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Interannual variation in diapausing copepods and associated water masses in a continental shelf basin, and implications for copepod buoyancy

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ABSTRACT

Oceanographic surveys were conducted in Roseway Basin, western Scotian Shelf, during late-summer from 2007 through 2009 to measure the magnitude of interannual variation in the spatial distribution of diapausing copepods Calanus finmarchicus and C. hyperboreus and associated water mass characteristics. Calanus spp. abundance, energy density and hydrography were measured at depths >50 m along transects using a Towed Underwater Biological Sampling System equipped with an Optical Plankton Counter (OPC) and a conductivity-temperaturedepth (CTD) sensor, as well as at fixed stations using a Biological Net and Environmental Sampling System equipped with nets, OPC and CTD. Water mass density and in some cases salinity explained variation in the deep copepod layer across both time and space, whereas temperature did not. Water mass density, copepod energy density and thickness of the copepod layer were statistically lower during 2008 than 2007 or 2009. The copepod layer was absent from the western Basin margin during 2008 where low density continental water resided that year, whereas during 2007 and 2009 higher density continental slope water and copepods were each present along the western margin. Our results suggest that water mass density is an important characteristic defining the spatial and interannual ecology of the deep copepod layer in Roseway Basin. The 26 σ_t isopycnal may be a lower density limit to diapausing Calanus spp. habitat on continental shelves with shallow bathymetry, that helps the animals maintain neutral buoyancy during diapause.

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1. Introduction

Copepods of the genus Calanus are ubiquitous, abundant and energy-rich zooplankton that form the food base for higher trophic levels throughout the North Atlantic (Hirche, 1983). As an adaptation to survive winter food shortages at high latitudes. *Calanus* spp. have developed an overwintering life history strategy that includes ontogenetic vertical migration, arrested development and reduced metabolism, known as diapause (Hirche, 1996). Before entering diapause, Calanus spp. accumulate energy-rich lipid (wax esters), and in late summer and early autumn the animals enter diapause, sink through the water column and become concentrated in thick layers at depth (Hirche, 1996; Michaud and Taggart, 2007). Most Calanus populations reside in the deep ocean over the continental slope and abyssal plain and may diapause at depths > 1000 m where they remain for extended periods, presumably maintaining neutral buoyancy (Hirche, 1996; Kogeler et al., 1987; Visser and Jonasdottir, 1999). Some aggregations enter diapause over the continental shelf and the depth at which they diapause is

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particularly Calanus finmarchicus and C. hyperboreus (Baumgartner et al., 2003; Davies et al., 2014), and the Basin is a known critical feeding habitat for endangered North Atlantic right whales (Kraus and Rolland, 2007) and other copepod predators. Explaining the spatial and temporal variation in the distribution and abundance of deep Calanus layers within and among continental shelf basins, and the associated mechanisms driving their supply, formation and maintenance, provides insights into variation in predator habitat use. In Roseway Basin, Calanus spp. are supplied from at least two major upstream sources (Head et al., 1999; Herman et al., 1991; Sameoto and Herman, 1990; Tremblay and Roff, 1983; Zakardjian et al., 2003). The first is a cold, relatively fresh water mass that originates

in the Gulf of St. Lawrence and contains cold-adapted (Arctic) C. glacialis

restricted by the relatively shallow bathymetry (100 to 300 m, Murison and Gaskin, 1989; Herman et al., 1991; Woodley and Gaskin, 1996;

Baumgartner et al., 2003; Michaud and Taggart, 2007). These bathymet-

rically restricted diapausers become passively aggregated near bottom

within shelf basins due to bathymetric steering of slow circulation

(Herman et al., 1991). The thick, deep, lipid-rich layers in the shelf ba-

sins are an energetically valuable food resource for larger zooplankton,

fish and whales. One such basin, Roseway Basin on the western Scotian

Shelf (NW Atlantic, Fig. 1a), contains a rich supply of calanoid copepods,





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Fig. 1. Bathymetric charts depicting survey coverage in the Roseway Basin study area (a) on the western Scotian Shelf (WSS), (b) the three oceanographic Basin regions, (c) the relative probability of sighting a right whale in the Basin, and (d–f) the zooplankton and water mass surveys conducted in (d) 2007, (e) 2008 and (f) 2009, respectively. In panels d–f, each BIONESS tow location is identified by B0x labels, each CTD profile by CTDxx, and TUBSS transect survey transects by solid black lines identified by numbers 1 to 13 (1–10 in 2008; 11–13 in 2009). Solid blue labels and symbols denote the subset of profiles that were included in the statistical analyses. Isobaths panels b through f are spaced at 25 m with the 100 m and 160 m isobaths labelled in (b).

and *C. hyperboreus* that are transported southwest along the inner Scotian Shelf by the Nova Scotia Coastal Current (NSCC). The second is the warm, salty, continental slope water that transports high concentrations of *C. finmarchicus* – a sub-Arctic and boreal species – from the slope onto the Scotian Shelf through deep channels and into basins such as Roseway. The addition of slope water to the central and western Scotian Shelf plays a pivotal role in the population dynamics of *C. finmarchicus* on the Shelf (Head et al., 1999; Zakardjian et al., 2003), and interannual variation in slope water intrusions to Roseway explains some variation in *C. finmarchicus* and right whale abundance in the Basin (Patrician and Kenney, 2010).

Davies et al. (2013, 2014) used extensive survey data collected in Roseway Basin during 2008 to evaluate kilometer- to habitat-scale spatial and tidal variation in the distribution of diapausing copepod abundance at depth in relation to water masses and their advective characteristics. The studies demonstrated that the diapausing copepods were concentrated below the 120 m isobath and particularly so along the southeastern Basin margin (120 - 160 m isobath) and central basin (>160 m isobath, Fig. 1b), where high density continental slopeinfluenced water was dominant. Both the basin-scale spatial distribution of copepods and the upslope extent of the deep copepod layer during tidal advection were limited vertically by the 1026 σ_t (kg m⁻³) isopycnal. This observation led the authors to hypothesize that the 1026 isopycnal represented a shallow density limit to diapausing copepod habitat, below which the dormant copepods will tend to sink and remain with a neutrally buoyant density. Davies et al. also divided the Basin into different regions based on water mass variation; the southeastern slope margin, the central Basin and the western Basin margin (Fig. 1b). The southeastern slope margin is a location where right whales (copepod predator) consistently congregate (Vanderlaan et al., 2008) and where the copepod layer and isopycnals tilted upslope toward shallower depths in 2008. The central, deepest area of the Basin contained high concentrations of copepods associated with warm, salty slope water (Davies et al., 2014). The western Basin margin (120 - 160 m) is a shallow, wide region where in 2008 low-density NSCC water dominated, and the deep copepod layer was absent. Given these observations, the authors hypothesized that: (1) diapausing *Calanus* in Roseway may be generally associated with high-density slope water and not low-density shelf (NSCC) water; and (2) in years when water mass density is higher throughout the Basin (i.e., the influence of slope-water strengthens) the suitable water-density habitat for the diapausing *Calanus* may expand toward the shallow and wide western margin (Fig. 1b). The extent to which the copepod field, water masses, and copepod aggregation processes vary among years in the Roseway Basin has not been investigated, and such information is valuable for explaining the strong spatial and interannual variation observed in the occupancy by right whales (Fig. 1c, Brown et al., 2001; Patrician and Kenney, 2010; Vanderlaan et al., 2008).

