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Event scale and persistent drivers of fish and macroinvertebrate distributions on the Northeast US Shelf

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The Northeast US Continental Shelf Large Marine Ecosystem is experiencing warming at a rate exceeding that of many other large marine ecosystems and has undergone significant climate-related changes. We examined the effect of thermal events and shifting patterns of primary and secondary productivity on the distribution of fish and macroinvertebrate species during the period 1968–2016. Though subject to inter-annual change, the along-shelf centre of gravity of chlorophyll concentration lacked a trend. Similarly, zooplankton bio-volume and total abundance along-shelf distance were also found to be without trend. However, the trend in the centre of gravity of copepod taxa diverged from the trends in bio-volume and non-copepod zooplankton abundance, suggesting most of these taxa had shifted in distribution to the northeast. The centres of gravity of fish and macroinvertebrate species have trended significantly to the northeast, suggesting copepods may play a key role in the distribution of higher trophic levels. Analysis of thermal events suggest that abrupt change in temperature can actuate persistent change in the distribution of fish and macroinvertebrate species. In aggregate, these broad trophic level patterns imply that distributional changes affecting upper trophic levels were dominated by thermal mechanisms, whereas lower trophic productivity, although subject to the same thermal conditions, exhibited less of a response. We hypothesize this lack of distributional response at lower trophic levels is due to their higher rates of production and turnover, and hence reflect a capacity to better integrate seasonal thermal changes. Furthermore, distributional changes of upper trophic levels may also be significantly impacted by feeding interactions at specific life history stages, where temperature affects both predator and prey.

Keywords: chlorophyll concentration, climate change, fish distribution, thermal habitat, zooplankton.

Introduction
In recent decades, the thermal conditions for the Northeast US Continental Shelf Large Marine Ecosystem (hereafter the Northeast US Shelf, or NEUS) have changed, with the ecosystem experiencing a rate of warming among the fastest worldwide (Belkin, 2009; Mills *et al.*, 2013; Pershing *et al.*, 2015). Such warming can have profound impacts on the ecophysiology of marine organisms (Neill *et al.*, 1994) through the biological processes influenced by temperature (Brett, 1979). Hence, changes in temperature can alter the habitats of marine fish and macro-invertebrates with significant impacts on growth and mortality (Anderson, 1988; Pepin, 1991), with these impacts often focused on the essential life history stages of a species (Anderson *et al.*, 2013). Contrasting regions of changing habitat quality of a species will likely cause local abundances to vary with concomitant changes in species distribution. For many NEUS marine fish and macroinvertebrate taxa, thermal habitat preferences are well understood (Kleisner *et al.*, 2017), which when coupled with the expected warming of this ecosystem under future climate scenarios (Saba *et al.*, 2016), suggest that the distribution of many species may shift beyond current ranges. This creates an expectation that the ecosystem will be redefined and the

manner in which humans interact with it will change as well (Hare *et al.*, 2016).

In the NEUS, the influence of climate change on marine fish populations has often been represented through changes in latitude and depth distribution (Nye *et al.*, 2009; Lucey and Nye, 2010; Pinsky and Fogarty, 2012; Pinsky *et al.*, 2013a; Kleisner *et al.*, 2015, 2016). More nuanced work has addressed changes in the population abundance over species-specific life stages (Walsh *et al.*, 2015) and how distribution changes may be related to changes in habitat suitability for a given species (Hare *et al.*, 2012; Lynch *et al.*, 2015; McManus *et al.*, 2018). Several methods have been used to quantify spatial distribution shifts for marine populations; each varying based on the abundance and distance units of measure and desired outcome products (Pinsky *et al.*, 2013b; Thorson *et al.*, 2016; Adams, 2017). Centre of gravity estimates have been one of the more commonly used indicators used to assess changes in spatial distribution (Woillez *et al.*, 2007), which provide insight into the average movement over time. While spatial distribution indicators and thermal relationships have been described for many NEUS marine fish and macroinvertebrates, similar evaluations for lower trophic levels in the region are fewer.

The NEUS has higher trophic connectivity than many other marine systems (Link *et al.*, 2010), making it imperative to understand changes in distribution across trophic levels. Furthermore, this high level of connectivity suggests that adaptability rather than specificity of predators may play a larger role in shaping marine distributions than thermal and thermally related stressors. As a significant prey source for pelagic fish and the early life history stages of many fish species, zooplankton, particularly copepods, have been used as an indicator of marine ecosystem regime shifts (Sherman *et al.*, 1998). Long-term changes in zooplankton biomass and species composition have also been linked to large shifts in the biomass and recruitment success of upper trophic levels in the NEUS and other marine systems (Beaugrand *et al.*, 2003; Alheit and Niquen, 2004; Mackas *et al.*, 2007; Hipfner, 2008; Bi *et al.*, 2011; Hunt *et al.*, 2011; Tanasichuk and Routledge, 2011; Friedland *et al.*, 2013). In turn, zooplankton have a trophic dependence on phytoplankton, which defines the length of the food chain and the pathways from primary productivity to higher trophic levels (Ryther, 1969; Canales *et al.*, 2016). While phytoplankton constitute the base of the NEUS food web, evaluating both phytoplankton and zooplankton are important when assessing trophic impacts on fish and macroinvertebrate populations. For example, on global scales, the amount of primary productivity channeled to mesozooplankton is more highly correlated with fishery yields than primary productivity itself (Friedland *et al.*, 2012). Shifts in fish and macroinvertebrates are well documented in this ecosystem, yet those of zooplankton and phytoplankton are relatively under examined.

To understand how the different trophic levels of the NEUS ecosystem are responding to climate change and ocean warming, we investigated prospective distribution shifts for phytoplankton, zooplankton, and fish and macroinvertebrate taxa over a period of five decades. Three centre of gravity metrics were used to characterize distributional change: distance along the coast, distance to the coast, and depth. The different metrics allowed us to compare the various potential responses a given trophic level may exhibit in response to a set of forcing factors. These metrics account for potential movements latitudinal along the coast and for response to gradients that may be associated with depth and coastal influences. The observed changes in distribution were further tested using change-point detection statistics to determine whether event-scale processes drove the changes in observed distribution and whether species return to their previously established locations after an event. Finally, the temperatures of occurrence for species were compared with ocean temperature to evaluate its role in distributional shifts across trophic levels.

Material and methods
Study system and distribution metrics
A long-term monitoring program for the NEUS ecosystem has been measuring fish and macroinvertebrate populations for approximately five decades over the period 1968–2016. Complimentary programs have measured zooplankton populations within a similar period, 1977–2015, noting that were interruptions to these time series in the 1990s. Chlorophyll *a* concentration has not been measured synoptically on the Northeast Shelf in a consistent fashion by any monitoring program; therefore, we relied on remote sensing data to characterize the distribution of primary producers during the period 1979–2016, noting there was an interruption in the remote sensing data during the late 1980s into the early 1990s. Collectively these data, which will be described in detail below, allow for the comparison of spatial–temporal shifts over multiple trophic levels within the ecosystem. Change in distribution was characterized with three spatial distribution metrics applied to chlorophyll *a* concentration, zooplankton bio-volume, zooplankton taxon abundance, and fish and macroinvertebrate taxon abundance within the extent of the ecosystem (Figure 1a). The three centre of gravity metrics included along-shelf distance, depth of occurrence, and distance to the coastline. Along-shelf distance was taken as the distance from the origin of a transect originating at 76.53°W 34.60°N extending to 65.71°W 43.49°N at a point closest to the position of the subject taxon. The distance is expressed in km, with examples of along-shelf position estimates illustrated in Figure 1a; lower along-shelf distances correspond to positions in the southwest portion of the ecosystem and higher values more in the northeast. The along-shelf distance centre of gravity was the weighted mean distance using the abundance measure of the subject taxon as the weighting factor. Depth of occurrence represents the depth (depth of the seabed) associated the abundance measure, the centre of gravity depth expressed in meter. Distance to the coast is the distance to the closest position on the coastline associated with the abundance measure, the centre of gravity distance expressed in units of kilometers.

Water temperature
Surface and bottom water temperature was considered a potential factor in actuating distribution events. Temperature fields for the extent of the ecosystem were developed using an optimal interpolation approach where annual data were combined with seasonal climatologies over the period 1968–2016. Temperature on the NEUS was collected using conductivity/temperature/depth (CTD) instruments, with the most complete sample coverage in spring (February–April) and fall (September–November). To correct for the differences in date of collection between years, temperatures were standardized to a collection date of April 3 for spring collections and 11 October for fall, which were the mean dates for the data collections by season. The corrections were
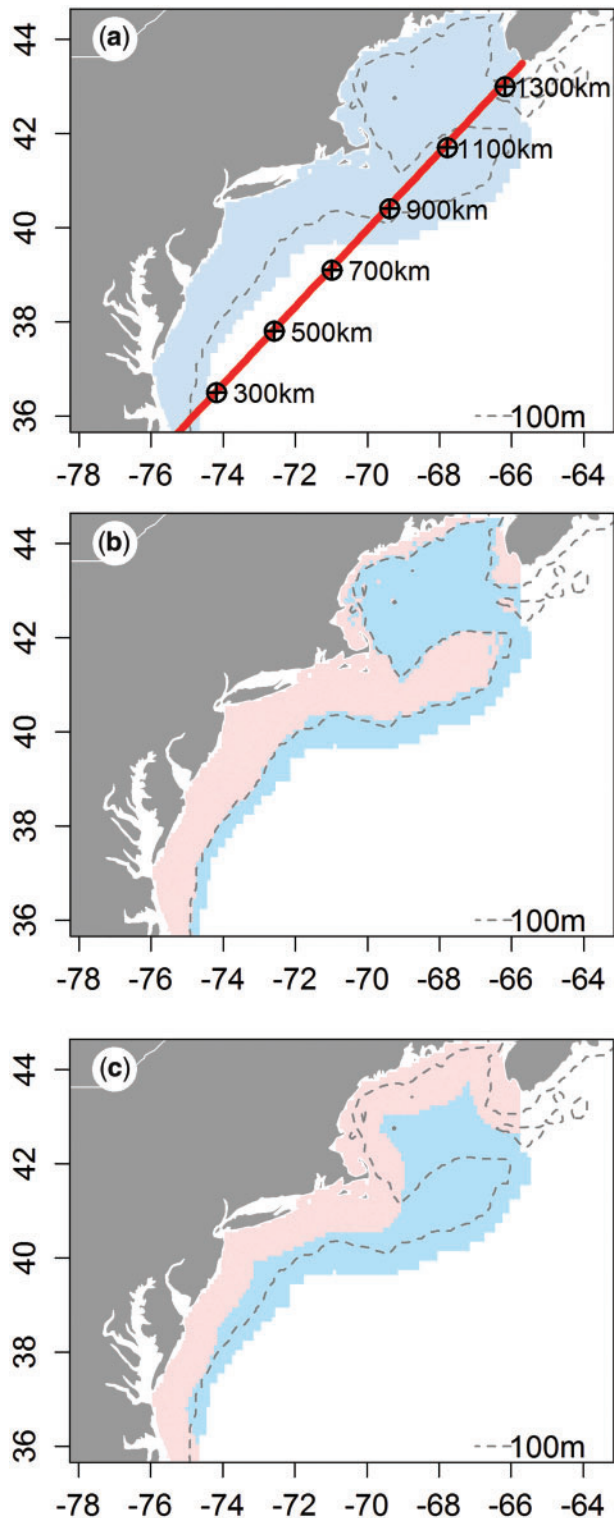
Figure 1. Map of the US Northeast Shelf showing the extent of the ecosystem as shaded region (a). Line marks along-shelf reference line with reference distances marked. Maps of differential depth (b) and distance to the coast (c) in the ecosystem with lighter red regions representing the areas less than the median in terms of depth and distance, darker blue regions greater than the median.

