dogfish, and affect the abundance of benthic scavengers via "food falls."

METHODS

Gelatinous Zooplankton Abundance

Defined as scyphozoans, siphonophores, ctenophores, and salps, GZ abundance was sampled on dedicated plankton monitoring, bottom trawl, and dredge surveys of the National Marine Fisheries Service (NMFS), Northeast Fisheries Science Center (NEFSC; Azarovitz, 1981; Kane, 2007; NEFSC, 2014). Beginning in 1977, all samples were collected seasonally, approximately 6 times per year with a 61-cm bongo frame fitted with a 333 µm mesh net towed obliquely to 5 m above the bottom to a maximum depth of 200 m for the Mid-Atlantic Bight, Georges Bank, and Gulf of Maine regions of the northeast U.S. continental shelf (> 290,000 km^2; Fig. 1). Distributed uniformly within each region, 30 to 60 sampling stations were selected randomly either approximately 8 to 35 km apart or by depth strata (Fig. 1). A mechanical flowmeter at the center of the bongo frame measured the volume of water towed. At times, stations with more than approximately 2 liters of GZ were encountered. In these cases, the sample was carefully rinsed with salt water over a 4 mm sieve. The volume of GZ in excess of what is needed to fill two, 1-liter sample jars was recorded in the tow log and the excess GZ was discarded. Specimens were preserved in 5 % formalin. GZ were identified and enumerated along with all other zooplankton in the samples to the lowest possible taxa at the Polish Plankton Sorting and Identification Center in Szczecin, Poland with concentrations expressed in 100 m^3. Mean annual amounts of GZ for this study spanned 1977 through 2009.

Fish Consumption

A long-term, shelf-wide fish diet sampling program for the northeast U.S. continental shelf ecosystem directly monitors changes in fish feeding and indirectly identifies changes in ecosystem processes (Link and Almeida, 2000; Smith and Link, 2010). The standardized NMFS NEFSC bottom trawl survey program has been conducted seasonally since 1968 (Azarovitz, 1981; NEFC, 1988; Reid *et al.,* 1999). Beginning in 1973 and through to 2013, fish diet data were collected from a variety of species across the shelf from Nova Scotia to Cape Hatteras, North Carolina (Fig. 1). These seasonal multi-species surveys are designed to monitor trends in abundance and distribution and to provide samples to study the ecology of the large number of fish and invertebrate species inhabiting the region. They primarily have occurred in the spring

(March through May) and fall (September through November) across the entire time series, but winter (February; 1992 through 2007), and summer (July through August; 1977 through 1981, and 1991 through 1995) data are available.

Although the diet sampling program started in 1973, we focused our study on spiny dogfish stomachs from 1977 through 2013 (number = 70,401) for the entire range of the northeast U.S. shelf surveys (i.e., from Nova Scotia to Cape Hatteras, North Carolina), and account for approximately 90 % of all GZ prey occurrences observed in the NEFSC fish diet dataset. See Link and Almeida (2000) and Smith and Link (2010) for full details on the food habits sampling and data. Here we summarize these details with respect to spiny dogfish. From 1977 through 2013, spiny dogfish stomachs and prey were examined at sea immediately after the catch was sorted on deck. This alleviates concerns over the degradation of any GZ due to formalin or ethanol preservation (Purcell, 1988) or rapid digestion (Arai *et al.*, 2003). Total stomach volume (0.1 cm^3 minimum resolution), prey composition (%), numbers, and lengths were collected at sea. Additionally, a conversion from volumetric measurement of prey (cm^3) to mass (g) was used to obtain biomass estimates of food consumed (Link and Almeida, 2000). The size of dogfish sampled ranged from juveniles (~25 to 40 cm) to large, mature females (~110 cm), but were mostly the medium size classes (~65 cm).

GZ were readily identifiable in the stomachs of spiny dogfish at sea upon macroscopic inspection (Fig 2). They were predominantly ctenophores, but also included scyphozoans, siphonophores, and salps. Their firm-gelatin constitution, transparent bodies with visible internal organs, small and clear ball- or bell-like shape, and uniquely colored pinkish-gray masses and obvious ctene structures for ctenophores (relative to any other spiny dogfish prey) permitted coarse taxonomic level identification. Even after partial digestion, GZ in spiny dogfish stomachs were identifiable, particularly the ctene of Ctenophora. It appears that spiny dogfish do not masticate most GZ; rather they are ingested as whole prey items. When compared with direct methods of sampling GZ in the marine environment (e.g., nets), our stomach sampling methods largely eliminated concerns over specimens breaking apart and becoming unidentifiable and/or indistinguishable at these coarse taxonomic levels (Bailey *et al.*, 1994; Hamner *et al.*, 1975; Weisse *et al.*, 2002).

GZ consumption was estimated with the evacuation rate methods of Eggers (1977) and Elliot and Persson (1978). To include the winter and summer data when available, two half-year seasons were created which aggregated winter and spring diet data ("spring"; mean number per year = 1,262 and SE = 128), and summer and fall ("fall"; mean number per year = 641 and SE = 68); sampling for each half-year season spanned the entire shelf. Daily per capita consumption (g) of spiny dogfish per half-year season was modeled as

$$C_{spring/fall} = 24 \cdot E \cdot \bar{S}^{\gamma} \quad [1]$$

where 24 is the number of hours in a day, and $\bar{S}$ is the mean total amount of prey eaten per season. Mean total amount of prey equaled the sum of the mean individual prey amounts weighted by the number of spiny dogfish collected per 1 cm length bin, and weighted by the total number of spiny dogfish caught per station (similar to Link and Almeida 2000; Latour et al. 2008). The derived parameter γ was set to 1 (Gerking, 1994). E is the hourly evacuation rate modeled as

$$E = \alpha e^{\beta T} \quad [2]$$

where α and β were set to 0.002 and 0.115 respectively, and T is the bottom temperature associated with the presence of spiny dogfish collected during the NEFSC bottom trawl survey. The α and β values chosen were conservative estimates based on immature spiny dogfish in the Pacific (Hannan 2009) and demersal fishes of the northeast U.S. shelf (Durbin *et al.*, 1983). The sensitivities of these parameters were explored by NEFSC (2007).