Objective 1 of this study is to describe and quantify the magnitude of interannual variability in diapausing *Calanus* spp. abundance in relation to hydrography and bathymetry in Roseway Basin during 2007 through 2009. Objective 2 is to gain insights into the physical mechanisms that define diapausing *Calanus* aggregations within the Basin by exploring statistical relationships between diapausing Calanus and water masses across three years. This serves to help answer the question of how generalizable, across years, are the observations made in 2008 and the hypotheses drawn therefrom concerning Calanus and water mass density associations? Objective 3 is to describe the three dimensional spatial structure of water mass and Calanus distributions across years, with a particular focus on variation in the vertical thickness and concentration of *Calanus* aggregations between the shallow western Basin margin and the deeper southeastern margin. This helps answer the question: are there years when the western Basin margin is a measurably richer or poorer copepod habitat?

2. Methods

2.1. Biological and hydrographic data collection

Three surveys conducted in Roseway Basin in late-summer during 2007 through 2009 aboard the R/V *Dominion Victory* consisted of using towed gear for measuring zooplankton with net-tows and (or) optical plankton counters (OPC) coincident with conductivity, temperature, and depth (CTD) sensors deployed at several fixed stations and

along transects, respectively (Table 1, Fig. 1d-f). Zooplankton samples were collected at fixed stations using BIONESS (Bedford Institute of Oceanography Net and Environmental Sampling System; Sameoto et al., 1980), towed at a nominal 1 m s^{-1} and equipped with five to seven 333 μ m-mesh nets (1 m² aperture; 1.5 m length), either a Seabird-19 or -37 CTD (Seabird Electronics), an OPC (Focal Technologies; Herman, 1988, 1992), G.O. flow meters (General Oceanics) and pitch and roll sensors used to estimate filtered volume. The second kind of gear was the Towed Underwater Biological Sampling System (TUBSS, Taggart et al., 1996; Sprules et al., 1998) that consists of an OPC attached to an Endeco V-fin along with a Seabird-37 CTD, a G.O. digital flow meter and pitch and roll sensors (used for sampled volume estimation), deployed in an undulating (tow-yo) fashion between 50 m depth and ~10 m above bottom using a nominal vertical speed of 1 ms^{-1} and nominal vessel speed of 3 knots along a series of transects. The OPC streams plankton abundance-at-size data at 2 Hz, and from each of BIONESS and TUBSS the data streams were aligned with the coincident CTD, flow meter, pitch and roll, and vessel GPS data for use in subsequent analyses.

Five BIONESS tows were collected in the Basin during 2007, four during 2008 and three during 2009, each with collections at > 100 m in the diapausing copepod layer in locations where right whales and Calanus were known to be historically present (Fig. 1c). During 2007, BIONESS stations B01, B06 and B07 sampled the western slope margin, while stations B02 and B03 sampled the southeastern Basin margin (Fig. 1d). During 2008 four BIONESS tows were concentrated along the southeastern Basin margins (Fig. 1e), whereas during 2009 three tows were collected at the intersection of the western and southeastern slope margins. The sampling protocol consisted of Net-1 collecting a surface to ~10 m above bottom sample, then subsequent nets sequentially opening and closing to sample discrete depth strata between near bottom and the surface. Each year an additional BIONESS tow was completed with all nets opening and closing within the 130 to 160 m depth stratum. During 2008, a data stream failure from the real-time Seabird-19 CTD and the flow meters required use of an archival Seabird-37 CTD, and sample volume estimates for the net tows and the OPC were calculated using speed over ground recorded by vessel GPS and the change in depth recorded by the CTD. The calculation assumed that the relative speed over ground of the ship and the instrument are the same; a valid assumption because BIONESS weighs ~1 tonne and there is no catenary in the tow cable while under tow. A statistical comparison between speed calculated from flow meters and GPS during 2007 and 2009 showed no difference between the two metrics (t-test, P = 0.581). For all tows, volume filtered through the nets and the BIONESS-OPC was estimated as the product of net and OPC apertures, tow speed, and elapsed time.

2.2. Zooplankton taxonomic, size frequency and energy content analyses

All large and rare organisms (macrozooplankton; nominally >2 cm) were sorted from the formalin-preserved net collections, identified to family, and counted. The remainder of each sample (mesozooplankton; nominally 333 µm to 1 cm) was partitioned using a Folsom splitter until replicate sub-samples of 150 to 200 copepods were obtained. All zooplankton in each sub-sample were counted and identified: copepodids to genus, species and stage and the others to the highest taxonomic

Table 1 Survey periods and number of BIONESS tows, vertical CTD casts and TUBSS transects performed during each survey conducted in Roseway Basin during 2007, 2008 and 2009.

Year	Cruise dates (mm/dd)	BIONESS/CTD tows	Vertical CTD casts	OPC/CTD transects
2007	09/10-09/17	7	20	0
2008	09/04-09/13	4	6	10
2009	08/17-08/27	3	0	3

resolution possible. Sequential replicate sub-samples were examined until the coefficient of variation (CV) for both the dominant copepod species and stage and the total number of copepods either decreased to ~10% or less, or stabilized, or until a maximum of six sub-samples had been examined. Generally three to four replicates were required and the average CV for the total number of copepods and diapausing stages consistently ranged between 10 and 11%. Random subsamples of 20 to 100 individuals of *Calanus finmarchicus* diapausing stage (hereafter CF5) and *Calanus hyperboreus* diapausing stage (hereafter CH4) from each net collection were photographed under a dissecting scope, and their length and width measured using Image-J (v.141, freeware¹). The size distributions were used to sort the CF5s and CH4s into size classes (S_{net}) that corresponded to OPC digital bin classes (S_{opc}) that encompassed the observed S_{net} size frequency distribution (see Section 2.4 for details on S_{opc} and S_{net}).

Gross energy content (caloric, J) of individuals in each CF5 and CH4 size class was measured using a Parr® 1266 semi-micro oxygen-bomb calorimeter (complete details provided in Davies et al., 2012 and in Michaud and Taggart, 2007, 2011). This enabled us to apply sizespecific energy terms to the copepod abundance-at-size distributions measured by the OPC and thus calculate energy density $(Im^{-3}; detailed)$ below). The four CF5 digital bin-class (equivalent spherical diameter, ESD, µm) ranges were: 8 (823 - 936), 9 (943 - 1058), 10 (1064 -1182), and 11 (1187 - 1307). The three CH4 digital bin-class ranges were: 11 (1187 - 1307), 12 (1312 - 1434) and 13 (1439 - 1562). As there is no statistical difference in size-specific energy content between CF5 and CH4 (Davies et al., 2012), the data from bin-class 11, where the two species overlapped in size, were combined and thus the sizeclass-specific energy content estimates were: bin-class 8, 3.89 J; class 9, 5.71 J; class 10, 8.07 J; class 11, 9.31 J; class 12, 10.78 J; and class 13, 12.20 J, as in Davies et al. (2012).

