



A multivariate evaluation of environmental effects on zooplankton community structure in the western North Atlantic

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ABSTRACT

We report on our analysis of zooplankton community structure in the western North Atlantic based on spring and fall monitoring surveys from 1999 to 2011 of three large marine ecosystems (LMEs; Newfoundland Shelf, Gulf of St. Lawrence and Scotian Shelf). We aimed to synthesize knowledge of the distribution of zooplankton communities and to evaluate their relationship to environmental conditions as either biogeographic constraints or smaller-scale ecosystem drivers or both. A combination of exploratory and constrained analyses helped identify the dominant roles of bathymetry, surface salinity and temperature, subsurface biogeochemical inventories of nitrate and chlorophyll *a* on the macroscale distribution of zooplankton. These variables highlight the potential influences of vertical habitat features, latitudinal and estuary–ocean gradients, deep-water intrusions, and differences in the seasonal succession on community structure at biogeographic scales. The spatial pattern in the residual field of the constrained analysis suggests that mesoscale features may play a role in shaping community structure within each of the LMEs and point to the limitation of analytical approaches based principally on water mass tracers applied over broad-scales. Interannual variations in key environmental drivers had inconsistent abilities in predicting changes in community composition across LMEs. Organisms that had the greatest influence on the delineation of communities were similar between spring and fall surveys and consisted of roughly a dozen dominant and ubiquitous taxa. Determining the influence of environmental variations on productivity of key secondary producers requires an approach focussed at the scale of individual LMEs in order to address the consequence of dissimilarities in the dominant trophic relationships or the response to remote forcing across the region.

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Introduction

Knowing how distributions of marine plankton species are constrained by biogeophysical features of the pelagic environment is critical in understanding the ecological properties of regional ecosystems and their potential responses to a changing environment. Longhurst (2007) recognized the important link between the physical properties of the ocean and productivity of marine

ecosystems and used this knowledge not only to delineate biomes and major biogeographic provinces in the world oceans but also to provide a preliminary interpretation of ecosystem properties and their spatial boundaries. Longhurst's analysis relied heavily on satellite-derived observations of the distribution of surface temperature, sea-surface height and chlorophyll concentrations, which allowed him to put the ecology of plankton in context with atmosphere–ocean processes. He acknowledged, however, that the biogeographic classification of biomes and provinces did not take into consideration the spatial and temporal distribution of individual species or the communities they form. Moreover, the positions of biogeographic boundaries are dynamic and can be difficult to define as a result of variability in the position of water mass boundaries, transport processes across fronts, subduction of water masses at fronts and species ranges that span water mass boundaries (van der Spoel and Heyman, 1983; Boltovskoy, 1986;

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(Longhurst, 2007). At macro scales (1000s of km) in the open ocean, pelagic biogeographic classification is likely to provide a good representation of the major oceanographic ecosystems. In contrast, continental shelf pelagic communities are influenced both by their position relative to large-scale oceanic provinces and by smaller-scale processes, for example, interactions between circulation and bathymetry or the coast, coastal inputs of freshwater and nutrients, and pelagic–benthic biogeochemical and trophic interactions, and thus they exhibit greater variability at coarse (1–100 km) and mesoscales (10–1000 km) than oceanic communities (Haury et al., 1978; Briggs, 1995). Because the greatest pressure on exploited marine populations occurs on continental shelves, more detailed analyses of the environmental effects on distributions of key species in the continental shelf Large Marine Ecosystems (LME – Sherman and Alexander (1989)) may provide greater forecasting capacity for ecosystem responses to environmental change. Here, we have used multivariate analysis to examine patterns of zooplankton spatial distributions and their relationships to environmental drivers on the continental shelves of the Canadian northwest Atlantic.

Within the northwest Atlantic Shelf province (Longhurst, 2007), the Canadian continental shelf has three LMEs: the Scotian Shelf, Gulf of St. Lawrence and the Newfoundland and Labrador Shelf. Each of these LMEs has been the site of important fisheries and since 1999 all have been the subject of an integrated oceanographic observation program, the Atlantic Zone Monitoring Program (AZMP) of Fisheries and Oceans Canada, which aims to quantify the changes in the ocean's physical, chemical and biological properties (Theriault et al., 1998). The Scotian Shelf and southern Grand Banks are in a transition zone between the North Atlantic subpolar and subtropical gyres, and the three systems are linked by major equatorward currents and circulation features (Loder et al., 1998) (Fig. 1). Considerable understanding has been developed concerning factors that influence variation in circulation strength and properties in this region (Loder et al., 2001; Petrie, 2007; Han et al., 2008) as well as the exchange of water among LMEs (Han et al., 1999; Galbraith, 2006; Wu et al., 2012). The region is greatly influenced by the equatorward flow of the Labrador Current, which is closely tied to the continental slope, and by the outflow of freshwater from the Arctic and the Gulf of St. Lawrence, and both of these have a great influence on the region and have shown significant variations (e.g. temperature, currents) on decadal time scales (Galbraith et al., 2012; Han et al., 2014). Conditions in the region demonstrated a general warming trend since the later 1990s (DFO, 2013). In addition, oceanic processes associated with variability in Gulf Stream position, the intrusion of slope water onto the shelves, and deep convection in the Labrador Sea have had different effects on each of these LMEs (Loder et al., 1998). These three LMEs have demonstrated a varying degree of interannual-scale coherence in their physical properties in response to changes in atmospheric forcing (Petrie, 2007). Because of the large latitudinal extent of the Canadian continental shelf (41–55°N), there is considerable variability in their physical, chemical and biological oceanographic properties. Timing and duration of the seasonal primary production cycle is also highly variable, ranging from February to November off southern Nova Scotia with spring and fall blooms, to June to October off the coast of Labrador with a single peak in phytoplankton abundance. Furthermore, all three LMEs underwent significant changes in ecosystem structure and productivity as a result of anthropogenic and environmental pressures (Choi et al., 2005; Morissette et al., 2009; Dawe et al., 2012), and the degree to which each system has recovered has varied greatly (Link et al., 2011) which in turn is likely to affect the extent and magnitude of potential top-down effects which predators may have on lower trophic levels.

Mesozooplankton play a key role in the transfer of energy from primary producers, which are strongly affected by variations in physical conditions, to forage fish and upper trophic levels, which are often subjected to considerable pressure from commercial exploitation. Taxonomic diversity of zooplankton varies with latitude and has been strongly linked to water temperature (Rombouts et al., 2009; Yasuhara et al., 2012). Analyses of zooplankton community structure on continental shelves in the northwest Atlantic have determined that changes in composition were strongest along the across-isobath gradient in temperature and salinity, which mostly corresponds to the inshore–offshore direction (Tremblay and Roff, 1983; Plourde et al., 2002; Johnson et al., 2011; Pepin et al., 2011) but there is considerable variability in the strength of those relationships. Analyses of zooplankton community structure on the Newfoundland Shelf revealed a strong and consistent pattern in species composition among water masses that extends across seasons (Pepin et al., 2011). The Newfoundland and Labrador Shelves are at the intersection of several major oceanographic domains that result in the formation and persistence of spatially well-defined zooplankton communities. In contrast, Tremblay and Roff (1983) found that community composition on the Scotian Shelf was highly variable, which they attributed to the strong advective mixing processes which dominate the region. Johnson (unpublished data) has been able to establish that much of that variability was caused by variations in water mass composition. Despite these analyses that point to the association of zooplankton communities with major water masses, there remains limited understanding of the relative influence of macroscale, oceanic and mesoscale environmental variation on community structure.

The influence of the physical and biological environment may reflect macroscale biogeographic constraints on the distribution of different taxa and would reflect general physiographic features of the northwest Atlantic, similar to the association with major water masses. Alternatively, variations in community structure might reflect the influence of mesoscale or coarse-scale fluctuations in pelagic habitat characteristics on community interactions and productivity that reflect local, short-term processes within the broad physical geographic structure related to ocean currents. If biogeographic constraints predominate, then we should expect to see the greatest interannual changes in community composition in biogeographic boundary regions where environmental gradients are typically high, particularly on the Scotian Shelf and southern Grand Banks. In the NW Atlantic shelf system, where circulation has a strong influence on the spatial distribution of water properties, variability in circulation and biogeographic boundaries are likely to be strongly linked. Thus, it might be possible to gain greater understanding of interrelated changes in transport of zooplankton communities among LMEs if there is spatial coherence in community responses to environmental changes in boundary regions. On the other hand, if communities are more sensitive to locally-driven macro- and mesoscale scale physical variability, then there may be more limited spatial coherence in interannual variations in community composition among systems in response to changes in the physical environment. Coherent macroscale variability in atmospheric forcing, such as the record warm air temperatures that were associated with anomalously warm sea-surface temperatures across much of the Canadian NW Atlantic shelves in 2012, could also lead to coherent large-scale changes in zooplankton communities (DFO, 2013).

Analysis of community structure consists of identifying recurrent structures of association based on multivariate ecological data. Anderson and Willis (2003) recommended four elements in the analysis of multivariate ecological data: (1) a robust unconstrained ordination; (2) an appropriate constrained analysis with

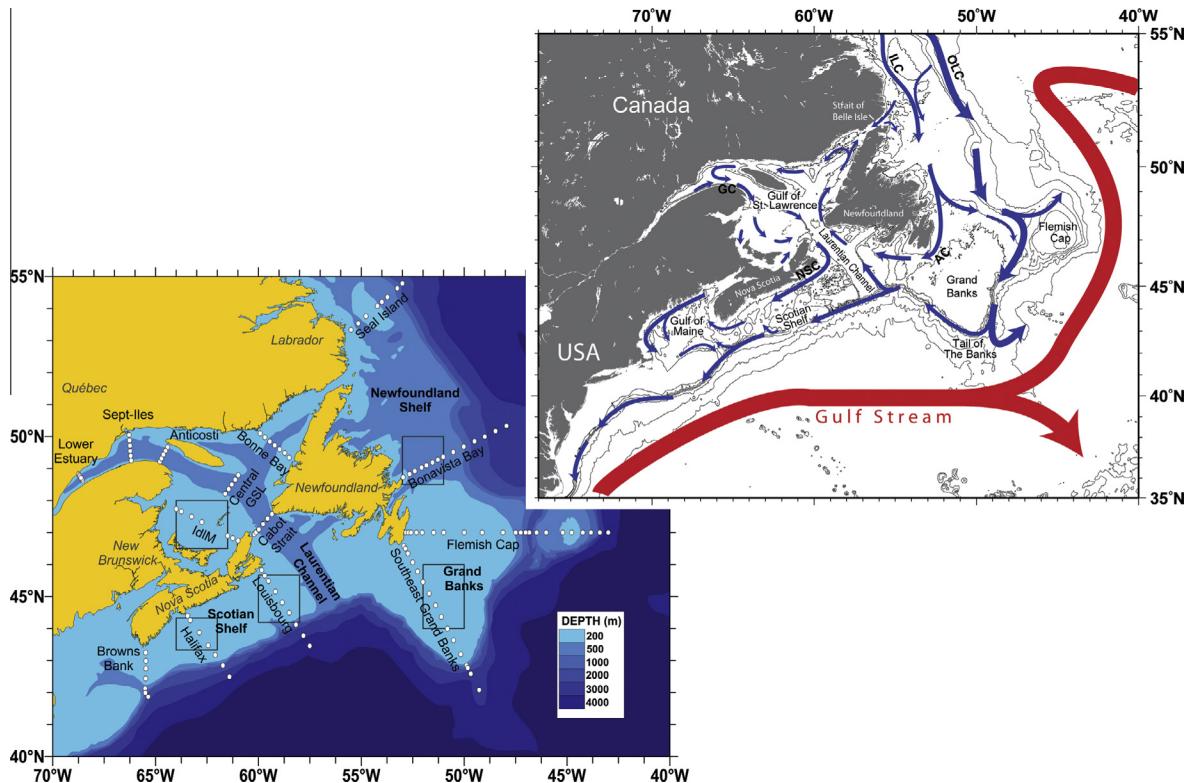


Fig. 1. Bathymetric map of the study region (lower left), showing the location of the 14 oceanographic sections and locations sampled by the program (Iles-de-la-Madeleine (IdIM) and Central Gulf of St. Lawrence (Central GSL)). Major bathymetric features are identified in bold. Gray boxes indicate the key areas over which semi-monthly composite images from satellite observations were obtained for each of the large marine ecosystems. Schematic diagram of the general circulation features in the study region (upper right) adapted from analyses by Hannah et al. (2001), Drinkwater and Gilbert (2004) and Fratantoni and McCartney (2010). Elements of Fratantoni and McCartney reprinted from Deep-Sea Research Part I – Oceanographic Research Papers, 57/2, Freshwater export from the Labrador Current to the North Atlantic Current at the Tail of the Grand Banks of Newfoundland, 258–283, 2010, with permission from Elsevier. Abbreviations represent OLC – Offshore branch of Labrador Current; ILC – Inner branch of Labrador Current; AC – Avalon Channel; GC – Anticosti Gyre-Gaspé Current; NCS – Nova Scotia Current.

reference to a specific hypothesis(es), such as driver-response associations identified in the unconstrained ordination; (3) a rigorous test of the hypothesis(es); and (4) characterization of the species responsible for the multivariate patterns. Unconstrained ordinations (e.g. principal component analysis, correspondence analysis, metric or non-metric multidimensional scaling) can be particularly useful in visualizing broad patterns of variations across the entire data set and can serve to determine whether *a priori* classifications are concurrent with the separation and dispersion among groups as well as any differences in within-group variability or spread (Legendre and Legendre, 1998). Constrained ordinations (e.g. redundancy analysis, canonical correlation analysis) use some form of *a priori* hypotheses to relate the responses of taxa to predictor variables (e.g. environmental variables) which allow the location of differences among groups to be seen, although they do not allow any assessment of either total or within-group variability.

This approach was used to analyze zooplankton community structure and environmental variability in the western North Atlantic, based on spring and fall surveys from 1999 to 2011. Our aims were to synthesize our knowledge of the distributions of zooplankton communities in the western North Atlantic and to evaluate their relationships to environmental conditions as either biogeographic constraints or smaller-scale ecosystem drivers or both. We achieved our goals by (1) describing the physical habitat available to zooplankton based on a number of summary variables that serve to describe the major features of the water column that can affect the suitability of the habitat for different zooplankton taxa; (2) carrying out exploratory and constrained multivariate analyses of zooplankton community structure to assess whether

the similarities and differences among groups and systems in their patterns of distribution are associated with variations in environmental conditions; and (3) providing a preliminary assessment of the regional coherence in interannual variations in community structure and environmental conditions. It is clear from previous investigations that temperature, salinity, ocean currents and regional productivity are important factors that govern the distribution of zooplankton communities (Longhurst, 2007). In this study, the patterns of variation in zooplankton community structure identified in the unconstrained analyses and their apparent association with biogeographic drivers served as the *a priori* basis for the constrained analyses, along with a suite of other factors that to our knowledge served as probable indicators of environmental influences and water-mass characteristics that were likely to affect zooplankton community structure.

Methods

Data collection

Our analyses were based on data collected during 13 years of AZMP sea-going missions. The project focused on the physical, chemical, and biological data collected at stations along 14 oceanographic sections (Fig. 1) during spring and fall cruises in three regions (Scotian Shelf (SS), Gulf of St. Lawrence (GSL), and Newfoundland and Labrador Shelf (NLS)) for the period 1999–2011.

The dataset included 77 cruises (25 for SS, 26 for GSL and 26 for NLS), which resulted in 1229 observations in the spring and 1171 in the fall. Although spring and fall surveys were performed in all

three regions, the AZMP sections were not sampled simultaneously among the regions or at exactly the same time each year within the regions. Spring surveys of the NLS were frequently sampled in April–May before or during the spring bloom, while April–May SS surveys typically followed the bloom, and GSL surveys were most often in June, much later than the bloom (Fig. 2). The fall surveys were typically in September–October for the SS, in October–November for the GSL and November–December for the NLS. These regional and interannual differences must be considered in interpreting large-scale patterns in environmental and lower trophic level variability. Not all stations were sampled during each survey, either as a result of poor weather conditions, logistical constraints, or ice cover during the spring surveys – for example, the northern-most section of the NLS was never sampled during the spring surveys.