Annual per capita consumption of GZ was generated by scaling $C_{spring/fall}$ from a daily estimate to each half-year season by multiplying by 182.5 (days in a half-year), multiplying by the seasonal proportion of GZ in spiny dogfish diet ($D_{spring/fall}$), and summing the half-year seasons:

$$C_{Annual} = \left(C_{Spring} \cdot D_{Spring} \cdot 182.5\right) + \left(C_{Fall} \cdot D_{Fall} \cdot 182.5\right) \quad [3]$$

The time series of annual per capita consumption of GZ spanned 1977 through 2013.

To quantify the dominance of GZ prey in spiny dogfish over time, the ratio of average GZ prey mass to all other prey by season was estimated for 1977 through 2013. Years with values greater than one indicate GZ prey dominance.

Benthic Scavenger Abundance

Depth-stratified mean numbers per tow of Atlantic hagfish (*Myxine glutinosa*) and grenadiers (Family: Macrouridae) were estimated by weighting the number of fish per tow by the area (km^2) of the stratum where they were collected during the NEFSC fall bottom trawl survey (NEFC, 1988). The two time series of benthic scavenger abundance spanned 1977 through 2013. A notable and consistent increase in grenadier abundance occurred post-2008 which was due to a vessel and gear change in 2009; thus, a simple conversion based on the time series average (1977 to 2008: 0.025 grenadiers per tow; 2009 to 2013: 0.346 grenadiers per tow) multiplied the post-2008 data by 0.07 to account for this change. In the northwest Atlantic, these taxa are distributed across the northeast U.S. continental shelf (Fig. 2), preferring the deep basin environments of the Gulf of Maine and along the continental shelf slope.

Environmental indices

Annual variability in water temperature was measured with two indices: mean sea surface (SST) and bottom (BT) temperatures collected during the NEFSC fall bottom trawl surveys (Azarovitz, 1981; NEFC, 1988). For each survey trawl, prior to 1990, temperatures were taken with water bottles and SST was checked with bucket samples. Beginning in 1990, BT and SST were measured with conductivity, temperature, and depth profilers (CTDs). Depth-stratified mean temperatures were generated by weighting the data by the area of the stratum (km^2) where collected. The two time series of SST and BT used here extended from 1977 to 2013.

Two time series of climatological oscillations for the northwest Atlantic include the Atlantic Multidecadal Oscillation (AMO) and the North Atlantic Oscillation (NAO). The AMO index is believed to be driven by thermohaline circulation and based on the detrended Kaplan sea surface temperature dataset (5° latitude by 5° longitude grid) from 0 to 70° N. Its positive periods are associated with warmer land and ocean temperatures, decreased rainfall, and increased droughts (Enfield *et al.*, 2001). Monthly AMO data were downloaded as standardized time series (mean = 0 and SD = 1) from NOAA, Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/data/timeseries/AMO/index.html). The annual average AMO time series for this study was from 1977 to 2013.

The NAO index is estimated as the difference in sea-level atmospheric pressure between the Azores (high) and Iceland (low). We used the mean winter (December to March) index as most of the variability in the NAO occurs during this time and it fully incorporates the range of this higher variance. The NAO is the only distinct teleconnection pattern present throughout the year in the northern hemisphere (Hurrell *et al.*, 2003). For the northeast U.S. continental shelf, a positive index has been attributed to cooler air and sea surface temperatures, and with its connectivity to water circulation, decreases in intense storm activity as weather patterns shift northeastward toward Newfoundland and northern Europe. Monthly NAO data from December through March were downloaded as standardized time series (mean = 0 and SD = 1) from NOAA, National Weather Service, Climate Prediction Center (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml). The annual winter average NAO time series was from 1977 to 2013 for this study.

Analysis

Dynamic factor analysis (DFA) was used to statistically identify common trends in GZ abundance for this northwest Atlantic shelf and determine if the explanatory variables: spiny dogfish consumption of GZ, the abundance of Atlantic hagfish and grenadiers, and the four environmental indices are related to GZ abundance. Similar to other dimension reduction techniques such as principle component analysis and factor analysis, DFA models *N* observed time series in terms of *M* common trends while choosing *M* as small as possible without losing too much information (Zuur *et al.,* 2003a; Zuur *et al.,* 2003b). All time series were standardized (mean = 0; SD = 1) to identify the number of common trends and relate the explanatory variables to GZ abundance. Modeling was accomplished with the MARSS (Multivariate Auto-regressive State-Space) package in R (version 3.0.2; R Core Team, 2013) having the structure:

$$\begin{gathered} y_{it} = Z_{ij}x_{jt} + n_{it} \text{ where } n_{it} \sim \mathrm{MVN}(0, R) \\ x_{jt} = x_{jt-1} + e_{jt} \text{ where } e_{jt} \sim \mathrm{MVN}(0, Q) \\ x_{j0} = 0 \end{gathered} \qquad [4]$$

where y_{it} (GZ abundance value for the *i*th region at time *t*) is modeled as a linear combination of *j* common trends (x_{jt}) and factor loadings (Z_{ij}) plus respective noise (n_{it} and e_{jt}). The covariance matrix *R* was one of three structures types: diagonal and equal, diagonal and unequal, or unconstrained, and covariance matrix *Q* was set equal to the identity matrix. All parameters including the parameters of the *R* covariance matrices were generated with maximum likelihood estimation (Zuur *et al.*, 2003a). Model selection criteria were based on Akaike's information criterion corrected for sample size (AICc) and tested the three different *R* covariance matrix structures, the number of common trends associated with GZ abundance, and with the addition of explanatory variables, the importance of these covariates relative to GZ abundance. If the addition of explanatory variables with a time lag of zero did not reveal an association with GZ abundance, the data were lagged by 1, 2, and 3 years independently for each variable and retested. Model averaging was accomplished by weighting the predicted data by the probability that each model is best (i.e. Akaike weight; Anderson, 2008).