2.3. TUBSS-OPC data collection

In 2008 and 2009, zooplankton abundance-at-size estimates, particularly for the CF5 and CH4 combined size distribution, were obtained using the TUBSS-OPC (Fig. 1e, f, Table 2). During 2008, five cross-Basin transects (Tr-1 to Tr-4, Tr-8), each 15 to 30 km in length, were oriented in a generally NW to SE zig-zag pattern, and sampled across the deep basin and southeastern slope regions (Fig. 1e). Tr-8 was ~35 km in length and intersected Tr-4 and Tr-5. Three cross-Basin transects (Tr-5 to Tr-7) sampled the shallow western Basin slope margin. Two along-Basin transects (Tr-9, Tr-10) intersected the seven cross-Basin transects. Tr-9 sampled west-to-east along the western slope margin, and Tr-10 sampled SW-to-NE along the southeastern margin. In 2009, sampling was limited to two cross-Basin transects (Tr-11 and -12) ~18 km in length on opposite sides of the Basin that sampled the deep Basin and southeastern margin regions, interrupted by one along-Basin transect (Tr-13) at 52 km in length that transected the middle of the Basin from the western slope margin across the deep basin (Fig. 1f). Tr-12 crossed Tr-13 at the 15 km mark on the western Basin margin, whereas Tr-11 crossed Tr-13 at the 40 km mark near the eastern margin. TUBSS data were collected during the day (Tr-11 and 12) and at night (Tr-13).

In 2009, the TUBSS data streams were realigned to a 1 Hz sampling frequency. Some data recording and storage was interrupted at ~1 h intervals (file management) though interruption was generally less than 3 s. Volume filtered was determined using the product of flow meter speed, elapsed time and OPC sampling tunnel aperture where the latter was corrected for pitch. Flow meter speeds were systematically lower when TUBSS was descending, leading to higher zooplankton particle concentrations relative to the previous and (or) subsequent ascent (Suppl. Fig. 1a). To determine which of the ascending or descending portion of the tow was biased, tow speed was estimated from the vessel

¹ http://rsbweb.nih.gov/ij/.

Table 2

Summary characteristics of each transect sampled using TUBSS in Roseway Basin during 17 through 27 August 2009, including start and end date, time (ADST), latitude and longitude, as well as nominal transect heading, extent, and maximum sampling depth.

Year	Transect No.	Start Date (mm/dd)	Start Time (hh/mm)	End Date (mm/dd)	End Time (hh/mm)	Start Lat	Start Lon	End Lat	End Lon	Heading (true)	Extent (km)	Max depth sampled (m)
2008	1	09/06	01:31	09/06	03:10	43.077	-65.002	43.100	-65.097	NW	8.27	161
	2	09/11	12:39	09/11	17:01	42.922	-64.977	43.112	-65.174	NW	27.00	163
	3	09/11	07:44	09/11	12:03	43.074	-65.278	42.930	-64.982	SE	29.90	160
	4	09/09	17:17	09/09	21:06	42.814	-65.201	43.038	-65.268	NW	26.17	161
	5a	09/13	20:11	09/13	17:37	42.967	-65.480	42.875	-65.315	SE	17.00	144
	5b	09/09	15:22	09/09	17:17	42.875	-65.318	42.814	-65.201	SE	12.08	143
	6	09/08	22:10	09/09	01:50	42.960	-65.477	42.780	-65.433	SE	21.09	132
	7	09/09	01:50	09/09	04:47	42.780	-65.433	42.903	-65.568	NW	17.89	128
	8	09/13	20:11	09/14	00:45	42.967	-65.480	42.976	-65.089	E	31.88	161
	9	09/05	21:00	09/06	01:30	42.898	-65.164	43.076	-65.002	NE	28.25	156
	10a	09/09	07:43	09/09	15:21	42.832	-65.775	42.875	-65.320	E	24.16	143
	10b	09/13	15:30	09/13	17:39	42.889	-65.154	42.876	-65.316	W	23.99	153
2009	11	8/26	09:16	8/26	14:00	43.053	-65.211	43.053	-65.208	NW	18.28	166
	12	8/25	09:40	8/25	13:30	42.931	-65.340	42.790	-65.245	SE	19.70	144
	13	8/25	21:44	8/26	07:57	42.825	-65.499	43.095	-65.041	NE	52.35	157

GPS (as above for the 2008 BIONESS), and the resulting metric was compared statistically to the flow meter estimates on adjacent ascents and descents (Suppl. Fig. 1). A positive linear relationship between flow meter and ship tow speed on the ascent had a slope that was not significantly different from 1 (P < 0.001, slope = 1.068 ± 0.148 S.E.), whereas during the descent the flow meter speed systematically underestimated GPS speed (P < 0.001, slope = 0.88 ± 0.11 S.E., Suppl. Fig. 1a), and we therefore concluded that the descending portions of the tows were biased. Michaud and Taggart (2011) observed the same phenomenon using the same equipment during a similar survey and attributed the bias to a 'shielding' of the flow meter by the tow body during nose-down descent. We therefore developed a calibration equation to correct the biased volume sampled estimates (Suppl. Fig. 1b, downward_{corrected} = 1.02•downward_{raw} + 0.37, P < 0.001, r² = 0.78).

During 2008, tow-cable faults prevented recording of pitch and flow meter data from the platform and we were required to use Seabird-37 CTD in archival mode recording data at 20 or 6 s intervals, and then upload the data following the completion of each deployment. In lieu of flow meter data, tow speed was estimated from the vessel GPS and TUBSS depth as described above for the 2008 BIONESS, a procedure which we already validated using the 2009 comparison between ship GPS and flow meter speed (Suppl. Fig. 1). Again, the volume filtered estimates were determined using the product of tow speed, elapsed time and OPC aperture. No correction for downward tows was required because flow speeds estimated from the vessel GPS do not systematically differ between the ascending and descending portions of the tow (Suppl. Fig. 1b). All data were interpolated, where needed, to 1 Hz.

2.4. OPC data analyses

The majority of BIONESS-OPC and TUBSS-OPC data analyses followed Michaud and Taggart (2011). In summary, the plankton particles are classified by the OPC in 4096 digital bin-classes (DS_{opc}), each proportional to particle area. The particle equivalent spherical diameters (ESD_{opc} , μ m) were then calculated from DS_{opc} using the following empirical equation (Taggart et al., 1996):

$$ESD_{opc} = 10^{(0.575 \log[(DS_{opc}) + 1.870)]}$$
(1)

To simplify the analysis, the number of digital bin-classes was reduced to 64 by using the integer value of $DS_{opc}^{1/2}$. Each ESD_{opc} measurement was the assigned one of the 64 bin classes, denoted by S_{opc} . The number of particles in each S_{opc} bin class sampled at 2 Hz was then recalculated at 1 Hz, and *Calanus* concentration was estimated by summing the S_{opc} bin classes that corresponded to the BIONESS-net (S_{net}) size distribution (see Supplement for S_{opc} - S_{net} calibration details) and

dividing by the sampled volume. *Calanus* concentration in each size class was then multiplied by the size-class-specific energy content (J, Section 2.2), and the resulting energy density (kJ m⁻³) series was integrated over all *Calanus* size classes. A statistical comparison between the S_{net} and S_{opc} energy density estimates across all three years was assessed using linear regression, and estimates were strongly correlated ($r^2 = 0.94$) with a slope not different from 1 (P < 0.001, slope = 0.9688 \pm 0.0307; see Suppl. and Fig. S4 for details). Thus, the TUBSS-OPC, BIONESS-OPC and BIONESS-net collections provide comparable energy density estimates, and no correction among instruments or years was required to compare across them.

2.5. Additional CTD profiles

During 2007 several CTD profiles were collected throughout the Basin using a vertically profiling Seabird-25 (Fig. 1d). Additional CTD casts were few in 2008 and absent in 2009 because the TUBSS profiles provided high resolution, broad scale sampling of the hydrography (Fig. 1e, f).

