



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

BRIAN E. SMITH,^{1*} MICHAEL D. FORD² AND JASON S. LINK¹

¹NOAA Fisheries, 166 Water Street, Woods Hole MA 02543, U.S.A.

²NOAA Fisheries, SSMC3 12525, 1315 East-West Highway, Silver Spring Maryland, 20910, U.S.A.

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 10–15 yr. Conservative estimates of annual removal of GZ by spiny dogfish ranged from approximately 0.3–298 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-yr 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.

Key words: climate change, gelatinous zooplankton bloom, northwest Atlantic, scavenging, time series analysis, trophic ecology

INTRODUCTION

The 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 a 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

*Correspondence. e-mail: brian.smith@noaa.gov

Received 17 December 2015

Revised version accepted 3 May 2016

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 m² 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.*, unpublished data), 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' after 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,b) 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 six times per year with a 61-cm bongo frame fitted with a 333- μ m 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 km²; Fig. 1). Distributed uniformly within each region, 30–60 sampling stations were selected randomly either approximately 8–35 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 L of GZ were encountered.

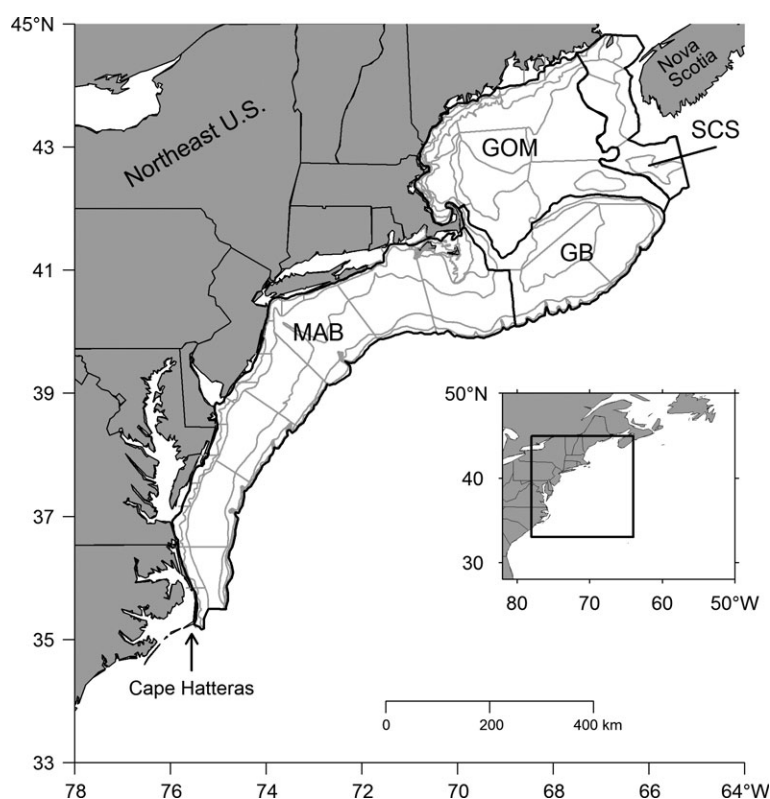


Figure 1. Map of the northwest Atlantic (inset) and northeast U.S. continental shelf (detailed). Regions defined as MAB: Mid-Atlantic Bight; GB: Georges Bank; GOM: Gulf of Maine; and SCS: Scotian Shelf. Cape Hatteras, North Carolina and Nova Scotia labeled for reference. Gray lines denote depth strata.

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-L 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 . The mean annual amounts of GZ for this study spanned 1977 through to 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 a 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 to August; 1977 through to 1981, and 1991 through to 1995) data are available.

Although the diet sampling program started in 1973, we focused our study on spiny dogfish stomachs from 1977 through to 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 to 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 owing to formalin or ethanol preservation (Purcell, 1988) or rapid digestion (Arai *et al.*, 2003). The total stomach volume (0.1 cm^3 minimum resolution), prey composition (%), numbers, and lengths were collected

at sea. Additionally, a conversion from the 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 (~25–40 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

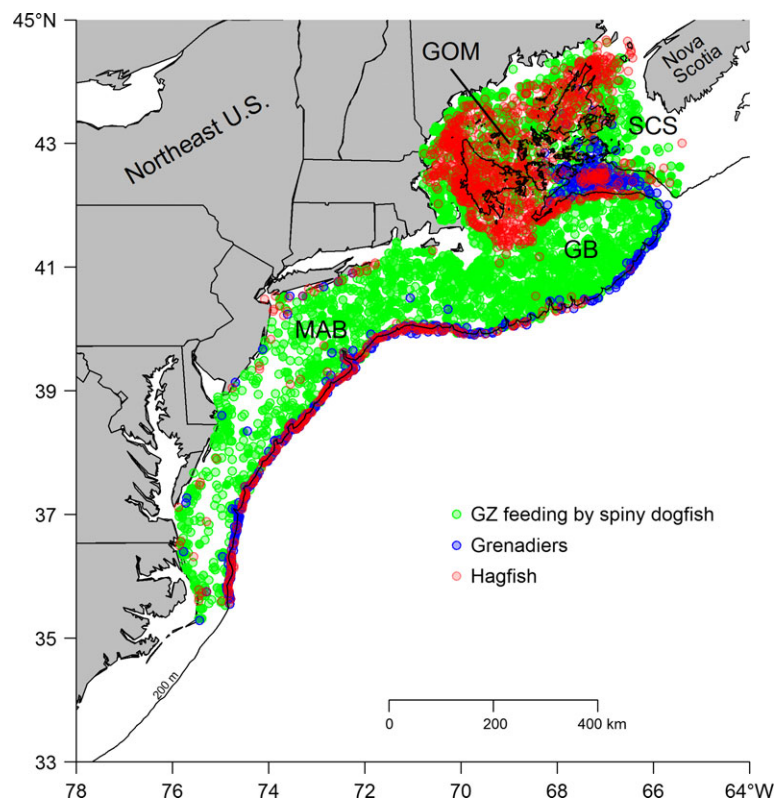
indistinguishable at these coarse taxonomic levels (Hamner *et al.*, 1975; Bailey *et al.*, 1994; Weisse *et al.*, 2002).