RESULTS

Similar time series trends in GZ abundance were observed for the three major regions of the northeast U.S. continental shelf (Fig. 3a). Each region was defined by high GZ abundance around 1980, a low in the mid-1980s to early 1990s, followed by a maximum from the late 1990s to early 2000s then meandering around the time series mean thereafter. Episodic GZ blooms with 10 to 15 year periods were observed. Dynamic factor analysis identified one common trend among shelf-wide GZ abundance and an unconstrained error covariance matrix best fit the multivariate data with the lowest AICc (base model prior to adding explanatory variables; Model 1; Table 1). This suggests that there was covariance among regions (time series) along with concurrent trends in GZ abundance.

The time series of GZ consumption by spiny dogfish displayed 3 major feeding episodes from 1977 through 2013 (Fig. 3b). The years 1984, 1988, and 2003 had 236 to 298 g individual^{-1} of consumed GZ, which was approximately 4 to 5 times greater than the time series mean of 61 g individual^{-1}. Interestingly, these feeding episodes corresponded to the blooms of GZ, and for the fall or spring, the ratio of GZ prey to other prey was greater than one, indicating GZ was also the dominant diet component by mass relative to all other prey observed (Fig. 4).

Trends in benthic scavenger abundance (i.e. Atlantic hagfish and grenadiers) were variable for much of the time series from 1977 through 2013; however, patterns coinciding with the timing of GZ blooms were present (Fig. 3c). For Atlantic hagfish, the data indicated an increase in abundance around 1980 at 0.15 number tow^{-1}, to a low from the early-1980s to early-1990s of 0.01 number tow^{-1}, followed by distinct increases > 0.28 number tow^{-1} in 2003, 2007, and 2010 compared to the time series mean (0.12 number tow^{-1}). For grenadiers, abundance was high (> 0.048 number tow^{-1}) in 1984, 1986, 1989, and 1990, then stayed low from 1994 to 1999 with an average of 0.01 number tow^{-1} before reaching the time series peak in 2003 (0.08 number tow^{-1}). Following 2003, grenadier abundance remained around the time series mean of 0.02 number tow^{-1}.

The standardized indices of AMO, SST, and BT had similar trends with negative values early in the time series averaged from 1977 through 1994 (AMO: -0.13; SST: -0.30; BT: -0.36) and positive values averaged from 1995 through 2013 (AMO: 0.17; SST: 0.50; BT: 0.21), albeit the trend in bottom temperature was less dramatic with higher interannual variability (Fig. 3d). Conversely, the standardized winter NAO index had a positive average value early in the time series from 1977 through 1996 (0.01) and a negative average value from 1997 through 2013 (-0.21; Fig. 3d).

Addition of the explanatory variables (spiny dogfish consumption, Atlantic hagfish and grenadier abundance, and the four environmental indices) to the base dynamic factor model with one common trend and an unconstrained error covariance structure provided a variable series of improved or degraded model fits (Table 1). For modeling GZ abundance, the lowest AICc was achieved with the addition of 2-year lagged spiny dogfish consumption, 2-year lagged Atlantic hagfish abundance, 2-year lagged grenadier abundance, and SST (Model 19). Although the addition of 2-year lagged grenadier abundance did not substantially decrease AICc as compared to Model 17, its addition (Model 12) demonstrated an association with GZ abundance; thus, Models 19 and 17 were chosen as optimal. We interpret these results to demonstrate a shelf-wide response to GZ blooms by multiple fishes and the warming of SST. Interestingly, a 2-year lag in spiny dogfish consumption of GZ was notable relative to the timing of GZ blooms across the shelf. A similar result was also observed with hagfish and grenadier abundance. This suggests a 2-year delay in predatory response and productivity whether feeding directly in the water column (spiny dogfish) or near the seafloor via “food falls” (Atlantic hagfish and grenadiers).

The predicted data from the optimal models (Models 17 and 19; Table 1) were averaged and fit to each of the annual GZ abundance for the three regions of the shelf (Fig. 5). For the Gulf the of Maine, Georges Bank, and Mid-Atlantic Bight, this model was characterized by four events beginning around 1980 with an increase in GZ abundance followed by a low through most of the 1980s until the early to mid-1990s when a second and more persistent high abundance of GZ was apparent. This second bloom period occurred through the early 2000s and was in greater abundance compared to the 1980 bloom. For the remainder of the 2000s, modeled GZ abundance fell just below the time series mean demarcating a second low, and was consistent for the three regions.

DISCUSSION

We demonstrate distinct temporal oscillations in GZ abundance for the northeast U.S. continental shelf and tie these patterns to the fish community via feeding and benthic scavenger abundance. Increases (blooms) and decreases (declines) in GZ abundance occurred over 10 to 15 year periods and were positively related to the warming of SST. Regional patterns in GZ abundance were similar across the shelf, indicating synchrony in bloom timing that link lower and upper trophic levels, and suggest couplings between GZ and benthic environments. Synchrony among lower and upper trophic levels due to climate (Beaugrand and Reid, 2003; Alheit and Niquen, 2004) and fishing (Frank *et al.*, 2005) has been shown repeatedly for continental shelves. We selected GZ because of its suspected minimal ecosystem importance, and any detectable patterns would further confirm the case for broad-scale trophic-level synchrony. Here GZ was the dominant prey of spiny dogfish and a potential direct or indirect carbon source for benthic scavengers following periods of high GZ abundance. This reveals possible energetic/trophic value for these taxa and their synchrony with the fish community. Confirming our hypotheses, with a lag of two years following bloom periods, consumption of GZ by spiny dogfish was approximately one-half order of magnitude greater than the average GZ consumption for the decades sampled. Similarly lagged by two years, Atlantic hagfish and grenadier abundances were approximately two times greater than their respective time series averages following GZ blooms, but this was most evident with the second bloom (late 1990s).