2.6. Statistical analysis and comparisons

Statistical comparisons were made among various metrics that defined the diapausing copepod layer calculated from each BIONESS-OPC/CTD and (or) TUBSS-OPC/CTD profile. These included the average, maximum and depth-integrated Calanus energy density and the vertical thickness of the layer. Integrated energy density and layer thickness were calculated at all depths below the minimum depth where a threshold energy density of 8.79 kJ m⁻³ was reached. The threshold was chosen because it is the minimum food energy density required to meet the basal metabolic demand of a major copepod predator in Roseway; the North Atlantic right whale (Kenney et al., 1986). The threshold thus has biological significance for at least some predators (i.e., large baleen whales), as well as being in agreement with the inflection point that represents a rapid increase in energy density at the shallowest point of the deep layer. Layer thickness was calculated assuming that the bottom of the layer lay 5 m above the seafloor, consistent with observations made in Roseway Basin (Davies et al., 2013). The average energy density was calculated over all depths where energy density exceeded the threshold, and also over all depths exceeding 100 m, for different purposes. Water mass metrics associated with each biological metric were also calculated for each profile. These included latitude, longitude and bathymetric depth, profile depth, temperature, salinity and density at the top of the deep copepod layer, at the depth of maximum energy density, and as averaged over the thickness of the deep layer. From the BIONESS-net data, three metrics defining species composition in net samples below 100 m were used: the proportion of C5s and C4s relative to the total copepod concentration, and the Shannon Index of species diversity (Legendre and Legendre, 2012). All *Calanus* energy density estimates were normalised for statistical analysis using a logarithmic transform. Only the data sampled at bathymetric depths between 138 and 157 m were included for statistical analyses because this was the depth range sampled in all three years. Further, data along the northern slope margin were excluded because this region was not sampled in 2007 (Fig 1d-f). Data included in the statistical analyses are colour-coded blue in Fig. 1d-f. These restrictions meant that no interannual comparison could be made for the deep basin region, but interannual comparisons could be made along the western and southeastern Basin margins, which are the most important areas for right whale feeding aggregations (Fig. 1c).

Objective 1, quantifying the magnitude of interannual variability, was addressed statistically by assessing differences within each biological or physical oceanographic variable among years and across profiles. Correlations among the biological characteristics that defined the deep layer were assessed using Pearson's correlation coefficient (r). Statistical differences within each biological and physical characteristic defining the layer among years were assessed using a Welch-corrected analysis of variance (ANOVA; Legendre and Borcard, 2008). Welch's ANOVA is appropriate when variances and sample sizes are unequal (2007 n = 5, 2008 n = 91, 2009 n = 20). Estimates are reported as the average \pm one standard deviation. Variation in water masses among years were then described in relation to the statistical comparisons using temperature-salinity diagrams.

Objective 2, assessment of statistical relationships between diapausing *Calanus* estimates and source water mass characteristics (hydrography) was achieved using an Analysis of Covariance (ANCOVA) with the hydrographic variable as the continuous predictor and year as the fixed categorical factor. The first set of tests determined whether general relationships across years were apparent between the maximum Calanus energy density within the deep layer and the corresponding hydrographic variables at the maximum. Regions where the energy density threshold was never reached were not included in the analyses (28 % of profiles in 2008). The second set of tests determined whether general relationships across years were apparent between the average Calanus energy density below 100 m and the coincident hydrographic variables. The average below 100 m was used rather than the average over the deep copepod layer so that regions where the energy density threshold was never reached could be included in the analysis. The third set of tests determined whether general relationships existed across years between the shallowest point of the deep copepod layer and either the hydrographic variables at that point or the associated bathymetry. These analyses helped determine if there were vertical limits to the diapausing copepod habitat.

Disparate observations in 2007, variation in water mass presence and distribution among years, and variation in sampling location among years, together prevented rigorous multivariate statistical comparison of *Calanus* energy density among regions, years, and water masses in one analysis. Therefore, Objective 3, describing the three dimensional spatial structures of water masses and *Calanus* distributions across years, was addressed by building on the quantitative assessments addressed Objectives 1 and 2 using additional qualitative comparisons, where possible, between the western slope margin, the southeastern margin and the central basin. First, the relative contributions of three end-member water masses that contributed to the basin hydrography were calculated for each profile using the average temperature (T) and salinity (S) of each profile below 100 m, and solving the following set of linear equations:

 $aT_{source1} + bT_{source2} + cT_{source3} = T_{deep_basin}$ (2)

 $aS_{source1} + bS_{source2} + cS_{source3} = S_{deep_basin}$ (3)

$$\mathbf{a} + \mathbf{b} + \mathbf{c} = \mathbf{1} \tag{4}$$

where a, b and c are the desired proportions, and subscripts represent each of the source and basin water masses. Geographic variation in water mass end-member composition (relative proportions) and hydrography (T-S signature) was described among years and regions using T-S diagrams. The geographic patterns in water mass end-members included CTD profiles collected in 2007 that had no concurrent measurements of *Calanus* energy density (Fig. 1d). Then, geographic variation in water mass hydrography (TS signature) and end-members in relation to copepod energy density where the two measures were co-located (Fig. 1, blue colored locations) within the deep layer (>100 m) was described among years using T-S diagrams.

3. Results

3.1. Magnitude of interannual variability

The metrics that defined diapausing copepod energy density in the water column of Roseway Basin were positively correlated with each other (Pearson's r > 0.90 in all cases) and all metrics were lower in 2008 than in either 2007 or 2009 (Welch's ANOVA, $p \le 0.001$ in all cases). Deep-layer-averaged energy density in 2008 (9 \pm 4 kJ m⁻³) was less than half that estimated in 2007 (23 \pm 1 kJ m⁻³) and 2009 $(21 \pm 2 \text{ kJ} \text{ m}^{-3})$. Depth-integrated energy density was significantly different among all three years; during 2008 (94 \pm 18 kJ m⁻²) it was an order of magnitude less than 2007 (1019 \pm 2 kJ m $^{-2})$ and less than 2009 $(362 \pm 5 \text{ kJ m}^{-2})$ by a factor of four. Maximum energy density in 2008 $(19 \pm 3 \text{ kJ m}^{-3})$ was half that in either 2007 $(37 \pm 1 \text{ kJ m}^{-3})$ or 2009 $(36 \pm 2 \text{ kJ m}^{-3})$. The diapausing copepod layer was half as thick in the vertical dimension during 2008 (25 \pm 19 m) than during 2007 (55 \pm 32 m) or 2009 (52 \pm 26 m) and this was related to the deep layer beginning 20 m deeper during 2008 $(111 \pm 11 \text{ m})$ compared to 2007 (92 \pm 30 m) and 2009 (91 \pm 24 m). Furthermore, 28 % (22 of 78) of the profiles in 2008 did not reach the threshold energy density, compared to 1 profile (5 %) in 2009 and none in 2007, over the same bathymetric range sampled each year. The profiles where the threshold was not reached occurred at significantly shallower bathymetric depths $(145 \pm 4 \text{ m})$ compared to profiles where the threshold was reached $(151 \pm 5 \text{ m}, t\text{-test}, P < 0.001)$. Copepod diversity in the deep layer did not change among years (P = 0.267) and *C. finmarchicus* was always the dominant species, comprising 56 to 71 % of the total mesozooplankton concentration (P < 0.001). However, the relative composition of arctic versus temperate *Calanus* spp. was different (P < 0.001) among years; the relative proportion of diapausing C. hyperboreus C4 declined in 2009 to 5 \pm 2% compared to 2007 at 19 \pm 6 % and 2008 at 19 ± 7 %. At the same time, the proportion of C. finmarchicus C5 increased significantly each year from 56 \pm 11 % in 2007 to 63 \pm 8 % in 2008 to 71 \pm 10 % in 2009 (P = 0.015).