based on linear regressions of temperature versus day of the year for a half-degree grid of the ecosystem. For the same grid, mean bottom temperature was calculated by year and season. For grid locations that had data for at least 80% of the time series, which preserved most of the locations on the shelf, the data from those locales were used to calculate a seasonal mean temperature. The annual seasonal means were used to calculate temperature anomalies, which were combined over the time series to provide seasonal surface and bottom temperature anomaly climatology. Returning to the raw data, the observations for a year, season, and depth were then used to estimate an annual field using universal kriging with depth as a covariate (R package automap ver. 1.0–14). The annual field was then combined with the climatology anomaly field, adjusted by the annual mean, using the variance field from the kriging as the basis for a weighted mean between the two. The variance field was divided into quartiles with the first quartile (lowest kriging variance) carrying with it a weighting of 4:1 between the annual to climatology values. Hence, the optimal interpolated field at these locations were skewed toward the annual data reflecting their proximity to actual data locations, reflected by low kriging variance associated with them. The weighting ratio shifted to 1:1 in the highest variance quartile reflecting less information from the annual field and more from the climatology.

The temperature fields were applied as yearly seasonal means and as temperature differentials based on two partitioning schemes associated with the centre of gravity metrics. In one scheme, the ecosystem was divided by depth with a shallow zone based on the depth locations below the median depth and a deep zone for those above the median (Figure 1b). The temperature depth differential was computed as the mean for the shallow minus the mean of the deep. In the other scheme, the ecosystem was divided by distance to the coast with a close zone based on the distance locations below the median distance and a distance zone for those above the median (Figure 1c). The temperature distance differential was computed as the mean for the close minus the mean of the far.

Chlorophyll concentration

We analysed centre of gravity of chlorophyll a concentration using data extracted from remote-sensing databases. Chlorophyll a concentration (mg m^{-3}) data from 1979 to 1986 were provided by the Coastal Zone Color Scanner (CZCS) sensor (Gregg and Conkright, 2002), available from the Ocean Color Website (oceancolor.gsfc.nasa.gov/). The data were analysed at a 9 km-resolution and resampled to match a 0.1° grid over the extent of the ecosystem (Figure 1a). Chlorophyll a concentration during the period 1997–2016 was based on measurements made with the Sea-viewing Wide Field of View Sensor (SeaWiFS), Moderate Resolution Imaging Spectroradiometer on the Aqua satellite (MODIS), Medium Resolution Imaging Spectrometer (MERIS), and Visible and Infrared Imaging/Radiometer Suite (VIIRS) sensors. We used the Garver, Siegel, Maritorena Model (GSM) merged data product obtained from the Hermes GlobColour website (hermes.acri.fr/index.php). These four-sensor time series were combined using a bio-optical model inversion algorithm (Maritorena et al., 2010). The data was downloaded at a 4 km

resolution and resampled to match a 0.1° grid over the extent of the ecosystem.

Annual mean spring and fall chlorophyll *a* concentration maps were developed, from which along-shelf distance, depth, and distance to the coast centres of gravity for chlorophyll *a* concentration were calculated. We evaluated the time series changes in distribution metrics using Mann–Kendall non-parametric trend analysis. We calculated Kendall's tau test for the significance (two-tailed test) of a monotonic time series trend (Mann, 1945) for centre of gravity of along-shelf distance, depth, and distance to the coast. We also calculated Theil–Sen slopes of trend, which is the median slope joining all pairs of observations (R package wql, version 4.9).

Zooplankton bio-volume and abundance

Zooplankton abundance has been measured within the context of multiple sampling programs with varying sampling designs. The two most comprehensive monitoring programs over the study period were the Marine Resources Monitoring, Assessment, and Prediction Program or MARMAP (1977–1987) and the Ecosystem Monitoring Program or EcoMon (1992–present) programs, both serving as shelf-wide surveys of the ecosystem (Sherman *et al.*, 1998; Kane, 2007). In addition, there were two sampling programs with more specific spatial and temporal foci, the Herring–Sandlance study (1988–1993) and the US GLOBEC program (1994–1999), both of which were mainly focused on sampling in the Georges Bank area (Beardsley *et al.*, 2003). The raw zooplankton abundance data are made publicly available at ftp://ftp.nefsc.noaa.gov/pub/hydro/zooplankton_data/. In all of these surveys, zooplankton were sampled obliquely through the water column to within 5 m of the sea floor or a maximum depth of 200 m using paired 61-cm Bongo samplers equipped with 333-micron mesh nets. However, sample distribution has not been consistent through time, with segments of the time series comprised of differing combinations of fixed, random, and regionally focused stations. In addition, vessel availability has resulted in years lacking a distributional balance in zooplankton samples over the ecosystem.

From this collection of sample stations, we considered candidate taxa to represent the distribution of secondary production in the ecosystem. For each station, we analysed the settled bio-volume (a proxy for total planktonic biomass) in the units of ml per m^3, and taxa-specific abundance in units of number per m^3. From a set of 38 candidate taxa (i.e. these higher abundance taxa), 21 met the criterion of occurring in at least 38 years of one or both of the seasonal time series. This metric resulted in 17 taxa for the spring data (9 of which were copepod species) and 20 taxa in fall, with 11 representing copepods. Of these taxa, 16 occurred in both seasons (Supplementary Table S1). Because of the aforementioned issues of sample distribution, we elected to interpolate the zooplankton data over the extent of the ecosystem (Figure 1a) using ordinary kriging; the data was logarithm ($\log_{10}(x+1)$) transformed before interpolation. The interpolated fields by year and season were then used to determine the centre of gravity of along-shelf distance, depth, and distance to the coast for seasonal bio-volume and zooplankton taxa. The overall time series of zooplankton data extended from 1977 to 2015; however, due to data adequacy concerns, the years 1989, 1990, 1991, and 1994 of the spring data and years 1989, 1990, and 1992 of the fall data were excluded from analyses.

Fish and macroinvertebrate species abundance

The principal fishery independent survey on the NEUS is the bottom trawl survey conducted by the Northeast Fisheries Science Center, which provides both spatial and temporal depictions of fish and macroinvertebrate abundances (Grosslein, 1969). The survey began in the fall of 1963, but for consistency, we restricted the analysis to the years 1968–2016. The survey data are publicly available at http://comet.nefsc.noaa.gov/cgi-bin/ioos/ioos.pl. Surveys are conducted in the spring and fall and are based on a stratified random design. Catch from the survey tows can be identified to species, genus, functional group, or an unidentified category. We restricted this analysis to catch identified to species since most of the catch is identified to this level and provides the most reliable information on change in fish and macroinvertebrate distribution. Species were also assigned functional groups based on their adult prey preference and vertical presence to assess broader ecosystem changes: benthivores, demersal piscivores, pelagic piscivores, or planktivores. We first considered seasonal lists of candidate species that included taxa that occurred in at least 100 tows during the study time series. This exercise produced lists of 122 and 174 species in spring and fall, respectively. The distribution metrics were then calculated for each candidate species by season. In spring, 72 of the candidate species had catches distributed over the time series and were thus included in the analysis (Supplementary Table S2). Another 16 taxa were found to have catch distributed over only part of the time series, and though of interest in terms of distributional change, these partial time series raised concerns over change in availability and identification of these taxa in the survey. In fall, 79 of the candidate species had catches distributed over the time series (Supplementary Table S3); another 34 were found to have partial time series. Our centre of gravity calculations were similar to the methods used in previous analyses of these data (Nye *et al.*, 2009; Bell *et al.*, 2015) that applied calculations to catch from a core set of survey strata consistently sampled over the time series. In addition, we applied a tow per strata weighting to ameliorate the differences in the allocation of stations to strata (Bell *et al.*, 2015).

Change in distribution events

Distributional change events for fish and macroinvertebrates were identified using change point statistics and contextualized with step change data from bottom and surface temperature time series. Change events for fish and macroinvertebrates were detected using the sequential averaging algorithm Sequential *t*-test Analysis of Regime Shifts, or STARS (Rodionov, 2004, 2006), which finds the change points in a time series. Consistent with other applications of this approach (Lavaniegos and Ohman, 2007), the STARS algorithm parameters were specified *a priori*: the alpha level used to test for a change in the mean was set to $\alpha = 0.1$; the length criteria, the number of time steps to use when calculating the mean level of a new regime, was set to 10; and, the Huber weight parameter, which determines the relative weighting of outliers in the calculation of the regime mean, was set to 3. Positive and negative change points were summed each year. A year with a total number of change points equal or greater than two standard deviations above the mean were considered of interest for further analysis. For events that occurred early in the times, the species that had a change in distribution were examined further to determine how long after the event they remained at the new distribution. The intention was to provide evidence as to whether an event results in a persistent change in distribution. For comparison, time series of step change in bottom and surface

temperature were represented as residuals from a loess fit curve, noting that the fits were not used to suggest significance, but instead to offer a consistent basis to visualize potential outliers. The same treatment was applied to the bottom and surface depth differential temperature and distance to coast temperature differential.

Occupancy bottom temperature

Occupancy temperature was taken as the mean standardized bottom temperature associated with each tow by species. For each spring taxon with data over the full time series, the standardized bottom temperature for tows within the study domain were averaged, and in turn, an annual mean was taken of the species means. The same procedure was done for the fall taxa with data over the full time series. Species trends were evaluated with Mann–Kendall non-parametric trend analysis.

Multivariate analysis

Multivariate relationships between fish and macroinvertebrate distribution responses and zooplankton and temperature explanatory variables were analysed with canonical correlation analysis. We correlated a response variable set that included the along-shelf

distribution metrics for benthivores, demersal piscivores, pelagic piscivores, and planktivores to an independent variable set consisting of distribution metrics for other zooplankton and copepods and bottom and surface temperature indices (R package CCA ver. 1.2). For each zooplankton category, along-shelf, depth, and distance to the coast metrics were variables. The temperature variable set included bottom and surface temperature, depth temperature differential, and distant to the coast temperature differential. This was repeated for two other response sets of variables including fish and macroinvertebrate depth and distance to the coast distance metrics with the same independent variable sets.