Documenting synchrony among abiotic and biotic factors, and developing indicators of environmental change are critical for predicting regime shifts within ecosystems (Scheffer *et al.*, 2001; Möllmann *et al.*, 2009; Carpenter *et al.*, 2011). Considering fish diet variability and changes in prey availability (GZ abundance observed here), the topics of prey preference, diet switching, feeding strategies, and functional feeding responses are well studied for various environments (e.g. Lechowicz, 1982; Moustahfid *et al.,* 2010; Buren *et al.,* 2012). Particularly for temperate continental shelves with relatively low biodiversity, generalist feeding strategies are globally common among fishes (Hayden *et al., In review*). For the northeast U.S. shelf, opportunistic generalist feeding is conventional for many fishes, regardless of trophic guild (Garrison and Link, 2000; Smith and Link, 2010), and prey switching in response to external drivers has been observed (e.g. fishing pressure; Link and Garrison, 2002; Smith *et al.*, 2013). Our work extends these efforts, documenting a feeding response of spiny dogfish and suggesting increases in Atlantic hagfish and grenadier abundance throughout the shelf in relation to GZ-bloom periods. Although tracking abrupt changes in abundance of marine taxa can be difficult such as with GZ, we suggest fish diets (see Fahrig *et al.,* 1993, Link and Ford, 2006, Smith *et al.*, 2014) and abundance are useful indicators capable of monitoring ecological-pulse events as potential precursors to regime changes.

The relationship of GZ and benthic scavenger abundance (namely hagfish) suggests these taxa may be useful indicators of GZ oscillations or at least be indicative of the degree of bentho-pelagic coupling on this shelf (Graf, 1992). Interestingly, bentho-pelagic coupling can have a variable influence on benthic communities (e.g. shelf versus oceanic areas; Valiela, 1984; Miller, 2004); however, the response of the benthos can provide insight on the dynamics of the pelagic environment as shown here and by others (Smith *et al.*, 2006). Considering community-level responses to surges of prey, a link between benthic scavenger productivity and GZ blooms suggests a connection between pelagic and benthic communities and energy transfer between photic and aphotic water layers of the northwest Atlantic similar to other systems (Gili *et al.,* 2006; Lebrato and Jones, 2009; Lebrato *et al.,* 2013a).

What is the mechanism behind the 2-year lag in spiny dogfish feeding and benthic scavenger abundance relative to GZ abundance? Asexual and sexual reproduction, coupled with fast growth rates (Alldredge, 1983), allow GZ to rapidly increase their populations when environmental conditions are favorable; however, these conditions are generally short-lived. Yet, longer-term relationships between GZ and the environment have been documented (this study; Brodeur *et al.,* 2008; Richardson *et al.,* 2009; Purcell, 2012). For this shelf, bloom-years of high GZ abundance persisted for approximately 5 years. The dietary presence of high GZ abundance lasted for 1 to 2 years. Not surprisingly, the sampling efficiencies of these two samplers (net versus diet) were different as shown with other studies making similar comparisons with fish diets (e.g. Smith *et al.*, 2013). With the patchiness of GZ distributions, their breaking apart due to sampling (Hamner *et al.*, 1975), and use of formalin for sample preservation (Purcell, 1988), net sampling of GZ is challenging. Yet nets collect a wider size-range of organisms compared to spiny dogfish. This predator will naturally select larger GZ that would also be sampled by direct means. Digestion may also render smaller GZ or pieces of GZ unidentifiable. Therefore, with these considerations, one hypothesis is that the GZ selectivities of the plankton net and spiny dogfish were not equal, producing a lag in fish responses.

Secondly, spiny dogfish may also be feeding on aged or dead GZ near the seafloor. GZ mortality (non-predatory) varies by taxa, but can be on the order of 2+ years for *Aurelia labiata* (Albert, 2005), 1+ years for ctenophores (Pitt *et al*. 2013), and possibly immortal for some basal metazoan groups (Petralia *et al.*, 2014). In this study, all spiny dogfish were collected with a bottom trawl; thus, with their fast rate of digestion (Arai *et al.*, 2003) and quick transport to the deep sea (hundreds to over one thousand meters day^{-1} [Lebrato *et al.*, 2013a]), bottom feeding may be occurring here. As abundance of GZ increases following a bloom, spiny dogfish prefer GZ approximately 2 years following peak GZ abundance. This preference may be the result of GZ aggregating near the seafloor as shown with Ctenophora (inshore Argentina; Costello and Mianzan, 2003). Within the years following feeding, GZ abundance remains low suggesting this fish as well as other predators may contribute to a top-down control in response to these pulses (Carpenter *et al.*, 1985; Power, 1992; Halpern *et al.*, 2006), albeit, this is not likely the sole factor at play (e.g. oscillating favorable GZ conditions [Richardson *et al.*, 2009]). In one instance, a large increase in GZ consumption was observed during a low period of abundance > 2 years post-bloom (i.e. 1988). We categorize this as positive prey preference following a bloom period (Lechowicz, 1982), but we cannot totally rule out net limitations reiterating the caveats of both sampling techniques previously mentioned.

