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Linking zooplankton assemblages with oceanographic zones in an Atlantic coastal ecosystem.

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ABSTRACT

Shallow (5 – 35 m depth) coastal waters, with their proximity to human populations, are likely to experience greater changes to ecosystem structure and functions from climate change and human impacts than offshore waters. Concerns of declining fisheries landings and deteriorating habitat quality in Northumberland Strait led to an assessment by Fisheries and Oceans Canada of the state of the environment and biota including zooplankton during the summer. In this paper we describe spatial structure of zooplankton (three distinct assemblages) and determined that two oceanographic zones can explain the spatial variation. Using distance-based linear models, bottom water temperature and surface water salinity explained 16 to 25 percent of the variation in zooplankton composition for each year of the survey. We used retrospective analyses to estimate what the zooplankton assemblage may have resembled in the early 1990s from data of oceanographic conditions. Given the prediction of warming oceans by the Intergovernmental Panel on Climate Change, we provide a means of predicting zooplankton composition and their distribution, with implications for the planktivorous fishes that prey upon them.

KEY WORDS: zooplankton assemblage, oceanography, climate change, spatial pattern, coastal habitat, hypoxia, Northumberland Strait, Gulf of St. Lawrence

INTRODUCTION

In the southern Gulf of St. Lawrence (sGSL), the coastal ecosystem (5 – 35 m depth) still supports an economically valuable fishery for American lobster (*Homarus americanus*) (Hanson and Lanteigne 2000; Hanson 2009; DFO 2016), whereas the offshore ecosystem (> 35 m depth) supported groundfish fisheries, many of which have collapsed (Savenkoff et al. 2007; Morissette et al. 2009; Bundy et al. 2009). The collapse of populations of offshore, piscivorous, demersal

fishes has released predator pressure on planktivorous fishes whose abundance has increased and appears to have resulted in decreased abundance of their zooplankton prey (Myers et al. 2007; Benoît and Swain 2008; Bundy et al. 2009). In contrast, there is much less information available for coastal ecosystems in Canadian marine waters, mainly due to a near absence of research survey time series.

A short research-trawl survey time series exists (beginning in 2000) for Northumberland Strait, a coastal ecosystem within the sGSL. Despite the short time series, significant increases have been detected in planktivorous fish abundances concurrent with near elimination of piscivorous demersal fishes (Bosman et al. 2011; Hanson 2011; Kelly and Hanson 2013). Bosman et al. (2011) suggested that these changes may affect food-web structure in coastal waters. In addition to fisheries impacts, coastal ecosystems are also likely to experience changes due to anthropogenic land-use in adjoining small estuaries and along the coastline.

In response to stakeholder perceptions of declining fisheries landings and deteriorating habitat quality in Northumberland Strait, the Minister of Fisheries and Oceans Canada established a working group to examine these concerns in 2005 (AMEC 2007). The working group identified introduction of invasive species, increased nutrient and silt loading from nearby land sources, and local effects of climate change such as coastal erosion, sea level rise, warming temperature, acidification, and increased storm activities as the key uncertainties that may affect the state of this ecosystem (Forbes et al. 2004; AMEC 2007; Zeebe et al. 2008; Shaw et al. 2008). However, the lack of baseline information against which to make comparisons prevented resource managers from discerning the degree to which these factors are natural in cause or anthropogenic and that might be alleviated by changes to human activities (AMEC 2007;

Mercer-Clarke et al. 2008; DFO 2010). Consequently, a coastal ecosystem research program within Northumberland Strait was initiated to increase understanding of ecosystem functions. The tasks of the program were to quantify: oceanographic conditions, the composition of the zooplankton and fish communities; and the predator-prey interactions in the pelagic and benthic food webs.

Zooplankton in temperate coastal and estuarine ecosystems support commercially important marine planktivorous fishes as well as the larvae and small juveniles of a variety of demersal predatory fishes (Darbyson et al. 2003; Hanson 2011; Nunn et al. 2011). For example, during the summer, the Northumberland Strait is a feeding ground for Atlantic mackerel (*Scomber scombrus*) Atlantic herring (*Clupea harengus*), juvenile Atlantic cod (*Gadus morhua*), white hake (*Urophycis tenuis*), and winter flounder (*Pseudopleuronectes americanus*) (Hanson and Courtenay 1996; Darbyson et al. 2003; Bosman et al. 2011; Hanson 2011). Unlike the well-studied offshore zone, the Strait also serves as a major feeding area for diadromous fishes, especially rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) (Bosman et al. 2011). Changes to zooplankton abundance and species composition can influence the recruitment and productivity of commercially exploited fish species (Beaugrand et al. 2003; Castonguay et al. 2008). Understanding how physical, chemical, and biological processes influence the distribution and abundance of zooplankton species (or groups) is necessary for developing models capable of discerning and predicting the effects of natural and anthropogenic perturbations on ecosystem structure and economic sustainability of fisheries (Marasco et al. 2007; Fulton 2010; Fulton et al. 2011). The composition and dynamics of the zooplankton community within Northumberland Strait and adjacent waters are poorly known because previous, small-scale, studies were completed over 30 years ago and may not reflect the current

state of this coastal ecosystem (Citarella 1982; Hargrave et al. 1985; de Lafontaine et al. 1991; de Lafontaine 1994). Similar to other marine ecosystems which have had perceived changes to fisheries and the biota that support them (Pershing et al. 2015; Sinclair et al. 2015), we were interested in testing two hypotheses regarding influences on the spatial structure of the zooplankton community; (1) top-down: predator-prey interactions and (2) bottom-up: spatial abiotic environmental conditions. Herein we test the second hypothesis; the first hypotheses will be tested in subsequent work.

In this study we report the results of zooplankton surveys carried out in Northumberland Strait during the summers of 2008 and 2009. Objectives of this study were to: 1) provide indices of zooplankton abundance; 2) quantify and map distinct assemblages of zooplankton taxa and oceanographic habitats using a Bayesian conditional probability method of classification; and 3) evaluate the association between zooplankton assemblage structures and concurrently measured oceanographic conditions using distance-based linear analysis. The outputs from distance-based linear models allowed us to provide retrospective estimates of zooplankton in the 1990s, based on oceanographic data collected at that time.

MATERIALS AND METHODS

Study Area

Northumberland Strait (ca 16,000 km² in area) is the shallow body of water that separates Prince Edward Island from the mainland in Atlantic Canada (Fig. 1). Water depth is mostly less than 20 m in the central part of the Strait and the maximum depths of 40 m and 50 m occur at the western and eastern ends of the Strait, respectively. The water column in the central area is well

mixed and bottom-water temperatures during summer can exceed 22 °C (Hanson and Courtenay 1996; Voutier and Hanson 2007; Bosman et al. 2011). The water columns in the east and west ends of the Strait are strongly stratified and waters >35 to 40 m deep are part of the cold (< 1 °C) intermediate layer (Koutitonsky and Bugden 1991; Gilbert and Pettigrew 1997). Both sea ice and land-fast ice develop during most winters resulting in bottom water temperatures < -1.6 °C (Hanson and Courtenay 1996). Movement of ice often causes seabed gouging to a depth of about 15 m in the Strait (Brown et al. 2001).