Results

Trends in chlorophyll distributions

The centre of gravity distribution metrics for chlorophyll *a* concentration had some discernable trends. The spring along-shelf distance for chlorophyll *a* concentration was approximately 850 km at both the beginning and end of the time series (Figure 2a). Along-shelf distance in fall was less dispersed at the beginning of the time series and suggested a centre of gravity closer to 900 km (Figure 2b). However, neither the spring nor the fall chlorophyll *a* concentration
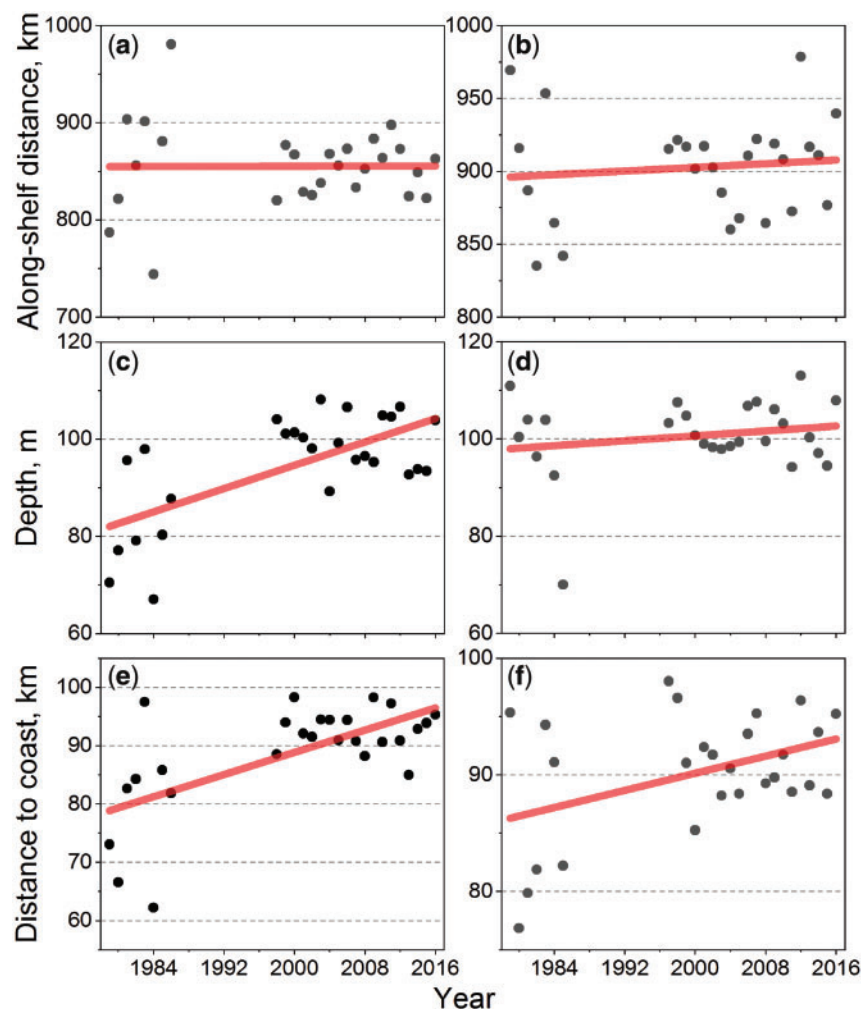

Figure 2. Time series of chlorophyll concentration centre of gravity based on remote sensing date. Spring time frame data along-shelf distance (a), depth (c), and distance to coast (e); fall data for along-shelf distance (b), depth (d), and distance to coast (f). Red lines are linear regression lines.

Table 1. Theil–Sen slope and Mann–Kendall trend test probability (*p*, bold indicates significance at *p*=0.05) for time series of annual centre of gravity of along-shelf distance, depth, and distance to the coast for spring and fall spring and fall chlorophyll concentration, zooplankton abundance and bio-volume, and fish and macroinvertebrate abundance.

Group	Season	Along-shelf distance		Depth		Distance to coast	
		Slope	*p*	Slope	*p*	Slope	*p*
Chlorophyll	Spring	0.020	0.999	0.435	**0.033**	0.345	**0.020**
Chlorophyll	Fall	0.211	0.707	−0.002	0.999	0.155	0.338
Zooplankton abundance	Spring	0.758	0.293	−1.893	0.173	0.096	0.532
Zooplankton bio-volume	Spring	−1.030	0.244	−0.198	0.609	0.234	0.410
Zooplankton abundance	Fall	0.216	0.817	−3.787	**0.037**	0.009	0.902
Zooplankton bio-volume	Fall	−0.060	0.892	0.103	0.614	0.237	0.105
Fish and macroinvertebrates	Spring	1.807	**0.000**	0.075	0.365	−0.007	0.938
Fish and macroinvertebrates	Fall	0.843	**0.000**	0.023	0.724	−0.100	**0.006**

along-shelf distance time series were found to have significant trends (Table 1). The spring centre of gravity depth distribution was generally at the 80 m isobaths during the start of the time series and increased to approximately 100 m during the more contemporary time period (Figure 2c). The fall centre of gravity depth was without trend and remained at approximately 100 m throughout (Figure 2d). The spring depth trend was significant whereas the fall trend was non-significant. The spring and fall distance to the coast centre of gravity trended in similar fashion as depth, tending toward further distances from the coast. The spring time series suggested a change from 80 to 95 km from the coast (Figure 2e), whereas the fall time series suggested an increase from 85 to 95 km (Figure 2f). The spring trend was significant whereas the fall was non-significant.

Trends in zooplankton distributions

Most of the metrics for centre of gravity distribution for zooplankton biomass and abundance did not exhibit significant trends through time. Spring zooplankton abundance and bio-volume along-shelf distances were found to be without trend (Table 1), with positions at approximately 800 and 900 km for abundance and bio-volume, respectively (Figure 3a and d). Along-shelf distance centre of gravity time series were nearly the same for fall abundance and bio-volume (Figure 3g and j, respectively) and their trends were found to be non-significant. Centre of gravity depth distributions for abundance and bio-volume were dramatically different. In both spring and fall, zooplankton abundance depth centre of gravity tended to exceed 100 m (Figure 3b and h, respectively). In contrast, bio-volume depth centre of gravity tended to be less than 100 m in both seasons (Figure 3e and k, respectively). The fall abundance depth centre of gravity time series trend was significant, whereas the other trends were non-significant. There were no significant trends in the zooplankton distance to the coast centre of gravity data. Zooplankton abundance distance to the coast centre of gravity data tended to be approximately 100 km (Figure 3c and i, spring and fall, respectively) whereas the bio-volume distant to the coast was closer to 80 km (Figure 3f and l, spring and fall, respectively).

The trends among zooplankton bio-volume, abundance of non-copepod taxa, and copepod taxa suggest differing distributional responses among these groups. Theil–Sen slopes of centre of gravity of along-shelf distance for copepods averaged approximately 2 km year^{-1} where the slope for bio-volume and the mean slope for the other taxa were negative (Figure 4a and b, spring and fall, respectively). The positive slopes indicated a shift in location to the northeast. Theil–Sen slopes of the centre of gravity for depth were

near zero for bio-volume and other taxa, but the mean slopes for copepod taxa were negative in both spring and fall (Figure 4c and d, spring and fall, respectively). The negative slopes suggested a shift to deeper depths. Theil–Sen slopes of centre of gravity of distance to the coast for copepods were negative, indicating a shift to locations closer to the coast; the slope for bio-volume and the mean slope for the other taxa were both positive, indicating shifts further from shore (Figure 4e and f, spring and fall, respectively).

Trends in fish and macroinvertebrate species distributions

Since the late 1960s, most fish and macroinvertebrate taxa have shifted northeast, as indicated by the higher along-shelf distance centres of gravity. The mean along-shelf distance for fish and macroinvertebrates was approximately 800 km at the beginning of the time series and has increased to greater than 850 km in the most recent years in both spring and fall seasonal surveys (Figure 5a and d). The trends for these time series were also significant (Table 1). Mean depth centre of gravity for fish and macroinvertebrates time series had no discernable trends; however, mean depth tended to be slightly higher in spring than in fall (Figure 5b and e). Seasonal differences in distance to the coast centre of gravity reflect the differences noted in depth distributions, with mean spring distances at approximately 100 km and fall distance at 90 km (Figure 5c and f). The time series trend in the fall data was significant; however, the trends may have been anomalously high values in the beginning of the time series.

The trends among benthivores, demersal piscivores, pelagic piscivores, and planktivores taxa suggest differing distributional responses among these groups. Theil–Sen slopes of centre of gravity of along-shelf distance for planktivores were generally twice the rate for other taxonomic groups (Figure 6a and b, spring and fall, respectively). All these groups had positive slopes, indicating a shift in location to the northeast, with the exception of pelagic piscivores in fall, which had mean slope of zero. Theil–Sen slopes of the centre of gravity for depth were similar for benthivores, demersal piscivores, and planktivores and distinctly lower for pelagic piscivores (Figure 6c and d, spring and fall, respectively). The negative slopes for pelagic piscivores suggest a shift to deeper depths. Theil–Sen slopes of centre of gravity of distance to the coast were similar for all groups (Figure 6e and f, spring and fall, respectively).