Considering the 2-year lag with benthic scavenger abundance, the ecological processes and hypotheses described for predation by spiny dogfish apply here as well, although transport of GZ to the benthos plus the integration of GZ energy (directly or indirectly) for population growth are definite factors. Rates of jelly transport in this study were unknown, but suspected to be relatively fast on the order of hundreds to over one thousand meters day^{-1} (Lebrato *et al.*, 2013a). Thus, in combination with GZ longevity (1-2+ years Albert, 2005, Pitt *et al.*, 2013; Petrailia *et al*., 2014), the availability of GZ carrion for benthic scavengers and the subsequent increase in scavenger abundance per tow is not observed until 2 years following the increase in GZ abundance. Since blooms occurred for approximately 5 years, GZ energy may reach the benthos following the initial year of high abundance on this continental shelf. A hypothesis is that GZ contributes additional energy for fish recruitment (e.g. Friedland *et al*., 2008; Leaf and Friedland, 2014). It is also possible these scavengers may not be consuming GZ carrion. They could be feeding on living GZ aggregations as these scavengers were collected in relatively shallow waters (average depth for Atlantic hagfish: 186 m; grenadiers: 273 m) of this shelf environment versus the deeper waters beyond the shelf slope. More likely, these scavengers may also favor increases in other benthos consuming or in association with "jelly falls" or living jelly aggregations (e.g. decapod shrimp, galatheid crabs, and amphipods; Sweetman and Chapman, 2011; Sweetman *et al.*, 2014). The limited diet data available for hagfish (number = 4 stomachs) and grenadiers (number = 31 stomachs) of this shelf indicate hagfish consume fish remains (e.g. scales) and grenadiers: large amounts of amphipods, polychaetes and other benthic invertebrates. Grenadiers also have a high frequency of unidentifiable remains in their diets and hagfishes rasp their food. Hagfish have also been observed to actively prey on living fishes (Zintzen *et al*., 2011), so the exact link or combination of events linking these scavengers to GZ remains uncertain. We note that the spatial overlap of GZ and benthic scavengers in this study was limited to the edge of the continental shelf excluding the Gulf of Maine. This may have weakened the relationships or delayed the responses observed. Nonetheless, a shelf-wide relationship between GZ and scavenger abundance was found suggesting these fishes may benefit from GZ blooms. Related hypotheses specific to the Gulf of Maine have merit as well as examining trends in abundance of additional scavengers in relation to GZ abundance for this shelf (Sweetman *et al.*, 2014). The exclusion of invertebrate scavengers here was solely because of minimal spatio-temporal data available. Akin to the Falkland Islands (South Atlantic), our findings support Arkhipkin and Laptikhovsky (2013) which inferred increases in rock cod (*Patagonotothen ramsayi*) abundance favor GZ presence following their consumption. The time between GZ blooms to increases in rock cod abundance was not examined; however, it shows synchrony in their abundances and further suggests GZ to be a valuable trophic resource and a potential fish recruitment mechanism for multiple Atlantic ecosystems. We note that additional hypotheses regarding the 2-year lag in GZ-fish synchrony of this shelf are equally valid; nevertheless, we kept our focus on feeding given the theme of our work.

Population success for many species has often been correlated with food availability, abundance, and energy (e.g. Lambert and Dutil, 2000; Österblom *et al.,* 2008; Mills *et al.,* 2013). Notably, shifts in prey quality and energy tradeoffs can occur when fish predators switch to other prey when their abundance is high. With spiny dogfish, routine prey include fishes (e.g. clupeids and Atlantic mackerel *Scomber scombrus*) and squids in the northwest Atlantic (Smith and Link, 2010). These items have 5 to 10 KJ/g wet weight of energy in comparison to the GZ considered here with only 0.1 to 0.4 KJ/g wet weight (Steimle and Terranova, 1985; Arai, 1988). Given these differences, one might expect fish population success to be hindered by GZ blooms and subsequent feeding. However, with an exceptional rate of digestion (Arai *et al.,* 2003), and known increases in energy density for reproductive GZ (Milisenda *et al.,* 2014), these feeding events may provide comparable energy resources particularly if their routine fish prey are less available (e.g. predation of fish eggs and larvae; Purcell and Arai, 2001; Lynam *et al.,* 2005). To note, spiny dogfish abundance was excluded as a covariate in this study due to the effect of fishing pressure on this species, particularly unregulated fishing during the years 1977 to 2000 examined here (NEFSC, 2006). More importantly, we chose conservative parameter estimates for modeling GZ evacuation based on Durbin *et al*, (1983) and Hannan (2009). Albeit the trend in GZ consumption and its relationship to GZ abundance would remain unchanged, increasing parameter estimates by one order of magnitude (applicable to the northwest Atlantic) would equally increase the scale of GZ consumption (g individual^{-1}; NEFSC, 2007). Beyond the trophic interactions considered here, high energy flows and nutrient pathways for several ecosystems involve jellyfish and biota in association with jellyfish (e.g. leatherback sea turtles [*Drmochelys coriacea*; Healsip *et al.* 2012], microbes [Condon *et al.* 2011; Tinta *et al.* 2012], and seabirds [Sato *et al.* 2015]). Akin to these studies, our work suggests an increased importance in these GZ-community links during bloom periods.

Considering the benthic scavengers included in this study, increased GZ presence via “jelly falls” or saturation of the water column can provide a surge of energy to a somewhat energy-limited, patchy fish community of the deep-shelf benthos relying heavily on imported nutrition sinking from the euphotic zone (Miller, 2004). Studies have shown amounts of carbon available following “jelly falls” are on the order of 0.3 to 1.4 mg C m^{-2} (Lebrato *et al.,* 2013b) or even up to 78 g C m^{-2} (Billett *et al.,* 2006), in some cases exceeding the annual downward transport of carbon. On the northeast U.S. shelf, sediment samples indicate the majority of the shelf contains low amounts of carbon (< 0.5 % by weight) with small patches and some areas (Gulf of Maine) with slightly higher amounts (0.5 to 1.99 % by weight; Theroux and Wigley, 1998). Although periodic swarms of salps with strong diel vertical migrations overlap the shelf edge into deeper waters of this ecosystem (Madin *et al*., 2006), amounts of jelly carbon transported to the benthos remain unreported to our knowledge. We believe GZ blooms provide surges of energy to the shelf benthos, including benthic prey for scavenging fishes (e.g. Priede *et al.,* 1994; Sweetman and Chapman, 2011; Sweetman *et al.* 2014). This energy signal should be evident as seen with large-carrion falls (~4 % daily carbon flux rate; Higgs *et al.,* 2014), but it may also exceed annual downward carbon transport akin to other areas (Arabian Sea; Billett *et al.,* 2006).