Sampling Design

Data and samples were collected as part of research-trawl surveys conducted during July-August, 2008 and 2009. Sampling locations were based on a random block design of nine survey strata (blocks) that were defined based on substrate composition (from Kranck 1971; Loring and Nota 1973; Caddy et al. 1977); stratum 4 is not identified in this study because it was an obsolete designation based on a boundary line between American lobster fishing zones. Stratum 4 stations were redistributed into stratum 3 and 5 based on the most common substrate composition (Fig. 1). Stratum 8 is not part of Northumberland Strait and was not sampled during this study (Fig. 1). There are about 1100 possible stations based on a 3.7 x 3.7 km grid placed over a chart of the Northumberland Strait (starting point: 47°00.00'N; 64°00.00'W). Samples were collected in a west to east direction to avoid conflict with the commercial lobster season. While all survey blocks have been covered in other survey years, mechanical breakdowns resulted in parts of strata 7, 9 and 10 not being sampled in 2008, and remnants of two hurricanes prevented sampling in part of stratum 10 and all of stratum 9 in 2009. Due to the discrepancy in spatial coverage, we performed separate analyses for each survey year.

Surface-water samples (2-m depth), conductivity-temperature-depth profiler (CTD) casts, and zooplankton samples were obtained during 2008 and 2009. During the 2008 survey, water samples were collected at 119 stations, CTD profiles at 124 stations, and zooplankton samples at 117 stations. During 2009, water samples were collected at 117 stations, CTD profiles at 227 stations, and zooplankton samples were collected at 116 sites. Contour maps of near-surface and bottom-water characteristics and abundance of dominant zooplankton groups were based on all sites sampled in each year. Similarly, characterization of zooplankton group assemblages and oceanographic zones were based on all available zooplankton sample and CTD profile sites, respectively. Finally, distance-based linear models (DSTLM; see below) were based on concurrent sampling of zooplankton samples and CTD profiles at 117 and 116 sites in 2008 and 2009, respectively.

Zooplankton Collection

Zooplankton were collected with a 5-m long, 1-m diameter, conical net (500 μ m mesh) equipped with a flow meter (Model 2030R, General Oceanics, Miami FL). The net was towed at a speed of 0.50 m/s for 5 minutes in a stepped oblique fashion with towing times of at least 1 minute at each of 1-m above the bottom, mid water-column depth, and 0.5-1.0 m below the surface. Samples were preserved in 5% buffered formalin-seawater and taken to the laboratory for processing. Not all zooplankton taxa were included in the collection (e.g., ctenophores and jellyfishes were excluded) because the overall research program focused on zooplankton taxa typically preyed upon by planktivorous fish (O'Brien 1979; Checkley 1982; MacNeill and Brandt 1990). While ctenophores and jellyfishes undoubtedly play a major role (as predators and prey) in this and many other ecosystems (Richardson et al. 2009), quantitative collection of

jellyfishes (in particular the very large *Aurelia aurita* and *Cyanea capillata*), would require a dedicated survey using different sampling gear, a task beyond the scope of this study.

In the laboratory, large debris and organisms were removed (e.g. macroalgae, fishes, and jellyfish; *Aurelia aurita*, *Cyanea capillata*, and *Aglantha digitale*). A Folsom plankton splitter was then used to reduce the number of remaining organisms to 400 to 500 individuals per fraction. Using a Leica Ez4D dissection microscope, zooplankton were then identified to the lowest practical taxonomic level and counted. Zooplankton specimens that were not identified to species level were grouped into the lowest taxon identified and henceforth referred to as a zooplankton group. For example, adults of large-bodied *Calanus* copepods (>2500 µm long) were easily discernible from small-bodied copepods (500-1000 µm long) and were separately counted. Zooplankton abundance was expressed as number/m³.

Sampling physical and chemical variables

Vertical profiles (CTD casts) were taken with a Sea-Bird electronics SBE-25 SEALOGGER CTD profiler (Sea-bird Electronics, Inc., Bellevue, Washington, USA) equipped with a SBE 43 dissolved oxygen sensor, a LiCor LI-193SA spherical quantum sensor to measure photosynthetically active radiation (PAR), and a Wetlab ECO-FLNTU (RT) sensor to measure fluorescence of chlorophyll *a* and turbidity of the water. For each station, a vertical profile of temperature (°C), salinity, oxygen [mL/L], PAR (µmol/s · m), turbidity (NTU), and chlorophyll *a* concentration [µg/L] was produced. Before each cast, the location (latitude and longitude) and water depth (depth sounder) were recorded. The CTD profiler was held at a depth of 2 meters for 3 minutes to equilibrate and then lowered at a rate of 0.5 m/s until a weight, suspended 0.5 m beneath the water intake, touched the ocean floor. In 2008, the ECO-FLNTU (RT) probe was not

connected resulting in missed profiles of chlorophyll *a* fluorescence and turbidity levels for 52 stations in the western part of the Strait. Consequently, for 2008, we did not use chlorophyll *a* fluorescence and turbidity measurements in multivariate analyses.

Benthic photosynthesis is limited to depths where there is sufficient PAR (Millet et al. 2009). The percentage of surface PAR reaching the ocean-floor at each station was calculated to estimate where benthic photosynthesis could occur in the Strait. We chose >1% of surface PAR to be a measure of habitat in which benthic photosynthesis could occur (Kelble et al. 2005; Runcie et al. 2008; Millet et al. 2009).

Seawater was collected at a depth of 2 meters using a horizontal van Dorn bottle. Five hundred mL of the seawater were filtered through 25-mm Whatman GF/C glass micro-fibre filters. The filters were then placed in aluminum foil, frozen, and transported to the laboratory for analysis to estimate chlorophyll *a* concentrations using methods described in Yentsch and Menzel (1963) and Parsons et al. (1984).

Mapping zooplankton groups and environmental conditions

Contour maps of near-surface and bottom-water characteristics, and abundance of dominant zooplankton groups (see below), were plotted by means of natural neighbour interpolation (Sibson 1981; Sukumar et al. 2001) using the software ESRI ArcGIS™ (v. 9.3, ESRI, Redlands, CA).

Species selection and mathematical transformation

Following procedures in Souissi et al. (2001), we removed sixteen of 32 zooplankton groups identified for analyses, as they were present in less than 5% of the samples. Groups were

separated into dominant zooplankton groups and secondary zooplankton groups if they were present in greater than or less than 0.5% of total zooplankton abundance found in all samples (in numbers per m³), respectively. Secondary zooplankton groups do not contribute much to the overall assemblage structuring (Strmecki et al. 2010). Eight zooplankton groups were retained in the dominant zooplankton group.