Distribution change events

Twelve distributional change events were identified in the time series of fish and macroinvertebrate distribution metrics, two of
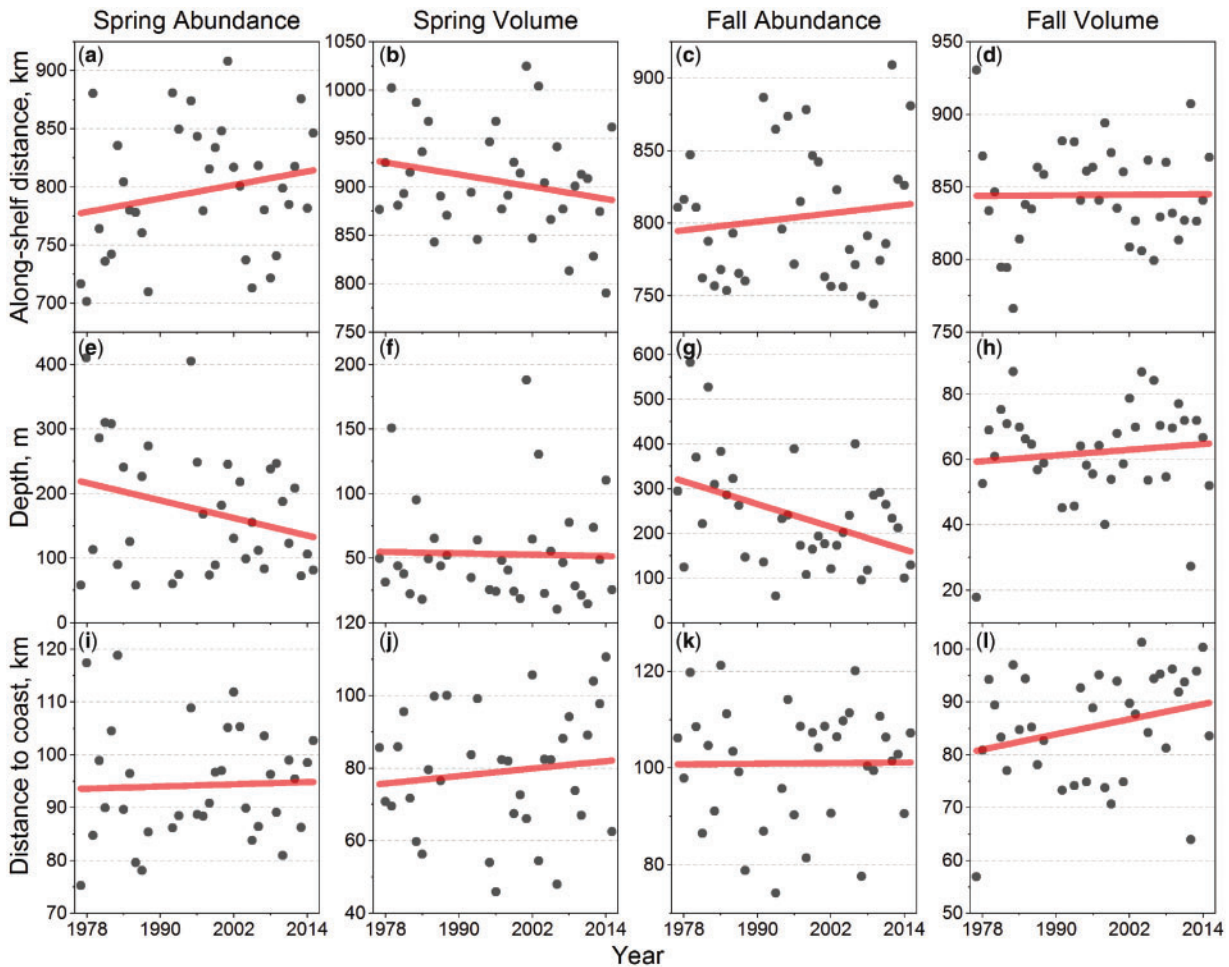
Figure 3. Mean along-shelf distance for spring zooplankton abundance (a) and bio-volume (b) and for fall abundance (c) and bio-volume (d). Mean depth for spring zooplankton abundance (e) and bio-volume (f) and for fall abundance (g) and bio-volume (h). Mean distance to coast for spring zooplankton abundance (i) and bio-volume (j) and for fall abundance (k) and bio-volume (l). Red lines are linear regression lines.

which occurred early enough in the time series to test whether these events led to persistent changes in distribution. On average, four taxa had an identifiable change point in a given year. Most change point events were found in the along-shelf distance data. Two events, in 1986 and 2013, were found in the spring along-shelf data (Figure 7a). The greatest number of events were found in the fall along-shelf data including an event in 1977 and four additional events at the end of the time series (Figure 7b; Table 2). There were three events in the depth data (Figure 7c and d) and two in the distance to the coast data (Figure 7e and f); these events were near the end of the series and were not analysed further since persistent changes could not be tested.

Two along-shelf distance events occurred early in the time series and were evaluated in respect to persistence in distributional change. The spring 1986 event involved 15 species that had an abrupt change in distribution (Table 2). Ten of these species stayed at the new distribution centre of gravity for the rest of the time series with three appearing to return to their original distribution within two decades and the rest after approximately one decade. The group of species persisting at new distributions was taxonomically diverse including an elasmobranch, a clupeid, a pelagic piscivore, a crustacean, and a host of benthic species.

The species responding to this event stayed at their new distribution for more than two decades on average. The fall 1977 event involved 11 species, 4 of which stayed at the new distribution to the end of the time series with 2 returning to their original distribution after approximately three decades and the rest after approximately one decade. A Crustacean, two elasmobranchs, a pelagic piscivore, and two benthic species were among the persistent migrating species, so like the 1986 event a cross section of taxa was impacted. The species responding to this event also stayed at their new distribution for more than two decades on average.

Distributional events were compared with step changes in temperature and temperature differential time series. Bottom and surface temperatures have significantly increased on the order of 1°C over the time series in both spring and fall seasons (Figure 8a, b, e, and f; Table 3). Loess residuals of these time series reveal several distinct temperature step changes in spring bottom and surface temperatures, specifically surface temperature in 1976 and bottom and surface temperatures in 2012 (Figure 8c and g). The only fall temperature change of note was in the bottom temperature during fall 1985 (Figure 8d and h). The fall 1985 bottom temperature change appeared potentially related to the distribution shift in the spring of 1986 given their one season of separation. The spring 1976 temperature change may
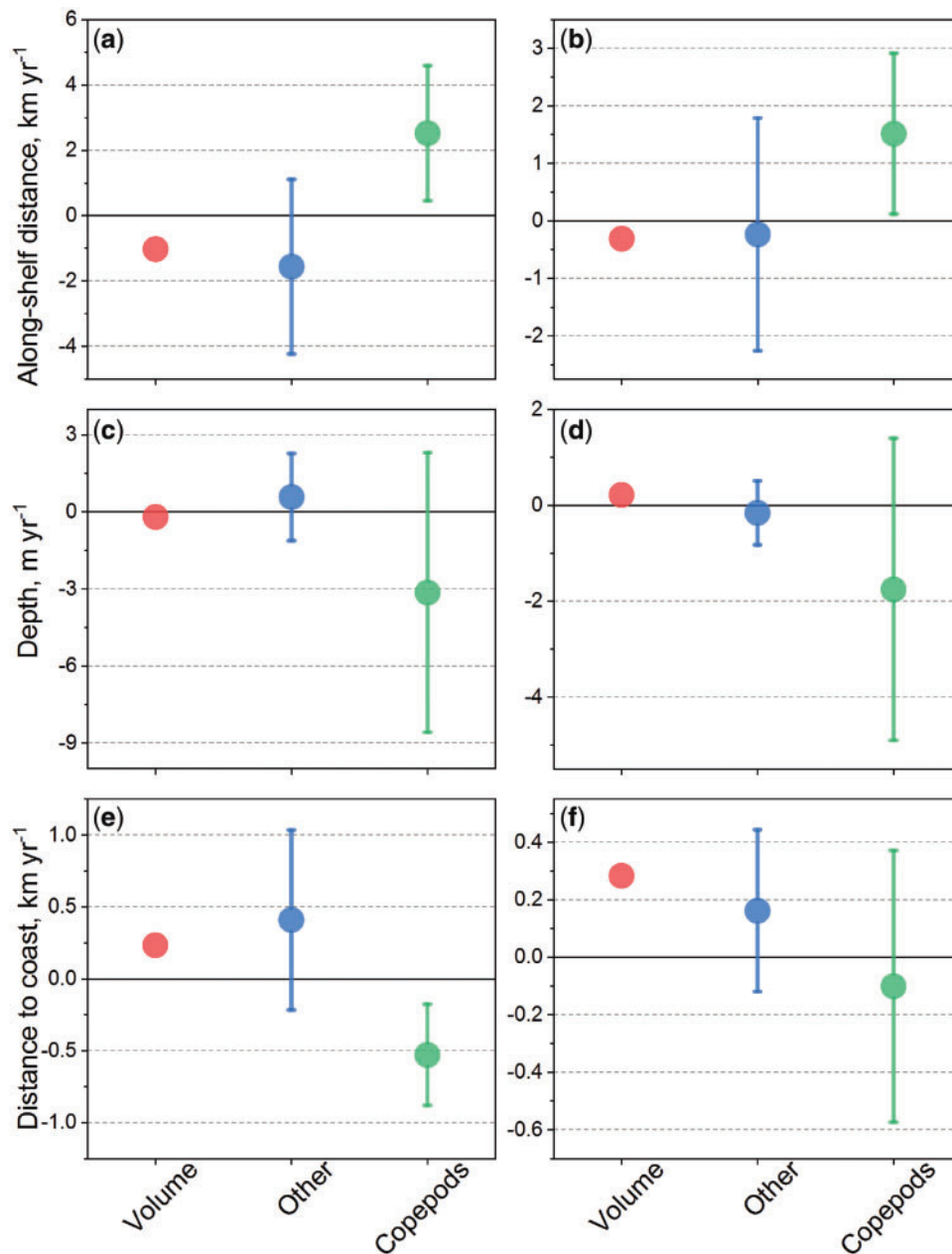
Figure 4. Mean Theil–Sen slope of centre of gravity of spring zooplankton bio-volume (volume), non-copepod zooplankton taxa (other), and copepods (copepods) along-shelf distance (a), depth (c), and distance to the coast (e); for fall along-shelf distance (b), depth (d), and distance to the coast (f). Error bars are 95% confidence intervals.

be related to the fall 1977 distribution shift, but causality with a three-season lag seems unlikely. There are numerous distributional shifts beginning in spring of 2013 and in following years that may be related to the exceptional step change in temperature that occurred in 2012.

Bottom and surface depth temperature differential time series were without significant trends (Supplementary Figure S1a, b, e, and f). There was a spring bottom temperature differential step change in 1975 that preceded the 1977 distribution event by 2.5 years (Supplementary Figure S1g); with such a long lag between thermal and distribution events it does not appear that these events are related. The other step changes in these data were unrelated to the 1977 or 1986 distributional events, but did

include spring change in 2012 and a notable change in 1994 (Supplementary Figure S1c, d, and h). Bottom and surface distance to the coast temperature differential time series were significant in only one instance: the fall surface time series (Supplementary Figure S2a, b, e, and f). None of the step changes in these data were in proximity to the 1977 or 1986 distributional events or related to the recent events beginning in 2012 (Supplementary Figure S2c, d, g, and h).