At each station, a vertical profile of water-column properties was collected from the surface to the bottom using a rosette-mounted conductivity–temperature–depth (CTD) sensor (Seabird 911). In addition, a Seabird 43 probe was used to measure dissolved oxygen and a Chelsea Aqua III *in situ* fluorometer was used to measure chlorophyll *a* concentration. The CTD was lowered continuously at a targeted speed of 50 m min⁻¹ to the maximum depth for the station, or 3400 m on some surveys. Water samples were collected at standard depths (5, 10, 20, 30, 40, 50, 75, 100 m and near bottom) for sensor calibration and determination of nutrient (silicate, nitrate, phosphate) and chlorophyll *a* concentrations. Zooplankton samples were collected using 0.75 m diameter – 202 µm ring nets towed vertically from 10 m above bottom, to a maximum of 1000 m, at 1 m s⁻¹. After the net was rinsed out, large gelatinous zooplankton were removed from the catch, identified according to major taxonomic category (e.g. siphonophore, ctenophore, medusae), measured volumetrically and a sub-sample of this gelatinous zooplankton catch was preserved separately for confirmation of identification. Samples were preserved in 2% formaldehyde for subsequent identification and enumeration.

CTD data were verified and processed using standard quality-control techniques (Emory and Thomson, 1997). Nutrient

concentrations were determined using a sequential-flow auto-analyzer, and chlorophyll *a* concentrations were determined from acetone-extracted samples using a modification of the Holm-Hansen et al. (1965) procedure or that of Welschmeyer (1994). The preserved zooplankton samples were analyzed for species composition and abundance. After pouring off the formalin, all organisms larger than 1 cm were manually separated out. The remainder of the sample (i.e. all organisms less than 1 cm) was split once using a Motoda splitter. One half of the sample was used for dry weight determination, where the animals were collected on a pre-weighed shark skin filter, dried at 60 °C for 48 h and weighed. Dry weight biomass (g m⁻²) was also measured but not used in this study. The other half of the sample was used for the determination of taxonomic composition and abundance. For identification and enumeration, sub-samples of the remaining half of the original sample were taken such that a minimum of 200 organisms per net were counted and identified to the lowest taxonomic level possible. Once the 200 organism count has been achieved, additional aliquots were taken until a total of approximately 75–100 *Calanus* spp. had been identified and staged. Copepods were staged and identified to species whenever possible. Copepodites of *Pseudocalanus* spp. were identified only to the genus level. Zooplankton abundance was estimated as the abundance per unit area (m⁻²) based on the count from the subsample and the mouth area of the net (0.442 m²) and assuming 100% filtration efficiency. Aerial abundance was chosen as most appropriate to represent abundance because of the variation in the depth of tows in the study region. Complete details of field and laboratory protocols are available from Mitchell et al. (2002).

Environmental variables

Environmental variables were derived from CTD profiles of temperature, salinity and oxygen and from profiles of nutrient (nitrate, phosphate, and silicate) and chlorophyll concentrations from water samples collected at a standard set of nominal depths. A set of standard environmental variables was defined to summarize and characterize environmental variability in the region with the

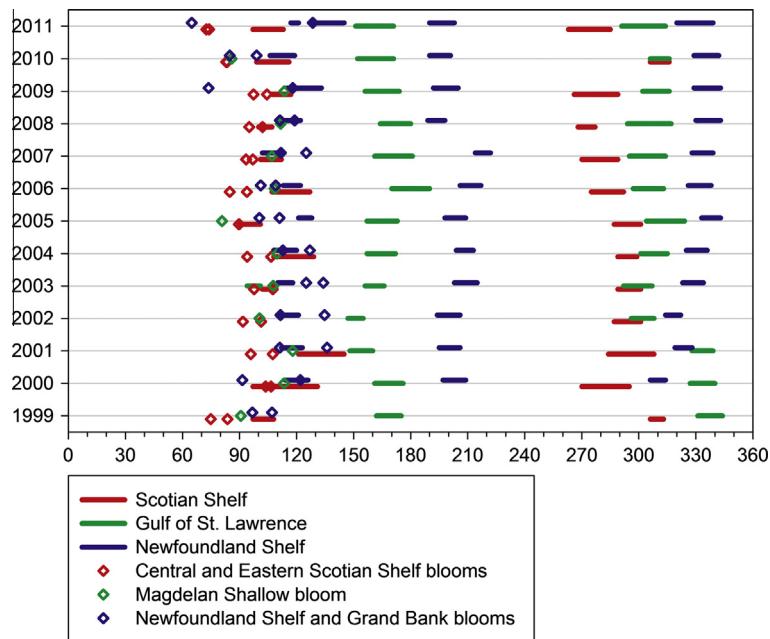


Fig. 2. Schematic illustration of the timing of surveys on the Newfoundland Shelf, Scotian Shelf and Gulf of St. Lawrence in relation to day of year over the study period (1999–2011). Diamonds indicate the timing of the peak spring phytoplankton concentration determined by fitting a shifted Gaussian to time series of semi-monthly areal estimates of surface chlorophyll concentrations derived from composite images of satellite observations for key areas in each of the regions (Wu et al., 2007). Summer surveys of the Newfoundland Shelf were excluded from the analyses.

overall goal of providing general descriptors of the pelagic habitat. Those variables were computed for each station occupation and consist of physical, nutrient and chlorophyll indices.

The physical variables derived from CTD data include the following: average seawater temperature, 0–50 m (T0_50 m); average salinity, 0–50 m (S0_50 m); stratification index 0–50 m (STRAT); average dissolved oxygen concentration, 0–50 m (O2_050 m); cold Intermediate Layer thickness using temperature thresholds appropriate for each region (CIL). The variables derived from the bottle profiles include: integrated nitrate concentration in the surface (0–50 m–NIT0_50 m) and subsurface (50–150 m–NIT50_150 m) layers; integrated silicate concentration in the surface (0–50 m–SILO_50 m) and subsurface (50–150 m–SIL50_150 m) layers; integrated phosphate concentration in the surface (0–50 m–PHO0_50 m) and subsurface (50–150 m–PHO50_150 m) layers; integrated chlorophyll concentration, 0–100 m (CHLO_100 m); excess silicate, 0–50 m (XSILO_50 m); and excess phosphate, 0–50 m (XPHO0_50 m).

The variables were derived using common processing strategies and protocols in order to standardize the information. As part of the standardization, a set of nominal depths was derived for each standard station location. Use of nominal depths is preferable to real depths for consistent estimation of near-bottom and averaged properties. If the maximum nominal depth was less than 50 m, the average water temperature, salinity and dissolved oxygen in the surface layer were computed from 0 m to the nominal depth. The stratification index was determined as the density difference between 5 and 50 m (or the nominal depth). Because of spatial differences in deep-water temperature among the three regions, the regional index of the cold intermediate layer (CIL) was reported as the thickness of a layer in the water column with temperature less than 0 °C for the NLS, less than 4 °C for the SS and less than 2 °C for the GSL.

Integration of the nutrient and chlorophyll profiles to generate shallow and subsurface inventories was performed using a trapezoidal integration procedure (Johnson et al., 2014). At stations where the nominal depth was less than the bottom depth of the desired layer (50 or 150 m) the integration was performed to the nominal depth instead. Excess silicate in the layer 0–50 m was computed as the difference between silicate and nitrate concentrations in the layer (Silicate–Nitrate) and excess phosphate as: *Excess Phosphate = Phosphate concentration – Nitrate concentration/16*.

Zooplankton species names were updated based on the World Register of Marine Species (WoRMS) (Boxshall et al., 2014) using the Taxon Match Tool. For this analysis, non-copepods were grouped into coarse taxonomic groups for more consistent representation among years and regions (Table 1). Rare taxa were left out of the analysis, based on occurrence, defined as the percentage of station occupations at which the taxon was present. Taxa with 3% occurrence or greater in one or both seasons in at least one LME were included in the analysis. For copepod genera with only one species observed throughout the study area, the genus and species were grouped and included in the analysis if one or both had at least 3% occurrence in one or both seasons in at least one LME. For copepod genera with multiple species, only those identified to species were included if they had at least 3% occurrence in one or both seasons in at least one LME. Exceptions include *Clausocalanus* spp. (genus and species grouped together due to taxonomic uncertainties that could bias analysis), *Pseudocalanus* spp., *Corycaeus* spp., and Aetideidae (each genus or family was grouped together, as species identifications are uncommon in some or all regions), and Euchaetidae (omitted).

We calculated two indices of biodiversity: (1) taxonomic richness (*S*), which is simply the average number of taxa at each sampling location based on all sampling events, (2) the average of

Shannon's index of diversity ($H' = -\sum_{i=1}^S p_i \ln(p_i)$, where p_i is the relative abundance of each taxa and *S* is the number of taxa in each sample), and (3) Pielou's evenness index ($J' = H'/\ln(S)$) at each location. Shannon's index is a weighted average of the proportional abundance of taxa; a low value implies greater dominance by a few taxa while a higher value reflects more even distribution of taxa to the overall community at a location while Pielou's evenness index is an alternate metric that quantifies the numerical equality of the community.

Multivariate analyses

To reveal the distribution patterns in zooplankton community structure, we undertook a series of multivariate analyses that aimed to first provide an exploration of the major trends in composition followed by an assessment of the influence of environmental variables which we had identified as potentially important influences on plankton distributions. Analyses were performed on the spring and fall datasets separately, rather than taking an approach without *a priori* assumptions which combined both seasons to assess their separation in multivariate space. We chose to separate seasons because we know from seasonal sampling at high-frequency sites that there are significant differences in zooplankton communities and that each season represents a different phase in the seasonal succession of environmental conditions, taxonomic composition and developmental stages or state of key species. Environmental conditions are very different during the two sampling periods, so combining both seasons could lead to erroneous relationships because of seasonal rather than biogeographic effects. Furthermore, a number of taxa are present in one season but not the other, which will strongly influence the outcome of the analysis. Finally, separating the data from the two seasons provided an opportunity to evaluate the consistency and importance of different environmental drivers between periods.

The first steps consisted of unconstrained analyses of the environmental and zooplankton community datasets performed separately using Principal Component Analysis (PCA), which aims to represent the data along a reduced number of orthogonal axes and identify the main trends of each dataset. By treating environment and community separately, these analyses allowed us to identify the general spatial structure across the regions. PCA is a passive form of analysis and the interpretation is done *a posteriori*. A preliminary analysis of the environmental variables demonstrated significant differences in the underlying distribution of values, which would have significantly influenced the accuracy of our analyses. As a result, a fourth-root transformation was applied to subsurface (50–150 m) nutrient inventories, and log-transformation was applied to depth, temperature (+2 °C), stratification, CIL thickness (log or 0), surface (0–50 m) nutrient inventories, and chlorophyll (0–100 m) inventories. Oxygen concentrations, salinity and excess nutrient estimates were not transformed. A fourth-root transformation was applied to the zooplankton abundance data.

Redundancy analysis (RDA) served as the basis of the constrained analysis in this study. It is founded on a principal components analysis (PCA) of the multivariate (i.e. multiple responses) multiple linear regression fitted to a combination of explanatory variables that best account for the variation in the response matrix. In addition to the analysis of fitted values, we also performed an analysis of the residuals. Use of both fitted and residual fields provided us with the opportunity to identify patterns of variation in zooplankton community structure at the broad- and mesoscales that reflect the associations of regional and local variations in environmental variables as well as hint at factors not included in our analysis. An alternative approach would have been to use canonical

Table 1

List of taxa, their occurrence (proportion of observations in which the taxa was identified) and average abundance of non-zero occurrences during the spring and fall surveys. Note that copepod taxa identified only to genus levels but for which older stages could be accurately identified to species were not included in the analyses.

Taxa	Spring		Fall	
	Occurrence	Abundance (m^{-2})	Occurrence	Abundance (m^{-2})
Calanoida				
<i>Calanus finmarchicus</i>	0.995	22,138	0.989	19,097
<i>Pseudocalanus</i> spp.	0.939	25,347	0.895	18,482
<i>Microcalanus</i> spp.	0.844	8521	0.807	7947
<i>Metridia longa</i>	0.665	3193	0.636	3666
<i>Temora longicornis</i>	0.559	9933	0.624	26,008
<i>Calanus hyperboreus</i>	0.901	9254	0.624	6533
<i>Metridia</i> sp.	0.411	2700	0.485	7779
<i>Calanus glacialis</i>	0.824	4078	0.434	1230
<i>Metridia lucens</i>	0.351	5763	0.394	5588
<i>Scolecithricella minor</i>	0.435	1952	0.382	1518
<i>Paracalanus</i> sp.	0.044	3364	0.369	19,515
<i>Aetideidae</i>	0.307	1382	0.284	1452
<i>Paraeuchaeta norvegica</i>	0.316	2195	0.253	700
<i>Centropages typicus</i>			0.232	18,821
<i>Acartia longiremis</i>	0.172	720	0.198	1047
<i>Clausocalanus</i> spp.	0.096	5228	0.187	8079
<i>Centropages hamatus</i>	0.190	2508	0.160	2672
<i>Euchaeta</i> sp.	0.294	2435	0.127	933
<i>Mecynocera clausi</i>			0.123	4555
<i>Spinocalanus</i> spp.	0.090	2021	0.097	2813
<i>Acartia</i> sp.	0.111	918	0.096	826
<i>Heterorhabdus</i> sp.	0.082	1081	0.089	890
<i>Pleuromamma</i> sp.			0.072	8547
<i>Pleuromamma borealis</i>			0.054	3737
<i>Nannocalanus minor</i>			0.051	1701
<i>Pleuromamma robusta</i>			0.041	1118
<i>Acartia hudsonica</i>			0.040	508
<i>Calocalanus pavo</i>			0.039	1090
Cyclopoida				
<i>Oithona similis</i>	0.995	53,797	0.994	77,285
<i>Oithona atlantica</i>	0.490	4596	0.599	6470
Harpacticoida				
<i>Microsetella</i> sp.	0.093	661	0.062	569
Poecilostomatoida				
<i>Triconia borealis</i>	0.268	2191	0.246	1977
<i>Triconia conifera</i>	0.157	1586	0.148	1481
Non-copepod				
Gastropoda	0.760	4238	0.741	5130
Chaetognatha	0.740	615	0.736	708
Larvacea	0.837	18,558	0.671	5074
Euphausiacea	0.753	4766	0.581	658
Amphipoda	0.440	192	0.546	127
Cnidaria	0.490	754	0.471	681
Bivalvia	0.304	3807	0.461	5843
Ostracoda	0.432	4693	0.449	4448
Polychaeta	0.716	3289	0.310	615
Mysidacea	0.263	162	0.284	113
Bryozoa	0.053	380	0.267	2862
Decapoda	0.417	224	0.262	20
Ctenophora	0.184	27	0.205	20
Echinodermata	0.180	5992	0.182	1964
Cladocera	0.063	2411	0.178	3390
Cirripedia	0.347	6436	0.051	3012
Tunicata			0.041	3181
Isopoda	0.031	239		

correspondence analysis (CCA) in which species are ordered along the canonical axes following their ecological optima (i.e. a unimodal response) based on the χ^2 distance among sites, in contrast to the linear response assumed in RDA. However, [Legendre and Gallagher \(2001\)](#) noted that differences in the abundance of common species contributed less than for a rare species. [Borcard et al. \(2011\)](#) recommended that use of CCA be restricted to cases in which rare species were well sampled. Because the coverage and sample sorting protocols of the program place emphasis on abundant taxa rather than rare species, the limitations of CCA led us to decide on the use RDA in this study.