Multinormality of data is necessary to apply computations of Bayesian probabilities. However, mathematical transformations (e.g., double square root, log-log) did not provide multinormality when tested using the Dagnelie Method (Souissi et al. 2001; Legendre and Legendre 2012). To obtain multinormality, Principal Component Analysis (PCA) was performed on log-transformed species counts from each year (PCA performed on non-transformed data also failed to provide multinormality). PCA scores from 6 axes provided maximum multinormality and were retained; these explained 90% and 97.5 % of the total variance in 2008 and 2009, respectively. Hierarchical classifications were applied to PCA scores from each year, using the Euclidean distances with flexible links clustering with beta = -0.25 (Legendre and Legendre 2012) to achieve separation into groups for subsequent mapping. This technique allowed for the production of a dendrogram in which sampled sites were grouped together based on similarity. Sampled sites (i.e. objects) were selected from the dendrogram at cut-off levels (i.e., as the dendrogram splits samples into small groups) and were considered to represent zooplankton assemblages (Souissi et al. 2001; Anneville et al. 2002).

Bayesian conditional probability method of zooplankton assemblage mapping

Following procedures described by Souissi et al. (2001); Anneville et al. (2002); and Eastwood et al. (2006), Bayesian conditional probabilities were calculated to determine the

likelihood that a sampled site belonged to a particular zooplankton assemblage defined by the clustering analysis (Harff and Davis 1990; Harff et al. 1993). Using the PCA scores calculated for each sampled site, the probability of membership of an object, O_i in a zooplankton assemblage G_j was given by

(2)
$$P(O_i \in G_j) = \frac{p_j |\Sigma_j|^{-1/2} \exp[-d_j^2(i)/2]}{\sum_{k=1}^g p_k |\Sigma_k|^{-1/2} \exp[-d_k^2(i)/2]}$$

where, p_j is an *a priori* probability representing the proportion of sites in a zooplankton assemblage G_j to the total number of sampled sites in each year, and $d_j^2(i)$ is the generalized Mahalanobis distance between G_j and O_i :

(3)
$$d_j^2(i) = (O_i - m_j^G)' \Sigma_j^{-1} (O_i - m_j^G)$$

where m_j^G is the centroid of the zooplankton assemblage G_j , based on the scores from the principal axes of the cut-off group samples, without retaining the object of interest (i.e., Σ^{-1}). A pooled variance-covariance matrix was used instead of using a normal dispersion matrix when computing the generalized Mahalanobis distance d^2 .

Probability-based method for mapping zooplankton assemblages

Consideration of an appropriate cut-off level for the dendrograms was necessary, as one level greater or less in similarity could substantially change the number of zooplankton assemblages being mapped (Eastwood et al. 2006). To decide an appropriate dendrogram cut-off at each hierarchical level (k), the median probability $Pm(k)$ of the maximum probabilities for a sample to belong to a particular assemblage was calculated as

235 (4)
$$P_m(k) = \text{median } P_{max}(k)$$

236 This provided an average measure of within-group homogeneity for each hierarchical level.
237 Lower cut-off levels were only considered to be mapped if they provided a larger $P_m(k)$ value.

238 Conditional probabilities for each object to belong to a particular assemblage were then
239 treated as regionalized variables (Harff et al. 1993) and plotted using standard geostatistical
240 tools. Specifically, contours of conditional probabilities for zooplankton assemblages at each cut-
241 off level were obtained by using a spherical variogram model and kriging. The set of maps
242 provides an estimate of the probability that each grid cell belongs to a given zooplankton
243 assemblage. These maps were collated into a single assemblage map, whereby the zooplankton
244 assemblage that has the highest probability was plotted. We plotted the zooplankton assemblages
245 at cut-off levels 2 and 3, because further partitioning into 4 cut-off levels for zooplankton
246 assemblages showed a reduction for the median probability $P_m(k)$.

247 *Characterization of zooplankton group assemblages*

248 An indicator value index (IndVal) of Dufrêne and Legendre (1997) was used to
249 determine which zooplankton group(s) characterized zooplankton assemblages identified at each
250 cut-off level. To obtain the indicator value index, the specific fidelity for a zooplankton group
251 within a zooplankton assemblage was measured relative to all other zooplankton assemblages.
252 The maximum specificity value occurred when a zooplankton group was present in only one
253 zooplankton assemblage and the maximum fidelity value occurred when a zooplankton group
254 was present in all objects (sampled sites) within a zooplankton assemblage. The indicator value

index (IndVal) is the product of species fidelity (F) and specificity (S) and is expressed as a percentage:

$$(5) \quad IndVal = (S \cdot F) \times 100$$

The maximum indicator value (100%) occurs when a zooplankton group is observed at all sites and only within one zooplankton assemblage. Following Dufrêne and Legendre (1997), species that had an indicator value greater than 25% were retained to characterize a zooplankton assemblage (Souissi et al. 2001; Anneville et al. 2002; Eastwood et al. 2006).

Multivariate regionalization mapping of oceanographic zones.

Mapping of oceanographic zones followed the same procedures as mapping zooplankton assemblages. Unlike the method used for to map zooplankton assemblages, all oceanographic variables available were included in the analysis because each variable could be important to influence the spatial structure and composition of zooplankton assemblages. For both years of mapping, we used water depth, temperature, salinity and oxygen levels measured in the bottom-water (0.5 m above the ocean floor) and in the surface water (2 m depth) as well as percentage PAR (measured at 2 m) reaching the ocean floor. In 2009, four variables were also included: bottom-water turbidity, surface-water turbidity, maximum chlorophyll a concentration using fluorescence, and the depth at which the chlorophyll a maximum concentration occurred. Thus, 8 and 12 environmental variables were used to plot oceanographic zones for 2008 and 2009, respectively. As with the zooplankton data, principal component analyses (PCA) were performed on log-transformed oceanographic variables from each year because simple mathematical transformations did not provide multinormality when tested using the Dagnelie Method (Souissi

et al. 2001; Eastwood et al. 2006; Legendre and Legendre 2012) and PCA performed on non-transformed data also failed to provide multinormality. PCA scores from 6 and 3 axes provided maximum multinormality, were retained, and explained 97.5% and 82.1 % of the total variance in 2008 and 2009, respectively. The maximum conditional probability for each object was computed from dendrogram cut-off level 2 and 3; cut-off levels 4 and onward had a lower median conditional probability and were not considered.

Evaluating correlation between zooplankton and environmental predictor variables

To determine whether the composition and distribution of zooplankton groups were related to physical and chemical oceanographic characteristics, we performed distance-based linear models (Clarke and Warwick 2001; Clarke and Gorley 2006; Anderson et al. 2008). Distance based linear models use distance-based redundancy analysis (dbRDA) and permutation methods to test the plausibility of the null hypothesis (i.e., no relationship between resemblance matrix of the PC scores of zooplankton data and one or more environmental predictor variables) by obtaining a p-value. To reduce redundancy in the dbRDA and the possibility of overestimating precision, we conducted preliminary correlation and principal components analyses (PCA) of the eight and 13 environmental variables that were considered for DSTLM (see supplementary analyses for documentation of variable selection). For each year of the survey, two environmental variables were retained for analyses: surface water salinity and bottom water temperature. We chose surface water salinity and bottom water temperature over other variables as they are commonly available for oceanographic studies. All dbRDA were performed using 9999 unrestricted simultaneous permutations of the rows and columns in Gower's centered dissimilarity matrices of zooplankton community. Single variable and two

variable solutions were assessed to determine which environmental variables explained the most variation using R^2 . Statistical analyses were performed using R Statistical Language (R Core Team 2017) and the ‘vegan’ package (Oksanen et al. 2017).