Frequently shown, climate directly affects oceanographic processes (e.g. Miller, 2004; Drinkwater *et al.,* 2009), can lower phytoplankton concentrations (Boyce *et al.*, 2010), and modify fish distributions (Nye *et al.,* 2009). Here, warming SST was related to increases in GZ abundance as seen with other studies around the world (e.g. Richardson *et al.,* 2009; Condon *et al.,* 2013). Limited (AMO) or an absence of evidence (NAO and BT) was found for the other environmental indices tested; however, other indices not considered here may have also played a synergistic role with SST as shown by Brodeur *et al.,* (2008) in the eastern Bering Sea. The global fear is that GZ may be able to withstand climatic and environmental disturbances when other biota are negatively impacted (Jackson, 2008; Qiu, 2014). Thus, our work suggests further studies to relate additional climatic and environmental indices to GZ blooms and explore their synergies are warranted for this region.

For the northeast U.S. continental shelf, GZ blooms occur as widespread events that are connected to the fish community and the environment. Interestingly, the fishes considered here responded positively to the oscillations of GZ directly as prey or from suspected “food falls” and subsequent increases in prey following blooms. At this scale, we show a novel coupling between the plankton and fish communities spanning pelagic and benthic environments of this ecosystem. Reports of high GZ abundance have generally been negative (Dong *et al.,* 2010; Schrope, 2012; Graham *et al.*, 2014), but we show the general flux of GZ abundance on the shelf and how select members of the fish community can benefit from ecological pulse events, noting the utility of GZ frequently considered to be avoided by biota of upper trophic levels. As inputs for ecosystem models, documenting trends in GZ abundance and their connectivity to the fish community and the environment has implications for advancing our understanding of whole-shelf ecology (Link *et al.*, 2010). For the communities of this northwest Atlantic shelf, GZ carbon is not ignored and its effects on ecosystems from the fish community to humans are widely important, which need to be explained and will receive continued interest given their profound yet variable effects.

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TABLES

Table 1. Dynamic factor models applied to the three gelatinous zooplankton abundance time series. Akaike's information criterion (AICc) corrected for sample size was used for model selection. Δ_i is the difference between AICc and the minimum AICc; w_i is the weight associated with one model's AICc relative to the other models. M is the number of common trends identified which was equal to one and applied to all models with covariates. Multimodel averaging of the predicted data was applied with models 17 and 19; thus, w_i was reestimated and equaled 0.425557 (17) and 0.574425 (19) with negligible probability gained from the other models shown.

Model	AICc	Δ_i	w_i
1. Data = M common trends + error	132.4	19.0	0.000035
2. Data = M common trends + consumption + error	137.4	24.0	0.000003
3. Data = M common trends + 2-year lagged consumption + error	120.9	7.5	0.010903
4. Data = M common trends + AMO + error	130.9	17.5	0.000073
5. Data = M common trends + NAO + error	138.0	24.6	0.000002
6. Data = M common trends + SST + error	133.2	19.8	0.000023
7. Data = M common trends + BT + error	138.2	24.8	0.000002
8. Data = M common trends + 2-year lagged consumption + AMO + SST + error	119.5	6.1	0.021956
9. Data = M common trends + hagfish abundance + error	133.5	20.1	0.000020
10. Data = M common trends + 2-year lagged hagfish abundance + error	130.7	17.3	0.000081
11. Data = M common trends + grenadier abundance + error	138.1	24.7	0.000002
12. Data = M common trends + 2-year lagged grenadier abundance + error	130.3	16.9	0.000099
13. Data = M common trends + 2-year lagged consumption + 2-year lagged hagfish abundance + 2-year lagged grenadier abundance + error	117.2	3.8	0.069342
14. Data = M common trends + 2-year lagged consumption + AMO + 2-year lagged hagfish abundance + 2-year lagged grenadier abundance + error	119.9	6.5	0.017976
15. Data = M common trends + 2-year lagged consumption + AMO + SST + 2-year lagged hagfish Abundance + error	119.0	5.6	0.028193
16. Data = M common trends + 2-year lagged consumption + AMO + SST + 2-year lagged hagfish Abundance + 2-year lagged grenadier abundance + error	120.8	7.4	0.011462
17. Data = M common trends + 2-year lagged consumption + SST + 2-year lagged hagfish abundance + error	114.0	0.6	0.343455
18. Data = M common trends + 2-year lagged consumption + SST + 2-year lagged grenadier abundance + error	118.7	5.3	0.032755
19. Data = M common trends + 2-year lagged consumption + SST + 2-year lagged hagfish abundance + 2-year lagged grenadier abundance + error	113.4	0.0	0.463616
20. Data = M common trends + other covariate combinations + error	>117.4	NA	NA

FIGURE CAPTIONS

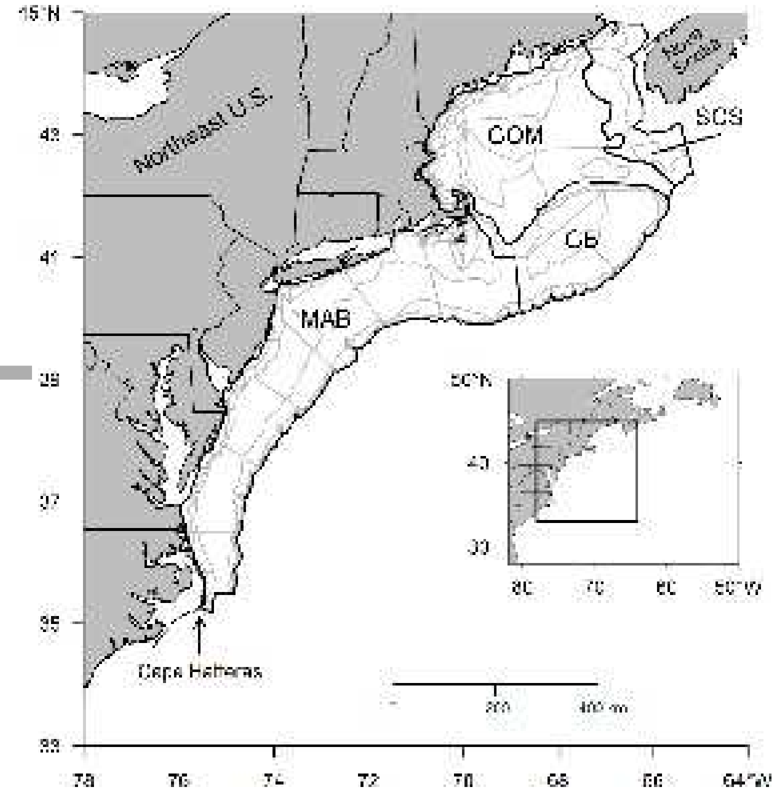
Figure 1. Map of the northwest Atlantic (inset) and northeast U.S. continental shelf (detailed). Regions defined as MAB: Mid-Atlantic Bight; GB: Georges Bank; GOM: Gulf of Maine; and SCS: Scotian Shelf. Cape Hatteras, North Carolina and Nova Scotia labeled for reference. Gray lines denote depth strata.