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'; the mean number per year = 1262 and SE = 128), and summer and fall ('fall'; the 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:

$$C_{\text{spring/fall}} = 24 \times E \times \bar{S}^{\gamma} \quad (1)$$

where 24 is the number of hours in a day, and \bar{S} is the mean total amount of prey eaten per season. The 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

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.



$$E = \alpha e^{\beta T} \quad (2)$$

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 $C_{\text{spring/fall}}$ 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 ($D_{\text{spring/fall}}$), and summing the half-year seasons:

$$C_{\text{Annual}} = (C_{\text{Spring}} \times D_{\text{Spring}} \times 182.5) + (C_{\text{Fall}} \times D_{\text{Fall}} \times 182.5) \quad (3)$$

The time series of annual per capita consumption of GZ spanned 1977 through to 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 to 2013. Years with values >1 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 to 2013. A notable and consistent increase in grenadier abundance occurred post-2008 which was a result of a vessel and gear change in 2009; thus, a simple conversion based on the time series average (1977–2008: 0.025 grenadiers per tow; 2009–2013: 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, before 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 SST, and with its connectivity to water circulation, decreases in intense storm activity as weather patterns shift northeastward toward Newfoundland and northern Europe. The monthly NAO data from December through to 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.

Statistical analysis

Dynamic factor analysis (DFA) was used statistically to 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 principal 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,b). 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:

$$\begin{aligned} y_{it} &= Z_{ij}x_{jt} + n_{it} \text{ where } n_{it} \sim \text{MVN}(0, R) \\ x_{jt} &= x_{jt-1} + e_{jt} \text{ where } e_{jt} \sim \text{MVN}(0, Q) \\ x_{j0} &= 0 \end{aligned} \quad (4)$$

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 structure 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 yr 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 after that. Episodic GZ blooms with 10- to 15-yr periods were observed. Dynamic factor analysis identified one common trend among shelf-wide GZ abundance and an

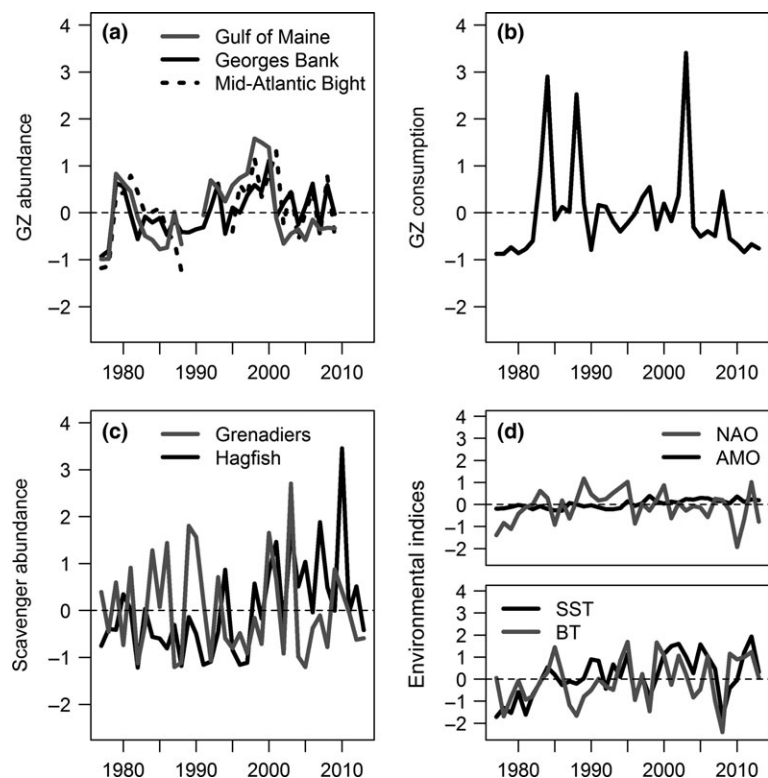


Figure 3. Standardized time series for the northeast U.S. continental shelf. (a) Gelatinous zooplankton abundance (GZ) by region. (b) Spiny dogfish consumption of GZ. (c) Scavenger abundance as number per tow for grenadiers and Atlantic hagfish. (d) Environmental indices (NAO: North Atlantic Oscillation,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

unconstrained error covariance matrix fit the multivariate data best with the lowest AICc (base model before 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 three major feeding episodes from 1977 through to 2013 (Fig. 3b). The years 1984, 1988, and 2003 had 236–298 g individual⁻¹ of consumed GZ, which was approximately 4–5 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 >1, 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 to 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). After 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 to 1994 (AMO: -0.13; SST: -0.30; BT: -0.36) and positive values averaged from 1995 through to 2013 (AMO: 0.17; SST: 0.50; BT: 0.21), albeit the trend in the bottom temperature was less dramatic with higher inter-annual variability (Fig. 3d). Conversely, the standardized winter NAO index had a average positive value early in the time series from 1977 through to 1996 (0.01) and a negative average value from 1997 through to 2013 (-0.21; Fig. 3d).