Occupancy bottom temperature

Occupancy temperature for fish and macroinvertebrate species in spring had a differential response compared with the response
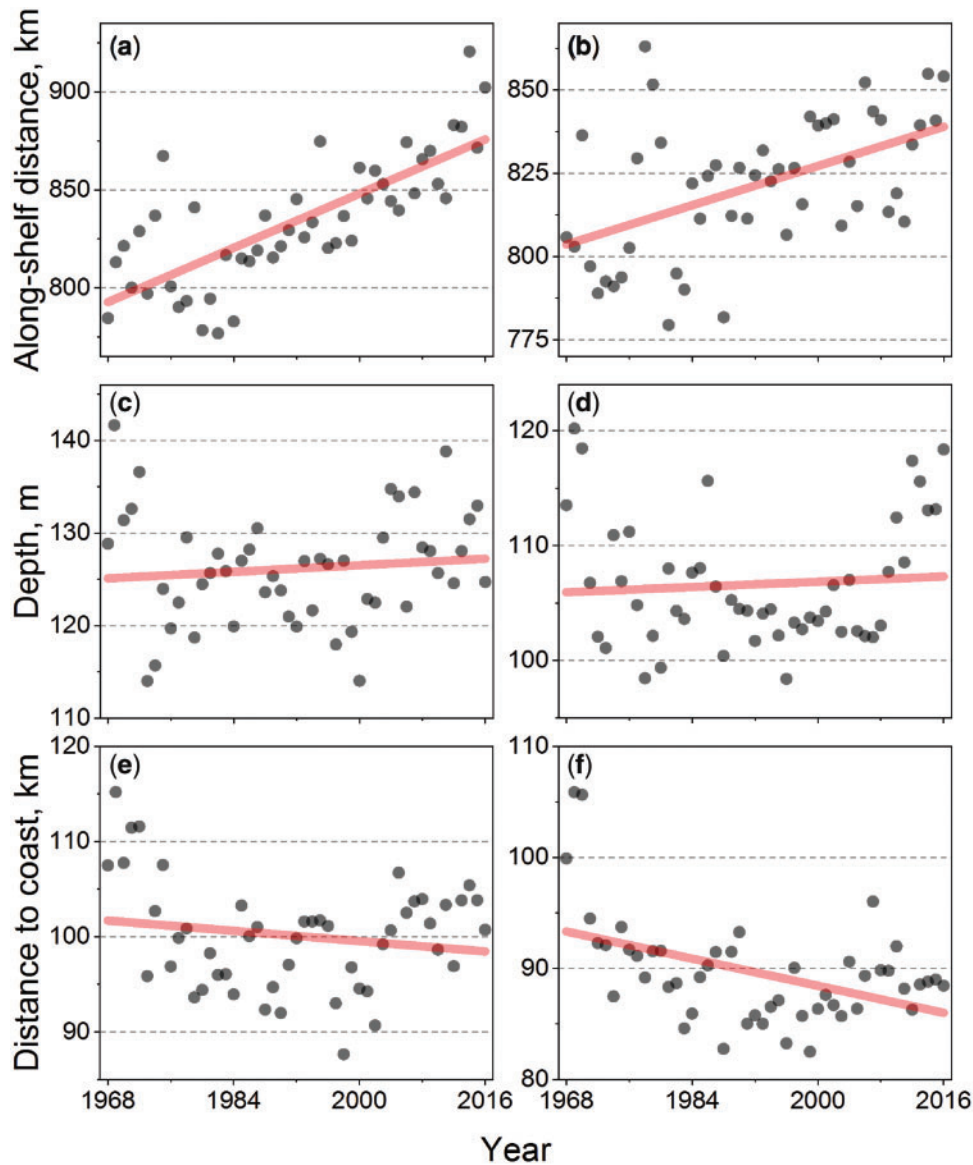
Figure 5. Fish and macroinvertebrate mean spring along-shelf distance (a), depth (c), and distance to the coast (e), and mean fall along-shelf distance (b), depth (d), and distance to the coast (f). Red lines are linear regression lines.

for fall species. Occupancy temperature was without trend for the mean of all spring species (Figure 9a), which is in contrast to the increasing trend in spring ecosystem temperatures (same data repeated from Figure 8a). The trend of the ecosystem temperature, as noted previously, was significant, whereas the trend for the mean occupancy temperature was non-significant (Table 3). The rate of change in occupancy temperature average about zero for pelagic piscivores and planktivores and were only slightly positive for benthic and demersal species (Figure 9c). This result would be consistent with fish and macroinvertebrates adjusting their distributions to maintain a constant thermal habitat over time despite changes in the distribution of thermal conditions in the ecosystem. In contrast, occupancy temperature for fish and macroinvertebrate species in fall changed over time, albeit not to the same extent as ecosystem temperatures (Figure 9b). The trends suggested by both time series were significant (Table 3). The excursion for ecosystem temperature was about

1.25°C as suggested by the start and end of the regression line, whereas the excursion of occupancy temperature was less, approximately 0.75°C. All fall functional groups had positive mean trends, exceeding the spring means for all groups (Figure 9d). The fall thermal regime has warmed faster than the spring regime; and, fall taxa have occupied progressively warmer water over time, thus not maintaining a consistent thermal habitat.

Multivariate analysis

Canonical correlation analysis suggests closer multivariate relationships between zooplankton and fish and macroinvertebrate distributions than with temperature variables. Fish and macroinvertebrate along-shelf distribution metrics were most clearly separated from zooplankton and temperature variables along canonical variate 2 (Figure 10a and b). Proximity of variables
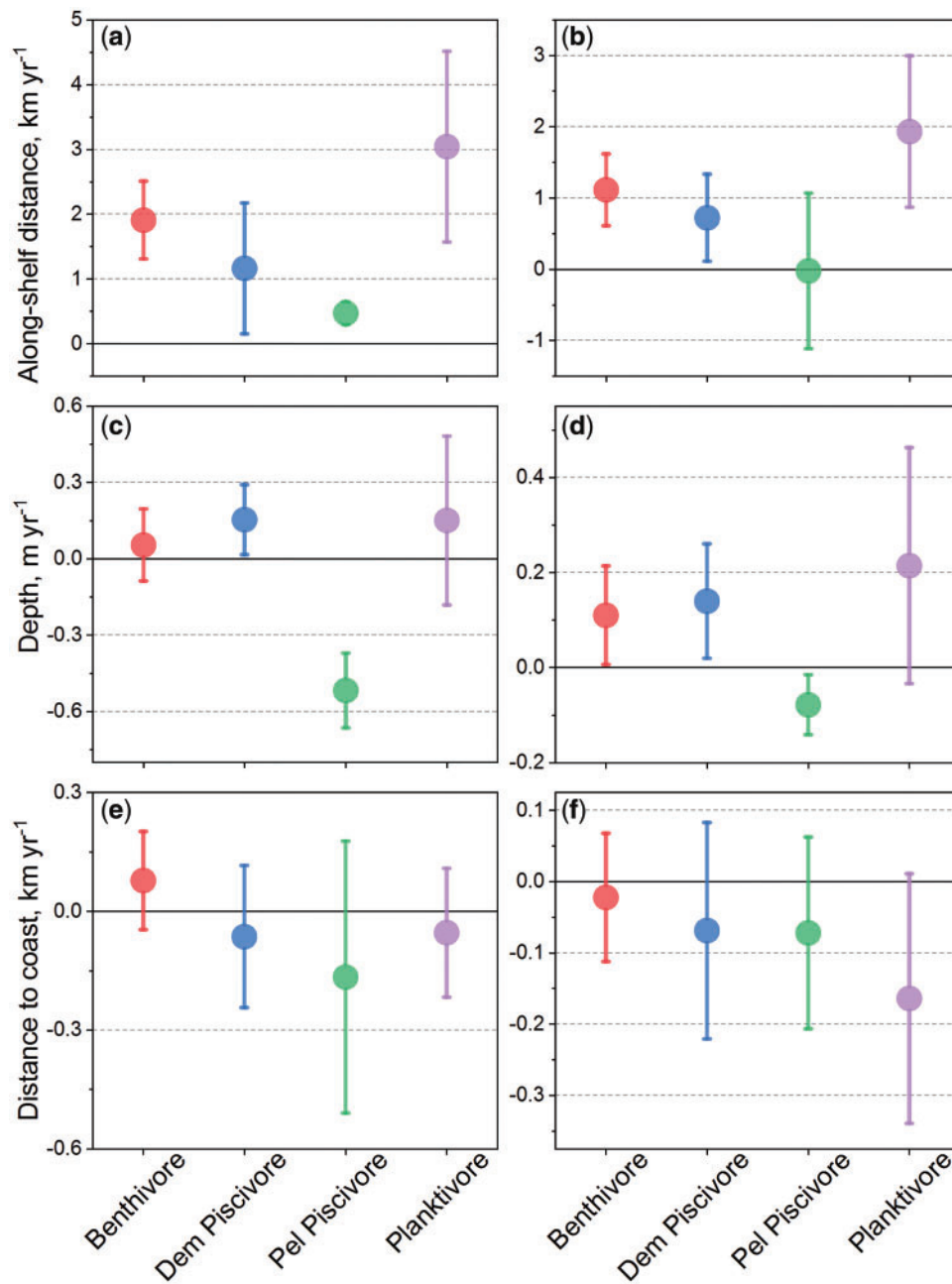
Figure 6. Mean Theil–Sen slope of centre of gravity of spring fish and macroinvertebrates by benthivore, demersal piscivore, pelagic piscivore, and planktivore along-shelf distance (a), depth (c), and distance to the coast (e); fall along-shelf distance (b), depth (d), and distance to the coast (f). Error bars are 95% confidence intervals.

suggest an association with the along-shelf distribution of copepods in spring and other zooplankton taxa in fall. The fish and macroinvertebrate depth differential metrics were separated along canonical variate 1 (Figure 10c and d). The spring variable separation suggests a weak correspondence to the temperature variables, where the fall data suggests a close relationship between fish and macroinvertebrate distribution and bottom and surface water temperature variables. The fish and macroinvertebrate distance to the coast metrics were clearly separated along canonical variate 1 in the spring (Figure 10e), suggesting weak correlation with the temperature variables and stronger correlation with the

zooplankton data. There are few discernable patterns in the fall data (Figure 10f).