For the constrained analyses (RDA), environmental data were transformed in the same manner as in the unconstrained analyses. We did not synthesize the environmental data to reduce dimensionality of the predictor variables because we sought to assess the importance of each descriptor independently in light of the potential covariance among variables, which was evaluated in the PCA of the environmental data for each season. A Hellinger transformation ($y'_{site,species} = \sqrt{y_{site,species}/y_{site+}}$) was applied to the zooplankton abundance data in order to standardize among taxa with widely-varying abundance levels. Following the RDA, we also

applied a forward-selection multiple regression approach (Blanchet et al., 2008), based on the adjusted coefficient of multiple determination (R_{adj}^2), to determine if a more parsimonious set of variables could be applied to the RDA. Significance levels were evaluated based on a permutation test ($N = 999$). To verify the robustness of the RDA results and assess the potential extreme influence that a few species may have had on the outcome, we also carried out distance-based RDA (dbRDA) based on presence–absence, in which an RDA was applied to the results of a principal coordinate analysis (PCoA) of Bray–Curtis dissimilarity measures among samples. The presence–absence transformation of the data should reduce the possible effects of ubiquitous taxa that demonstrate strong variation in abundance along environmental gradients on the analytical results.

SIMPER (similarity/dissimilarity percentages species contribution) analysis, based on a Bray–Curtis similarity matrix of the fourth-root transformed abundance data, was performed to identify the key taxa that contribute to the contrast between observations that demonstrated positive and negative loadings along each of the first three RDA axes.

To illustrate the potential value of multivariate analyses of community structure, we performed a preliminary investigation to test whether the environmental relationships identified in the RDA analyses reflect broader biogeographic constraints or interannual variations in environmental features. We selected the results from RDA2 from the fall survey results of the constrained analyses *post hoc* to contrast with interannual variations in transformed temperature (T0_50 m) because of the strong positive loading on this axis. Furthermore, temperature is often a correlate of changes in zooplankton abundance or species composition (e.g. Astthorsson and Gislason, 1995; Beaugrand, 2003; Mackas and Beaugrand, 2010) and would provide a useful evaluation of the potential strength or weakness of the multivariate approach in forecasting local interannual responses to environmental variation across a broad geographic area.

Analyses were performed using a combination of PRIMER v 6.0 (Clarke and Warwick, 2001) with PERMANOVA+ V 1.0.3 (Anderson et al., 2008) and R V 2.15.3 (R Core Team, 2013).

Results

Environmental conditions

The pattern of variation in both surface and subsurface nutrient inventories during the spring surveys was strongly associated with depth along the first principal component (PC1), with greater inventories occurring in deeper water (Fig. 3). Loadings on PC2 demonstrated the strong inverse relationship of salinity and temperature with stratification, excess silicate and the thickness of the cold intermediate layer (CIL). PC3 revealed that higher chlorophyll concentrations occurred in areas with cooler temperatures and weaker stratification, but higher phosphate, excess phosphate and oxygen concentrations; patterns which are in keeping with photosynthetic oxygen production by silicate-dependent diatom communities. Together, the first three PCs explain 62.8% of the variation in environmental variables from the spring surveys.

The patterns of variation explained by the first three PCs of the fall survey data accounted for 66.1% of the overall variance, but the separation of variables indicated that the observations reflect a more complex set of interactions compared to the pattern observed in the spring (Fig. 3). Nutrient inventories and oxygen concentrations loaded positively along PC1 and were inversely related to the average temperature and salinity in the surface layer. However, nutrient inventories in surface and bottom layers showed separation along PC2, with higher bottom

inventories occurring in the more saline deeper parts of the region. Higher chlorophyll inventories demonstrated an association with higher salinity in surface waters along PC3 and were inversely related to warmer temperatures, thicker CIL and excess levels of silicate.

The spatial distributions of the average spring PC scores for each station revealed patterns in the environmental associations (Fig. 4). Positive PC1 scores occurred mainly in the deep-waters north and east of the Grand Banks, in the northwest Gulf of St. Lawrence and off the Scotian Shelf. Negative PC1 scores occurred principally at depths <200 m. Negative PC2 scores were associated with the deep-water off the Newfoundland and Scotian Shelves but also occurred along the SE Grand Banks and Flemish Cap sections, while PC2 scores were positive in the Gulf of St. Lawrence and inshore eastern Scotian Shelf and Newfoundland Shelf. Negative PC3 scores mainly occurred on the Newfoundland Shelf and inshore eastern Scotian Shelf, while positive PC3 values occurred at most stations inside the Gulf of St. Lawrence and in deep-water off the Scotian Shelf and Tail of the Bank.

The fall PC scores exhibited similar regional-scale spatial coherence to those in spring surveys, but their spatial distributions differed from those observed in spring (Fig. 4). The occurrence of positive PC1 scores in fall was limited to the inshore Newfoundland Shelf and throughout the Gulf of St. Lawrence, and PC1 scores were negative at stations east of the Grand Banks as well as along the SE Grand Banks section and all sites on the Scotian Shelf, reflecting a shift to an inverse relationship between nutrient inventories and temperature in fall from an association between depth and nutrient inventories. In spring positive PC2 scores were found mainly in deep-waters off the shelf and in the deep channels of the Gulf of St. Lawrence, reflecting the loading of depth on PC2 in fall. Positive PC3 scores occurred on the Labrador and Newfoundland Shelves and the Grand Banks, while PC3 was mainly negative on the Scotian Shelf and in the Gulf of St. Lawrence.

Zooplankton community – unconstrained analyses

Taxonomic diversity

Spatial patterns in species richness and diversity were similar in both spring and fall (Fig. 5). Species richness and diversity were generally greater at locations off the continental shelf and in the deep channels of the Gulf of St. Lawrence. Sampling sites on the Grand Banks and in the southern Gulf of St. Lawrence had the lowest levels of richness and diversity, whereas stations in the Labrador Current and Scotian Shelf slope waters had the highest levels of both metrics. Average richness, diversity and evenness across the entire region were higher but less variable in the spring than in the fall. Average richness was greater on the continental shelf in the spring whereas richness was greater in slope and oceanic waters in the fall. In contrast, diversity was greater in the spring at 82% of the stations, with no clear bathymetric pattern in the distribution of positive and negative differences. Richness and diversity were highly correlated in the spring (Spearman $r_s = 0.73$) but the correlation was weaker in the fall ($r_s = 0.54$). During both seasons, sites in the Labrador Sea had higher levels of diversity (H') for a given taxonomic richness, and the same can be said for Scotian Shelf slope waters in the fall, whereas shallow parts of the Gulf of St. Lawrence, and to a lesser extent the southern parts of the Grand Banks, had lower levels of diversity relative to richness. Evenness did not demonstrate as strong a bathymetric influence in either spring or fall when contrasted with richness and diversity. On average, evenness was greatest on the Newfoundland Shelf and lowest in the Gulf of St. Lawrence in both seasons, with the contrast being strongest in the fall.

We applied a forward-selection approach to investigate the relationships between environmental variables with species

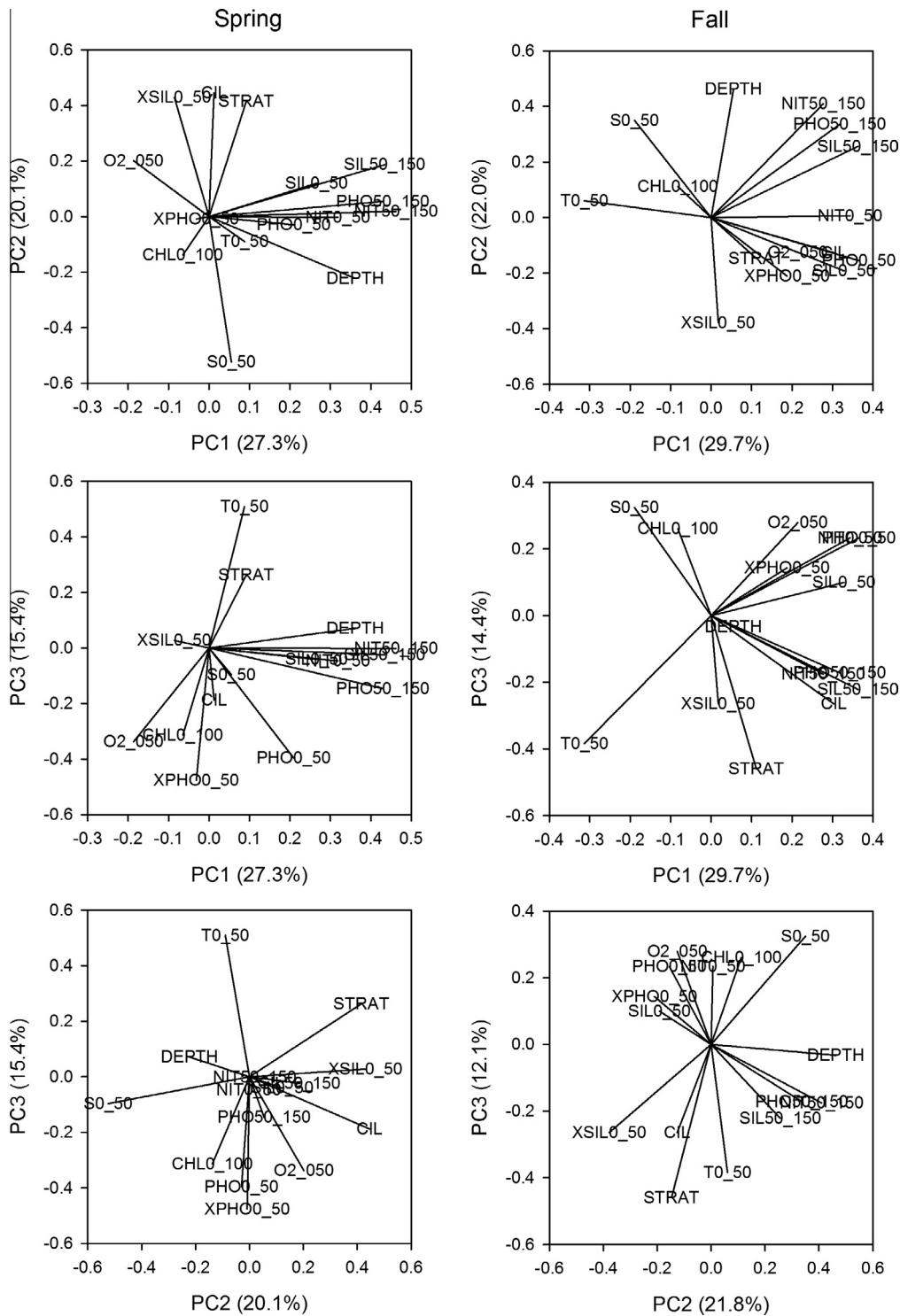


Fig. 3. Patterns of variation in environmental variables from the spring (left) and fall (right) oceanographic surveys based on the first three axes (PC1–PC3) derived from a principal component analysis. The percentage of variation associated with each axis appears in brackets next to the title. Symbols represent: DEPTH (m); T0_50 (average temperature 0–50 m); S0_50 (average salinity 0–50 m); NIT0_50 (integrated nitrate inventory 0–50 m); SIL0_50 (integrated silicate inventory 0–50 m); PHO50_150 (integrated phosphate inventory 50–150 m); NIT50_150 (integrated nitrate inventory 50–150 m); SIL50_150 (integrated silicate inventory 50–150 m); PHO50_150 (integrated phosphate inventory 50–150 m); O2_050 (average oxygen concentration 0–50 m); XSIL0_50 (excess silicate inventory 0–50 m); XPHOO_50 (excess phosphate inventory 0–50 m); CHLO_100 (integrated chlorophyll concentration 0–100 m); STRAT (Stratification Index); CIL (thickness of the cold intermediate layer).

richness or diversity. Spring richness was significantly related by 11 of the 16 environmental variables ($R^2_{adj} = 0.65$), with (in descending order of importance) subsurface water silicate, surface temperature, CIL thickness, bottom depth and surface salinity accounting for 91.8% of explained variance. Only five environmental

variables (depth, surface salinity, excess silicate, and subsurface inventories of silicate and nitrate) were significantly associated with diversity ($R^2_{adj} = 0.329$) with depth and salinity explaining 93.9% of that variance. Eight environmental variables were significantly correlated with spring evenness ($R^2_{adj} = 0.14$), with three variables

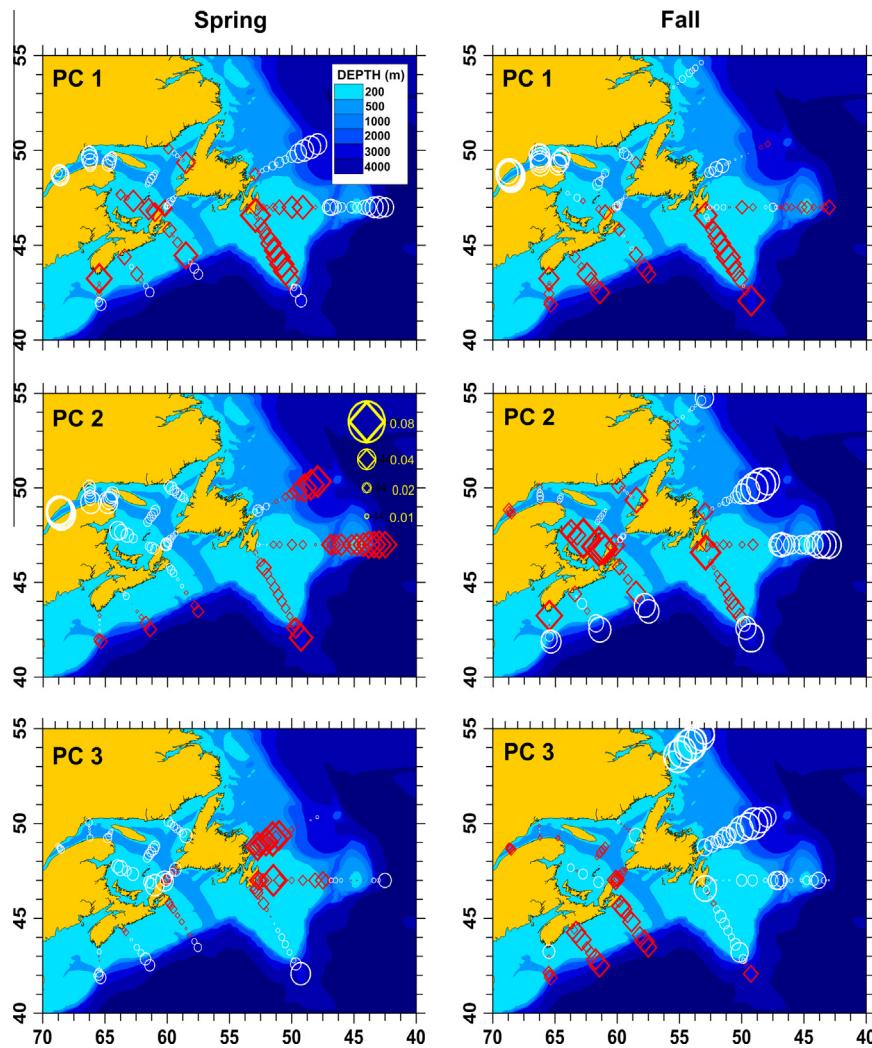


Fig. 4. Expanding symbol map of the average component score of the first three axes (PC1 – top panel; PC2 – middle panel; PC3 – bottom panel) of the principal component analysis of environmental data from the spring (left) and fall (right) surveys. Diamonds represent negative values; circles represent positive values; the size of each symbol scales in accordance to the value (the scale appears in yellow in the middle panel). Positive and negative values are consistent with the outcomes from the principal components analyses and have not been rotated to provide consistent views between seasons. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(depth, surface temperature and CIL thickness) accounting for 89.8% of explained variance. Nine variables were significantly associated with the spatial pattern in fall species richness ($R^2_{adj} = 0.571$) with depth, surface salinity and temperature accounting for 94.4% of explained variance. Diversity was significantly related to seven variables ($R^2_{adj} = 0.413$), with depth and surface oxygen inventories accounting for 91.2% of explained variance. Nine variables had a significant association with fall evenness ($R^2_{adj} = 0.27$) with 5 (surface salinity, surface nitrate, depth, CIL thickness and excess phosphate) explaining 93.1% of the fitted relationship.