The 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-yr lagged spiny dogfish consumption, 2-yr lagged Atlantic hagfish abundance, 2-yr lagged grenadier abundance, and SST (Model 20). Although the addition of 2-yr lagged grenadier abundance did not substantially decrease AICc as compared with Model 18, its addition (Model 12) demonstrated an association with GZ abundance; thus, Models 20 and 18 were chosen as optimal. We interpret these results to demonstrate a shelf-wide response by multiple fishes to GZ blooms and the warming of SST. Interestingly, a 2-yr 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-yr 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 18 and 20; Table 1) were averaged and fitted to each of the annual GZ abundances for the three regions of the shelf (Fig. 5). For the Gulf 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-yr 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 links lower and upper trophic levels, and suggest couplings between GZ and benthic environments. Synchrony among lower and upper trophic levels owing to climate (Beaugrand and Reid, 2003; Alheit and Niquen, 2004) and fishing (Frank *et al.*, 2005) has repeatedly been shown for continental shelves. We selected GZ because of its suspected minimal ecosystem importance, and any detectable patterns would further confirm the case for

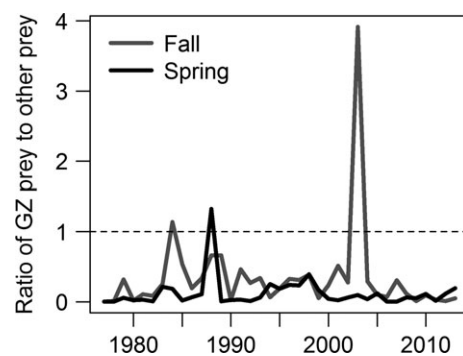
Table 1. Dynamic factor models applied to the three gelatinous zooplankton abundance time series.

Model	AICc	Δ_i	w_i
1. Data = M common trends + error	132.4	19.0	0.000033
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	0.010259
4. Data = M common trends + AMO + error	130.9	17.5	0.000069
5. Data = M common trends + NAO + error	138.0	24.6	0.000002
6. Data = M common trends + SST + error	133.2	19.8	0.000022
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	0.020660
9. Data = M common trends + hagfish abundance + error	133.5	20.1	0.000019
10. Data = M common trends + 2-year lagged hagfish abundance + error	130.7	17.3	0.000076
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	0.000093
13. Data = M common trends + 2-year lagged consumption + SST + error	117.4	4.0	0.059039
14. Data = M common trends + 2-year lagged consumption + 2-year lagged hagfish abundance + 2-year lagged grenadier abundance + error	117.2	3.8	0.065248
15. Data = M common trends + 2-year lagged consumption + AMO + 2-year lagged hagfish abundance + 2-year lagged grenadier abundance + error	119.9	6.5	0.016915
16. Data = M common trends + 2-year lagged consumption + AMO + SST + 2-year lagged hagfish Abundance + error	119.0	5.6	0.026528
17. Data = M common trends + 2-year lagged consumption + AMO + SST + 2-year	120.8	7.4	0.010786

Table 1. (Continued)

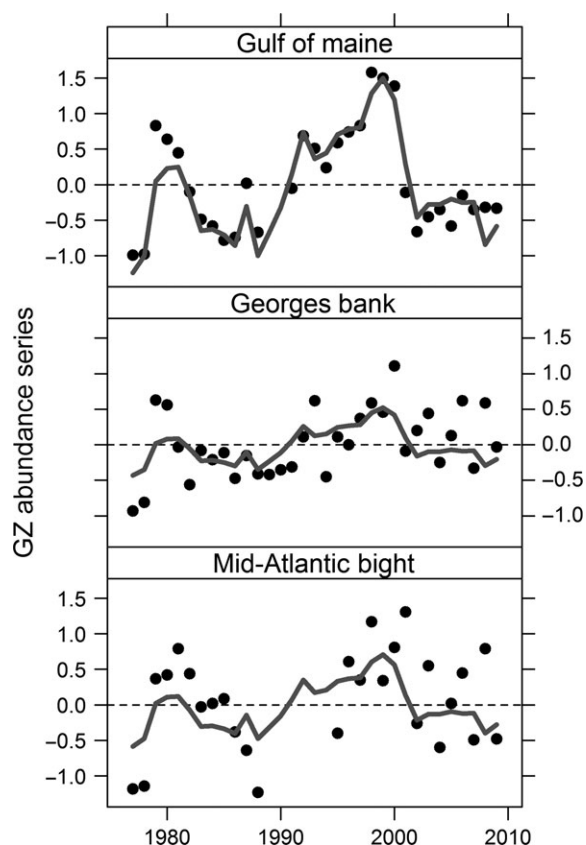
Model	AICc	Δ_i	w_i
lagged hagfish Abundance + 2-year lagged grenadier abundance + error			
18. Data = M common trends + 2-year lagged consumption + SST + 2-year lagged hagfish abundance + error	114.0	0.6	0.323178
19. Data = M common trends + 2-year lagged consumption + SST + 2-year lagged grenadier abundance + error	118.7	5.3	0.030821
20. Data = M common trends + 2-year lagged consumption + SST + 2-year lagged hagfish abundance + 2-year lagged grenadier abundance + error	113.4	0.0	0.436244

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 18 and 20; thus, w_i was reestimated and equaled 0.425557 (18) and 0.574443 (20) with negligible probability gained from the other models shown.