Discussion
Centre of gravities
Aggregated fish and macroinvertebrate centre of gravities in the NEUS shifted poleward, and to an extent inshore through time, concurrently with warming water conditions and changes in secondary production. Similar distributional shifts have been reported for several species within the NEUS and linked to
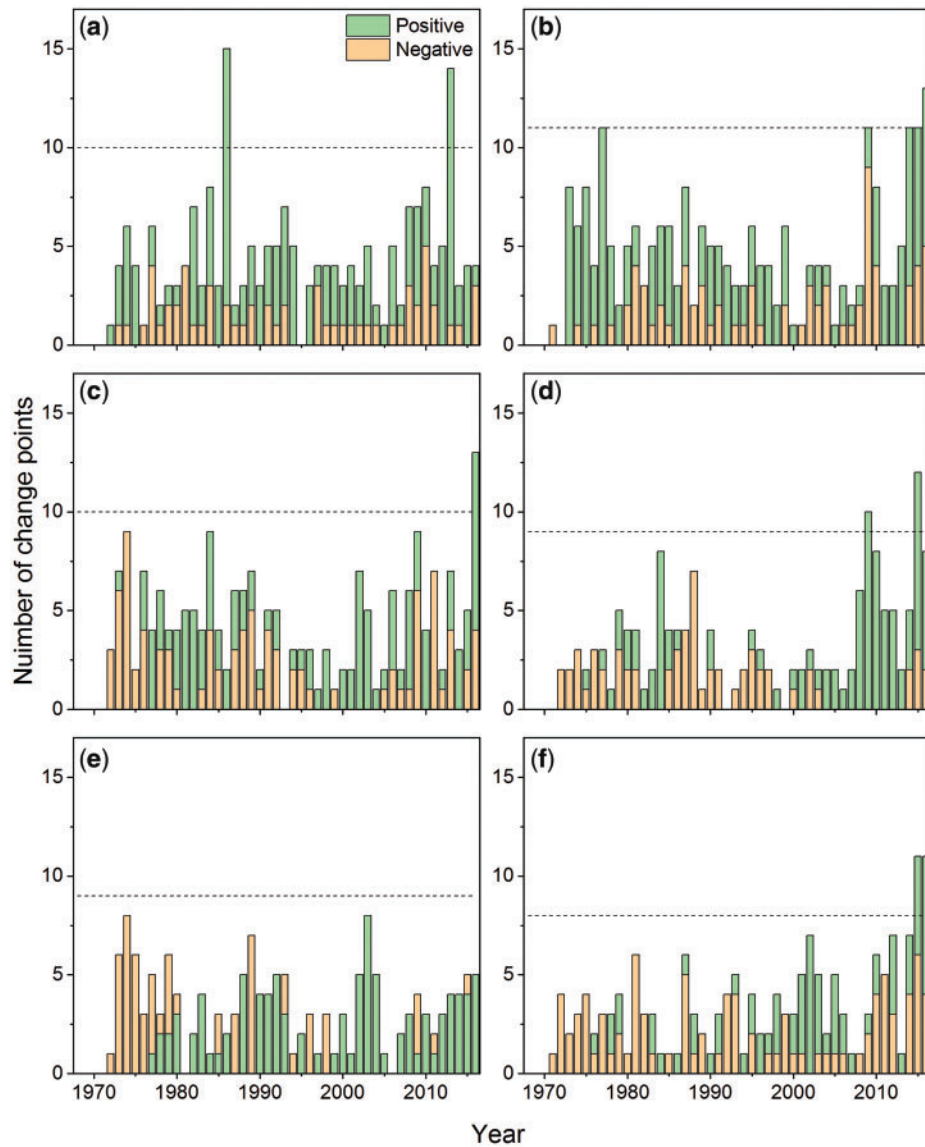
Figure 7. Number of positive and negative change points in spring along-shelf distance (a), depth (c), and distance to the coast (e); fall along-shelf distance (b), depth (d), and distance to the coast for fish and macroinvertebrate species. Dashed line marks two standard deviations above the mean.

thermal conditions and climate oscillations (Nye *et al.*, 2009; Lucey and Nye, 2010; Pinsky *et al.*, 2013b; Kleisner *et al.*, 2017). These results further support the operating hypothesis that a warming NEUS directly affects marine population distributions through their ecophysiology. Centre of gravity metrics, patterns may be weaker or stronger based on feeding strategies, with planktivores often exhibiting the strongest responses. For species living at the southern edge of their ecological range in the NEUS, distributional shifts may cause a contraction of the population and a functional extinction of the population within this region. For example, in the western Gulf of Maine, changes in the timing of the northern shrimp hatch have been linked to water temperatures, with hatch initiating earlier and lasting longer concomitant with increased bottom temperature (Richards, 2012). These earlier hatches are associated with decreased survival of larval stages and declining abundance of the population (Richards and Jacobson, 2016).

Similar thermal mechanisms have been identified with a range of marine species with associated change in their population dynamics, including impacts on American lobster and Atlantic cod (Pershing *et al.*, 2015; Rheuban *et al.*, 2017; Le Bris *et al.*, 2018).

Centre of gravity for aggregated zooplankton metrics do not indicate any significant poleward shifts in response to increasing temperatures, with the only significant shift indicating a shallowing depth distribution during the fall. However, within the zooplankton community, differences emerge in the distribution response of taxonomic groups; spring and fall copepod centre of gravity estimates indicate poleward, shallower, and inshore movements, while non-copepods and other zooplankton indicated little or no change in distribution through time. Demarcation between copepods and other zooplankton may relate to differences in vertical distribution in the water column through their life, with copepods primarily pelagic and many of the non-copepod

Table 2. Year and season associated with total change points at or above two standard deviations above the mean.

Season	Parameter	Event year	Year bin	Count	Species
Spring	Along-shelf distance	1986	6	1	*Scyliorhinus retifer*
			11	1	*Conger oceanicus*
			18	1	*Geryon quinquedens*
			24	2	*Malacoraja senta, Loligo pealeii*
			32	10	*Dipturus laevis, Alosa pseudoharengus, Urophycis regia, Pseudopleuronectes americanus, Helicolenus dactylopterus, Myoxocephalus octodecemspinosus, Hemitripterus americanus, Macrozoarces americanus, Lophius americanus, Homarus americanus*
	Along-shelf distance	2013			
	Depth	2016			
Fall	Along-shelf distance	1977	11	3	*Prionotus carolinus, Centropristis striata, Prionotus evolans*
			12	1	*Leucoraja erinacea*
			15	1	*Trachurus lathami*
			25	1	*Cancer irroratus*
			28	1	*Merluccius bilinearis*
			40	4	*Mustelus canis, Enchelyopus cimbrius, Raja eglanteria, Micropogonias undulates*
	Along-shelf distance	2009			
	Along-shelf distance	2014			
	Along-shelf distance	2015			
	Along-shelf distance	2016			
	Depth	2009			
	Depth	2015			
	Distance to coast	2015			
	Distance to coast	2016			

Notes: For along-shelf position in spring 1986 and in fall 1977, the number of years a taxa remained at the new level associated with the initial change is summarized by duration of the change (year bin) and the frequency of these changes (count), and the mean and median of the duration.

taxa analysed here having sessile life stages, and thus limited in their ability to move with habitat changes.

Copepod shifts in centre of gravity align with those of fish and macroinvertebrates and may explain the seasonal differences in the occupancy temperature of fish and macroinvertebrates. Planktivores feeding on copepods seem to drive the overall nekton shift, further supporting the bottom-up effect of zooplankton (Suca *et al.*, 2018). Similar shifts suggest that thermal environment influences copepods and fish and macroinvertebrate populations in some equivalent way; or, fish and macroinvertebrate distributional shifts may be due to more complex interactions beyond thermal tolerances, more specifically prey availability. Copepods are dominant prey for the early life history stages of many marine species, including Atlantic cod, haddock, redfish, and Atlantic mackerel (Runge, 1988; Castonguay *et al.*, 2008). Changes in zooplankton species composition and abundance can determine the prey available for larval fish and the local recruitment and abundance of components of a meta-population (Friedland *et al.*, 2013), particularly for species that have fish larvae with copepod-specific diets (Robert *et al.*, 2008; Wilson *et al.*, 2018). Copepod community structure shifts have been linked to regime change in the recruitment of a number of fish stocks (Perretti *et al.*, 2017); more specific linkages have been described between Gulf of Maine and Georges Bank cod and haddock recruitment and change in climate and zooplankton (Mountain and Kane, 2010; Friedland *et al.*, 2013). Our multivariate analysis suggests stronger concordance between copepods and specific fish and macroinvertebrate groups than with thermal covariates; however, the relationships are highly variable depending on the centre of gravity metric considered. The maintenance of a constant occupancy temperature by fish and macroinvertebrates in spring

would suggest distributions were thermally driven whereas the change in fall occupancy temperature over time would suggest trophic interactions played a relatively larger role. It is worth noting that the rate of along-shelf movement of copepods was lower in the fall than the spring and the excursion of ecosystem temperatures was less in the spring than in the fall. It would appear that fall fish and macroinvertebrate distribution were at variance to thermal trends because of the less pronounced shift in distributions of copepods in that season.

Phytoplankton centre of gravity metrics generally indicated little change in the distribution within the NEUS through time. Trophic influences between primary and secondary production may operate in the spring, but do not appear in the fall data. While phytoplankton biomass does not appear to have shifted through time, bloom phenology has changed, particularly with blooms initiating earlier and lasting longer (Friedland *et al.*, 2015). Further, changes in bloom dynamics have in part been attributed to grazing effects (Friedland *et al.*, 2015; 2016), indicating that the interaction reported between phytoplankton and zooplankton may be stationary or spatially variable through time. Bloom phenology changes attributed have been attributed to warming waters (Friedland *et al.*, 2018); however, warming sea temperatures do not correspond to geographic shifts in the bloom centre of gravity. In addition to temperature, phytoplankton biomass and primary production rates are influenced by solar irradiance, mixed-layer depth, freshwater inputs, stratification, nutrient concentrations, and grazing pressure (Sverdrup, 1953; Friedland *et al.*, 2015). In the Gulf of Maine and Georges Bank areas, physical forcing such as wind stress, heat flux, stratification, and source water entering the deep Gulf of Maine have been considered as or of greater importance to bloom formation than
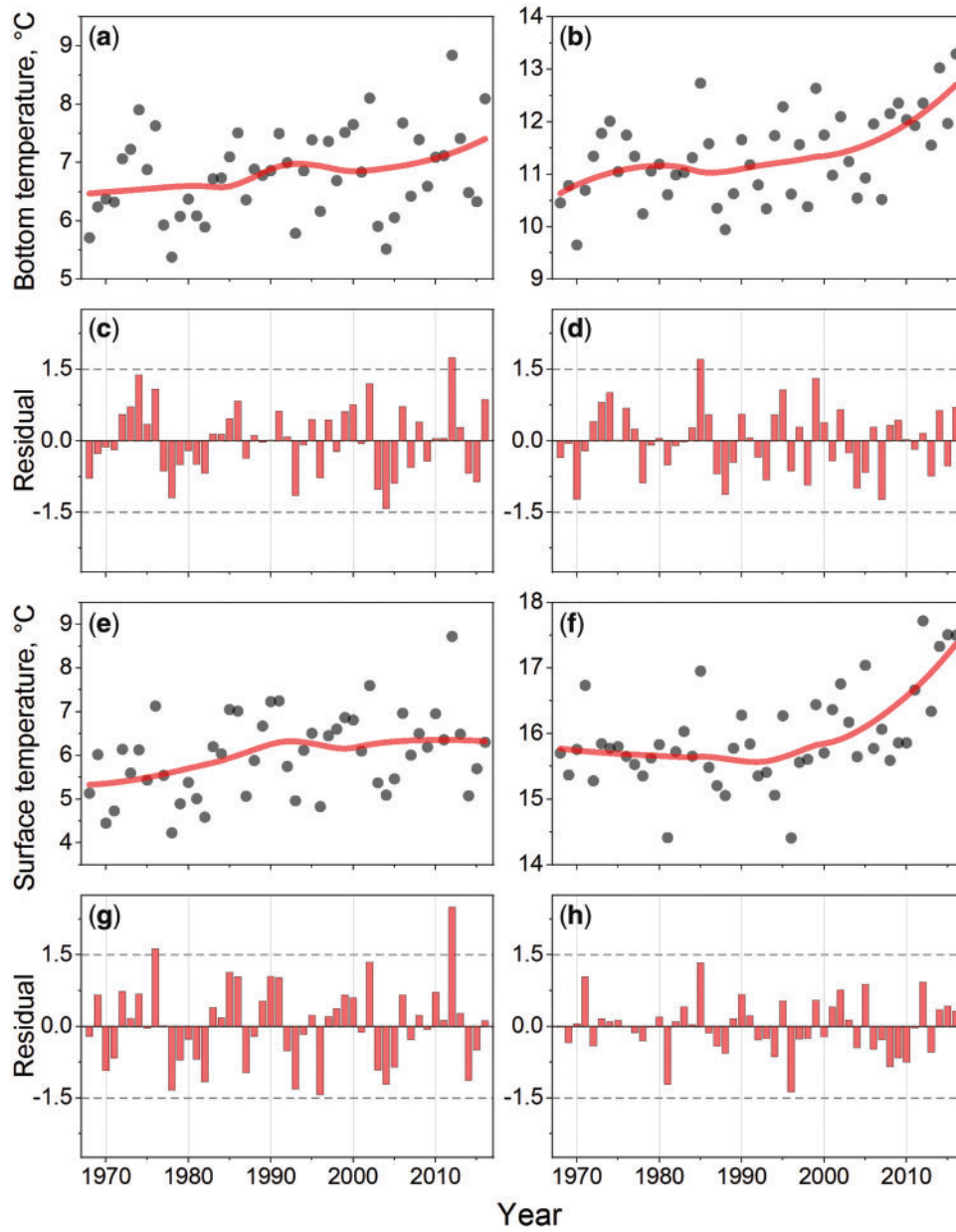
Figure 8. Annual spring (a) and fall (b) bottom temperatures for the Northeast Shelf ecosystem with residuals from their respective loess fits (c, d). Spring (e) and fall (f) surface temperature with residuals from loess fits (g) and (h), respectively. Red lines are loess fits.