Retrospective estimates of zooplankton composition: changes in zooplankton community?

A series of surveys conducted during July-August of 1993 to 1996 (Waite et al. 1997a; 1997b; 1997c; 1997d) collected physical and chemical measurements of temperature, salinity, surface chlorophyll *a* concentration and depth of maximum chlorophyll *a* fluorescence. These data presented an opportunity to consider whether oceanographic conditions are changing in Northumberland Strait and, if so, whether the composition and distribution of zooplankton may have changed based on existing information. First, we evaluated whether oceanographic characteristics found in the 2008-2009 surveys were similar to the previous survey period using unpaired two-tailed student t-tests with unequal variance. We used a dbRDA with the predictor variables surface water salinity and bottom water temperature which considered sample sites that had overlapping spatial coverage in 2008 and 2009 as well as 1993-1996 surveys (results not shown). We estimated the zooplankton composition that would have been present in 1993-1996 at each sample site based on the dbRDA output of predictor variables. Following this analyses, we provided contour maps of the hindcasted zooplankton composition. We then performed a PERMANOVA to compare the zooplankton composition in 2008-2009 surveys to those estimated for the 1990s. PERMANOVA allows the multivariate information to be partitioned according to the full experimental design (including all interaction terms), and does not make assumptions regarding the distributions of the original variables, as all P-values are obtained by permutation (Anderson et al. 2008). For our comparison between zooplankton compositions, we

nested the factor stratum within the factor survey period to account for spatial congruence of sampled sites between survey periods.

RESULTS

Zooplankton Abundance and Distributions

Eight zooplankton groups were identified as the dominant species and comprised 99% of the total abundance of zooplankton in Northumberland Strait: small-bodied copepods (mainly *Acartia tonsa*, *A. clausi*, *Centropages hamatus* and *Oithona similis*); *Podon* sp. (a cladoceran); *Calanus* copepods; crab zoeae (mainly *Cancer irroratus*, with *Ovalipes ocellatus* collected at a few stations in Stratum 3); Thecosomata (*Limacina retroversa*); hermit crab larvae (*Pagurus* sp.); invertebrate eggs; and chaetognaths (*Sagitta elegans*) (Table 1). The secondary species included: fish larvae (mainly *Clupea harengus*); *Evadne* sp. (a cladoceran); polychaetes; crab megalops (*Cancer irroratus* and *Ovalipes ocellatus*); shrimp larvae (mainly *Crangon septemspinosa*); American lobster larvae (*Homarus americanus*); hyperiid amphipods (mainly *Hyperia galba*); gammarid amphipods; capprellid amphipods; mysids (*Mysis* spp. and *Neomysis americana*); larvaceans; cumacean shrimp; bivalve larvae; and echinoderm larvae.

Small-bodied copepods were widely distributed, with the highest abundance in the western half of the Strait (Fig. 2a). Cladocera (*Podon* sp.) were most abundant along the eastern shoreline of Prince Edward Island and were absent from the central Strait (Fig. 2b). *Calanus* copepods were only captured in the deepest-water sites at the eastern and western ends of the Strait with the highest abundance observed at the western end of the Strait (Fig. 2c). Crab zoeae abundance was highest in stratum 3, but they also occurred near the Prince Edward Island and

Nova Scotia shorelines (Fig. 2d). The highest numbers of hermit crab larvae occurred in the west-central part of the Strait, and they were rarely caught in deep-water stations at the ends of the Strait (Fig. 2e). *Thecosomata* were most common in the central portion of the Strait and were seldom caught in the deep-water stations at the ends of the Strait (Fig. 2f). Invertebrate eggs (Fig. 2g) and chaetognaths (Fig. 2h) were mainly collected in the deep-water stations at the ends of the Strait.

Spatial structure and composition of zooplankton assemblages

Mapping of Bayesian conditional probabilities resulted in spatially distinct zooplankton assemblages at cut-off levels 2 and 3 (Fig. 3). At the hierarchical cut-off level 2, Group I (i.e. West Zooplankton Assemblage) occurred on the west end of the Strait in 2008 but at both ends of the Strait in 2009, while Group II (i.e. Center Zooplankton Assemblage) occurred in the central portion of the Strait. At hierarchical cut-off level 3, Group III (i.e. East Zooplankton Assemblage) occurred mainly in the East end of the Strait, but also occurred in a small area between the West and Center assemblages groups. At both cut-off levels, the West Zooplankton Assemblage occurred in deeper waters with a median depth between 24 to 30 m, the East assemblage at median depth between 16 to 33 m deep and the Center Zooplankton Assemblage at median depth between 12 to 22 m deep.

The indicator values for zooplankton groups, both dominant and secondary, were calculated for hierarchical cut-off levels 2 and 3 based on Bayesian conditional probability analysis for each year (Table 2). All eight dominant and four secondary zooplankton groups were considered to be important for these analyses, as the threshold indicator value was greater than 25%. For both years, the most important indicator zooplankton groups were *Calanus* copepods

for the West Zooplankton assemblage (Group I), *Thecosomata* for the Center Zooplankton Assemblage (Group II) and *Podon* sp. for the East Zooplankton Assemblage (Group III). Small-bodied copepods, chaetognaths, and fish larvae were other zooplankton groups that consistently characterized the West Zooplankton Assemblage. In 2009, at hierarchical levels 3, small-bodied copepods instead characterized the Center Zooplankton Assemblage (Group II), indicating that this group was widely distributed in the center and west region of the Strait. Hermit crab larvae, crab zoea, also consistently characterized the Center Zooplankton assemblage.

Oceanographic Zones

Two distinct oceanographic zones were identified in similar locations in both years: the Deep-Stratified (Group A) and Shallow-Mixed (Group B) oceanographic zones (Fig. 4). The Deep-Stratified zone occurred at the eastern and western ends of the Strait, and the Shallow-Mixed zone occurred in the center and central-west region of the Strait. The median depth for the Deep-Stratified oceanographic zone was 28.8 and 26.3 m for 2008 and 2009, respectively. For the Shallow-Mixed zone, the median depth was 15.5 and 13.9 m for 2008 and 2009, respectively.