Figure 4. Ratio of gelatinous zooplankton (GZ) prey to other prey of spiny dogfish by season. Values >1 indicate years with GZ being the dominant diet component.

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 after periods of high GZ abundance. This reveals a possible energetic/trophic value for these taxa and their synchrony with the fish community. Confirming our

Figure 5. Fitted values (gray lines) for annual gelatinous zooplankton (GZ) abundance (black dots) by region. The optimal model (Models 18 and 20 averaged; see Table 1) contains 1 trend and the explanatory variables: 2-yr lagged spiny dogfish consumption, 2-yr lagged Atlantic hagfish and grenadier abundance, and sea surface temperature.



hypotheses, with a lag of 2 yr after bloom periods, consumption of GZ by spiny dogfish was approximately a one-half order of magnitude greater than the average GZ consumption for the decades sampled. Similarly lagged by 2 yr, Atlantic hagfish and grenadier abundances were approximately two times greater than their respective time series averages after GZ blooms, but this was most evident with the second bloom (the 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; Möllman *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.*, unpublished data). 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 benthic-pelagic coupling on this shelf (Graf, 1992). Interestingly, benthic-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 into 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-yr 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 increase their populations rapidly when environmental conditions are favorable; however, these conditions are short-lived. 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 yr. The dietary presence of high GZ abundance lasted for 1–2 yr. Not surprisingly, the sampling efficiencies of these two samplers (net versus diet) were different as shown in 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 the use of formalin for sample preservation (Purcell, 1988), net sampling of GZ is challenging. 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, and possibly variable for spiny dogfish, 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+ yr for *Aurelia labiata* (Albert, 2005), 1+ yr for ctenophores (Pitt *et al.*, 2013), and possibly immortal for some basal metazoan groups (Petraria *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 per day [Lebrato *et al.*, 2013a]), bottom feeding may be occurring here. As the abundance of GZ increases after a bloom, spiny dogfish prefer GZ approximately 2 yr 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 yr post-bloom (i.e., 1988). We categorize this as positive prey preference after 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-yr 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. The 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 per day (Lebrato *et al.*, 2013a). Thus, in combination with GZ longevity (1–2+ yr Albert, 2005; Pitt *et al.*, 2013; Petraria *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 yr after the increase in GZ abundance. As blooms occurred for approximately 5 yr, GZ energy may reach the benthos after 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 after 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-yr 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 includes fishes (e.g., clupeids and Atlantic mackerel *Scomber scombrus*) and squids in the northwest Atlantic (Smith and Link, 2010). These items have 5–10 KJ g⁻¹ wet weight of energy in comparison to the GZ considered here with only 0.1–0.4 KJ g⁻¹ 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 owing to the effect of fishing pressure on this species, particularly unregulated fishing during the years 1977–2000 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 per individual; 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 [*Dermochelys coriacea*; Heaslip *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 after ‘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 suspect 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 in other studies around the world (e.g., Richardson *et al.*, 2009; Condon *et al.*, 2013). Limited evidence (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 after 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; Schroepe, 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 north-west 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.

ACKNOWLEDGEMENTS

We acknowledge the many people involved with the sampling and maintenance of various oceanographic and fish ecology datasets used in this study. In particular, we are grateful for NOAA Fisheries' support with the continuation of long-term, continental shelf-wide ecosystem surveys which are priceless data streams. We also thank J. Hare for his guidance with the plankton data, and thank two anonymous reviewers for their comments on prior versions of this manuscript.