The strongest differences in hydrographic properties associated with the deep copepod layers occurred in 2008 when Roseway experienced less dense deep water masses than in either 2007 or 2009. At the depth of the maximum energy density within the layer, water mass density was lower (P < 0.001) by 0.9 kg m⁻³ in 2008 (26.1 \pm 0.03 kg m⁻³) than in either 2007 (27.0 \pm 0.2 kg m⁻³) or 2009 (26.7 \pm 0.2 kg m⁻³). Though water density is a function of temperature (T) and salinity (S), neither S (P = 0.258) nor T (P = 0.08) at the depth of maximum energy density were significantly different among years. The same statistical patterns of hydrographic properties were found in relation to (1) the shallowest depth of the deep copepod layer (i.e., the top of the layer in the vertical) and (2) the average properties measured over the deep layer.

The hydrographic properties of water mass end-members that contributed to the waters found in Roseway Basin have been defined (Davies et al., 2014) as basin water (BW), intermediate basin water (iBW), and modified basin water (mBW), and their contributions to the water masses differed among each years (Fig. 2). In 2007, only 2 end-members were present (BW and iBW) while in 2008 and 2009 all



Fig. 2. Temperature-salinity diagram with lines of constant density (σ_t , dotted lines labelled at 25.6, 26 and 26.6) illustrating horizontal spatial variation in the deep-basin copepod energy density (color bar) among water masses during each of 3 annual surveys in Roseway Basin where each datum represents the 100 to 160 m stratum-average of BIONESS profiles (2007, square) or TUBSS transect profiles (2008, circle; 2009, triangle) and where water mass end-members are identified as BW (Basin Water), iBW (intermediate Basin Water), and mBW (modified Basin Water). East – west directionality of the water mass gradient is depicted by double-ended arrow.

three water masses were present. The limited contribution of warm mBW in 2007 meant the waters in the Basin tended to be colder. The BW and iBW masses in 2007 were more saline and more dense than in 2008 or 2009, and the BW was ~1 °C colder (Fig. 2). Thus, the deep waters of the Basin in 2007 tended to be colder, saltier and denser relative to 2008 and somewhat so relative to 2009. All three contributing end-members were warmer and more saline in 2009 relative to 2008 which led to the entire water mass structure in the Basin being slightly denser than in 2008 (Fig. 2). There was a particularly strong contrast in the hydrographic properties of iBW between 2008 and 2009, with 2008 being colder and fresher.

3.2. Relationship between Calanus and water mass properties

Water mass density explained a significant amount of variation in maximum copepod energy density across years (ANCOVA, P < 0.001, $r^2 = 0.27$, $log_{energy} = 0.69 \sigma_t - 17$), and the slope of the relation was not different across years (P = 0.072). Similarly, the relationship between salinity and maximum energy density was also significant (ANCOVA, P < 0.001, $r^2 = 0.37$, $log_{energy} = 1.23^*$ density - 39), which is not surprising since salinity is the primary driver of density variation in the Basin. The relationship between maximum energy density and temperature was not significant (P = 0.187). Although there was a significant (P < 0.001) log-linear relation between average copepod energy density and σ_t below 100 m (log_{energy} = 0.5 σ_t - 12), the explained variance was low ($r^2 = 0.11$). The relation between average *Calanus* and T and S below 100 m were insignificant (P > 0.05). These results suggest that water density and salinity are important characteristics explaining variation in diapausing copepod abundance distribution in Roseway Basin

We have previously argued that the 26 σ_t isopycnal represents a lower density limit for the formation of highly concentrated diapausing copepods in Roseway (Davies et al., 2013, 2014), and here we tested whether this argument held using a multi-year statistical analysis. We found that water mass density was meaningful in defining the vertical dimension of the deep copepod layer across years, where the 26 σ_t isopycnal was a clear limit; 2008 being a very different year than either 2007 or 2009 (Fig. 3). During 2008, the threshold energy density that defined the deep layer was never reached in waters with a density less than 26 σ_t (28 % of profiles). The depths at which the copepod energy density did exceed the threshold occurred between 78 and 134 m, where the water densities ranged from 26.0 to 26.18 $\sigma_{\rm t}$ (Fig. 3). The relationship between the depths at which the threshold was reached and the associated water mass densities at those depths was linearly positive (P < 0.001, $r^2 = 0.51$, Fig. 3). The relationships between the depths of the top of the copepod layer and water mass density at those depths in 2007 and 2009 were also linearly positive $(P < 0.001, r^2 = 0.77, Fig. 3)$, though with a statistically lower slope than in 2008 (P < 0.001). Further, in 37 % of the profiles collected during 2007 and 2009, the shallowest point of the deep layer began at a shallower depth than in 2008 (Fig. 3), resulting in the top of the deep layer being statistically deeper on average during 2008 than the other years (Section 3.1). Despite beginning at shallower depths, water mass densities associated with the top of the deep copepod layer during 2007 and 2009 ranged from 26.2 through 27.0 $\sigma_{\rm r}$; i.e., exceeding the water densities observed in 2008. One simple interpretation of the above results is that during 2007 and 2009 the expansion of water mass densities >26 σ_t in the vertical dimension to shallower depths also allowed the deep copepod layer to occur at shallower depths than during 2008 when the copepod layer was restricted to the deeper water, at depths exceeding the 26 $\sigma_{\rm t}$ isopycnal. As there was no relationship in any year between the shallowest point of the deep layer and water mass temperature, salinity or bathymetry (P > 0.05 in all cases) we again conclude, as above, that water mass density appears to be the most important physical characteristic (of those we considered) defining diapausing copepod habitat. However, water mass density only explains ~ 1/3 of the variation in copepod energy density spatially and temporally, and there remains much unexplained variation. For example, there were some areas of the Basin in 2008 where the average density below 100 m depth exceeded 26 σ_t but *Calanus* energy density remained low, and vice versa (Fig. 2).

3.3. A description of geographic distributions of Calanus and water masses in Roseway Basin

Charts depicting the general horizontal spatial distribution and relative proportions of end-members that contributed to the waters in



Fig. 3. Relations between the depth (m) at which copepod energy density in the deep layer exceeds a threshold of 8.79 kJ m⁻³ and the water mass density (σ_t) at that depth, collected during Roseway Basin surveys in 2007, (square), 2008 (circle), and 2009 (triangle). The linear regression models describing the relations are not significantly different between 2007 and 2009.

Roseway Basin in each year, and in relation to Basin bathymetry, show that interannual variation in water mass distribution can be characterized based on how far into the Basin and over the southern margin and onto the bank the mBW slope water intruded (Fig. 4, green data points). In all three years, the deepest part of the Basin was filled primarily with slope-origin iBW (red data points in Fig. 4), while the shelf water mass, BW (blue data points in Fig. 4), was dominant at the western Basin margin. The presence of fresh BW at the western margin caused the water in that region to be less dense at any given depth than in either the central basin or on the southeast margin. In 2007, BW extended its influence across the entire southwestern margin, where it then mixed with iBW water on the southern margin and on the bank (Fig. 4a). No mBW water intruded over the bank or into the Basin in 2007. In 2008, the BW was sharply adjacent (frontal region) to the mBW that had intruded over the southern bank and margin, and into the deep water of the Basin on the southeastern margin (Fig. 4b). In 2009, the mBW mass was present but restricted to the bank, and both iBW and BW waters intruded farther southward than in 2008 (Fig. 4c).