Spring surveys

The first three principal components explained 44.7% of the variance (PC1 21.4%; PC2 15.3%; PC3 8.0%) beyond which only PC4 explained more than 5% of the variance. The pattern of eigenvector coefficients (loadings) on the first two principal components among species was dome-shaped (Fig. 6), suggesting a degree of non-linearity in the relationships among species. Larvacea, *Pseudocalanus* spp., and *Temora longicornis*, three neritic taxa, had the strongest negative loadings on PC1 while the deep-water taxa consisting of *Microcalanus* spp., *Metridia longa*, *Oithona atlantica* and Ostracoda had the strongest positive loadings. Bivalve and

polychaete larvae also had negative loadings on PC1. *Metridia lucens*, Euphausiacea and *Calanus finmarchicus* had strong positive loadings on PC2 while Cirripedia and *Centropages hamatus* had weak negative loadings. The third principal component highlighted the separation of *O. atlantica* and Gastropoda from *Paraeuchaeta norvegica*, *Triconia borealis*, Cnidaria and *Calanus hyperboreus* and contrasted communities in open ocean areas from those in the Gulf of St. Lawrence.

The spatial distribution of the average PC scores for each station revealed clear patterns in the taxonomic assemblages (Fig. 7). Positive PC1 scores occurred principally beyond the continental shelf (defined by the 200 m isobaths) and in the deep channels of the Gulf of St. Lawrence, while sites on the continental shelves and in shallow waters of the Gulf of St. Lawrence had negative average scores. Average PC2 scores appeared to distinguish sites off Newfoundland (negative) from those on the Scotian Shelf and the deep channels of the Gulf (positive). Sites along the Bonne Bay, St. Lawrence Estuary and Magdalen Shallows sections also had moderate negative loadings suggesting that zooplankton assemblages at these locations were more similar to those off Newfoundland than to communities sampled on the Scotian Shelf and in the remainder of the Gulf. Sites with negative average PC3 scores were located

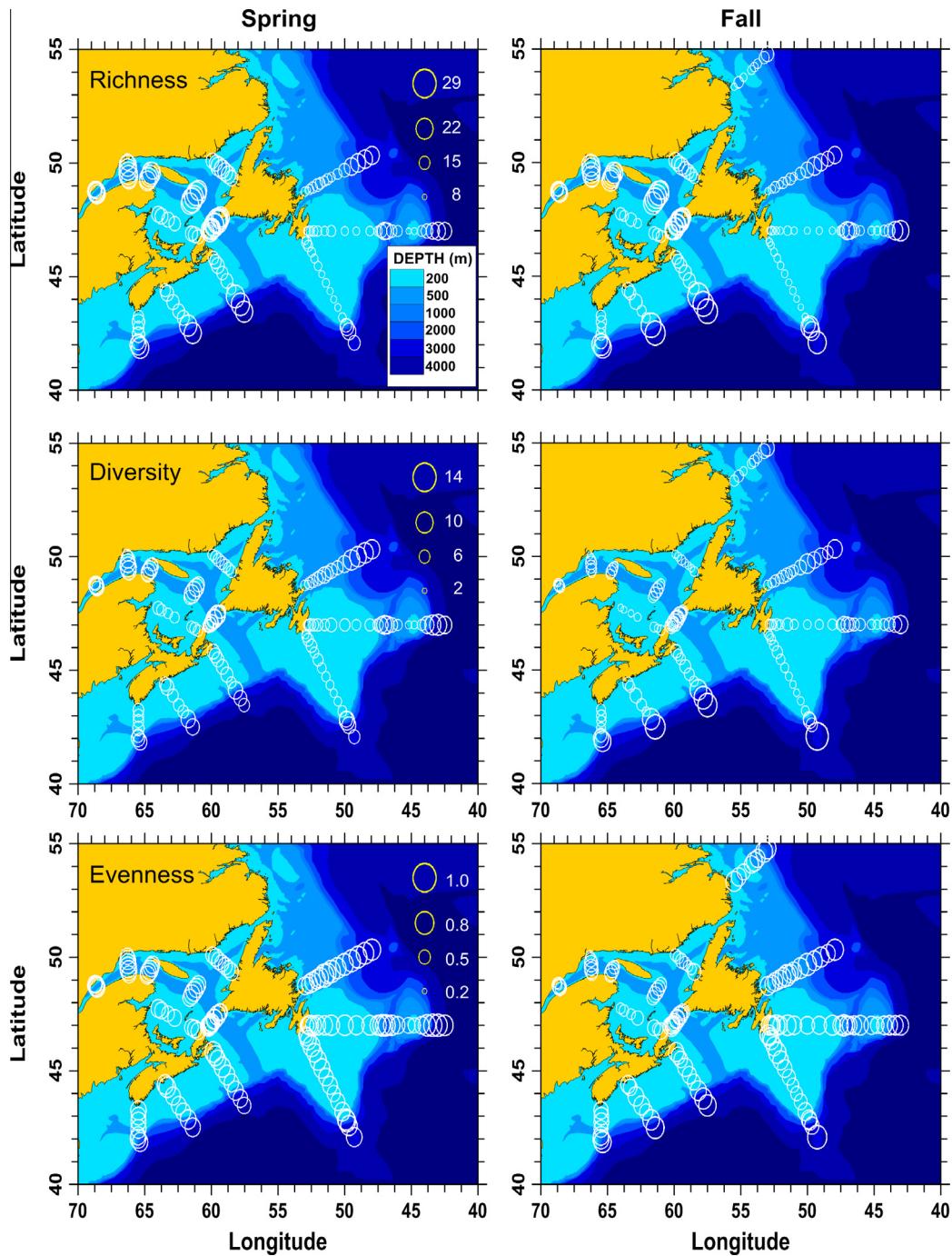


Fig. 5. Expanding symbol map of the average taxonomic richness (top panels) and Shannon's diversity index (middle panels) and Pielou's evenness index (bottom panels) for the spring (left column) and fall (right column) surveys. Legends for each index are located in the left panels; the size of each symbol scales in accordance to the value.

mostly in the Gulf of St. Lawrence while sites with positive averages were located principally at sites in the Atlantic Ocean. There were a few sites with weak negative average PC3 scores on the Grand Banks and at stations near the eastern coast of Newfoundland.

Fall surveys

The first three PCs explained 48.8% of the variance in the fall dataset (PC1 – 23.1%; PC2 – 14.9%; PC3 – 10.8%) beyond which only PC4 explained more than 5% of the variance (Fig. 6). The loadings of individual taxa were more uniformly distributed on PC1 and PC2 than in the analysis of the spring dataset. The neritic taxa

Pseudocalanus spp., *T. longicornis*, and *Bivalvia* had the strongest positive loading on PC1 while the deep-water taxa *Microcalanus* spp., *O. atlantica* and *M. lucens* had the strongest negative loadings. *Calanus hyperboreus*, *C. finmarchicus*, primarily cold-water taxa, and Ostracoda had the strongest positive loadings on PC2 whereas the warm-water taxa *Paracalanus* sp., *Centropages typicus*, *Clausocalanus* spp. and *M. lucens* had the strongest negative loadings. Positive loadings on PC3 were dome-shaped and most strongly affected by *Paracalanus* sp., *C. typicus* and *M. lucens*.

The spatial distribution of the average PC scores for each sampling location from the fall surveys revealed patterns that were generally similar to those apparent in the spring (Fig. 7). Negative

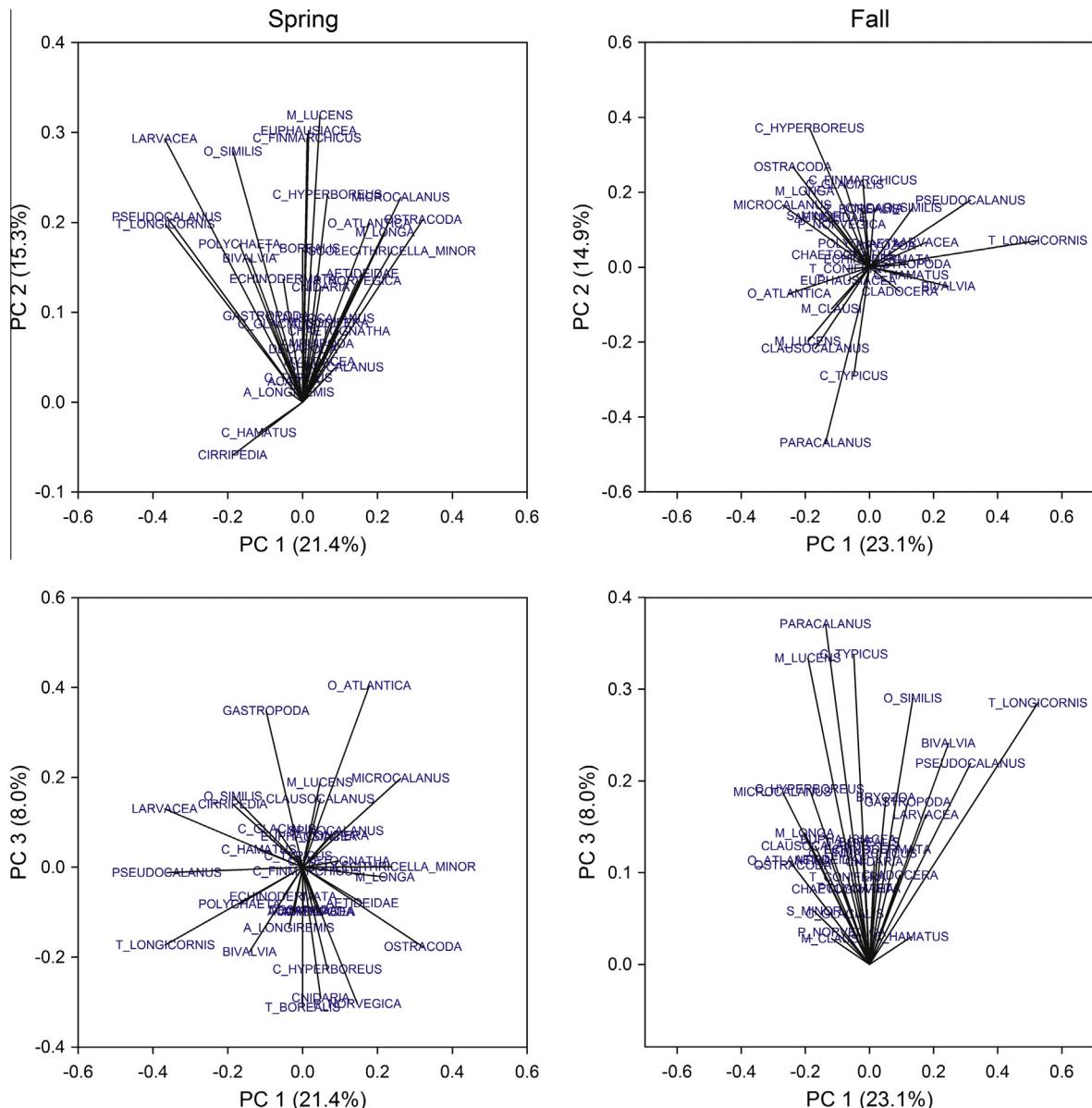


Fig. 6. Pattern of variation in species composition along the first three axes (PC1–PC3) of the principal component analysis of the spring (left) and fall (right) surveys. The percentage of variation associated with each axis appears in brackets next to the title. The name of each taxon appears at the end of each vector.

PC1 scores demonstrated a contrast principally of sites beyond the continental shelf (defined by the 200 m isobaths) and in the deep channels of the Gulf of St. Lawrence with those from the shallower sites. In contrast to the pattern noted in the spring, there appeared to be some distinction between most of the sites north of the Grand Banks and in the Gulf of St. Lawrence (PC2 positive scores) from those on the southern Grand Banks, Scotian Shelf and Cabot Strait (PC2 negative scores). Average PC3 scores were nearly all positive at sites on the Scotian Shelf and in the deep channels in the Gulf of St. Lawrence, whereas sites on the Newfoundland Shelf and in shallow parts of the Gulf of St. Lawrence exhibited negative scores.

Zooplankton community – constrained analysis

Spring surveys

All 15 environmental variables included in our analyses had a highly statistically significant ($p < 0.002$) effect on zooplankton community structure and accounted for 36.7% of the overall variance, although only the first 10 RDA axes were statistically

significant (Table 2). Depth alone accounted for 16.0% of the variance, which together with subsurface silicate inventories and average surface layer temperature and salinity accounted for a total of 28.9% of the variance (78% of explained variance). The remaining environmental variables each explained less than 2% of the overall variance. The first three axes of the RDA account for 31.8% of the total variance. As in the PCA of the environmental variables, there is clearly a strong association among many of the environmental variables (Fig. 8). Taxa contributing heavily to the structure in zooplankton community reflected the strong cross-shelf gradient in species composition along the first axis, with shallow shelf species (e.g. *Pseudocalanus* spp., *T. longicornis*, larvaceans) demonstrating separation with taxa that are more prevalent in deeper waters (e.g. *O. atlantica*, *Microcalanus* spp., *C. finmarchicus*, Ostracoda). Although many of the species were ubiquitous throughout much of the region, their relative importance changed in different environments. Larger species (e.g. *C. hyperboreus*, *C. finmarchicus*, *P. norvegica*) were more prevalent in areas where the abundance of smaller species was low (e.g. *Oithona similis*, *O. atlantica*, pelagic gastropods). The spatial pattern of average scores along the first

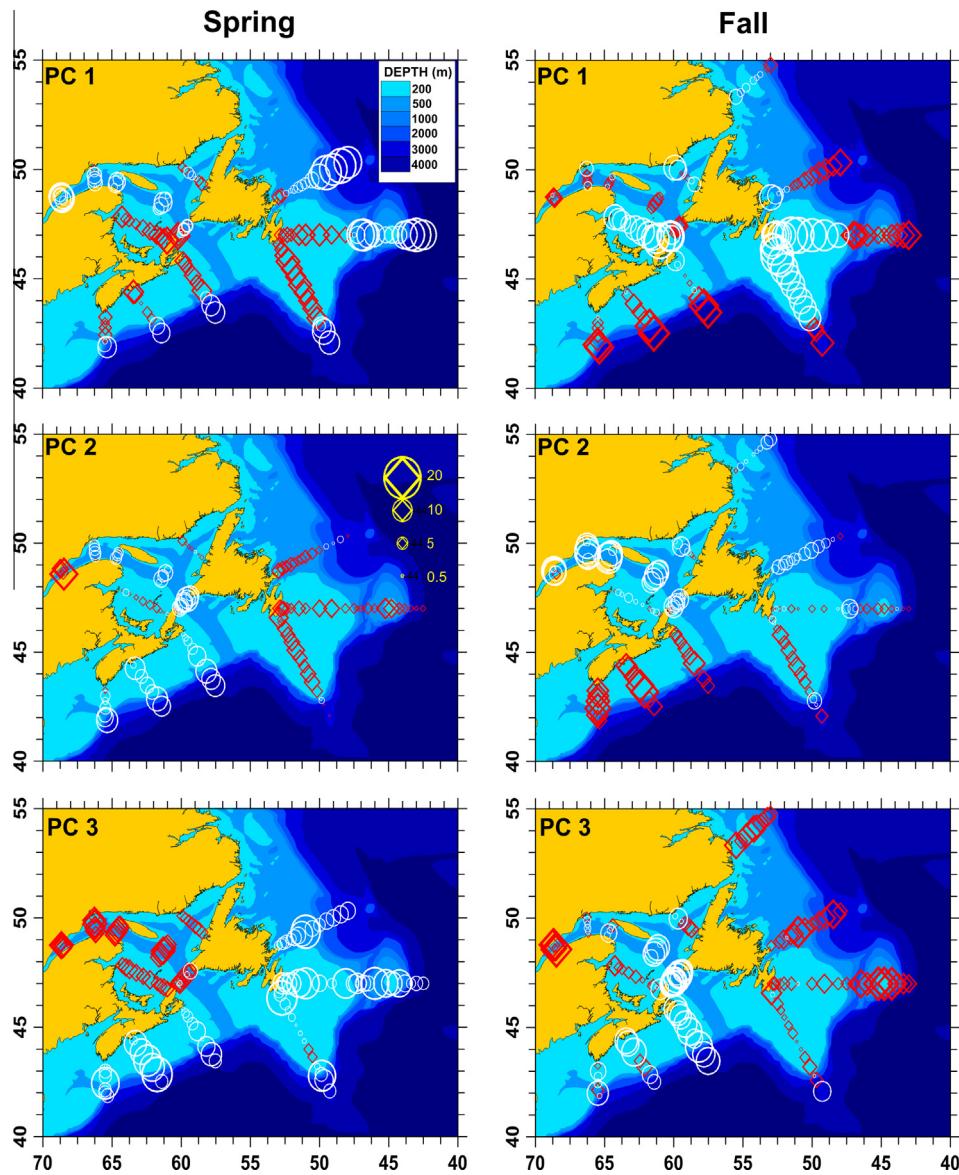


Fig. 7. Expanding symbol map of the average component score of the first three axes (PC1 – top panel; PC2 – middle panel; PC3 – bottom panel) of the principal component analysis of zooplankton data from the spring (left) and fall (right) surveys. Diamonds represent negative values; circles represent positive values; the size of each symbol scales in accordance to the value (the scale appears in yellow in the middle panel). Positive and negative values are consistent with the outcomes from the principal components analyses and have not been rotated to provide consistent views between seasons. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

axis (RDA1) demonstrated the clear influence of bathymetry on the distribution of zooplankton (Fig. 9), while the separation of the communities from the Gulf of St. Lawrence and inner Scotian Shelf (although the loadings for the latter were much weaker) from those found on the Newfoundland Shelf and Scotian Slope water was evident in the loadings on RDA2. The spatial pattern of positive RDA2 values may reflect the influence of the outflow of low-salinity water from the Gulf of St. Lawrence through Cabot Strait. There was considerable spatial structure in the average loadings on RDA3, which contrasts areas with higher temperatures (positive loadings) from cooler ones as temperature had a strong loading on RDA3. This pattern may reflect the influence of the inshore and offshore branches of Labrador Current flow on the Newfoundland Shelf and contrast the warmer and cooler portions of the Scotian Shelf and Gulf of St. Lawrence.