Figure 2. Map of feeding occurrences of gelatinous zooplankton (GZ) by spiny dogfish (*Squalus acanthias*), and grenadier (Family: Macrouridae) and Atlantic hagfish (*Myxine glutinosa*) distributions on the northeast U.S. continental shelf. Regions defined as MAB: Mid-Atlantic Bight; GB: Georges Bank; GOM: Gulf of Maine; and SCS: Scotian Shelf.

Figure 3. Standardized time series for the northeast U.S. continental shelf. (a) Gelatinous zooplankton abundance (GZ) by region. (b) Spiny dogfish consumption of GZ. (c) Scavenger abundance as number tow^{-1} for grenadiers and Atlantic hagfish. (d) Environmental indices (NAO: North Atlantic Oscillation, AMO: Atlantic Multidecadal Oscillation, SST: sea surface temperature, and BT: bottom temperature. Values expressed as annual averages of monthly or seasonal anomalies.

Figure 4. Ratio of gelatinous zooplankton (GZ) prey to other prey of spiny dogfish by season. Values greater than one indicate years with GZ being the dominant diet component.

Figure 5. Fitted values (gray lines) for annual gelatinous zooplankton (GZ) abundance (black dots) by region. The optimal model (Models 17 and 19 averaged; see Table 1) contains 1 trend and the explanatory variables: 2-year lagged spiny dogfish consumption, 2-year lagged Atlantic hagfish and grenadier abundance, and sea surface temperature.



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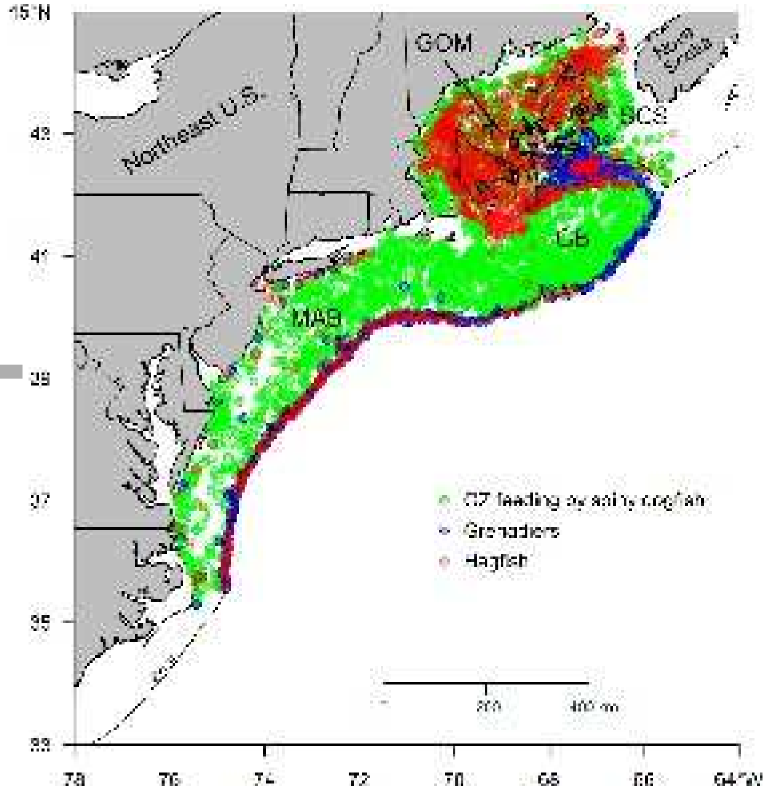