The above water mass distributions appeared to be related to the meridianal gradients in the magnitude and thickness of the deep copepod layer each year. Year 2008 saw a strong west (low) to east (high) gradient in the magnitude of copepod energy density that was not present in the other two years (Fig. 2). At the eastern margin, a slope-water intrusion brought high density (>26 σ_t) mBW water into the Basin, and copepod energy densities within the mBW water mass were locally as high as in 2009 (Fig. 2). At the western margin, the lower-density BW was dominant and particularly low in density (<26 σ_t) in 2008, and within this low density water the copepod energy density estimates were ${<}1~kJ~m^{-3}$ (Fig. 2). Thus, the slope water intrusion at the eastern margin influenced the mBW (>26 σ_t), and the particularly low density BW at the western margin created a strong east to west spatial gradient in the deep copepod layer. This east to west gradient was not observed in other years, nor were there any clear horizontal spatial associations between the magnitude of Calanus energy density and different water mass end-members during 2007 or 2009 (Fig. 2). This lack of gradient appears to be related to the deep copepod layer observed at the western Basin margin during both 2007 and 2009, whereas this layer was absent near the western margin during 2008 (Fig. 5).

While the deep copepod layer was present at the western margin during 2007, there was a clear west to east gradient in the vertical thickness of the deep copepod layer that year (Fig. 6). At the western margin (stations B07 and B01) the layer was thin and concentrated close to



Fig. 5. Regional (western Basin vs. southeast margin) and interannual (2007,'08, '09) variation in the vertical distribution of diapausing *Calanus* copepod energy density (kJ m⁻³) in Roseway Basin derived from BIONESS-OPC profile stations B07 (western Basin) and B03 (southeast margin) in 2007 (Fig. 1d) and from TUBSS-OPC transect-9 (2008) and -11 (2009) profiles located nearest to the two BIONESS stations (Fig. 1e, f).

bottom because low density BW water resided above the deep layer, and this study suggests that low density water vertically limits the deep copepod layer (Fig. 3). In contrast, at the southeastern margin during 2007 (stations B02 and B03), *Calanus* were distributed throughout the water column below 50 m depth, and these layers occupied the higher density iBW (Figs. 2, 6).

In summary, 2008 was oceanographically a very different year regarding the deep waters of Roseway Basin compared to 2007 and 2009. The deep diapausing layer was absent from the western margin, contained fewer copepods, and was vertically thinner when compared to the other years, and each of these observations was correlated with the presence of lower density water during 2008 than during 2007 or 2009. Our results suggest that water mass density is an important characteristic defining the spatial and interannual ecology of the deep copepod layer in Roseway Basin.



Fig. 4. Bathymetric chart illustrating the color-coded horizontal spatial distribution of water masses identified as BW (Basin Water, red), mBW (modified Basin Water, green) and iBW (intermediate Basin Water, blue) in (a) 2007, (b) 2008, and (c) 2009 in the deep waters of Roseway Basin where intermediate colors reflect gradients (mixing of adjacent water masses). Isobath contours are spaced at 25 m and the 100 m and 150 m contours are labeled in (a).

4. Discussion

4.1. Interannual variation in Scotian Shelf oceanography and its effect on Roseway Basin during 2007 - 2009

Abundance, energy and species composition of copepods residing in Roseway Basin during late-summer are two important factors that determine the amount of copepod food-energy available to predators, and each of these quantities were found to vary interannually. Total integrated energy density of the deep diapausing copepod layer was higher in 2007 than in the other years, partly because during that year a greater proportion of larger, Arctic-borne C. hyperboreus inhabited the basin, and partly because the total abundance of Calanus sp. was higher. Conversely, all metrics defining the deep copepod layer were lower during 2008 than in other years. To what extent can this variation be explained by annual cycles of copepod production on the Scotian Shelf, and/or to variation in water mass advection from other regions? The interpretation is aided by CTD data and *C. finmarchicus* abundance estimates derived from depth-integrated ring-net collections at six sampling stations (St-1 to -6) on the Browns Bank Line (BBL) that are annually occupied in April and October by the Fisheries and Ocean Canada Atlantic Zone Monitoring Program (AZMP) in the Roseway Basin region (Fig. 7a). The value of this comparison lies in that the transect samples the cold, fresh BW water mass (Fig. 7a, St-1 & -2), the western margin of Roseway Basin (Fig 7a, St-3 & -4) and the continental slope water (Fig. 7a, St-5 & -6).

The physical dynamics on the Scotian Shelf during 2007 were influenced primarily by an extremely cold sub-surface flow from the Arctic (Labrador Slope Water, LSW). Advection of LSW onto the Scotian Shelf during winter through summer of 2007 led to cold and fresh bottom-water anomalies and record high biomass of the Arctic species *C. hyperboreus* (Galbraith et al., 2010; Harrison et al., 2008; Petrie et al., 2008). This was the first major penetration of LSW onto the Shelf since 1998. The largest temperature anomalies, -2° C, were found on the western Scotian Shelf where Roseway Basin is located (Petrie et al., 2008). These observations are consistent with our species composition data and hydrographic observations in the deep water of Roseway (strong *C. hyperboreus* influence, highly dense water). By October of 2007, Petrie et al. (2008) noted that negative temperature anomalies persisted on the Shelf. However, at the same time the shelf break anomalies had decreased on the eastern and central Shelf and had become positive anomalies on the western Shelf south of Roseway, indicating the end of the LSW intrusion into the Roseway Basin region by autumn.

How the advection of LSW onto the Shelf during winter through summer interacted with the seasonal pattern of Shelf and slope copepod production and advection to culminate in relatively high abundances of diapausing C. finmarchicus in Roseway during the latesummer of 2007 are unclear. During spring, the most notable biological event in 2007 was a large-magnitude and extensive spring bloom in April that reached near-record levels relative to the 1998 - 2006 average on the Shelf, though the bloom was short-lived and biomass levels outside the bloom declined (AZMP, 2008). High abundances of early-stage copepods comprising 60 – 90 % *Calanus* spp. were measured during the bloom at AZMP Halifax St-2 (central Shelf), however broad-scale concentrations of C. finmarchicus on the Shelf during spring were below normal, were paradoxically low across the Shelf-portion of BBL near Roseway compared to 2008 or 2009 (~4.0 $\times 10^3$ – 5.0 $\times 10^3$ m⁻², Fig. 7b, St-1 & -2) and increased only modestly over the slope-portion of the BBL compared to 2008 or 2009 (~ 8.0 $\times 10^3$ – 2.7 $\times 10^4$ m⁻², Fig 7b St-5 and -6, Harrison et al., 2008; Johnson et al., 2012). The Arctic species C. hyperboreus and glacialis comprised a larger proportion of the shelf community than normal during spring, consistent with the presence of LSW.