There was considerable residual variance (63.3%) in zooplankton community structure that was not accounted for by the linear model estimated in the RDA. Some of this variance is likely the result of

sampling variability and counting errors associated with the protocols used in the program. However, there was also considerable spatial structure in the scores associated with the first three PCs of the analysis of residuals (Fig. 9) which accounted for 23.8% of the overall variance. In contrast to the results of the constrained analysis, the spatial structure in the residual PC analysis demonstrated a high degree of spatial fragmentation in average scores in which apparently distinct environments, such as the Grand Banks and Scotian slope waters, are more similar to one another in zooplankton composition than they are to the Labrador Current, Laurentian Channel and Scotian Shelf (Fig. 9). The spatial distribution of average loadings on individual PCs were partly the result of the influence of a few species that in some instances demonstrated relationships in their relative abundance which departed from statistical normality. There was a strong inverse loading of *C. finmarchicus* (-0.35) and *C. hyperboreus* (-0.45) relative to *O. similis* (0.75) along the first residual PC, while larvaceans loaded inversely to these three species along PC2 (0.78 versus -0.35,

Table 2

Details of the redundancy analysis (top portion of the table) of the spring surveys and results for the forward selection regression procedure (bottom portion of the table), based on adjusted R^2 -squared (R_{adj}^2), that was applied to determine whether the number of variables included in the multivariate analysis contributed significantly to the outcome.

	Degrees of Freedom	Variance	Percent of total variance	Cumulative percentage	F-value	P
RDA1	1	0.062	0.210	0.210	401.48	0.001
RDA2	1	0.020	0.068	0.278	130.83	0.001
RDA3	1	0.012	0.040	0.318	76.58	0.001
RDA4	1	0.004	0.015	0.333	28.13	0.001
RDA5	1	0.004	0.013	0.345	24.76	0.001
RDA6	1	0.003	0.009	0.354	17.21	0.001
RDA7	1	0.001	0.004	0.359	8.10	0.001
RDA8	1	0.001	0.003	0.361	5.34	0.001
RDA9	1	0.001	0.002	0.363	3.56	0.001
RDA10	1	<0.001	0.001	0.365	2.36	0.008
RDA11	1	<0.001	0.001	0.365	1.65	0.061
RDA12	1	<0.001	0.001	0.366	1.12	0.339
RDA13	1	<0.001	<0.001	0.366	0.91	0.551
RDA14	1	<0.001	<0.001	0.367	0.47	0.97
RDA15	1	<0.001	<0.001	0.367	0.34	0.997
Residual	1213	0.187				

Variable	R^2	Cumulative R^2	Cumulative R_{adj}^2	F-value	P
DEPTH	0.160	0.160	0.159	233.08	0.001
SIL50_150	0.057	0.217	0.216	89.70	0.001
T0_50	0.047	0.264	0.262	77.70	0.001
S0_50	0.026	0.289	0.287	44.27	0.001
NITO_50	0.017	0.307	0.304	30.54	0.001
CHLO_100	0.014	0.321	0.318	25.76	0.001
CIL	0.011	0.331	0.328	19.24	0.001
XSILO_50	0.007	0.339	0.334	13.13	0.001
NIT50_150	0.007	0.345	0.341	12.56	0.001
PHOO_50	0.004	0.350	0.344	7.84	0.001
XPHOO_50	0.009	0.358	0.352	16.18	0.001
STRAT	0.003	0.361	0.355	6.42	0.001
PHO50_150	0.002	0.363	0.357	3.81	0.001
SILO_50	0.002	0.365	0.358	3.54	0.001
O2_050	0.002	0.367	0.359	2.97	0.003

–0.20, and –0.28, respectively). Non-normality in the abundance of some ubiquitous species did not influence the overall findings, however, as the results of the distance-based RDA using presence/absence transformations of the data did not alter these basic results (not shown), although the constrained analysis explained slightly more of the variance (43.3%) relative to the RDA. An evaluation of the information content based on application of a forward-selection model using the R_{adj}^2 criteria revealed that all environmental variables provided statistically highly significant contributions to the explanation of variations in zooplankton community structure (Table 2).

SIMPER analysis, contrasting observations with positive and negative scores on RDA1–RDA3, reveals that 12–13 taxa accounted for approximately 50% of the dissimilarity between groups along all three axes. Of those, 11 taxa contributed to the top 50% of dissimilarity along all three axes (Table 3). Differences in the abundance of larvaceans, *T. longicornis*, *Pseudocalanus* spp., *C. hyperboreus* and *Microcalanus* spp. were highly influential. For each RDA axis, twenty-seven taxa accounted for 90% of the dissimilarity between observations with positive and negative scores; these 27 taxa represent 77% of the taxa included in the analyses.

Fall surveys

As in the analysis of the spring surveys, all 15 environmental variables had a statistically significant influence on zooplankton community structure ($p < 0.004$) and explained 37.8% of the overall variance (Table 4). Depth accounted for 14% of the overall variance, and together with surface temperature, salinity and subsurface

nitrates inventories accounted for 31% of the total variance (81% of the explained variance). The first three axes of the RDA accounted for 33.5% of the variance, but the association with environmental variables was more complex than for the spring surveys (Fig. 8). As with the spring surveys, a few taxa had considerable influence on the loadings along each axis. The influence of depth on species composition was clearly evident along the first RDA axis with *T. longicornis*, *Pseudocalanus* spp., and *O. similis* being more abundant in shallower waters while *O. atlantica*, *M. lucens*, *Clausocalanus* spp., and *C. finmarchicus* and *C. hyperboreus* were more abundant in deeper waters. Along RDA2, *Paracalanus* sp., *C. typicus*, *M. lucens* and *Clausocalanus* spp. were relatively more abundant in warmer waters while *C. finmarchicus*, *C. hyperboreus*, *Pseudocalanus* spp. and *O. similis* were more abundant in cooler areas. The effect of bathymetry was clearly apparent in the spatial distribution of average RDA1 scores (Fig. 10) although the contrast between the Laurentian Channel and the shallow parts of the Gulf of St. Lawrence did not appear to be as strong as for the spring surveys. RDA2 provided a separation of communities from the southern Grand Banks and Scotian Shelf from those in the Gulf of St. Lawrence and the Newfoundland Shelf, which appears to be a reflection of the contrasting thermal environments among these areas. Finally, RDA3 reflected differences in the communities off the eastern coast of Newfoundland from those of the Scotian Shelf and Gulf of St. Lawrence.

The residual variance (62.2%) demonstrated mesoscale patterns of coherence (~100–200 km) in the average scores for PC1 and PC2 but appeared to demonstrate coherence at large scales (100s of km) for the average scores of PC3 (Fig. 10). Species which exhibited strong loadings in the constrained analysis once again had significant associations and disparities along PC1 (*C. finmarchicus* (0.34), gastropods (0.2), *O. similis* (−0.65), *Paracalanus* sp. (−0.22), *Pseudocalanus* spp. (0.23), *T. longicornis* (0.49)) and PC2 (*C. finmarchicus* (0.51), *C. hyperboreus* (0.28), *O. similis* (−0.38), *Paracalanus* sp. (0.26), *T. longicornis* (−0.53)). Some degree of similarity among nearby sites should be expected because the multiple linear regression model used in the constrained analysis may not provide the ideal fit to the relationships among species, particularly if non-linearity in those relationships is substantial. We also note that some of the residual spatial structure was likely a reflection of local circulation features, such as the inshore arm of the Labrador Current near southeastern Newfoundland and the outflowing Nova Scotia Current along the northeastern side of Nova Scotia, and the Anticosti Gyre-Gaspé Current system in the northwest Gulf of St. Lawrence. These features have similar environmental properties to adjacent water masses but have sufficiently distinct zooplankton communities that may reflect connectivity between adjacent ecosystems. However, the spatial scale of coherence at mesoscales in the residual variance from the fall surveys is likely to be indicative of constraints and processes that were not considered in the RDA, such as differences in the relative state of community development along the seasonal cycle, differences caused by limitations in the range of some species, or the cumulative effect of trophic interactions. As in the case of the spring surveys, the results of the distance-based RDA using presence/absence transformations of the data did not alter our RDA basic results (not shown), and the overall variance explained by the constrained analysis was 40.8%, which was slightly more than the RDA, as in the spring analysis. An evaluation of the information content based on application of a forward-selection model using the R_{adj}^2 criteria revealed that all environmental variables provided statistically highly significant contributions to the explanation of variations in zooplankton community structure (Table 4).

SIMPER analysis, contrasting observations with positive and negative scores on RDA1–RDA3, reveals that 12 taxa accounted for approximately 50% of the dissimilarity between groups along

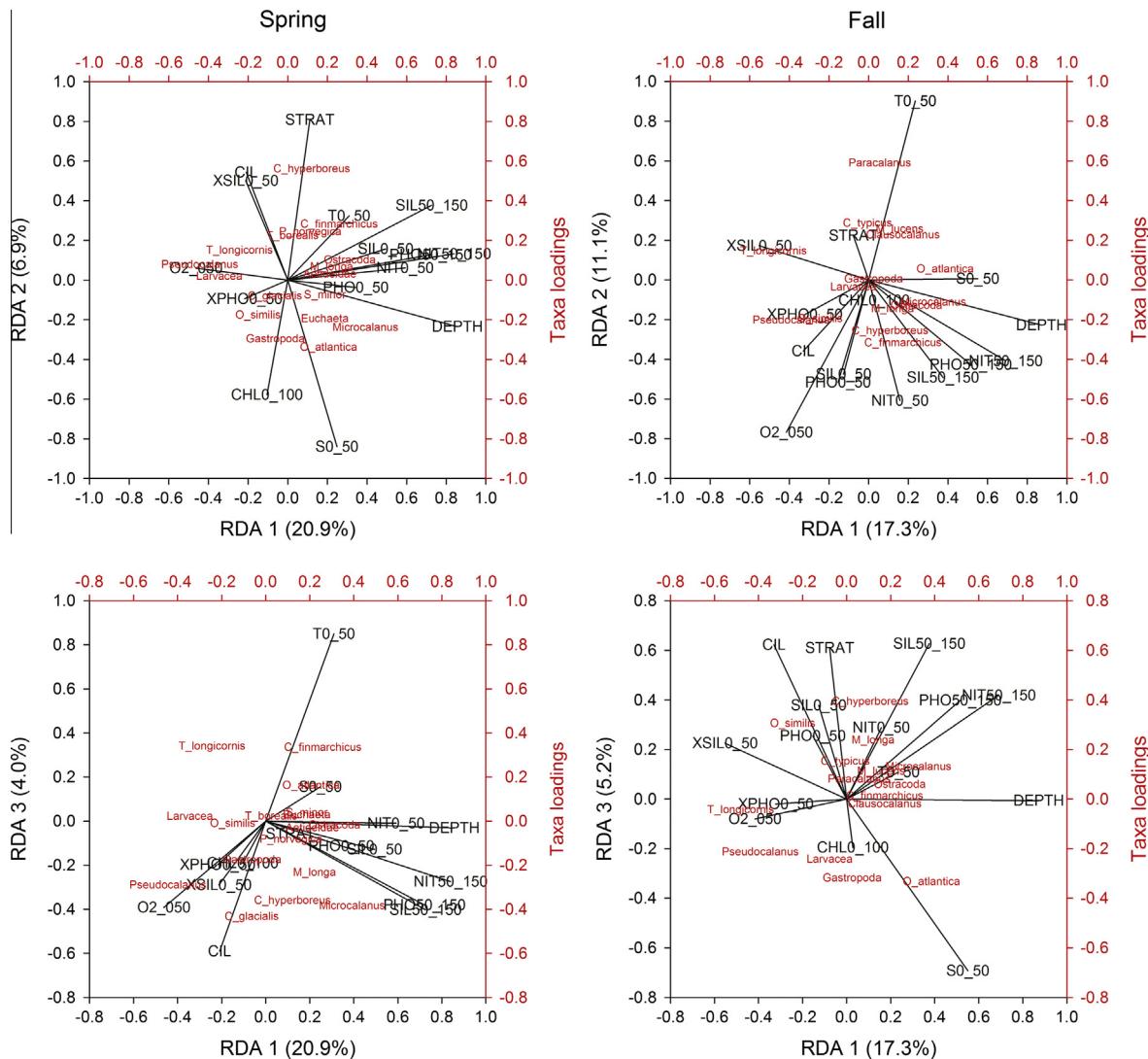


Fig. 8. Score along the first three axes of the redundancy analysis of each taxon (right and top axes) based on a Hellinger transformation of the zooplankton data from the spring (left column) and fall (right column) surveys. Only taxa with combined scores >0.2 on the first three axes are included in the plot. Vectors represent the relationships with and among the environmental variables (left and bottom axes). Symbols for environmental variables are as in Fig. 3.

all three axes. Of that, 11 taxa contributed to the top 50% of dissimilarity along all three axes (Table 5), and 9 of these taxa were also particularly influential in differentiating the RDA scores during the spring surveys. Differences in the abundance of *T. longicornis*, *Pseudocalanus* spp., *C. hyperboreus*, *O. atlantica* and *Paracalanus* sp. were highly influential. On each RDA axis, thirty to thirty-one taxa accounted for 90% of the dissimilarity between observations with positive and negative scores on each RDA axis, which represents ~68% of the taxa included in the analyses.