Bottom water salinity, bottom temperature, PAR intensity and surface chlorophyll *a* concentrations mainly distinguished the two oceanographic zones. The Shallow-Mixed zone had surface-water and bottom water temperatures up to 22 °C (Fig. 5a-d) and the water was relatively fresh (salinity 27-29) (Fig. 5e-h). In contrast, the Deep-Stratified zone had more saline (Salinity >29) and colder (>0 to 8 °C) bottom waters. Surface-water chlorophyll *a* concentrations were highly variable both temporally and spatially, but were higher in the Shallow-Mixed Oceanographic zone than the Deep-Water Oceanographic zone (Fig. 5i,j). In 2008, chlorophyll *a* concentrations ranged between 0.83 and 7.38 µg/L (mean ± SD: 2.83 ± 1.44 µg/L; Fig. 5i).

Chlorophyll *a* concentrations were lower in 2009 and ranged between 0.21 and 3.64 $\mu\text{g/L}$ (mean $\pm$ SD: $1.45 \pm 0.68 \mu\text{g/L}$; Fig. 5j).

There were little differences in oxygen concentrations and turbidity between the oceanographic zones, however there were differences in PAR and subsurface chlorophyll *a* maxima. Dissolved oxygen concentrations were similar throughout the Strait in both years (Fig. 6a-d). The mean ($\pm$ SD) level of dissolved oxygen was $5.25 \pm 0.33 \text{ mL/L}$ for both surface and bottom-water, which represents 80-110% saturation. In 2008, an area of substantially lower dissolved oxygen levels (3.2 mL/L; 55% saturation) was detected in the Shallow-Mixed zone (Fig. 6c). Subsurface chlorophyll *a* maxima were present at higher concentrations and located at deeper depths in the Deep-Stratified zone (1.5 and $> 3.0 \mu\text{g/L}$; 15-20 m depth) than the Shallow-mixed zone (0.5 to and 1.5 $\mu\text{g/L}$; 5-10 m depth; Fig. 6e-h). Bottom-water irradiance (PAR) was greater in the Shallow-Mixed zone than the Deep-Stratified zone (Fig. 6i, j) and exceeded 1% of surface levels in most areas, indicating adequate light for benthic photosynthesis. Near-shore regions of the Deep-Stratified Zone also received sufficient irradiance for benthic photosynthesis. Surface water turbidity was negligible at most locations, while bottom water turbidity ranged between 0.34 and 4.38 NTU in 2009 (mean $\pm$ SD: $1.35 \pm 0.82 \text{ NTU}$; maps shown in supplementary materials).

Environmental Correlates of Zooplankton Assemblages

In 2008, with the exception of percent PAR reaching the ocean floor, all single environmental variables explained a significant portion of variation in zooplankton assemblage structure (Table 3). Surface-water salinity explained the most variation ($R^2=0.19$) and bottom-water dissolved oxygen explained the least ($R^2=0.008$). The model which included bottom-water

temperature and sea surface salinity as predictor variables best explained variation in zooplankton assemblage structure ($R^2=0.25$).

In 2009, with the exceptions of surface-water dissolved oxygen, percent PAR reaching the ocean floor and surface water turbidity, all single environmental variables explained a significant proportion of the variation in zooplankton assemblage structure (Table 4). Surface salinity explained most variation in zooplankton assemblage structure ($R^2=0.10$). The model which included bottom-water temperature and sea surface salinity as predictor variables best explained variation in zooplankton assemblage structure ($R^2=0.16$).

For both years, we chose not to explore other combinations of predictor variables (see supplementary material) because there was collinearity among predictor variables. We chose temperature and salinity measurements over other environmental variables, as they are the most common measures taken during oceanographic surveys and are most likely to be directly impacted by climate change (IPCC 2013; Long et al. 2016).

Comparison of 2008-2009 surveys to 1993-1996 surveys.

Mean surface water temperatures were 0.6 °C higher in 2008-2009 than 1993-1996; using the Student t-test the difference was considered to be statistically significant (Table 5). Mean bottom water temperature did not differ significantly between the two sampling periods (Table 5). Mean surface chlorophyll *a* concentrations in 2008-2009 were more than three times the concentrations 1993-1996 (Table 5; $p < 0.0001$). Surface salinity values were not significantly different between sampling periods but bottom water-salinity was significantly more saline during the 2008-2009 sampling with an increase of 0.18 (Table 5; $p = 0.0468$).

Distributions of zooplankton groups, based on hindcasting with surface water salinity and bottom water temperature data for the 1993-1996 periods, were generally similar to those described in the 2008-2009 surveys (Fig. 7). Hindcasted estimates of zooplankton suggested that small-bodied copepods occurred mainly in the western portion of the Strait, *Podon* sp. occurred in the eastern portion of the Strait. *Calanus* copepods were hindcasted to have occurred in the western Strait, whereas crab zoea, hermit crab larvae, *Thecosomata* and eggs were estimated to have occurred in the stratum 3 of the Strait. Chaetognaths were hindcasted to have occurred on both ends of the Strait. Hindcasted distributions in 1993 to 1996 are more uniform than observed distributions in 2008 and 2009; which are more clumped.

Despite the similarity in appearance of zooplankton distributions in the 1990s and 2008-2009 surveys, significant differences in zooplankton composition were detected between the two time periods and between strata nested within time periods (Table 6). The small-copepods and *Calanus* zooplankton groups were hindcasted to have a reduced abundance when compared to the 2008-2009 surveys (Table 7). *Podon* sp., Crab zoeae, *Thecosomata*, hermit crab larvae, eggs, chaetognaths, and fish larvae had similar estimated abundance during the two survey periods.

DISCUSSION

Our analyses revealed three spatially distinct zooplankton assemblages and provided evidence that two distinct oceanographic zones can explain the spatial variation of zooplankton in Northumberland Strait. The Center zooplankton assemblage was composed primarily of small-bodied copepods and had higher abundances of *Thecosomata*, crab zoeae, and hermit crab larvae than elsewhere in the Strait. This is consistent with earlier reports of Atlantic rock crab larvae being found typically between 0.5 to 20 m depths in sGSL (Hargrave et al. 1985). In contrast, the

West and East Zooplankton Assemblages had a greater abundance of *Calanus* copepods and chaetognaths. Previous studies in the sGSL have also shown that *Calanus* copepods dominate the cold-intermediate-layer that is found at 30-100 m depth during daylight hours of July-August (Runge and Castonguay 1999; Tamigneaux et al. 1999; Roy et al. 2000; Zakardjian 2003; Maps et al. 2011). Coverage for stratum 7 and 10 was not complete for 2008 and 2009; therefore our results could have changed as a result of further sampling. However, we expect that because stratum 7 and 10 are stratified further sampling would have revealed similar composition throughout the stratum.

Our sampling was integrated over depths and cannot be used to identify vertical patterns of zooplankton composition, nor potentially distinct zooplankton assemblages within the water-column. We suggest that in the future, use of a depth-stratified sampling, using multiple opening/closing nets and environmental sampling system (MOCNESS), could be used to test whether there are vertical patterns in zooplankton species composition, particularly when sampling between temperature strata of the Deep-Stratified oceanographic zone.