Table 3. Theil–Sen slope and Mann–Kendall trend test probability (p, bold indicates significance at $p=0.05$) for time series of spring and fall bottom and surface temperature, temperature depth differential, temperature distance to the coast differential, and mean occupancy bottom temperature.

|		Temperature		Depth differential		Distance to coast differential	
Group	Season	Slope	p	Slope	p	Slope	p
Bottom temperature	Spring	0.017	**0.039**	0.001	0.776	0.001	0.803
Bottom temperature	Fall	0.028	**0.002**	0.012	0.046	0.008	0.131
Surface temperature	Spring	0.023	**0.020**	0.005	0.413	0.007	0.115
Surface temperature	Fall	0.021	**0.001**	−0.003	0.464	−0.008	**0.024**
Occurrence bottom temperature	Spring	0.006	0.413				
Occurrence bottom temperature	Fall	0.017	**0.004**				
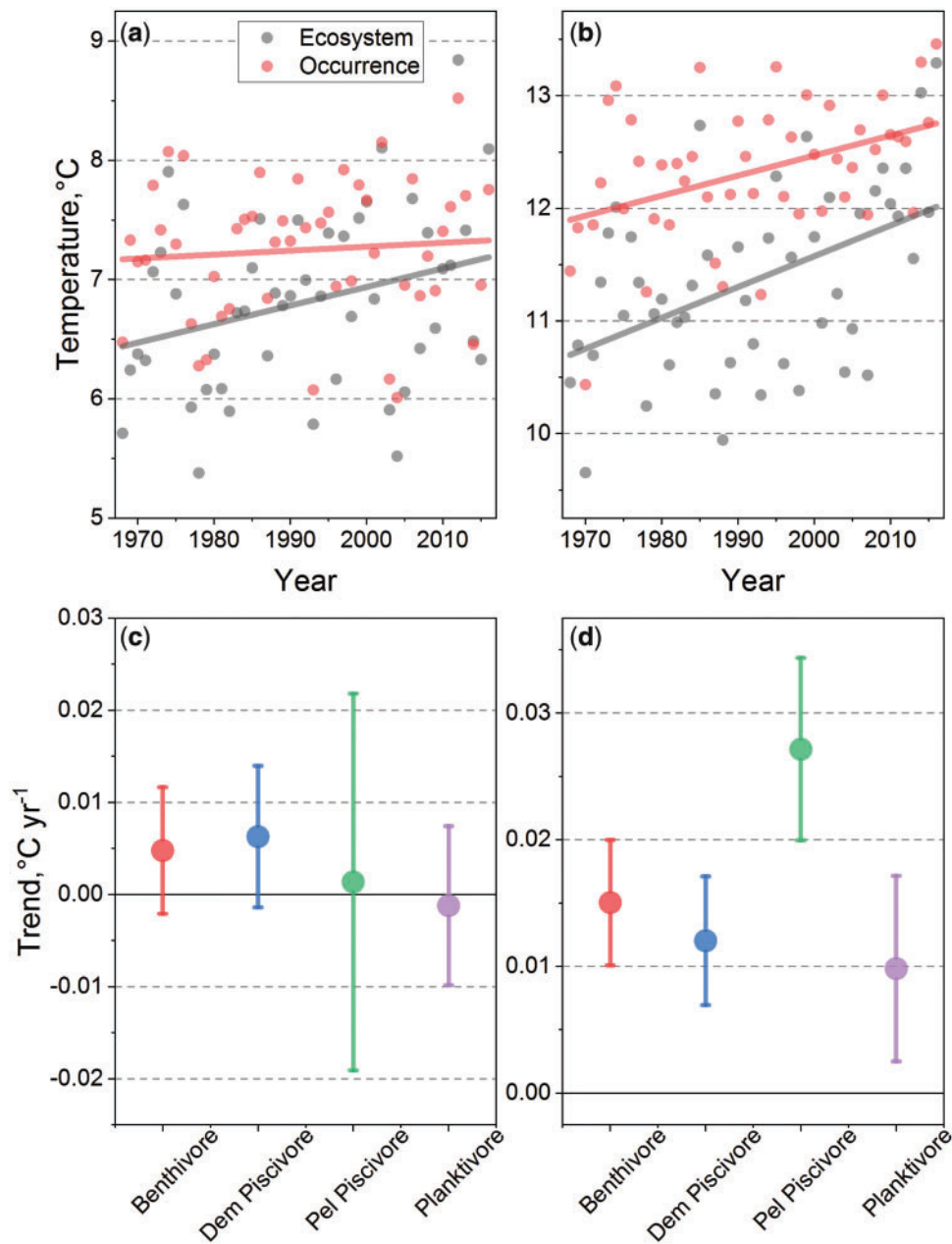
Figure 9. Annual spring (a) and fall (b) bottom temperatures for the Northeast Shelf ecosystem with mean occupancy temperature for fish and macroinvertebrates species. Lines are linear regression. Mean Theil–Sen slope of spring (c) and fall (d) occupancy temperature of fish and macroinvertebrates by benthivore, demersal piscivore, pelagic piscivore, and planktivore functional groups. Error bars are 95% confidence intervals.

nitrate availability (Ji *et al.*, 2008; Mountain and Kane, 2010; Saba *et al.*, 2015).

Our work supports the use of multiple metrics in identifying centre of gravity shifts since species and communities may respond to environmental changes differently. In an extensive analysis of adult fish and ichthyoplankton within the NEUS, Walsh *et al.* (2015) documented how geospatial shifts through time in marine fish are not necessarily uniform across species or life history stage. While centre of gravity shifts allow the assessment of population movements, climate change can affect marine fish distributions through other spatial effects, such as change in habitat areal extent or range modification. Adams (2017)

highlighted how the methods used to assess spatial movements can influence perception of climate effects on the distribution of butterfish (*Peprilus triacanthus*) demonstrating differences in distribution when the data is disaggregated by age or size.

Differential response to thermal conditions

Our study suggests that lower trophic levels differentially respond to change in thermal regime compared with upper trophic levels, a difference potentially attributable to the distinct scales at which these organisms interact with their environment as modulated by order of magnitude differences in their vital rates. Whereas upper
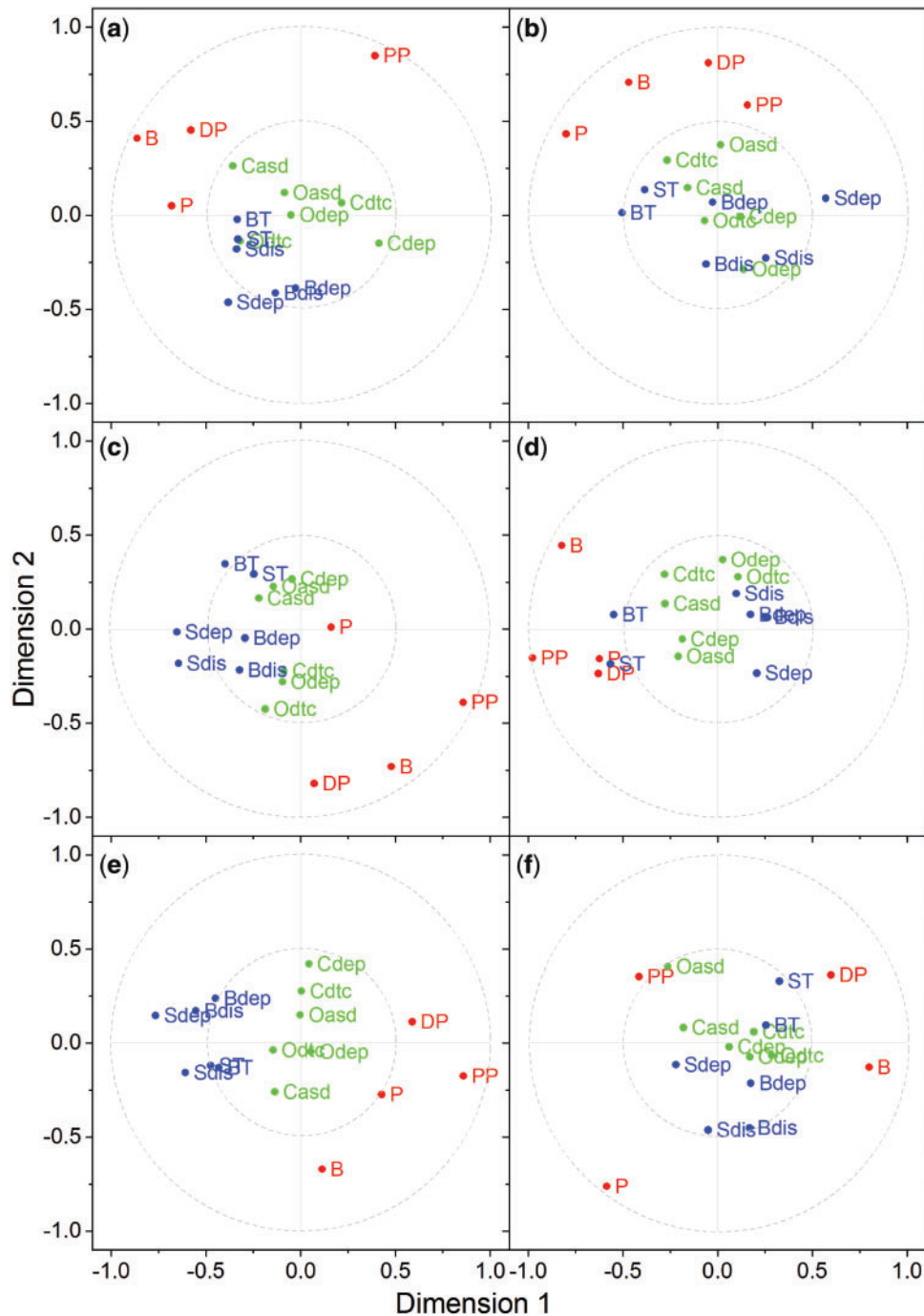
Figure 10. Canonical correlation analysis between fish and macroinvertebrate distribution responses (benthivores B, demersal piscivores DP, pelagic piscivores PP, and planktivores P), zooplankton (other zooplankton ASD Oasd, copepod ASD Casd, other zooplankton depth Odep, copepod depth Cdep, other zooplankton DTC Odtc, copepod DTC Cdtc), and temperature (bottom temperature BT, surface temperature ST, bottom depth temperature difference Bdep, surface temperature difference Sdep, bottom distance to coast temperature difference Bdis, surface distance to coast temperature difference Sdis) explanatory variables. Analyses are presented for spring along-shelf coast distance (a), depth (c), and distance to the coast (e), and fall along-shelf distance (b), depth (d), and distance to the coast (f).