Environmental relationships

Environmental variables included in the constrained analyses were selected not only because they have been demonstrated to affect the spatial distribution of plankton communities but also because interannual variations in some of these features, such as temperature and salinity, have been linked to fluctuations in the abundance and distribution of many components of marine ecosystems. To illustrate the potential value of multivariate analyses of community structure, we investigated whether the environmental relationships identified in the RDA analyses can reflect interannual variations in environmental features. We selected

RDA2 and the first three PCs of the RDA residuals from the fall period for illustrative purposes because temperature (T0_50 m) demonstrated a strong positive loading on RDA2 (Fig. 8) and there was strong separation of several ecologically-important large species along this axis (*M. longa*, *Euphausiacea*, *C. finmarchicus*, *Calanus glacialis* and *C. hyperboreus*). Two warm-water taxa that were strongly associated with RDA2, *Paracalanus* sp. and *C. typicus*, were not included in the analysis because they were absent or very low in abundance along sections in the northern part of the study region. Because our long-term objectives involve the development of indicators of ecosystem state, we based this assessment of the environment-community relationship for each section's average RDA2 scores and temperatures from each fall survey to provide indices similar to those used in regional environmental assessments. We also contrasted the average abundance of the five key species along each of the sections with average temperature to assess whether the fundamental relationships identified in the RDA held locally and interannually. Observations for all variables were transformed in the same manner as applied in the RDA. Finally, we also evaluated whether we could identify any relationship with interannual variations in temperature with PC1–3 of the RDA residuals along individual sections as a test of the local

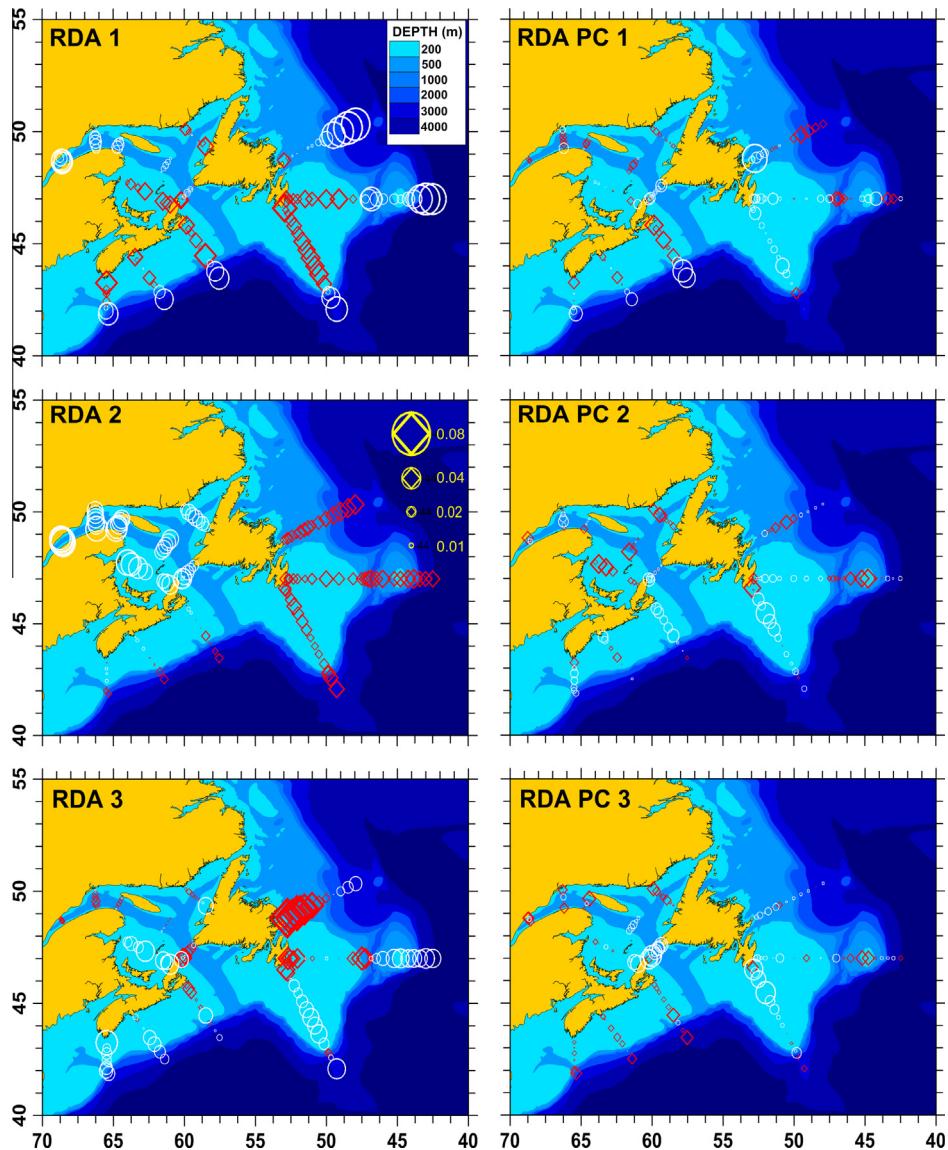


Fig. 9. Expanding symbol maps of the average component score of the first three axes (RDA1 – top panel; RDA2 – middle panel; RDA3 – bottom panel) of the redundancy analysis (left) and of the first three axes (RDA PC1 – top panel; RDA PC2 – middle panel; RDA PC3 – bottom panel) from a principal component analysis of the residual component of redundancy analysis (right) of zooplankton data from the spring surveys. Diamonds represent negative values; circles represent positive values; the size of each symbol scales in accordance to the value (the scale appears in yellow in the middle panel). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

accuracy of the general linear relationships derived in the constrained portion of the analyses.

The average fall temperature ranges observed on the sections varied from 1.6 on the Bonavista Bay section to 4.6 °C on the Halifax section (Table 6). Average temperatures were highest on the Scotian Shelf while temperatures were lower in the Gulf of St. Lawrence and off Newfoundland. The strength of the interannual relationship between average RDA2 scores and average temperature demonstrated considerable variability among sections, and correlations for the Scotian Shelf, Bonavista Bay and Cabot Strait (IML) sections were not significant. PC1 demonstrated statistically significant relationships with average fall temperature for the Anticosti Gyre section, which are weaker than the relationship between RDA2 and temperature, and for the Cabot Strait (IML) sections. Average PC2 scores had a strong positive association with temperature for the Louisbourg and Halifax sections, although only significantly for the latter. Statistically significant inverse relationships of temperature and PC2 scores were also

obtained for the St. Lawrence Estuary and Iles-de-la-Madeleine sections. The weak RDA2 association with interannual fluctuations in temperature along the Browns Bank section was not surpassed by any of the first three residual PCs. Forecasting the abundance of individual taxa based on average temperature along sections was highly variable, rarely significant, and the sign of the relationships was not always consistent with the average loadings identified in the RDA analysis. The correlations for the three species of *Calanus*, which all had negative loadings on RDA2, were generally stronger and more consistent in their sign than those for *M. lucens*. The associations of Euphausiacea with temperature were the poorest, which is not entirely unexpected given the weak loading of this taxon on RDA2 (Fig. 8). Moreover, vertical ring net sampling was not the most-suitable method for quantifying Euphausiacea because their strong swimming ability allows larger individuals to evade capture and oceanographic sections may not be ideal to characterize taxa with high degrees of patchiness.

Table 3

Results of the SIMPER analysis listing the average dissimilarity (Av.Diss), ratio of average dissimilarity to its standard deviation (Diss/SD), and cumulative percentage contribution of taxa that explain the top 90% of dissimilarity among observations with positive and negative loadings on RDA1–RDA3 for the spring surveys.

Taxa	RDA1			Taxa	RDA2			Taxa	RDA3		
	Av.Diss	Diss/ SD	Cumulative percentage		Av.Diss	Diss/ SD	Cumulative percentage		Av.Diss	Diss/ SD	Cumulative percentage
Larvacea	2.57	1.29	5.42	Larvacea	2.30	1.27	5.12	Larvacea	2.32	1.27	5.29
<i>Pseudocalanus</i> spp.	2.41	1.22	10.49	<i>T. longicornis</i>	2.12	1.18	9.84	<i>T. longicornis</i>	2.15	1.15	10.19
Ostracoda	2.35	1.62	15.45	<i>C. hyperboreus</i>	2.04	1.3	14.37	<i>Pseudocalanus</i> spp.	2.02	1.18	14.78
<i>T. longicornis</i>	2.33	1.23	20.35	<i>Pseudocalanus</i> spp.	1.99	1.17	18.80	<i>C. hyperboreus</i>	1.84	1.22	18.97
<i>Microcalanus</i> spp.	2.03	1.27	24.64	Gastropoda	1.81	1.31	22.82	<i>Microcalanus</i> spp.	1.83	1.19	23.13
<i>M. longa</i>	1.92	1.38	28.69	Euphausiaceae	1.78	1.34	26.78	Euphausiaceae	1.79	1.32	27.22
<i>O. similis</i>	1.84	1.25	32.56	<i>Microcalanus</i> spp.	1.76	1.24	30.69	<i>O. similis</i>	1.77	1.24	31.24
<i>O. atlantica</i>	1.82	1.18	36.39	<i>O. similis</i>	1.73	1.25	34.54	Gastropoda	1.71	1.26	35.13
<i>C. hyperboreus</i>	1.78	1.24	40.13	<i>O. atlantica</i>	1.71	1.16	38.35	<i>O. atlantica</i>	1.70	1.12	39.01
Euphausiaceae	1.77	1.34	43.86	Ostracoda	1.70	1.10	42.12	<i>M. longa</i>	1.69	1.22	42.86
<i>S. minor</i>	1.74	1.45	47.53	<i>C. finmarchicus</i>	1.65	1.26	45.80	Ostracoda	1.68	1.09	46.70
Gastropoda	1.72	1.26	51.15	<i>M. longa</i>	1.62	1.23	49.41	<i>C. glacialis</i>	1.68	1.21	50.53
Polychaeta	1.63	1.26	54.57	Polychaeta	1.59	1.28	52.95	<i>C. finmarchicus</i>	1.63	1.26	54.25
<i>C. finmarchicus</i>	1.60	1.23	57.94	<i>C. glacialis</i>	1.53	1.20	56.34	Polychaeta	1.59	1.25	57.87
Cirripedia	1.59	0.93	61.30	<i>M. lucens</i>	1.44	0.99	59.53	Cirripedia	1.47	0.88	61.22
<i>C. glacialis</i>	1.58	1.20	64.63	Cirripedia	1.43	0.88	62.72	<i>M. lucens</i>	1.41	0.94	64.43
<i>M. lucens</i>	1.42	0.95	67.62	<i>P. norvegica</i>	1.41	1.04	65.86	<i>S. minor</i>	1.34	1.10	67.47
<i>P. norvegica</i>	1.42	1.08	70.62	<i>S. minor</i>	1.31	1.11	68.78	<i>Centropages</i> spp.	1.27	0.83	70.35
<i>Euchaeta</i> spp.	1.41	0.99	73.59	<i>T. borealis</i>	1.30	1.01	71.67	<i>P. norvegica</i>	1.22	0.94	73.14
<i>Centropages</i> spp.	1.29	0.85	76.31	<i>Centropages</i> spp.	1.24	0.83	74.43	Bivalvia	1.15	0.83	75.77
Aetideidae	1.20	1.07	78.85	Bivalvia	1.23	0.89	77.16	<i>Euchaeta</i> spp.	1.14	0.85	78.37
Bivalvia	1.14	0.83	81.25	Cnidaria	1.19	1.22	79.81	<i>Chaetognatha</i>	1.05	1.17	80.76
Chaetognatha	1.11	1.21	83.58	<i>Euchaeta</i> spp.	1.13	0.86	82.32	<i>T. borealis</i>	0.98	0.80	82.99
Cnidaria	1.02	1.06	85.72	Chaetognatha	1.05	1.47	84.65	Aetideidae	0.98	0.89	85.21
<i>T. borealis</i>	1.00	0.82	87.83	Aetideidae	1.01	0.93	86.89	Cnidaria	0.96	1.02	87.39
<i>C. hamatus</i>	0.85	0.64	89.63	Echinodermata	0.78	0.63	88.64	<i>C. hamatus</i>	0.81	0.62	89.24
Echinodermata	0.72	0.59	91.14	<i>C. hamatus</i>	0.78	0.62	90.38	Echinodermata	0.72	0.59	90.87

An investigation of the RDA2 scores in relation to transformed temperature provides some insight into the possible cause of the variations in predictability among sections. Although the predicted values (RDA2) show a strong relationship with temperature (Fig. 11), there remains a degree of non-linearity in the distribution of observations, and the variance increases at higher temperatures. The latter, coupled with a small interannual signal, may be particularly important in explaining why variations in average temperature and RDA2 scores from the sections from the Scotian Shelf are weakly correlated.

Discussion

The Canadian northwest Atlantic continental shelf region included in this study spans nearly 14 degrees of latitude and is heavily influenced by the Labrador Current, which carries cold fresh waters of Arctic origin equatorward, and the Gulf Stream, which transports warm salty waters poleward. Gradients in environmental conditions are enhanced further by the significant and seasonally variable freshwater outflow through the Gulf of St. Lawrence from the St. Lawrence River, which has a drainage basin of 1.6 million km². The study region spans waters that are seasonally ice covered (Labrador and Newfoundland Shelf and Gulf of St. Lawrence) and areas that remain ice free throughout the year (central and western Scotian Shelf). Because our data span water masses that include sub-arctic to north temperate as well as estuarine and neritic to oceanic, it is not unexpected that we should identify important contrasts across the region. What may be unexpected, however, is the overall high degree of similarity in the relative

composition of the zooplankton community through varying environments, the relatively small number of taxa that contribute most to the observed dissimilarity, and that only a few of the environmental metrics we considered were required to provide meaningful predictors for the general spatial trends in community structure.

Environmental conditions

Principal components analysis of environmental conditions during the spring surveys identified a strong depth-related variation in surface and subsurface nutrient inventories that defines the onshore–offshore gradient. This variation was nearly orthogonal to the gradients in temperature–salinity versus the thickness of the cold intermediate layer and oxygen-excess silicate concentrations that essentially represent the transition from sub-polar to sub-tropical waters. These two major patterns of variation accounted for approximately 45% of the multivariate variance in environmental indices. The strong separation of depth and temperature effects at the northwest Atlantic scale study contrasts with analyses of environmental patterns limited to the Scotian Shelf and Newfoundland Shelf LMEs, where there are strong inshore–offshore temperature gradients driven by the influence of cold outflow (Gulf of St. Lawrence onto the inner Scotian Shelf, and inner arm of the Labrador Current on the Newfoundland Shelf) and warm waters offshore (Gulf Stream and Labrador Sea), respectively (Pepin et al., 2011, CL Johnson, unpublished data).

Several factors contribute to the strong association between depth and nutrient inventories on PC1 in spring. Subsurface nutri-

Table 4

Details of the redundancy analysis (top portion of the table) of the fall surveys and results for the forward selection regression procedure (bottom portion of the table), based on adjusted R^2 (R_{adj}^2) that was applied to determine whether the number of variables included in the multivariate analysis contributed significantly to the outcome.