Fig. 6. BIONESS-OPC vertical profiles of diapausing *Calanus* energy density (kJ m⁻³ (black line) and water mass density, σ_t , (open symbols) collected from west to east at BIONESS stations (a) B07, (b) B01, (c) B02 and (d) B03 during the 2007 survey in Roseway Basin. Sampling locations are depicted in Fig. 1d. Apparent anomalies in the profiles are related to small scale vertical undulations of TUBSS while under tow.

a) Geographic location of Browns Bank Line (BBL) sampling stations



Fig. 7. a. Chart of locations of six sampling stations on the Browns Bank Line (BBL) regularly occupied in b. April and c. October by the Atlantic Zone Monitoring Program (AZMP) in the Roseway Basin region, each illustrating variations in areal concentrations (m^{-2}) of all stages of *Calanus finmarchicus* in 2007 (dotted line), 2008 (solid line) and 2009 (dashed line). Data provided by AZMP.

During summer 2007, the late-stage copepodid entered diapause in July, which was one to two months later than usual, possibly due to the colder than normal conditions. A second maximum of early copepodid stages occurred in September indicating a late-in-the-year generation, and this is consistent with our observations of high adult abundances in September in Roseway. During the July groundfish surveys (Fisheries and Oceans Canada) that focus more closely on the deep basins, *C. finmarchicus* abundance was close to normal (Harrison et al., 2008).

During Autumn 2007, elevated concentrations in the Roseway region during October were evident in the AZMP collections along the BBL, with lower copepod concentrations shoreward (St-1 and -2) and on the Shelf-slope (St-5) compared to the western margin of Roseway and on Browns Bank (St-3 and -4), where concentrations were higher than in either 2008 or 2009 (Fig. 7c). This is entirely consistent with our observations of interannual variation along the western Basin margin (notably higher integrated energy density in 2007). Shelf-wide trawl surveys reported overall low mesozooplankton and average *C. finmarchicus* abundance during autumn (Harrison et al., 2008).

The fate of the strong pulse of C. finmarchicus measured at AZMP Halifax St-2 in the wake of the strong spring bloom is unknown, and it is possible that these animals were advected southwest during the spring and summer to form the diapausing population we observed in September in Roseway. No other notably strong blooms of copepods on the Shelf or the slope were observed that might explain our observations in Roseway. Intrusions of slope water onto the western Scotian Shelf are an important source of copepods to the basins (Davies et al., 2014; Head et al., 1999) but it is not clear whether or not the strong intrusions of LSW onto the Shelf that occurred throughout the year were responsible for transporting slope water rich in C. finmarchicus into the Basin during 2007. The strong spatial association between Calanus and iBW (the LSW-influenced water mass) in the Basin suggests this is a reasonable hypothesis, however the slope water did not appear particularly rich in Calanus, indeed it was much lower than either 2008 or 2009 (Fig. 7b).

Regional-scale variation in physical and biological oceanographic conditions across the western Scotian Shelf during 2008 are consistent with our observations that (1) the influence of LSW observed in 2007 did not recur but rather the area returned to warmer, saltier conditions, (2) the major source of diapausing C. finmarchicus in the Basin was from a small-scale intrusion of slope water containing slope spawned copepod populations, and (3) Shelf production was likely a minor source of copepods relative to the continental slope. During spring, bottom temperatures on the western Scotian Shelf and in the slope water were warmer compared to 2007 but remained colder than normal (Petrie et al., 2008), and the strong spring phytoplankton bloom noted in 2007 did not recur (Harrison et al., 2009). C. finmarchicus abundances along the BBL during spring at Shelf St-1 through St-3 were average at \sim 7.0 x 10³ m⁻², increasing by 2 to 3 orders of magnitude and to surprisingly high concentrations near and at the Shelf-slope stations (5.1×10^5) to $1.5 \times 10^6 \text{ m}^{-2}$; Fig. 7a,b). The same trend was observed along the BBL in October, although overall abundances were lower during autumn than spring (Fig. 7c). The high abundance of copepods we observed during a slope water intrusion into the deep waters of Roseway Basin is consistent with the AZMP observations of an extremely strong slopepopulation. However, the warm, salty intrusion of 2008 occurred at a much smaller scale than the cold LSW intrusion of 2007, hence the high concentrations we observed were likely localized and, outside this area, concentrations at depth were extremely low. Low concentrations in the shoreward BW mass in Roseway during late-summer suggest that the production of Calanus on the western Shelf was negligible during 2008, however AZMP data suggested that near- to above-average abundances of C. finmarchicus persisted from spring into autumn (Harrison et al., 2009)

Observations made along the Browns Bank Line during spring and autumn of 2009 are consistent with our observations that both the slope and the Shelf were each strong suppliers of C. finmarchicus to Roseway Basin during 2009 (Fig. 7). This is in contrast to 2008 when the slope water was clearly dominant, and to 2007 when the only large bloom of C. finmarchicus occurred on-Shelf. The magnitude of the spring bloom observed at AZMP Halifax St-2 in 2009 was considerably larger than the small bloom of 2008 and higher than the long-term average. Bloom duration in 2009 was also longer than normal (Johnson et al., 2012), which means it could support more generations of copepods (we measured three, and this is not uncommon; McLaren et al., 2011), particularly because development time would be relatively shorter due to the warmer temperatures compared to 2007 and 2008. Strong maxima in C. finmarchicus abundance were measured along the BBL during spring in the BW water mass (St-2: ~ $1.5 \times 10^{6} \text{ m}^{-2}$) and in the slope water mass (St-5: $9.6 \times 10^5 \text{ m}^{-2}$, Fig. 7b) and this pattern persisted into the autumn (Fig. 7c).

The strong inter-annual variability we measured in copepod abundance lends credence to the hypothesis of Patrician and Kenney (2010) that Roseway Basin is an ephemeral habitat for whales and their food, governed at least partially by annual cycles of copepod production and advection of Shelf-slope waters that vary in density. Decreased in situ salinity and density are hypothesized to be indicators of the changes in circulation during the 1990s that affected the advection of C. finmarchicus onto the Scotian Shelf and resulted in right whales presumably abandoning Roseway Basin for seven consecutive years (Patrician and Kenney, 2010). The authors concluded that during the abandonment period, low copepod concentrations in Roseway Basin were caused by increased transport of the NSCC that occurred because of a low salinity LSW pulse. At the same time, on-shelf transport of warm slope water, the major supplier of copepods to the Shelf in spring and summer, decreased (Greene and Pershing, 2004; Greene et al., 2013; Head et al., 1999). Although our observations are not entirely consistent with this interpretation (i.e., 2007 was a strong LSW year and 2008 and 2009 were not), the correlation between water mass density and C. finmarchicus does agree.

4.2. Distribution of water masses in Roseway Basin and their effect on Calanus

Interannual variation in the spatial distribution of water mass endmembers in Roseway Basin can be explained by variation in (1) transport of the NSCC, which carries BW, (2) the location of the shelf-slope front, which determines the on-Shelf extent of mBW and iBW, and (3) shelf-scale advection of cold LSW which affected all three water masses during 2007. The NSCC consists of an along-isobath throughflow on the inner Scotian Shelf with cross-Shelf meanders that are bathymetrically driven around the margins of Shelf basins (Hannah et al., 2001). The influence of the NSCC appeared as a wedge of BW that extended along-isobath around the northern and western margin of Roseway Basin. Volume transport of the NSCC reaches its annual low in summer, which creates a partial barrier to along-shelf flow on the western Scotian Shelf and results in greater off-shelf meandering toward the shelf-Break (Hannah et al., 2001). During 2007, when the Labrador Current was strong, BW dominated above the 160 m isobath on the northern and western margins of Roseway and also flooded the adjacent southeastern Bank, and this pattern can be attributed to greater off-Shelf transport of the NSCC that may have been driven by the strong upstream intrusion of LSW. This is in staunch comparison to 2008 when along-isobath flow of BW around the western margin of the Basin was halted far from the southern basin margin, which may be attributed to reduced off-Shelf transport by the NSCC and lack of LSW.