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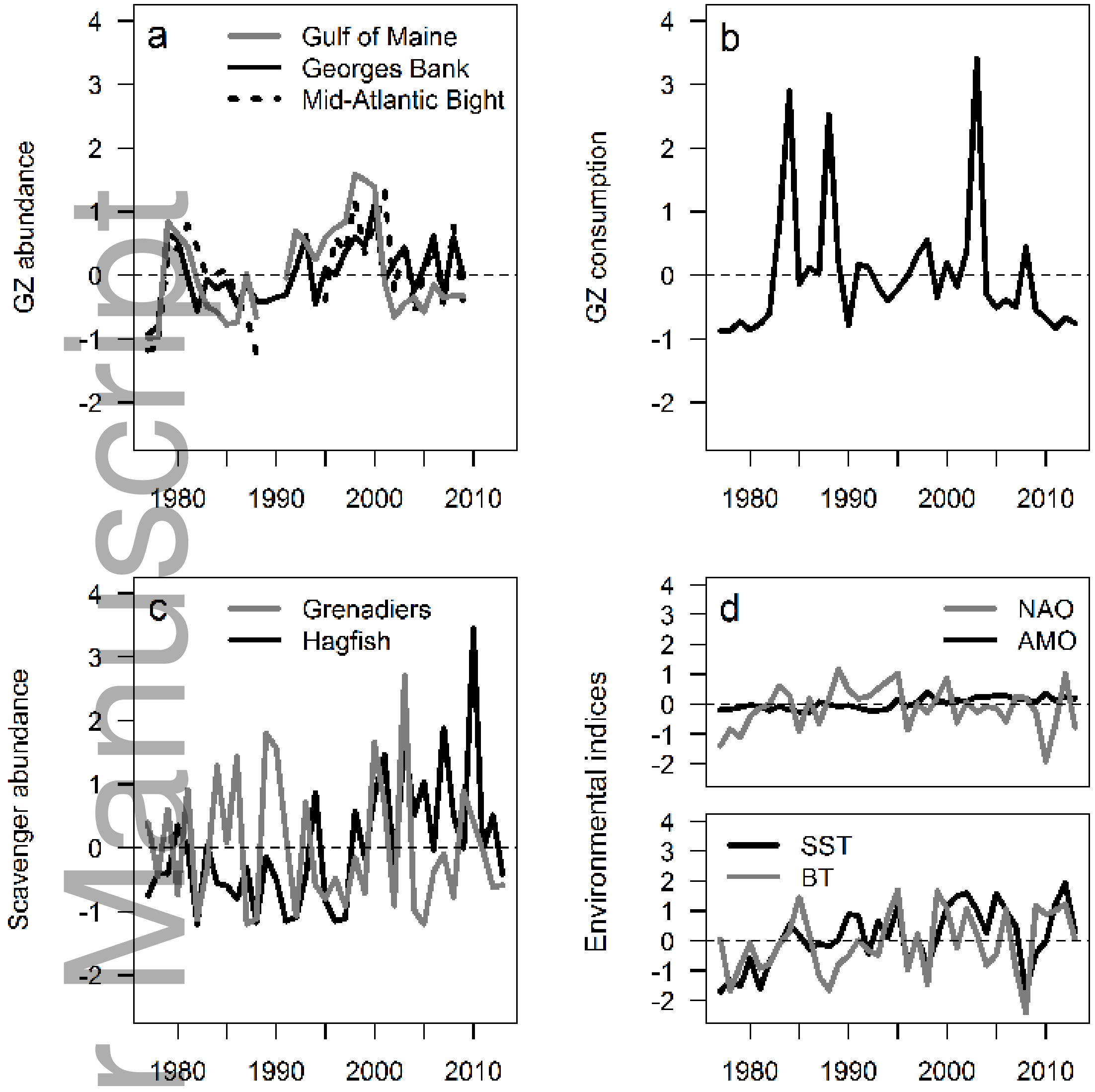

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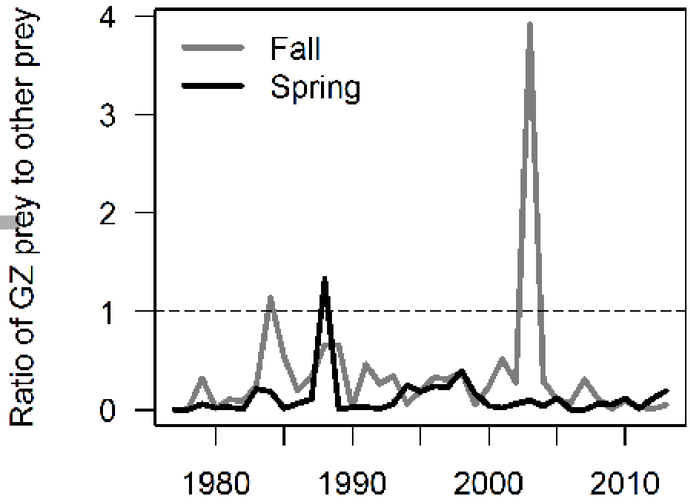

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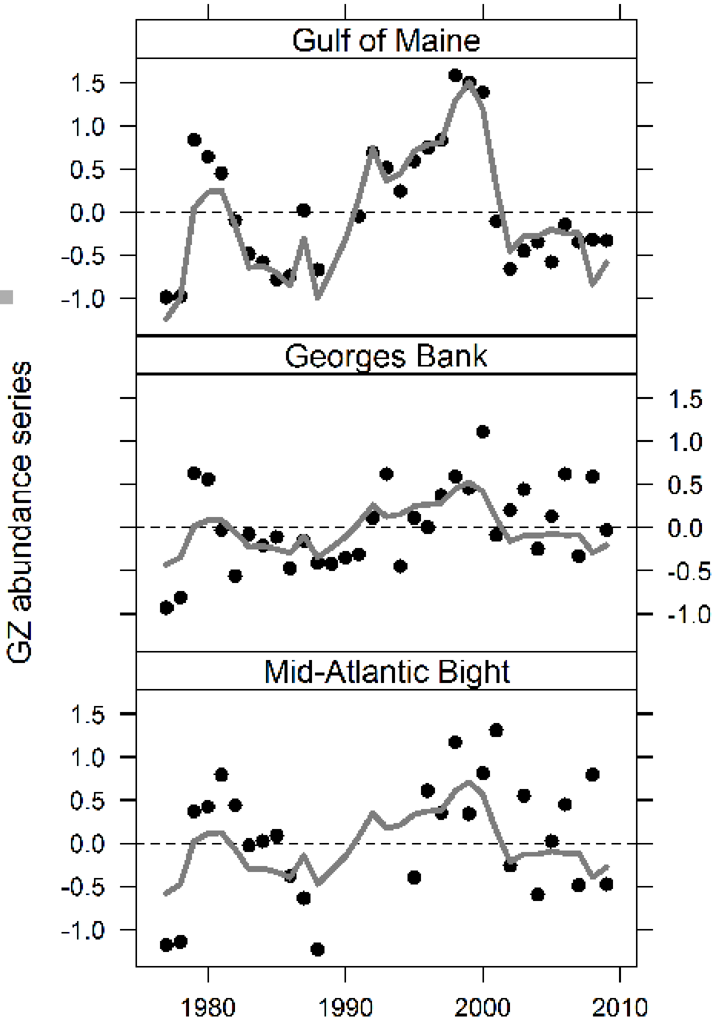

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