	Degrees of Freedom	Variance	Percent of total variance	Cumulative percentage	F-value	P
RDA1	1	0.057	0.173	0.173	320.68	0.001
RDA2	1	0.036	0.111	0.284	205.76	0.001
RDA3	1	0.017	0.052	0.335	95.66	0.001
RDA4	1	0.006	0.017	0.352	31.77	0.001
RDA5	1	0.003	0.010	0.362	18.16	0.001
RDA6	1	0.002	0.005	0.367	8.93	0.001
RDA7	1	0.001	0.004	0.371	6.95	0.001
RDA8	1	0.001	0.002	0.373	4.52	0.001
RDA9	1	0.001	0.002	0.375	3.10	0.002
RDA10	1	<0.001	0.001	0.376	2.17	0.021
RDA11	1	<0.001	0.001	0.377	1.57	0.098
RDA12	1	<0.001	0.001	0.377	1.44	0.138
RDA13	1	<0.001	<0.001	0.378	0.38	0.987
RDA14	1	<0.001	<0.001	0.378	0.34	0.996
RDA15	1	<0.001	<0.001	0.378	0.21	1
Residual	1155	0.204				

Variable	R^2	Cumulative R^2	Cumulative R_{adj}^2	F-value	P
DEPTH	0.140	0.140	0.139	190.04	0.001
T0_50	0.100	0.240	0.239	154.36	0.001
S0_50	0.039	0.279	0.277	62.54	0.001
NIT50_150	0.031	0.310	0.307	52.02	0.001
O2_050	0.017	0.327	0.324	30.28	0.001
NITO_50	0.013	0.340	0.337	22.67	0.001
SIL50_150	0.010	0.350	0.347	18.69	0.001
SIL0_50	0.006	0.356	0.352	10.85	0.001
PHO50_150	0.004	0.361	0.356	7.52	0.001
CIL	0.004	0.365	0.360	8.05	0.001
CHLO_100	0.003	0.368	0.362	5.98	0.001
PHOO_50	0.003	0.371	0.365	5.55	0.001
XPHOO_50	0.002	0.373	0.366	4.03	0.001
XSILO_50	0.002	0.376	0.368	4.46	0.001
STRAT	0.002	0.378	0.370	3.75	0.002

ent inventories represent an estimate of the total nutrient pool between 50 and 150 m depth, or between 50 m and the nominal bottom depth. This relatively-shallow depth stratum was chosen to include subsurface nutrient inventories at the majority of stations across a region that includes many shallow areas. The subsurface nutrient inventories reflect spatial variability in both water mass and local nutrient regeneration processes; for example, relatively-high nutrient concentrations are associated with the North Atlantic Central Water that forms the warm slope water, the dominant slope water type off the Scotian Shelf during 1999–2011, and also with strong nutrient regeneration in the St. Lawrence Estuary (Townsend et al., 2006). However, subsurface nutrient inventories are also systematically lower in water of less than 150 m depth because of the reduced depth range over which the inventory is integrated. Nutrients in this depth stratum are also influenced by primary production in the euphotic zone, which the stratum overlaps, and they may therefore reflect depletion as a result of the seasonal primary production cycle. The third PC axis of variation reflected an association between higher levels of chlorophyll and higher salinities, inversely related to temperature and excess levels of silicates. AZMP spring surveys were generally carried out after the spring phytoplankton bloom, and substantially later in the Gulf of St. Lawrence. Based on comparison with semi-monthly climatological patterns of chlorophyll variability across the study region, the spatial structure of the spring PC3 is likely influenced by differences in the timing of sampling relative to the spring bloom (Bedford Institute of Oceanography

Operational Remote Sensing). Because spring phytoplankton blooms in the region consist principally of diatoms, the inverse association with excess silicate levels is reasonable even though nitrate levels are generally the limiting factor in the study area (Harrison and Li, 2008; Harrison et al., 2013).

In contrast to spring, the strongest environmental gradient in the fall was associated with temperature, reflecting an increased latitudinal gradient related to the cumulative heat gain from the summer. Variations associated with depth were again nearly orthogonal to the temperature gradient. The fall surveys were carried out over a time interval of 2 months during which the vertical stratification of the water column begins to break down. This may have contributed to the inverse relationship between average surface temperature and surface nutrient inventories, which would increase as a result of enhanced mixing and thus may be more a reflection of the timing of individual surveys rather than broad-scale environmental patterns. Deeper locations had greater subsurface nutrient inventories, as in the spring, reflecting the contrast between oceanic and shelf environments, but surface nutrient inventories, with the exception of excess silicate, were not strongly related to water depth. As in the spring, the third PC axis identified the association between phytoplankton concentrations and surface salinity that were inversely related with excess silicate. Although it has been noted that the fall bloom consists of flagellates, dinoflagellates and diatoms (Head and Pepin, 2010; Johnson et al., 2013), our analysis highlights that much of biomass likely consists of diatoms. However, from the perspective of predicting the spatial patterns in zooplankton community structure, our analysis reveals that temperature–salinity–nutrient gradients are dominant signals in both spring and fall and that phytoplankton standing stock, along with corresponding biogeochemical variables, represents a variable habitat descriptor superimposed over macroscale environmental features.

Zooplankton community

The unconstrained analyses explained ~45–50% of the variation in zooplankton community structure in the first three principal components, indicating that the broad-scale biogeographic features identified in the analysis represent dominant characteristics of the pelagic environment in the region. Bathymetry proved to have the strongest and most consistent effect across space and time, as demonstrated by the distinction between communities from shelf (<200 m) areas and those in deeper waters, on both the slope and in the deep channels of the Gulf of St. Lawrence in spring and fall. Even the simple indices of taxonomic richness, diversity and evenness revealed the strong associations of bathymetry with zooplankton communities. These contrasts in diversity and community structure across bathymetric landscapes suggest that the vertical extent and variations in water column environmental features, not measured by indices that integrate over broad depth intervals, are likely important determinants of community complexity and habitat partitioning among taxa (Longhurst, 1985; Mackas et al., 1993). Energy storage strategies are known to affect the vertical distribution of mesozooplankton in response to spatial and seasonal changes in environmental conditions (Heath et al., 2004; Laakmann et al., 2012; Pond, 2012). For example, the distribution of different stages of the three *Calanus* species in the region is strongly affected by the onset of diapause (Huntley et al., 1983; McLaren et al., 2001; Plourde et al., 2001; Tittensor et al., 2003; Johnson et al., 2008; Pepin and Head, 2009). Competition among closely-related species (Laakmann et al., 2009), prey-predator interactions (Schulz et al., 2012) and ecophysiological niche adaptations (Irigoin et al., 2011) have also been identified as key factors that determine how the vertical extent of the water column can affect spatial patterns in zooplankton community

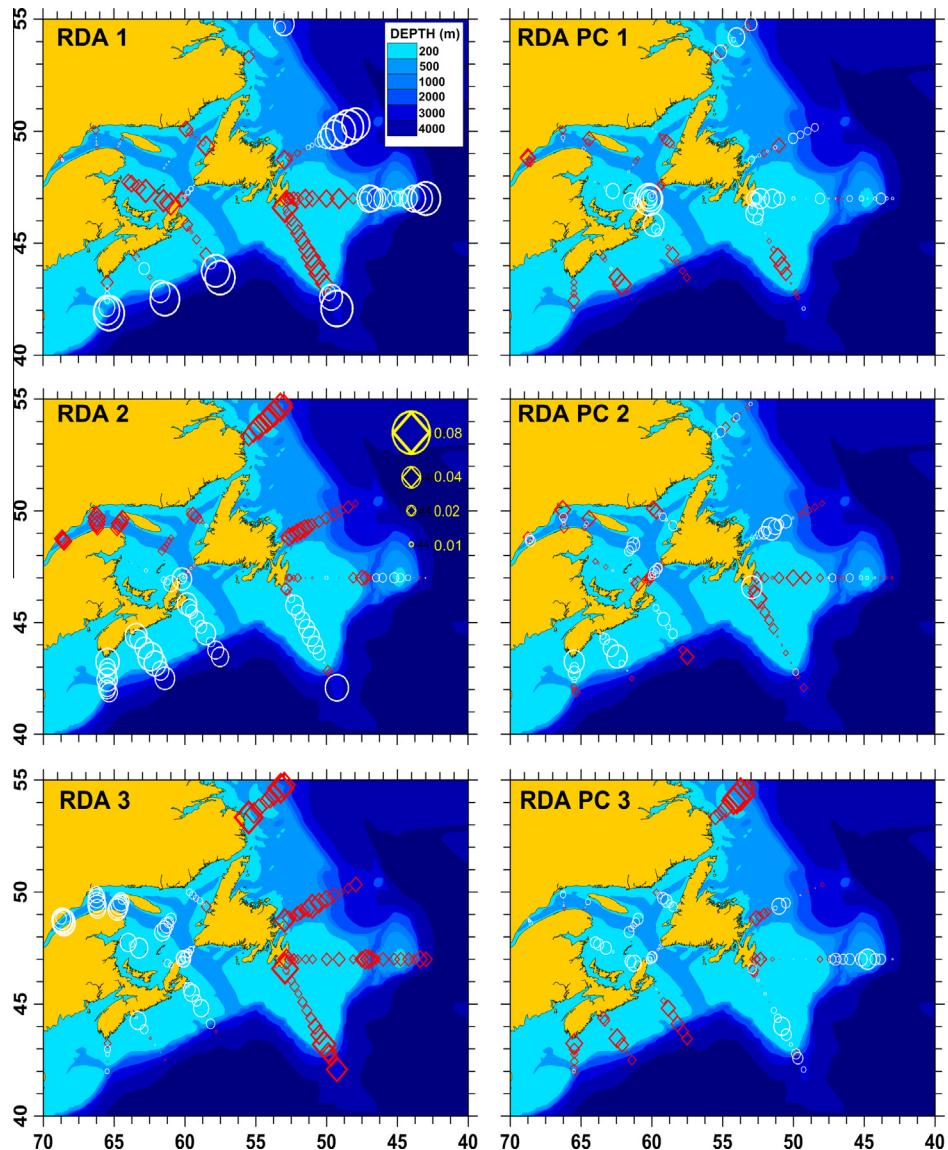


Fig. 10. Expanding symbol maps of the average component score of the first three axes (RDA1 – top panel; RDA2 – middle panel; RDA3 – bottom panel) of the redundancy analysis (left) and of the first three axes (RDA PC1 – top panel; RDA PC2 – middle panel; RDA PC3 – bottom panel) from a principal component analysis of the residual component of redundancy analysis (right) of zooplankton data from the fall surveys. Diamonds represent negative values; circles represent positive values; the size of each symbol scales in accordance to the value (the scale appears in yellow in the middle panel). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

structure. The potential significance of ecophysiological adaptation appears to be critical in many ways because the second and third PCs of the unconstrained analyses identified important latitudinal and estuarine-versus-oceanic gradients in community structure as significant signals following the apparent associations with bathymetry. The latitudinal pattern could reflect differences in the seasonal state of development of key taxa which reflect variations in the seasonal temperature cycle (Mackas et al., 2012), but observations from high-frequency sampling sites on the coastal shelf throughout the study area and in the Gulf of Maine have also revealed regional differences in community composition and annual community variability (CL Johnson, unpublished data). The effect of latitude is likely to be confounded with the gradient from the estuarine waters of the western Gulf of St. Lawrence, which are known to affect conditions on the Scotian Shelf via the outflow of water through the western Cabot Strait (e.g. Sameoto and Herman, 1992; Han et al., 1999) and reflected in the contrasts of temperature and salinity which affect community structure

throughout the western Atlantic (Gislason et al., 2009; Pepin et al., 2011; Estrada et al., 2012).

Constrained analyses revealed the dominant influence of only a few environmental variables and the role of a few dominant species in delineating the overall structure of the zooplankton communities in the northwest Atlantic. The overall variance accounted for by environmental variables was relatively small (<40% of the variance) when contrasted with the unconstrained analyses that highlighted the overall spatial structure in the communities, implying that factors other than those considered in our models are at play. In both seasons, depth was the dominant variable that influenced zooplankton communities, consistent with our interpretation of the unconstrained zooplankton community analysis, but the variability associated with depth in the RDA was less than the variability explained by zooplankton PC1 in both seasons. As discussed above, depth may serve as a proxy for deep-water pelagic habitat diversity that was not explicitly characterized in the analysis presented here, and thus the differences

Table 5

Results of the SIMPER analysis listing the average dissimilarity (Av.Diss), ratio of average dissimilarity to its standard deviation (Diss/SD), and cumulative percentage contribution of taxa that explain the top 90% of dissimilarity among observations with positive and negative loadings on RDA1–RDA3 for the fall surveys.

Taxa	RDA1			RDA2			RDA3				
	Av.Diss	Diss/ SD	Cumulative percentage	Av.Diss	Diss/ SD	Cumulative percentage	Av.Diss	Diss/ SD	Cumulative percentage		
<i>T. longicornis</i>	3.39	1.35	6.49	<i>T. longicornis</i>	2.96	1.19	5.78	<i>T. longicornis</i>	2.95	1.22	5.84
<i>Pseudocalanus</i> spp.	2.52	1.19	11.3	<i>Paracalanus</i> spp.	2.81	1.16	11.25	<i>Pseudocalanus</i> spp.	2.32	1.26	10.44
<i>O. atlantica</i>	2.47	1.38	16.03	<i>Pseudocalanus</i> spp.	2.35	1.18	15.83	<i>C. hyperboreus</i>	2.29	1.33	14.98
<i>C. hyperboreus</i> Ostracoda	2.32	1.39	20.46	<i>C. hyperboreus</i>	2.24	1.32	20.20	<i>O. atlantica</i>	2.20	1.29	19.34
<i>Microcalanus</i> spp.	2.21	1.28	29.03	<i>Microcalanus</i> spp.	2.07	1.22	28.39	<i>Paracalanus</i> spp.	2.15	0.92	23.59
<i>Paracalanus</i> spp.	2.17	0.95	33.19	<i>O. similis</i>	2.06	1.10	32.41	<i>Gastropoda</i>	2.09	1.30	27.74
<i>O. similis</i>	2.06	1.07	37.13	Larvacea	2.00	1.20	36.31	<i>O. similis</i>	2.08	1.12	31.87
<i>M. longa</i>	2.01	1.34	40.97	Gastropoda	1.95	1.23	40.12	<i>M. longa</i>	2.04	1.32	35.92
Larvacea	1.98	1.22	44.76	<i>M. longa</i>	1.94	1.25	43.90	Larvacea	2.04	1.23	39.96
Gastropoda	1.91	1.24	48.42	Ostracoda	1.89	1.17	47.58	<i>Microcalanus</i> spp.	1.99	1.2	43.91
Bivalvia	1.87	1.07	52.00	<i>M. lucens</i>	1.86	1.12	51.22	Bivalvia	1.83	1.03	47.53
<i>M. lucens</i>	1.79	1.07	55.42	Bivalvia	1.86	1.04	54.84	Ostracoda	1.82	1.14	51.13
<i>C. finmarchicus</i>	1.65	1.12	58.58	<i>C. finmarchicus</i>	1.83	1.13	58.41	<i>M. lucens</i>	1.71	1.04	54.51
<i>S. minor</i>	1.55	1.21	61.54	<i>C. typicus</i>	1.57	0.72	61.47	<i>C. finmarchicus</i>	1.69	1.13	57.85
<i>C. glacialis</i>	1.36	1.11	64.14	<i>C. glacialis</i>	1.45	1.16	64.30	<i>C. typicus</i>	1.38	0.65	60.60
<i>C. typicus</i>	1.33	0.65	66.67	<i>S. minor</i>	1.30	1.04	66.84	<i>C. glacialis</i>	1.34	1.11	63.25
Chaetognatha	1.22	1.29	69.01	<i>Clausocalanus</i> spp.	1.20	0.70	69.17	<i>S. minor</i>	1.28	1.03	65.79
Aetideidae	1.20	1.00	71.30	Chaetognatha	1.14	1.24	71.40	Chaetognatha	1.23	1.59	68.22
<i>Clausocalanus</i> spp.	1.17	0.68	73.55	Euphausiaceae	1.13	1.18	73.60	Cnidaria	1.20	1.15	70.60
Euphausiaceae	1.07	1.14	75.60	Cnidaria	1.06	1.04	75.67	Euphausiaceae	1.19	1.25	72.95
Cnidaria	1.03	1.03	77.56	Aetideidae	1.01	0.86	77.64	<i>T. borealis</i>	1.04	0.87	77.28
<i>T. borealis</i>	0.99	0.78	79.45	<i>T. borealis</i>	0.99	0.78	79.58	<i>Clausocalanus</i> spp.	1.00	0.62	79.26
<i>P. norvegica</i>	0.88	0.86	81.14	Cladocera	0.90	0.61	81.33	<i>P. norvegica</i>	0.84	0.82	80.94
Polychaeta	0.82	0.85	82.70	<i>P. norvegica</i>	0.83	0.81	82.94	Cladocera	0.83	0.58	82.58
Cladocera	0.79	0.58	84.21	<i>C. hamatus</i>	0.79	0.57	84.49	<i>A. longiremis</i>	0.80	0.65	84.17
<i>C. hamatus</i>	0.72	0.55	85.60	Polychaeta	0.79	0.81	86.03	Polychaeta	0.80	0.83	85.77
<i>M. clausi</i>	0.72	0.54	86.98	<i>A. longiremis</i>	0.74	0.62	87.48	<i>C. hamatus</i>	0.76	0.56	87.27
Echinodermata	0.70	0.63	88.33	Echinodermata	0.73	0.64	88.91	Echinodermata	0.74	0.64	88.74
<i>A. longiremis</i>	0.70	0.62	89.66	<i>M. clausi</i>	0.68	0.53	90.23	Amphipoda	0.67	1.10	90.07

Table 6

Average fall temperature and range in average temperature along oceanographic sections along with the correlation of annual average transformed temperature with average RDA and PC scores of the RDA residual variability as well as the Hellinger transformed abundance of five key taxa. Cabot Strait occupations by the Institut Maurice-Lamontagne (IML) and the Bedford Institute of Oceanography (BIO) are reported separately because the collections occur 15–30 days apart. Significant correlations are highlighted in bold.