trophic level taxa integrate thermal conditions across broad spatial and temporal scales, lower trophic level taxa, composed of phytoplankton and zooplankton, tend to experience thermal conditions at much finer scales. When coupled with shorter turnover times associated with lower trophic levels, such taxa have the opportunity and ability to optimize the timing and microscale

expression of their life histories at a given locale. In marine ecosystems, we have seen shifts in phenology of phytoplankton and zooplankton blooms (Friedland *et al.*, 2015; Kristiansen *et al.*, 2016). We have also seen shifts in fine-scale vertical location due to mixed-layer depth, stratification, nutrient concentrations, and predation pressure (Sverdrup, 1953; Friedland *et al.*, 2015) and

shifts in horizontal location due to wind stress, heat flux, freshwater inputs, and water mass movements (Ji *et al.*, 2008; Mountain and Kane, 2010; Saba *et al.*, 2015). Metabolic vital rate considerations, expressed as nutrient uptake for phytoplankton or grazing for zooplankton, mediate these shifts. For phytoplankton or zooplankton, given the speed of their vital rates that accumulate into what are relatively short production and generation times, the ability to wait until "conditions are right" (Tilman, 1981) is a reasonable outcome and likely why large-scale shifts in biomass are generally not widely observed for these taxa. The exception might be when current regimes change and thereby alter both the location of nutrients and phytoplankton cells at large spatial scales (Polovina *et al.*, 2008). Furthermore, we need to be mindful that chlorophyll concentration is indicative of community level abundance and does not address the potential for species level change in the phytoplankton community that may be responding differentially to climate forcing (Winder and Sommer, 2012). Lower trophic levels would appear to have a higher capacity to adapt to thermal change, whereas upper trophic levels with more complex life histories, and relatively slower vital rates, cannot afford to wait for the "right conditions" and hence move to more suitable habitat—expressed as shifts in distribution.

Ambient temperature affects all poikilotherms, but these effects are moderated by the organism's surface area relative to volume exposed to ambient temperatures (Froese, 2006). Lower trophic level organisms have a much higher ratio of surface area to volume, and thus are more directly susceptible to the influence of thermal conditions on their vital rates than larger organisms with a lower surface area to volume ratio (Planinsic and Vollmer, 2008). As such, lower trophic level taxa respond rapidly to environmental conditions and are able to make up for suboptimal conditions by taking advantage of thermal conditions that shift to suitable temperatures. Conversely, upper trophic level taxa are relatively less adaptable, having a lower range of possible vital rate changes, which results in lower metabolic rates and ultimately lower population-level production. When viewed at a population level at broad spatial scales, the lower metabolic rates and lowered production of upper trophic level taxa would lead to lower realized biomass at a given locale, which coupled with their need to move to suitable habitats, is expressed as a shift in distribution.

Another consideration that would lead to the differences observed in lower and upper trophic level shift in location is the ability of the former to enter dormant states. Phytoplankton can enter various cysts or similar resting stages that then respond to environment cues (such as temperature) that signal the activation of regular metabolism (Ellegaard and Ribeiro, 2018). Some zooplankton have diapausing capabilities (Baumgartner and Tarrant, 2017) that provide a similar function. Upper trophic level taxa, especially fishes, do not have dormant stages. Similar to the logic noted above, these dormant stages allow lower trophic level taxa to await suitable thermal conditions, and hence would resist the need to shift distribution. The instance of copepods exhibiting a weak, but discernable distribution shift represents an intermediary example between the patterns shown here for upper and lower trophic levels. Although true for many zooplankton, certain key facets of copepod life histories can more closely resemble, in both mechanism and magnitude, dynamics of upper trophic level taxa. These include the production of egg sac broods, the large potential migration distances relative to body size, relatively lower productivity and fecundity compared with other zooplankton taxa, and a lack of vegetative reproduction (Purcell, 2018).

Additionally, copepod hatching is often mismatched to production cycles because of thermal conditions (Baumgartner and Tarrant, 2017) and copepods have the capacity to store energy to a greater extent than most other zooplankton (Jager *et al.*, 2017). Collectively these facets of copepods life history likely contribute to the distributional behaviour we observed.

Change points

The greater number of distributional change points observed in recent years suggests greater system variability, and perhaps instability, than at other points in the time series. However, these recent shifts should be assessed with caution and reevaluated as data becomes available. The distinct shift seen in spring 2013 fish and macroinvertebrate along-shelf centre of gravity followed the anomalously warm year of 2012. This 2012 warming was pervasive throughout the NEUS, and most pronounced in the Gulf of Maine. The temperatures have been associated with the rare occurrence of longfin squid in the region and accelerated moulting of American lobsters that ultimately caused more legal-sized lobsters to recruit to the fishery and a lengthening of the fishing season (Mills *et al.*, 2013). In the case of the 2012 warming, effects were noticed within the same year; however, change points in fish and macroinvertebrate centre of gravities may be lagged responses from environmental or bottom-up changes in years prior. For example, altered season lengths can influence fish growth, maturity, and reproduction in a given year, with the resulting biology apparent years later in recruitment and spawning stock abundance (Henderson *et al.*, 2017). While this work analyses the NEUS in totality to capture holistic changes within the region, the heterogeneity between the NEUS subunits should be noted. Ecoregions within the NEUS have been shown to vary based on temperature (Thomas *et al.*, 2017), oceanography (Townsend *et al.*, 2006), phytoplankton blooms (Friedland *et al.*, 2015), zooplankton (Morse *et al.*, 2017), and fish assemblage (Lucey and Nye, 2010). Ecoregions with the NEUS may show differences in both central shifts and change points through time.

Within the NEUS, spring and fall zooplankton community regime shifts have been documented between the years 1989 and 2006 (Morse *et al.* 2017). The fish and macroinvertebrate centre of gravity shifts were largely found outside of this period, but those species with significant change points in their centre of gravities in 1977 and 1986 tended to show a persistent shift in distribution. Zooplankton community regime shifts have been linked predominantly to changes in temperature, stratification, and climate oscillations (Morse *et al.*, 2017), indicating that these forces may be greater determinants in zooplankton shifts in centre of gravity than the lower trophic level production. These regime shifts have also been presented as size shifts in the zooplankton community for ecoregions within the NEUS. The ratio of small (e.g. *Pseudocalanus* sp.) to large (e.g. *Calanus finmarchicus*) copepods have gone through three dominant phases: low ratio in the 1970s and 1980s, followed by a high ratio from the 1980s through 1990s, and a return to the smaller-sized regime in the early 2000s (Perretti *et al.*, 2017). These three copepod regimes correspond to low-high-low regimes of fish recruitment for several stocks in the NEUS (Perretti *et al.*, 2017), suggesting specifically the bottom-up effect of smaller-sized copepods on fish recruitment, and corroborating the synchronous centre of gravity shifts for copepods and higher trophic level nekton and the potential for a persistent shift (Rindorf and Lewy, 2006).

As with fish and temperature effects, zooplankton have also exhibited lagged relations with climate. For example, sea temperatures and *Calanus finmarchicus* have been shown to relate to basin-scale oceanographic changes from climate oscillations by up to 4 years (Xu *et al.*, 2015; Thomas *et al.*, 2017).

Conclusions

This work highlights the importance of both the availability of lower trophic level organisms and the physical environment in shaping higher trophic level distributional patterns over mesoscale to macroscale of an ecosystem. Movement of fish and macroinvertebrate taxa northeast and inshore seems to correspond with both warming waters and shifts in copepod populations. Dissimilar trends across multiple trophic levels further highlights how ecosystem responses can be non-linear or different across trophic levels, with trophic levels impacted differently by the environment. The phytoplankton standing stock does not exhibit similar shifts, but can vary in its centre of gravity annually and is likely still a prominent driver in higher tropic level production. The incongruous shifts between phytoplankton and fish and macroinvertebrates represent the differences in physiological reliance to temperature, or the suite of factors that differentially influence each trophic level. While sea temperature and prey fields are primary habitat components, several other habitat determinants not reviewed here—including salinity, sediment, dissolved oxygen, pH, and ocean circulation—have also changed through time (Poloczanska *et al.*, 2016) and likely contribute to distributional variability. Further, as highlighted by copepod and larger nekton interactions, habitat requirements can vary by life stage. Thus, changes at a given life stage can alter population connectivity between successive life stages, overall recruitment, and spawning stock biomass (Cowen *et al.*, 2007; Llopiz *et al.*, 2014). Finally, regardless of which specific mechanism, or cumulative effects thereof, the scales of interaction with the environment, vital rates, and life history traits differentially result in lower likelihood for lower trophic levels to exhibit large-scale distribution shifts in biomass relative to upper trophic level fish and macroinvertebrates.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

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