REFERENCES

- Albert, D.J. (2005) Reproduction and longevity of *Aurelia labiata* in Roscoe Bay, a small bay on the Pacific coast of Canada. *J. Mar. Biol. Assoc. U.K.* **85**:575–581.
- Alheit, J. and Niquen, M. (2004) Regime shifts in the Humboldt Current ecosystem. *Prog. Oceanogr.* **60**:201–222.
- Allredge, A.L. (1983) The quantitative significance of gelatinous zooplankton as pelagic consumers. In: *Flow of Energy and Materials in Marine Ecosystems: Theory and Practice*. M.J.R. Fasham (ed) New York: Plenum Press, pp. 407–433.
- Anderson, D.R. (2008) *Model Based Inference in the Life Sciences: A Primer on Evidence*. New York: Springer, 184 pp.
- Arai, M.N. (1988) Interactions of fish and pelagic coelenterates. *Can. J. Zool.* **66**:1913–1927.
- Arai, M.N., Welch, D.W., Dunsmuir, A.L., Jacobs, M.C. and Ladouceur, A.R. (2003) Digestion of pelagic Ctenophora and Cnidaria by fish. *Can. J. Fish Aquat. Sci.* **60**:825–829.
- Arkhipkin, A. and Laptikhovsky, V. (2013) From gelatinous to muscle food chain: rock cod *Patagonotothen ramsayi* recycles coelenterate and tunicate resources on the Patagonian Shelf. *J. Fish Biol.* **83**:1210–1220.
- Armstrong, J.D., Bagley, P.M. and Priede, I.G. (1992) Photographic and acoustic tracking observations of the behavior of the grenadier *Coryphaenoides (Nematonurus) armatus*, the eel *Synaphobranchus bathybius*, and other abyssal demersal fish in the North Atlantic Ocean. *Mar. Biol.* **112**:535–544.
- Azarovitz, T.R. (1981) A brief historical review of the Woods Hole laboratory trawl survey time series. In: Doubleday W.G., Rivard D. (eds). *Bottom trawl surveys. Can. Spec. Publ. Fish. Aquat. Sci.* **58**: 62–67.
- Bailey, T.B., Torres, J.J., Youngbluth, M.J. and Owen, G.P. (1994) Effect of decompression on mesopelagic gelatinous zooplankton: a comparison of in situ and shipboard measurements of metabolism. *Mar. Ecol. Prog. Ser.* **113**:13–27.
- Beaugrand, G. and Reid, P.C. (2003) Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Glob. Change Biol.* **9**:801–817.
- Billett, D.S.M., Bett, B.J., Jacobs, C.L., Rouse, I.P. and Wigham, B.D. (2006) Mass deposition of jellyfish in the deep Arabian Sea. *Limnol. Oceanogr.* **51**:2077–2083.
- Blenckner, T., Llope, M., Möllmann, C. *et al.* (2015) Climate and fishing steer ecosystem regeneration to uncertain economic futures. *Proc. R. Soc. B* **282**:20142809.
- Boero, F., Bouillon, J., Gravili, C., Miglietta, M.P., Parsons, T. and Piraino, S. (2008) Gelatinous plankton: irregularities rule the world (sometimes). *Mar. Ecol. Prog. Ser.* **356**:299–310.
- Boyce, D.G., Lewis, M.R. and Worm, B. (2010) Global phytoplankton decline over the past century. *Nature* **466**:591–596.
- Brodeur, R.D., Decker, M., Ciannelli, L. *et al.* (2008) Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. *Prog. Oceanogr.* **77**:103–111.
- Brotz, L., Cheung, W.W.L., Kleisner, K., Pakhomov, E. and Pauly, D. (2012) Increasing jellyfish populations: trends in large marine ecosystems. *Hydrobiologia* **690**:3–20.
- Buren, A.D., Koen-Alonso, M. and Montevecchi, W.A. (2012) Linking Predator diet and prey availability: common murre and capelin in the northwest Atlantic. *Mar. Ecol. Prog. Ser.* **445**:25–35.
- Burkholder, J.M., Noga, E.J., Hobbs, C.H. and Glasgow, H.B. Jr (1992) New 'phantom' dinoflagellate is the causative agent of major estuarine fish kills. *Nature* **358**:407–410.
- Carpenter, S.R., Kitchell, J.F. and Hodgson, J.R. (1985) Cascading trophic interactions and lake productivity. *Bioscience* **35**:634–639.
- Carpenter, S.R., Cole, J.J., Pace, M.L. *et al.* (2011) Early warning signs of regime shifts: a whole-ecosystem experiment. *Science* **332**:1079–1082.
- Condon, R.H., Steinberg, D.K., del Giorgio, P.A. *et al.* (2011) Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. *Proc. Natl Acad. Sci. USA* **108**:10225–10230.
- Condon, R.H., Graham, W.M., Duarte, C.M. *et al.* (2012) Questioning the rise of gelatinous zooplankton in the World's oceans. *Bioscience* **62**:160–169.
- Condon, R.H., Duarte, C.M., Pitt, K.A. *et al.* (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *Proc. Natl Acad. Sci. USA* **110**:1000–1005.
- Conley, K.R. and Sutherland, K.R. (2015) Commercial fishers' perceptions of jellyfish interference in the Northern California Current. *ICES J. Mar. Sci.* **72**:1565–1575.
- Costello, J.H. and Mianzan, H.W. (2003) Sampling field distributions of *Mnemiopsis leidyi* (Ctenophora, Lobata): planktonic or benthic methods? *J. Plankton Res.* **25**:455–459.
- Dong, Z., Liu, D. and Keesing, J.K. (2010) Jellyfish blooms in China: dominant species, causes and consequences. *Mar. Pollut. Bull.* **60**:954–963.