Our study focused on larger sized zooplankton that are typically preyed upon by juvenile and adult planktivorous fish; consequently, we used a 500 μm mesh net (Colton Jr et al. 1980; Checkley 1982; MacNeill and Brandt 1990). Nonetheless, many coastal zones are dominated by small-bodied zooplankton (Pitois et al. 2008; Vasilyeva et al. 2009) and about 50% of organisms are retained in a net with square meshes of the same size (Skjoldal et al. 2013). Sampling with a smaller mesh net would likely identify similar spatially distinct zooplankton assemblages but we would expect to see greater captures of small-bodied copepods, pteropods, and crab zoeae and potentially greater heterogeneity in the zooplankton composition of Northumberland Strait.

Identification of distinct marine habitats and quantification of co-occurring species are helpful in discerning and predicting the effects of natural and anthropogenic perturbations on ecosystem structure and economic sustainability of fisheries (Marasco et al. 2007; Fulton 2010; Fulton et al. 2011). Many statistical tools and approaches have been used to classify and map the spatial structure of species assemblages. Yet, many existing approaches such as principal components analysis (PCA) (e.g., Mahon et al. 1998) or cluster analyses (e.g., Doyle et al. 2002; Bosman et al. 2011) have limitations in delineating distinct spatial boundaries. These techniques map species assemblages by plotting different assemblages as symbols that are placed at sampled sites. By using mapped symbols, one cannot quantitatively describe boundaries between species assemblages using site-specific species assemblage mapping and descriptions must instead rely on qualitative visual inspection. Such problems are especially common when there are large distances between sites because it is more difficult to delineate the boundary between one assemblage and another. Herein, the use of the method developed by Souissi et al. (2001) allowed us to create contoured maps of assemblage structure based on the most probable composition of indicator species. It should be noted that other techniques exist for addressing this issue, such as bootstrapped PCA (PCA_{BTSP}; Jordaan et al. 2010) or Bayesian multinomial logit models (e.g. Jørgensen et al. 2011). Comparison among these approaches is beyond the scope of the present paper but would be a useful future contribution.

We linked spatial changes in zooplankton assemblage structure to changes in surface water salinity and bottom water temperature using dbRDA. These results suggest that, during summer months, changes in zooplankton compositions correlate with changes in environmental predictor variables. Our results are consistent with other studies which have found that spatial changes in zooplankton composition can be explained by changes in environmental variables

(Beare et al. 2002; Lee et al. 2005; Isari et al. 2005; Coyle 2005; Coyle et al. 2008). How this correlated spatial structure of habitat and zooplankton composition might further affect the fish species which are dependent upon zooplankton as a food source, is not as yet known for Northumberland Strait. This question is the subject of a subsequent study we performed on the diet composition of planktivorous fishes and their distribution.

Similar to other studies (Moore and Folt 1993; Yvon-Durocher et al. 2011; Rall et al. 2012; Alcaraz et al. 2013), we found that spatial differences in the distribution of zooplankton of different sizes are consistent with changes in water temperature. In the warmer waters of the Shallow-Mixed zone, zooplankton compositions were dominated by small-bodied zooplankton such as copepods, *Thecosomata*, crab zoeae and hermit crab larvae. In contrast, in the cold bottom layer of the Deep-Stratified zone, larger-bodied plankton such as *Calanus* copepods, chaetognaths and *Podon* sp., were dominant. Differences in zooplankton size and species are often attributed to changes in metabolic processes due to body-size (Ikeda 1985; Moore and Folt 1993). Smaller-bodied zooplankton may outcompete large-bodied zooplankton in warmer water temperatures because the respiration costs are greater for large-bodied zooplankton (Vidal 1980a; 1980b; 1980c; Moore and Folt 1993; Almeda et al. 2010). Conversely, given sufficient food availability, large-bodied zooplankton may outcompete small-bodied zooplankton in colder waters, due to decreased respiration costs.

Is Northumberland Strait ecosystem changing?

Our study also provided a means to estimate zooplankton community structure in Northumberland Strait. Using historical data on oceanographic conditions we used hindcasting to estimate what the zooplankton assemblage may have resembled in the early 1990s. There are

several uncertainties to the hindcasted estimates we provided herein. First, it is likely that these hindcasts for the early 1990s are too uniform with respect to density compared to observed zooplankton densities in 2008-2009, which appeared to be more clumped. Second, our study does not account for changes to species that prey upon zooplankton or changes in nutrient loading, both of which may impact the productivity and mortality of the zooplankton within the Strait.

With water temperatures in the sGSL predicted to increase between 0.3-4.8 °C by 2080 (IPCC 2013; Long et al. 2016), this analytical method could provide a means to predict zooplankton composition in the future, in particular with integration of predator abundance and distribution. We expect, for example that smaller-bodied zooplankton in the Center zooplankton assemblage may increase in abundance and range. As the depth of the warm surface layer increases and, consequently, the area of bottom in contact with these warm waters also increases (Long et al. 2016), the cold intermediate layer will become compressed. In general terms, the habitat of the cold-water associated zooplankton would likely be compressed, while that of small-bodied species would likely increase. Smaller-bodied zooplankton often are a less energy-valuable food-source for planktivorous fish than large-bodied zooplankton (Moore and Folt 1993) although whether the main fish planktivores will be able to compensate for smaller prey sizes with greater intake is unknowable. Moreover, we are not able to predict whether new zooplankton species may populate the area using the methods herein. Further work is necessary to evaluate whether shifts in zooplankton taxa have occurred since this first baseline study was completed and whether there have been concurrent changes in abundance, growth, and foraging ecology of fishes within the Strait.

Jellyfish, which depend on high water temperature and food availability for rapid growth, may increase in abundance in the Strait due to increased abundance of small-bodied copepods and warmer temperatures (Purcell et al. 2007). Thus, jellyfish disrupt the movement energy (and biomass) to fish populations (Richardson et al. 2009). While large jellyfishes are sufficiently abundant to attract predators such as, leatherback turtles (*Dermochelys coriacea*; Atlantic Leatherback Turtle Recovery Team 2006), almost nothing is known about their seasonal and annual abundances; even a single baseline estimate is lacking. Clearly, this lack of information on jellyfishes (and ctenophores) represents a major data-gap in understanding present and future structure and functioning of the Strait and main Gulf of St. Lawrence ecosystems

The ecosystem research program of Northumberland Strait began in response to concerns of declines in fisheries landings and a perception of physical and chemical degradation of habitat quality (AMEC 2007). In 2008, we detected oxygen concentrations in the center of the Northumberland Strait which would be low enough to kill fishes, crustaceans, and molluscs if persistent (e.g. 3.2 to 4 ml/l; Ribaud et al. 2005; Diaz and Rosenberg 2008). Further work is warranted to determine if low oxygen levels are a common or persistent occurrence in Northumberland Strait, to understand the cause, and to investigate the possibility of mitigating the problem.