	Temperature	Range	RDA2	PC1	PC2	PC3	<i>M. lucens</i>	Euphausiaceae	<i>C. finmarchicus</i>	<i>C. hyperboreus</i>	<i>C. glacialis</i>
Bonavista Bay	3.34	1.63	-0.08	-0.36	-0.17	-0.12	n/a	0.51	-0.46	-0.30	-0.39
Flemish Cap	5.73	4.02	0.67	0.04	-0.16	0.08	0.01	0.04	-0.08	-0.15	-0.73
Southeast Grand Banks	6.67	3.97	0.78	-0.17	0.07	-0.07	-0.09	0.01	-0.57	-0.51	-0.60
St. Lawrence Estuary	3.16	2.89	0.93	0.12	-0.74	-0.09	-0.39	0.23	0.11	-0.31	0.41
Sept–Iles	3.58	3.46	0.98	0.51	-0.38	0.38	0.53	0.22	-0.05	-0.25	-0.18
Anticosti Gyre	3.70	3.17	0.95	0.59	0.02	0.36	0.82	0.04	0.37	0.18	-0.08
Central Gulf	5.41	3.07	0.87	0.03	-0.20	-0.74	0.45	-0.02	-0.26	-0.49	-0.59
Iles-de-la-Madeleine (IdLM)	5.91	4.21	0.96	0.35	-0.77	-0.17	-0.29	0.68	-0.85	-0.49	-0.30
Bonne Bay	4.52	2.52	0.97	0.33	-0.21	0.02	0.22	-0.06	-0.46	-0.36	-0.27
Cabot Strait (IML)	6.63	4.38	0.34	0.62	0.09	-0.54	-0.51	-0.04	-0.39	0.01	0.22
Cabot Strait (BIO)	7.46	3.51	0.99	0.24	-0.22	0.04	0.18	0.46	-0.47	-0.51	0.15
Louisbourg	10.26	2.64	-0.05	-0.07	0.48	-0.56	0.35	-0.02	-0.61	0.11	-0.29
Halifax	12.04	4.55	0.27	0.05	0.60	-0.31	0.24	0.02	-0.18	-0.52	-0.07
Browns Bank	11.78	3.50	0.45	-0.01	-0.14	0.33	-0.03	-0.04	-0.22	-0.33	-0.18

between depth and the underlying habitat features they represent may reduce the strength of the relationship between depth and community composition in a predictive relationship. This distinction may also contribute to the differences between spatial distributions of zooplankton PC1 and RDA1 with respect to the intrusion of scores typical of deep-water into the deep Laurentian Channel,

especially in fall. After depth, temperature had one of the strongest relationships to zooplankton community variability, most strongly associated with RDA3 in spring and RDA2 in fall. The spring RDA3 differentiated some of the dominant north temperate species from the dominant subarctic species, while in fall warm temperatures were associated with summer-fall and warm-water shelf copepods

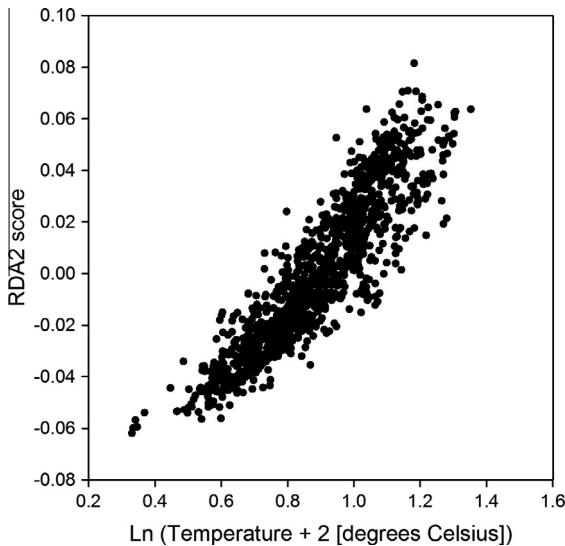


Fig. 11. RDA2 scores for each observations from the fall surveys versus temperature ($T_{0_50\text{ m}}$).

along RDA2, with positive RDA2 scores on the Scotian Shelf, southern Grand Banks and Flemish Cap. Similarly, the salinity–CIL axis (RDA2 in spring and RDA3 in fall) differentiated communities of the Gulf of St. Lawrence and its outflow on the inshore Scotian Shelf from the Labrador and Newfoundland Shelves. The effect of temperature on the zooplankton community was not unexpected given the importance of this environmental feature on virtually every aspect of the life history of poikilotherms. Our analysis revealed, however, that the effect of temperature was confounded with the influence of bathymetry and salinity to varying degrees between the two seasons. Likewise, the effect of salinity, which highlights the gradient between estuarine and oceanic environments, varied between spring and fall as a result of its relationship with the other dominant environmental variables. The varying importance of temperature and salinity between seasons highlights the need to interpret the significance of individual environmental variables based on analyses that consider the effects of seasonal and spatial context.

The dominant patterns of variability identified in the zooplankton PCA and the RDA provide perspective on the relative influence of the macroscale biogeographic context of the region and mesoscale processes on zooplankton communities. The influence of bathymetry was identified as a dominant factor influencing zooplankton community distribution with a notable shift in community composition at the edge of the continental shelf. While the shelf break is a clear boundary for a number of relatively-rare warm offshore species, likely associated with Gulf Stream waters, its influence on the more-dominant community was also evident in both analyses. The shelf break, where environmental gradients are strong, was identified by the multivariate analyses as a geographically-fixed region with strong changes in community structure, but in reality it represents an area where there is likely to be considerable episodic mixing between shelf areas and the deep ocean, with the degree of exchange varying across the region. Circulation along the Newfoundland slope is strongly associated with the outer branch of the Labrador Current but there is substantial flow of Labrador Sea water onto the shelf as the current sweeps in south of the Seal Island section and then off again as it encounters the northern Grand Banks, moving the deep-water community onto and off of the shelf area to varying degrees depending on the intensity of the current (Pepin et al., 2013). In contrast, circulation on the Scotian Shelf is influenced by the complex bathymetry of the region, by the outflow of relatively freshwater from the Gulf

of St. Lawrence and by slope water intrusions through the channels, especially on the western Scotian Shelf (Han and Loder, 2003; Loder et al., 2003; Urrego-Blanco and Sheng, 2012). In both systems, surface and deep offshore water masses can intrude onto the shelf (Petrie and Drinkwater, 1993), but since the most variable environmental variables we used to describe the pelagic habitat of zooplankton were those associated with the surface layer (0–50 m), the subsurface variables may not have been sufficiently variable or sensitive to highlight the spatial extent of the zone across which the different deep-water communities may be mixing. This may have contributed to the varying degree of success in applying interannual variations in environmental conditions to forecasting changes in zooplankton community structure along each oceanographic section. The predictive ability of changes in surface water temperatures may be limited in areas where subsurface water mass exchanges have a significant impact on community structure.

Despite a broad and diverse array of variables used to identify major environmental drivers of zooplankton distributions, the spatial pattern in the residual field of the constrained analysis identified mesoscale features that affect the spatial variations in community structure (e.g. Avalon Channel, link between GSL and SS through Cabot Strait). Earlier regional analyses had been able to identify the role of advective mixing (Tremblay and Roff, 1983) and major boundary currents (Pepin et al., 2011) on community structure, yet neither study had identified the potential influence of mesoscale features because the contrast between predicted and observed (residual) had not been considered. The occurrence of broad areas with similar residual values points to the limitation of analytical approaches based principally on water mass tracers (i.e. temperature, salinity, nutrients, etc.) that neglect or are unable to identify areas of convergence or divergence that are not associated with major frontal system but that have been demonstrated to strongly affect the aggregation of plankton (e.g. Helbig and Pepin, 2002). Furthermore, the spatial structure of communities could demonstrate non-linear or differential responses of some community components to changes in environmental descriptors that would likely result in significant spatial structure in the residual field of the RDA. Physiological processes as well as prey-predator interactions involve non-linear relationships which, when integrated across a broad number of taxa, are unlikely to yield simple linear relationships with environmental variables over the large geographic scale of the study region. Revisiting regional analyses could serve to identify the influence of mesoscale oceanographic features on the spatial distribution of zooplankton because weak or subtle gradients in environmental conditions might be less likely to be overwhelmed by the level of variation that occurs over broad geographic scales. Furthermore, the inclusion of indices of dynamic processes (e.g. convergence) based on regional circulation model outputs or the application of non-linear methods (e.g. regression trees, neural networks) could provide greater insight into the factors that are driving spatial variations in plankton composition. The spatial scale of the analysis and the choice of environmental descriptors will to some extent determine the scale of the features and environment–community relationships that we can expect to detect, but our analyses also revealed that the choice of taxa included in the analysis is also likely to constrain the study's outcome. Our results were greatly influenced by the occurrence of 10–14 key taxa, all of which were essentially ubiquitous throughout much of the region but varied in their relative proportions depending on environmental conditions and season. Focussing analyses on sub-dominant and uncommon taxa, which may be more strongly constrained in their distribution as a result of oceanographic or physiological limitations, could serve to better distinguish the effects of macro- and mesoscale features on the distribution of zooplankton as well as contrast the

simultaneous effects of water mass properties and local forcing that may affect changes in community structure.

Notwithstanding the constraints on our analyses, we were able to identify some emergent patterns in species associations across seasons that are likely a reflection of similar life history strategies or important ecological links. There is a group that appears to be principally restricted to deep-waters (*Scholaeicithricella minor*, *Heterorhabdus* sp., *Triconia conifera*, *Euchaeta* sp., *Spinocalanus* sp., *Pleuromamma* sp., Aetideidae, and Ostracoda) which often represent the warmer portions of the region but it may also be that these taxa are more broadly distributed in the water column and thereby require access to the deep waters of the Atlantic or the deep channels that cut across the Gulf of St. Lawrence. Many of these organisms are poorly studied and their roles in offshore ecosystems that border the study area are not well understood. Another group of species demonstrates high abundance in deep-water areas but can also be broadly distributed over some portions of the continental shelf in one season or another (*Clausocalanus* sp., *Mecynocera clausi*, *Microcalanus* sp., *Paracalanus* sp., *O. atlantica*, chaetognatha and Euphausiacea). The association between this group of small copepods and carnivorous zooplankton may be indicative of prey-predator assemblages with similar life history cycles. A third group consists of broadly-distributed taxa that appear capable of thriving in under a variety of environmental conditions and includes most of the large calanoid copepods (*C. finmarchicus*, *C. glacialis*, *C. hyperboreus*, *M. longa*, *M. lucens*, *P. norvegica*) that shift in distribution depending on the developmental state of their population, moving onto continental shelves around the time of the spring phytoplankton bloom and becoming more abundant in offshore areas in the fall as animals enter diapause. This group dominates the biomass of mesozooplankton in the NW Atlantic and provides a key pathway through which local production is channeled to upper trophic levels. The high adaptability to a broad range of environmental conditions may allow these species to take advantage of the high primary production found on the continental shelves (Ryther, 1969; Ware and Thomson, 2005) while taking shelter in offshore environments in which losses to predators may be lower (Pepin, 2013). A small group of species, consisting of *Acartia* sp., *T. longicornis*, bivalve larvae and to a lesser degree *Microsetella* sp. are more abundant in conditions in which there is an excess of silicate and waters are more strongly stratified, suggesting that they be better suited to environments in which dinoflagellates and flagellates predominate rather than those in which diatoms are more abundant. The groupings we identified appear to reflect common life history features and contributions to ecosystem functioning, aspects which were not part of the structure of our analytical design. Further research in this area would likely benefit from the application of a combination of broader range of approaches (e.g. RDA, CCA, multivariate regression trees) to take advantage of their different strengths and overcome possible limitations in an attempt to gain more comprehensive understanding of the structure in the observations.

Trophic cascades (i.e. bottom-up, top-down and intraguild interactions), which can influence zooplankton community structure through differential effects on species or stage-specific development rates and selective mortality (i.e. survival), were not considered in our analyses. Although we did consider the role of biogeochemical variables (reflected in surface nutrients, oxygen and chlorophyll) in the constrained analyses, they proved to have relatively-minor albeit biologically-meaningful influence on the results when contrasted with bathymetry and water mass tracers. Broad-scale surveys may detect the cumulative effects of local differences in the timing of the biological production cycle on the state of seasonal species succession because emergent spatial structures would be linked to the life cycles of the taxa in the local community. However, metrics based on concurrent measures of

nutrients or chlorophyll concentrations may not adequately reflect similar positions in the seasonal cycle as a result of regional differences in the timing and duration of blooms (Wu et al., 2007; Zhai et al., 2011; Zhao et al., 2013) or the effects of short-term changes in mixing or stratification (Han et al., 2012). How to interpret the effects of variations in phytoplankton production cycles on the outcomes of our analyses is therefore unclear. Furthermore, the early 1990s collapse of groundfish stocks in all regions (Scotian Shelf, Gulf of St. Lawrence, Newfoundland Shelf and Grand Banks) have been followed by different levels of recovery and changes in the abundance of small pelagic forage fish (Morissette et al., 2009; Dawe et al., 2012; Shackell et al., 2012; Buren et al., 2014) and patterns of fluctuations between lower trophic levels and forage fish appear to differ among regions (Frank et al., 2006; Petrie et al., 2009; Buren et al., 2014). Although it is well recognized that in freshwater systems planktivorous fish can significantly impact on community structure as a result of selective predation on different zooplankton taxa (e.g. Iglesias et al., 2011), the effect of forage fish and similar taxa has been difficult to demonstrate in marine ecosystems (Ruzicka et al., 2012; Suikkanen et al., 2013; Daewel et al., 2014). Although Daewel et al. (2014) noted that ecosystems with limited diversity and extreme environmental conditions were more likely to have demonstrated effects on zooplankton resulting from top-down control, they concluded there was limited evidence for prolonged periods of top-down control of zooplankton but that the combined effects of predation and bottom-up processes are important in shaping community structure. Furthermore, Neuheimer et al. (2010) concluded that different predator-prey interactions were key determinants of the mortality rates that regulated the seasonal cycle of recruitment in *Calanus finmarchicus* on the Newfoundland and Scotian Shelves. Given the complexity of interactions that would have to be considered, further analyses, possibly based on hierarchical or comparative approaches, will be necessary to determine how differences in the state of local ecosystems might have contributed the biogeographic patterns in community structure identified in this study.

Environmental factors have been shown to have direct effects on the production potential of some of the key taxa that define major patterns in the zooplankton community but the strength and nature of those relationships are spatially highly variable (Zakardjian et al., 2003; Kane, 2005; Maillet and Colbourne, 2007; Pershing et al., 2010; Stegert et al., 2010; Mackas et al., 2012; Head et al., 2013). A fundamental goal of the monitoring program from which our data were collected was to “understand the causes of oceanic variability … and provide the multidisciplinary datasets that can be used to establish the relationships between biological, chemical and physical” variables (Therriault et al., 1998). Our analyses have clearly revealed the dominant environmental drivers of the biogeographic distribution of zooplankton in the region, but further investigations will have to be carried out to determine whether interannual variations in these key factors are important determinants of fluctuations in the abundance and productivity of key secondary producers in the western north Atlantic. Beyond the expectation that species-specific responses are very likely to result in different responses to changes in the state of the physical environment among key zooplankters, the potential consequence of dissimilarities in the dominant trophic relationships (Neuheimer et al., 2010; Head et al., 2013) or the response to remote forcing (e.g. Petrie, 2007) may require an approach focussed at the scale of individual LMEs. Achieving capacity to predict changes in abundance, and possibly production potential, of zooplankton that play key roles in the three ecosystems considered in our analyses is becoming increasingly important if we are to anticipate the potential consequences and relative significance of short- (e.g. interannual, decadal) versus long-term (e.g. climatic) changes in the state of the ocean.

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