- Drinkwater, K.F., Mueter, F., Friedland, K.D. et al. (2009) Recent climate forcing and physical oceanographic changes in northern hemisphere regions: a review and comparison of four marine ecosystems. *Prog. Oceanogr.* **81**:10–28.
- Durbin, E.G., Durbin, A.G., Langton, R.W. and Bowman, R.E. (1983) Stomach contents of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, and estimation of their daily rations. *Fish. Bull.* **81**:437–454.
- Eggers, D.M. (1977) Factors in interpreting data obtained by diel sampling of fish stomachs. *J. Fish. Res. Board Can.* **34**:290–294.
- Elliot, J.M. and Persson, L. (1978) The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.* **47**:977–991.
- Enfield, D.B., Mestas-Nunez, A.M. and Trimble, P.J. (2001) The Atlantic Multidecadal Oscillation and its relation to rainfall and river flows in the continental U.S. *Geophys. Res. Lett.* **28**:2077–2080.
- Fahrig, L., Lilly, G.R. and Miller, D.S. (1993) Predator stomachs as sampling tools for prey distribution, Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*). *Can. J. Fish Aquat. Sci.* **50**:1541–1547.
- Fogarty, M.J. and Murawski, S.A. (1998) Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecol. Appl.* **8**:S6–S22.
- Ford, M.D. and Link, J.S. (2014) Bounds on biomass estimates and energetic consequences of Ctenophora in the northeast U.S. shelf ecosystem. *Int. J. Oceanogr.* **2014**:8.
- Frank, K.T., Petrie, B., Choi, J.S. and Leggett, W.C. (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**:1621–1623.
- Friedland, K.D., Hare, J.A., Wood, G.B. et al. (2008) Does the fall phytoplankton bloom control recruitment of Georges Bank haddock, *Melanogrammus aeglefinus*, through parental condition? *Can. J. Fish Aquat. Sci.* **65**:1076–1086.
- Garrison, L.P. and Link, J.S. (2000) Fishing effects on spatial distribution and trophic guild structure of the fish community in the Georges Bank region. *ICES J. Mar. Sci.* **57**:723–730.
- Gerking, S.D. (1994) *Feeding Ecology of Fish*. California: Academic Press, 416 pp.
- Gili, J.M., Rossi, S., Pagès, F. et al. (2006) A new trophic link between the pelagic and benthic systems on the Antarctic shelf. *Mar. Ecol. Prog. Ser.* **322**:43–49.
- Graf, G. (1992) Benthic-pelagic coupling: a benthic view. *Oceanogr. Mar. Biol.* **30**:149–190.
- Graham, W.M., Gelcich, S., Robinson, K.L. et al. (2014) Linking human well-being and jellyfish: ecosystem services, impacts, and societal responses. *Front. Ecol. Environ.* **12**:515–523.
- Haag, A. (2005) Whale fall. *Nature* **433**:566–567.
- Halpern, B.S., Cottenie, K. and Broitman, B.R. (2006) Strong top-down control in Southern California kelp forest ecosystems. *Science* **312**:1230–1232.
- Hamner, W.M., Madin, L.P., Aldredge, A.L., Gilmer, R.W. and Hamner, P.P. (1975) Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behavior. *Limnol. Oceanogr.* **20**:907–917.
- Hannan, K. (2009) Determination of gastric evacuation rate for immature spiny dogfish. In: *Biology and Management of Dogfish Sharks*. V.F. Gallucci, G.A. McFarlane & G.G. Bargmann (eds) Maryland: American Fisheries Society, pp. 253–258.
- Heaslip, S.G., Iverson, S.J., Bowen, W.D. and James, M.C. (2012) Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): video evidence from animal-borne cameras. *PLoS One* **7**:e33259.
- Higgs, N.D., Gates, A.R. and Jones, D.O.B. (2014) Fish food in the deep sea: revisiting the role of large food-falls. *PLoS One* **9**:e96016.
- Howarth, L.M., Roberts, C.M., Thurstan, R.H. and Stewart, B.D. (2014) The unintended consequences of simplifying the sea: making the case for complexity. *Fish Fish.* **15**:690–711.
- Hurrell, J.W., Kushnir, Y., Otttersen, G. and Visbeck, M. (2003) An overview of the North Atlantic Oscillation. In: *The North Atlantic Oscillation: climatic significance and environmental impact*. *Geophys. Monogr.* **134**:1–35.
- Jackson, J.B.C. (2008) Ecological extinction and evolution in the brave new ocean. *Proc. Natl Acad. Sci. USA* **105**:11458–11465.
- Kane, J. (2007) Zooplankton abundance trends on Georges Bank, 1977–2004. *ICES J. Mar. Sci.* **64**:909–919.
- Kideys, A.E. (2002) Fall and rise of the Black Sea ecosystem. *Science* **297**:1482–1484.
- Lambert, Y. and Dutil, J.D. (2000) Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. *Can. J. Fish Aquat. Sci.* **57**:815–825.
- Latour, R.J., Gartland, J., Bonzek, C.F. and Johnson, R.A. (2008) The trophic dynamics of summer flounder (*Paralichthys dentatus*) in Chesapeake Bay. *Fish. Bull.* **106**:47–57.
- Leaf, R.T. and Friedland, K.D. (2014) Autumn bloom phenology and magnitude influence haddock recruitment on Georges Bank. *ICES J. Mar. Sci.* **71**:2017–2025.
- Lebrato, M. and Jones, D.O.B. (2009) Mass deposition event of *Pyrosoma atlanticum* carcasses off Ivory Coast (West Africa). *Limnol. Oceanogr.* **54**:1197–1209.
- Lebrato, M., de Jesus Mendes, P., Steinberg, D.K. et al. (2013a) Jelly biomass sinking speed reveals a fast carbon export mechanism. *Limnol. Oceanogr.* **58**:1113–1122.
- Lebrato, M., Molinero, J., Cartes, J.E., Lloris, D., Mélin, F. and Beni-Casadella, L. (2013b) Sinking jelly-carbon unveils potential environmental variability along a continental margin. *PLoS One* **8**:e82070.
- Lechowicz, M.J. (1982) The sampling characteristics of electivity indices. *Oecologia* **52**:22–30.
- Link, J.S. and Almeida, F.P. (2000) An overview and history of the Food Web Dynamics Program of the Northeast Fisheries Science Center, Woods Hole, Massachusetts. *U.S. Dep. Commer. NOAA Tech. Memo. NMFS-NE-159*: 60 pp.
- Link, J.S. and Ford, M.D. (2006) Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. *Mar. Ecol. Prog. Ser.* **320**:153–159.
- Link, J.S. and Garrison, L.P. (2002) Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. *Fish. Res.* **55**:71–86.
- Link, J.S., Fulton, E.A. and Gamble, R.J. (2010) The northeast US application of ATLANTIS: a full system model exploring marine ecosystem dynamics in a living marine resource management context. *Prog. Oceanogr.* **87**:214–234.
- Litzow, M.A., Mueter, F.J. and Hobday, L.J. (2014) Reassessing regime shifts in the North Pacific: incremental climate change and commercial fishing are necessary for explaining