Summary

This study established that there is strong spatial structure within both the zooplankton and oceanographic conditions in Northumberland Strait, thus establishing a system to classify spatially distinct habitat. Examining spatial variation in feeding selectivity and diet overlap of planktivorous fishes with respect to observed spatial variation in the zooplankton resources is in

progress. We plan to use the analytical technique used in this study to also determine whether planktivorous fish assemblage structure correlates with variation in zooplankton structure. This information will be a critical input to any attempt to formulate ecosystem models that have sufficient spatial and temporal resolution to monitor and/or predict potential changes in Northumberland Strait and the sGSL.

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881 Figure Captions

882 **Fig. 1** Northumberland Strait study area, survey block boundaries (1-3,5-10), and stations
883 sampled in 2008 (open circles) and 2009 (filled squares). Stratum 4 is not identified because it is
884 an obsolete designation based on a boundary line between American lobster quota zones.
885 Stratum 4 stations were redistributed into stratum 3 and 5 based on the most common substrate
886 composition.

887 **Fig. 2** Contour maps of dominant zooplankton group abundance during 2009 Northumberland
888 Strait ecosystem surveys. 2008 contours are nearly identical to the 2009 contour maps;
889 consequently, they are not shown. Dominant zooplankton groups were (a) small-bodied

890 copepods, (b) *Podon* sp., (c) *Calanus* copepods, (d) crab zoeae, (e) hermit crab larvae, (f)
891 *Thecosomata*, (g) eggs, and (h) chaetognaths.

892 **Fig. 3** Maps of zooplankton assemblage hierarchical cut-off levels 2 (a,b) and 3 (c,d) in 2008 and
893 2009. Assemblage groups match with each zone designation at the hierarchical cut-off level: I
894 (West), II (Center) and III (East) Each colour represents the median depth of a zooplankton
895 assemblage group according to colour scale on the depth chart legend.

896 **Fig. 4** Maps of the oceanographic zones in (a) 2008 and (b) 2009. Oceanographic zones are each
897 zone designated at the branch level 2: A (Deep-Stratified) and B (Shallow-Mixed). Each colour
898 represents the median depth of an oceanographic zone according to colour scale on the depth
899 chart legend.

900 **Fig. 5** Contours of (a,b) surface temperature (°C) in 2008 and 2009, (c,b) bottom temperature
901 (°C) in 2008 and 2009, (e,f) surface salinity in 2008 and 2009, (g,h) bottom salinity in 2008 and
902 2009, and (i,j) surface water (2 m depth) chlorophyll *a* concentration [µg/L] collected from water
903 samples.

904 **Fig. 6** Contour maps of (a,b) surface water dissolved oxygen concentration [ml/l] in 2008 and
905 2009, (c,d) bottom water dissolved oxygen concentration [ml/l] in 2008 and 2009, (e,f)
906 concentration of the maximum subsurface chlorophyll *a* maxima (SCM) and (g,h) the associated
907 depth map of the SCM, and (i,j) the percent of irradiance reaching the ocean floor in 2008 and
908 2009. 2008 maps of SCM are incomplete due to a disconnected fluorometer probe.

909 **Fig. 7** Contour maps of hindcasted distributions of zooplankton based on sea surface salinity and
910 bottom water temperature measurements taken during the 1993-1996 oceanographic surveys of

911 the Northumberland Strait. Retrospective estimates of zooplankton group distributions and
912 abundance were (a) small-bodied copepods, (b) *Podon* sp., (c) *Calanus* copepods, (d) crab zoeae,
913 (e) hermit crab larvae, (f) *Thecosomata*, (g) eggs, and (h) chaetognaths. Two legends are
914 provided for zooplankton group abundance, the top legend is for panels a-d and the bottom
915 legend is for e-h.

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Table 1 Mean and standard deviation (SD) zooplankton group abundance (number/m³) by year, both years combined, and percentage of total estimated abundance of each zooplankton group taken from Northumberland Strait ecosystem surveys in 2008 and 2009

Zooplankton Group	Abundance by year		Years combined (n = 233)	Percentage (%)
	2008 (n =117)	2009 (n =116)		
Dominant zooplankton				
Small-sized copepods	273.7 ± 282.4	169.0 ± 141.2	221.1 ± 228.6	56.07
<i>Podon</i> sp.	49.0 ± 88.0	69.6 ± 121.3	59.4 ± 106.3	15.05
<i>Calanus</i> copepods	92.4± 226.3	15.0 ± 51.3	53.5 ± 167.9	13.58
Crab zoeae	32.9 ± 38.4	24.6 ± 48.6	28.7 ± 43.9	7.29
Hermit crab larvae	16.2 ± 17.9	12.2 ± 15.1	14.2 ± 16.6	3.59
<i>Thecosomata</i>	19.9 ± 30.8	18.3 ± 41.8	18.3 ± 41.8	2.33
Eggs	2.5 ± 3.6	3.1 ± 4.8	2.8 ± 4.3	0.71
Chaetognath	2.9 ± 8.8	2.1 ± 4.5	2.5 ± 6.9	0.63
Secondary zooplankton				
Fish Larvae	1.7 ± 2.1	1.0 ± 1.4	1.4 ± 1.8	0.34
<i>Evadne</i> sp.	1.3 ± 3.5	0.25 ± 1.0	0.81 ± 2.64	0.21
Mysids	<0.01	0.42 ± 1.80	0.42 ± 1.80	0.05
Polychaetes	0.23 ± 0.69	0.19 ± 0.60	0.21 ± 0.64	0.05
Crab Megalops	0.14 ± 0.69	0.16 ± 0.41	0.15 ± 0.57	0.04
Larvacean	0.08 ± 0.40	0.19 ± 0.74	0.14 ± 0.59	0.03
Cumacean shrimp	0.08 ± 0.49	<0.01	0.08 ± 0.49	0.01
Bivalves past veliger stage	0.062 ± 0.29	<0.01	0.06 ± 0.29	0.01
Cumulative Total	57191	36575	91872	

Table 2 Variations of the indicator value within each hierarchical level. Only zooplankton groups having indicator values greater than 25 % were retained. Zooplankton groups are labeled dominant and secondary groups. The indicator value is shown between parentheses and preceded by the number of the site group found on Fig. 4.

Year	2008		2009	
Zooplankton group label	Number of hierarchical levels		Number of hierarchical levels	
	2	3	2	3
Dominant zooplankton				
Small-sized copepods	I (75)	I (58)	I (61)	II (45)
<i>Podon</i> sp.	II (42)	III (58)	II (56)	III (74)
<i>Calanus</i> sp. Copepods	I (91)	I (90)	I (78)	I (74)
Hermit crab larvae	II (45)	II (34)	II (66)	II (58)
<i>Thecosomata</i>	II (73)	II (48)	II (91)	II (75)
Crab zoea	II (64)	II (59)	II (64)	II (65)
Eggs	II (48)	II (58)	I (44)	I (34)
Cheatognaths	I (58)	I (68)	I (34)	III (28)
Secondary zooplankton				
Evadne	II (45)	III (28)		
Crab Megalops				II (31)
Cumacean shrimp				
Bivalves past veliger stage				
Fish Larvae	I (48)	I (33)	I (59)	I (44)
Polychaetes		II (30)		
Larvacean				
Mysids				

Table 3 Distance-based redundancy analysis (db-RDA) correlations between zooplankton functional group composition and environmental variables in 2008.

Variable Solutions	df	Variance	Pseudo-F	<i>P</i> -value	R^2
Depth (D)	1	6406	5.470	0.006	0.05
Bottom-water temperature (BT)	1	10758	9.496	0.001	0.08
Surface-water temperature (ST)	1	3990	3.347	0.037	0.03
Bottom-water salinity (BS)	1	4278	3.596	0.034	0.03
Surface-water salinity (SS)	1	27763	28.224	0.001	0.20
Bottom-water dissolved oxygen (BO)	1	4525	3.810	0.030	0.03
Surface-water dissolved oxygen (SO)	1	6641	5.682	0.008	0.05
% of PAR reaching ocean floor (PAR)	1	1059	0.869	0.283	<0.01
BT and SS*	2	36741	20.122	0.001	0.25
Total Df	115				
Total Residual		139904			

Table 4 Distance-based redundancy analysis (db-RDA) correlations between zooplankton functional group composition and environmental variables in 2009. *Due to collinearity among single predictor variables, BT and SS were chosen among sets of non-correlated variables.

Variable Solutions	df	Variance	Pseudo-F	<i>P</i> -value	<i>R</i> ²
Depth (D)	1	3195	7.985	0.001	0.07
Bottom-water temperature (BT)	1	2071	5.047	0.007	0.04
Surface-water temperature (ST)	1	2510	6.175	0.002	0.05
Bottom-water salinity (BS)	1	3579	9.023	0.001	0.08
Surface-water salinity (SS)	1	4800	12.448	0.001	0.10
Bottom-water dissolved oxygen (BO)	1	2046	4.983	0.007	0.04
Surface-water dissolved oxygen (SO)	1	713	1.688	0.161	0.02
% of PAR reaching ocean floor (PAR)	1	1027	2.447	0.075	0.02
Subsurface Chlorophyll a Maxima	1	1762	4.265	0.010	0.04
Bottom Water Turbidity (Bturb)	1	2582	6.363	0.002	0.05
Surface water turbidity (Sturb)	1	123	0.287	0.653	<0.01
BT and SS*	2	7609	10.471	0.001	0.16
Total	112	47213			

Table 5 Comparison of temperature, salinities and surface chlorophyll *a* concentrations measured in Northumberland Strait during July-August 1993-96 to the present study (2008-2009) using a unpaired student t-test between survey periods.

Environmental Variable	Survey Period						p-value
	Waite et al. (1993-1996)			Present Study (2008-2009)			
	n	mean	SD	n	mean	SD	
Surface-water Temperature (°C)	174	18.26	1.74	287	18.88	1.80	0.0003
Bottom-water Temperature (°C)	174	12.99	5.22	287	12.04	5.30	0.0602
Surface-water chlorophyll <i>a</i> concentration [µg/l]	117	0.68	0.45	190	2.13	1.38	<0.0001
Surface-water Salinity	174	27.84	0.78	287	27.84	0.76	0.9868
Bottom-water Salinity	174	28.68	0.88	287	28.86	1.02	0.0468

Table 6 - Nested PERMANOVA tests psuedo-F and p-values for sampling period with stratum nested within sampling period to account for spatial congruence.

Variable	Degrees of Freedom	Sums of Squares	Mean Squares	Pseudo-F	P-Value
Survey Period	1	2.36	2.36	28.13	0.001
Stratum(Survey Period)	12	21.59	1.80	21.43	0.001
Residuals	395	33.17	0.08		
Total	408	57.12			

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Table 7 Mean and standard deviation (SD) retrospectively estimated zooplankton group abundance (number/m³) in 1993-2006 survey period (Waite et al. 1997a, 1997b, 1997c, 1997d) and observed abundance in 2008-2009 survey period.

Zooplankton Group	Survey Period			
	1993-1996		2008-2009	
	Mean	SD	Mean	SD
Small-sized copepods	194	101	221	234
<i>Calanus</i> copepods	41	63	52	168
<i>Podon</i> sp.	58	34	59	107
Crab zoeae	32	16	28	44
<i>Thecosomata</i>	23	14	19	36
Hermit crab larvae	15	6	14	16
Eggs	2	1	2	4
Chaetognath	1	2	2	7
Fish Larvae	1	1	1	2

Northumberland Strait study area, survey block boundaries (1-3,5-10), and stations sampled in 2008 (open circles) and 2009 (filled squares). Stratum 4 is not identified because it is an obsolete designation based on a boundary line between American lobster quota zones. Stratum 4 stations were redistributed into stratum 3 and 5 based on the most common substrate composition

Contour maps of dominant zooplankton group abundance during 2009 Northumberland Strait ecosystem surveys. 2008 contours are nearly identical to the 2009 contour maps; consequently, they are not shown. Dominant zooplankton groups were (a) small-bodied copepods, (b) *Podon* sp., (c) *Calanus* copepods, (d) crab zoeae, (e) hermit crab larvae, (f) Thecosomata, (g) eggs, and (h) chaetognaths.

Maps of zooplankton assemblage hierarchical cut-off levels 2 (a,b) and 3 (c,d) in 2008 and 2009. Assemblage groups match with each zone designation at the hierarchical cut-off level: I (West), II (Center) and III (East) Each colour represents the median depth of a zooplankton assemblage group according to colour scale on the depth chart legend.

Maps of the oceanographic zones in (a) 2008 and (b) 2009. Oceanographic zones are each zone designated at the branch level 2: A (Deep-Stratified) and B (Shallow-Mixed). Each colour represents the median depth of an oceanographic zone according to colour scale on the depth chart legend.

Contour maps of (a,b) surface water dissolved oxygen concentration [mL/l] in 2008 and 2009, (c,d) bottom water dissolved oxygen concentration [mL/l] in 2008 and 2009, (e,f) concentration of the maximum subsurface chlorophyll a maxima (SCM) and (g,h) the associated depth map of the SCM, and (i,j) the percent of irradiance reaching the ocean floor in 2008 and 2009. 2008 maps of SCM are incomplete due to a disconnected fluorometer probe.

Contour maps of hindcasted distributions of zooplankton based on sea surface salinity and bottom water temperature measurements taken during the 1993-1996 oceanographic surveys of the Northumberland Strait. Retrospective estimates of zooplankton group distributions and abundance were (a) small-bodied copepods, (b) *Podon* sp., (c) *Calanus* copepods, (d) crab zoeae, (e) hermit crab larvae, (f) Thecosomata, (g) eggs, and (h) chaetognaths. Two legends are provided for zooplankton group abundance, the top legend is for panels a-d and the bottom legend is for e-h.