- decadal-scale biological variability. *Glob. Change Biol.* **20**:38–50.
- Lynam, C.P., Heath, M.R., Hay, S.J. and Brierley, A.S. (2005) Evidence for impacts by jellyfish on North Sea herring recruitment. *Mar. Ecol. Prog. Ser.* **298**:157–167.
- Madin, L.P., Kremer, P., Wiebe, P.H., Purcell, J.E., Horgan, E.H. and Nemazie, D.A. (2006) Periodic swarms of the salp *Salpa aspera* in the Slope Water off of NE United States: biovolume, vertical migration, grazing, and vertical flux. *Deep-sea Res. I* **53**:804–819.
- Martini, F.H. (1998) The ecology of hagfishes. In: *The Biology of Hagfishes*. J.M. Jørgensen, J.P. Lomholt, R.E. Weber, H. Malte (eds) Netherlands: Springer, pp. 57–77.
- Milislenda, G., Rosa, S., Fuentes, V.L. et al. (2014) Jellyfish as prey: frequency of predation and selective foraging of *Boops boops* (Vertebrata, Actinopterygii) on the mauve stinger *Pelagia noctiluca* (Cnidaria, Scyphozoa). *PLoS One* **9**:e94600.
- Miller, C.B. (2004) *Biological Oceanography*. Oxford, UK: Blackwell Science Ltd, 402 pp.
- Mills, K.E., Pershing, A.J., Sheehan, T.F. and Mountain, D. (2013) Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Glob. Change Biol.* **19**:3046–3061.
- Moustahfid, H., Tyrrell, M.C., Link, J.S., Nye, J.A., Smith, B.E. and Gamble, R.J. (2010) Functional feeding responses of piscivorous fishes from the northeast US continental shelf. *Oecologia* **163**:1059–1067.
- Möller, H. (1984) Reduction of a larval herring population by jellyfish predator. *Science* **224**:621–622.
- Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M. and Axe, P. (2009) Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. *Glob. Change Biol.* **15**:1377–1393.
- NEFC (Northeast Fisheries Center). (1988) An evaluation of the bottom trawl survey program of the Northeast Fisheries Center. US Dep. Commer. NOAA Tech. Memo. NMFS-F/NEC-52: 83 pp.
- NEFSC (Northeast Fisheries Science Center). (2006) 43rd Northeast Regional Stock Assessment Workshop (43rd SAW) assessment report. US Dep Commer Northeast Fish. Sci. Cent. Ref. Doc. 06-25: 400 pp.
- NEFSC (Northeast Fisheries Science Center). (2007) 44th Northeast Regional Stock Assessment Workshop (44th SAW) assessment report. US Dep. Commer. Northeast Fish. Sci. Cent. Ref. Doc. 07-10: 661 pp.
- NEFSC (Northeast Fisheries Science Center). (2014) 59th Northeast Regional Stock Assessment Workshop (59th SAW) assessment report. US Dep Commer Northeast Fish Sci Cent Ref Doc 14-09: 782 pp.
- Nye, J.A., Link, J.S., Hare, J.A. and Overholtz, W.J. (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the northeast United States continental shelf. *Mar. Ecol. Prog. Ser.* **393**:111–129.
- Nye, J.A., Gamble, R.J. and Link, J.S. (2013) The relative impact of warning and removing of top predators on the northeast US large marine biotic community. *Ecol. Model.* **264**:157–168.
- Österblom, H., Olsson, O., Blenckner, T. and Furness, R.W. (2008) Junk-food in marine ecosystems. *Oikos* **117**:967–977.
- Paelr, H.W. and Huisman, J. (2008) Blooms like it hot. *Science* **320**:57–58.
- Petralia, R.S., Mattson, M.P. and Yao, P.J. (2014) Aging and longevity in the simplest animals and the quest for immortality. *Aging Res. Rev.* **16**:66–82.
- Pitt, K.A., Duarte, C.M., Lucas, C.H. et al. (2013) Jellyfish body plans provide allometric advantages beyond low carbon content. *PLoS One* **8**:E72683.
- Power, M.E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* **73**:733–746.
- Priede, I.G., Bagley, P.M. and Smith, K.L. Jr (1994) Seasonal change in activity of abyssal demersal scavenging grenadiers *Coryphaenoides (Nematonurus) armatus* in the eastern North Pacific Ocean. *Limnol. Oceanogr.* **39**:279–285.
- Purcell, J.E. (1988) Quantification of *Mnemiopsis leidyi* (Ctenophora, Lobata) from formalin-preserved plankton samples. *Mar. Ecol. Prog. Ser.* **45**:197–200.
- Purcell, J.E. (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Ann. Rev. Mar. Sci.* **4**:209–235.
- Purcell, J.E. and Arai, M.N. (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* **451**:27–44.
- Qiu, J. (2014) Coastal havoc boots jellies. *Nature* **514**:545.
- R Core Team. (2013) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reid, R.N., Almeida, F.P. and Zetlin, C.A. (1999) Essential fish habitat source document: fishery independent surveys, data sources, and methods. U.S. Dep. Commer. NOAA Tech. Memo. NMFS-NE-122: 39 pp.
- Richardson, A.J., Bakun, A., Hays, G.C. and Gibbons, M.J. (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol. Evol.* **24**:312–322.
- Sato, N.N., Kokubun, N., Yamamoto, T., Watanuki, Y., Kitaysky, A.S. and Takahashi, A. (2015) The jellyfish buffet: jellyfish enhance seabird foraging opportunities by concentrating prey. *Biol. Lett.* **11**:20150358.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. and Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature* **413**:591–596.
- Schrope, M. (2012) Attack of the blobs. *Nature* **482**:20–21.
- Sherman, K., Jaworski, N.A. and Smayda, T.J. (1996) *The Northeast Shelf Ecosystem: Assessment Sustainability and Management*. Oxford, UK: Blackwell Science, 564 pp.
- Smetacek, V. and Zingone, A. (2013) Green and golden seaweed tides on the rise. *Nature* **504**:84–88.
- Smith, B.E. and Link, J.S. (2010) The trophic dynamics of 50 finfish and 2 squid species on the northeast US continental shelf. U.S. Dep. Commer. NOAA Tech. Memo. NMFS-NE-216: 640 pp.
- Smith, C.R., Mincks, S. and DeMaster, D.J. (2006) A synthesis of benthic-pelagic coupling on the Antarctic shelf: food banks, ecosystem inertia and global climate change. *Deep Sea Res. II* **53**:875–894.
- Smith, B.E., Collie, J.S. and Lengyel, N.L. (2013) Effects of chronic bottom fishing on the benthic epifauna and diets of demersal fishes on northern Georges Bank. *Mar. Ecol. Prog. Ser.* **472**:199–217.
- Smith, B.E., Collie, J.S. and Lengyel, N.L. (2014) Fish trophic engineering: ecological effects of the invasive ascidian *Didemnum vexillum* (Georges Bank, northwestern Atlantic). *J. Exp. Mar. Biol. Ecol.* **461**:489–498.

- Steimle, F.W. and Terranova, R.J. (1985) Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. *J. Northw. Atl. Fish. Sci.* **6**:117–124.
- Stoner, E.W., Yeager, L.A., Sweatman, J.L., Sebilian, S.S. and Layman, C.A. (2014) Modification of a seagrass community by benthic jellyfish blooms and nutrient enrichment. *J. Exp. Mar. Biol. Ecol.* **461**:185–192.
- Sweetman, A.K. and Chapman, A. (2011) First observations of jelly-falls at the seafloor in a deep-sea fjord. *Deep Sea Res. I* **58**:1206–1211.
- Sweetman, A.K., Smith, C.R., Dale, T. and Jones, D.O.B. (2014) Rapid scavenging of jellyfish carcasses reveals the importance of gelatinous material to deep-sea food webs. *Proc. R. Soc. B* **281**:20142210.
- Theroux, R.B. and Wigley, R.L. (1998) Quantitative composition and distribution of the macrobenthic invertebrate fauna of the continental shelf ecosystems of the northeastern United States. *U.S. Dep. Commer. NOAA Tech. Rep. NMFS 140*: 240 pp.
- Tinta, T., Kogovšek, T., Malej, A. and Turk, V. (2012) Jellyfish modulate bacterial dynamic and community structure. *PLoS One* **7**:e39274.
- Utne-Palm, A.C., Salvanes, A.G.V., Currie, B. et al. (2010) Trophic structure and community stability in an overfished ecosystem. *Science* **329**:333–336.
- Valiela, I. (1984) *Marine Ecological Processes*. New York: Springer, 546 pp.
- Weisse, T., Gomoiu, M.T., Scheffel, U. and Brodrecht, F. (2002) Biomass and size composition of the comb jelly *Mnemiopsis* sp. in the north-western Black Sea during spring 1997 and summer 1995. *Estuar. Coast. Shelf Sci.* **54**:423–437.
- Zintzen, V., Roberts, C.D., Anderson, M.J., Stewart, A.L., Struthers, C.D. and Harvey, E.S. (2011) Hagfish predatory behavior and slime defence mechanism. *Sci. Rep.* **1**:131.
- Zuur, A.F., Fryer, R.J., Jolliffe, I.T., Dekker, R. and Beukema, J.J. (2003a) Estimating common trends in multivariate time series using dynamic factor analysis. *Environmetrics* **14**:665–685.
- Zuur, A.F., Tuck, I.D. and Bailey, N. (2003b) Dynamic factor analysis to estimate common trends in fisheries time series. *Can. J. Fish Aquat. Sci.* **60**:542–552.