The southwestward shelf-slope flow transports mBW and iBW in an along-isobath direction from northeast to southwest along the continental slope. This flow creates a shelf-slope front between the slopeinfluenced (mBW, iBW) and Shelf-influenced (BW) water masses, and the position of this shelf-slope front meanders seasonally northwestward (shoreward) and southeastward (toward the continental slope) on the western Scotian Shelf (Hannah et al., 2001). In 2008 the strong presence of mBW, which extended over the entire southeastern bank, through the deep channel separating Roseway and Baccaro Banks, and into the deep waters of Roseway Basin, suggests that the shelf-slope front extended further onto the Shelf that year, bringing copepods into the region. The shoreward extension of the shelf-slope front interrupted through-flow of the NSCC around the western margin of Roseway in comparison to 2007. In 2009, the shelf-slope front was limited to the adjacent southeastern Bank, and this allowed a wedge of BW to advect along-isobath and part way along the southeast Basin margin. In 2007 when the LSW intrusion was strong, the absence of mBW on the southeastern Bank suggests this water mass was displaced by LSW, coupled with increased on-shelf transport of the deeper iBW water mass which may have brought extremely high numbers of Calanus spp. into Roseway, and particularly along the western margin, where right whales are often aggregated (Fig. 1c).

Right whales in Roseway Basin are more aggregated east to west along the southern Basin margins than in the middle of the Basin (Fig. 1c). This may be related to reduced foraging at depth to achieve greater energetic efficiency because dive depths for right whales are in the 100 to 150 m depth range (Baumgartner et al., 2007). Our study suggests that during years when water mass density is lower in the Basin habitat, the copepod habitat for right whales moves toward the deeper central basin and may be absent along the basin margin. We observed this difference. In 2007 and 2009 the western margin contained a deep copepod layer. In 2008 the deep copepods layer was absent from the margin. Interannual expansions and contractions of water masses of a particular density along the shallow margins of Roseway Basin may be one driver of the interannual variability in right whale food, and thus right whale abundance, in this habitat.

4.3. Diapausing copepod buoyancy and the 26 σ_t isopycnal

The relationship between water mass density and the thickness and minimum depth of the deep diapausing copepod layer may be mechanistically explained by the dynamics of buoyancy regulation during diapause. There are three main components to diapausing copepod buoyancy regulation: (1) the animals have a large, full lipid sac (mostly wax ester), (2) they also have other biochemical constituents such as proteins and (3) at least some species have been shown to actively regulate their internal ionic composition. Concerning (1), wax ester has some interesting buoyancy properties in relation to seawater. Its thermal expansion coefficient is much larger than seawater, and to a lesser extent, lipid compressibility with pressure is also greater than sea water (Yayanos et al., 1978). Based on the buoyancy properties of wax ester alone, late-stage copepods are generally positively buoyant at the surface (copepod density = 9.1×10^2 to 9.15×10^2 kg m⁻³), and as they move downward to colder, higher pressure water, they become negatively buoyant (Visser and Jonasdottir, 1999). This means they cannot use lipids to help them sink when they enter diapause, however lipids will help them stay deep once they are resting. Copepod buoyancy models have been developed for C. finmarchicus populations that overwinter in the deep ocean waters (500 to1000 m depth) with a density between 31.3 and 32.8 σ_t (Campbell, 2008; Pond and Tarling, 2011; Visser and Jonasdottir, 1999). Based primarily on lipid dynamics, these models assume that positively buoyant animals swim downward to depths exceeding 500 m, where the animals can physiologically achieve neutrally buoyancy using their internal lipid supply. A mechanism has been proposed by which neutral buoyancy is achieved; namely at depths > 500 m, hydrostatic pressure and 50% unsaturation of lipid induces liquid-solid phase changes of wax ester, and these phase changes are accompanied by an increase in density of the lipid that reduces hydrostatic lift (Pond and Tarling, 2011). At the relatively higher temperature and lower pressure range experienced by the animals at the relatively shallow Scotian Shelf basin depths, these models predict that *C. finmarchicus* lipids will be positively buoyant and the animals will float toward the surface at ascent rates of ~100 m day⁻¹ (Visser and Jonasdottir, 1999). Thus, the results of such diagnostic models clearly do not extend to Shelf basin populations that overwinter at 100 to 200 m depths, and there is plasticity to their buoyancy regulation that has yet to be explored. Active buoyancy regulation using ion regulation may aid in achieving preferred density-depths, and maintaining those depths over the winter in the face of space and time variation in their local environment density and decreasing internal lipid content. A recent study shows that the diapausing copepod Calanoides acutus, an Antarctic relative of C. finmarchicus, can accumulate ammonium in exchange for the heavier sodium ion (Sartoris et al., 2010), which is a relevant finding because buoyancy properties appear to be extremely sensitive to biochemical composition (Campbell and Dower, 2003).

In our study, a correlation was found between diapausing copepods and the depth of the 26 σ_t isopycnal across space and time in Roseway Basin. Notably, diapausing C. finmarchicus also aggregate below the 1026 isopycnal in the Grand Manan Basin, another nearby right whale habitat (Michaud and Taggart, 2011). One explanation for this correlation is that diapausing copepods are negatively buoyant and sink when in water shallower than the 26 σ_t isopycnal, while they can achieve neutral buoyancy in water with density exceeding the 26 σ_{t} isopycnal. The most compelling data that show the 26 σ_t isopycnal has biological relevance come from two experiments on C. finmarchicus and C. hyperboreus in settling columns designed to measure their internal density in relation to the seawater (e.g., Kogeler et al., 1987; Visser and Jonasdottir, 1999). In the first experiment, live specimens of both species were caught every month for a year in the Fram Strait using a mid-water trawl, then placed immediately into a density column filled with seawater having an undisclosed temperature and a linear salinity gradient maintained using NaCl (Kogeler et al., 1987). The internal density of each animal was determined by the water density at which the animals stopped vertically moving (i.e., reached neutral buoyancy). The results showed that in September, during the time when the animals are entering diapause, their average internal density was not different from 26 $\sigma_{\rm t}$. The animals increased in density in February as their lipids depleted during reproduction. In the second experiment, C. finmarchicus were frozen upon capture from the Faroe-Shetland Channel and later thawed before being placed immediately into a settling column with a density gradient established using seawater diluted with sugar (Visser and Jonasdottir, 1999). The density of the animals was determined in the same manner as Kogeler et al. (1987). Afterward, the lipid and dry weight of each animal were measured, and the ratio of these two numbers was compared to the density of the animal. As expected, the density of the animals decreased as the lipid/dry weight ratio in the animal increased. At the maximum lipid/dry weight ratio measured ($\gamma = 0.30$), which is most comparable to the lipid content in the animals at time they enter diapause, the density of the animals was very close to 26 σ_{t} . What these experiments show is that, as a first approximation, the 26 σ_t isopycnal is near the density at which these animals reach neutral buoyancy near the surface (i.e. where the effect of pressure on lipids is negligible). It also predicts that below this isopycnal the animals will be positively buoyant, which is consistent with the predictions of modeling studies. However, these studies answer part of the question, because our observations in Roseway Basin show that the animals are aggregated below the 26 σ_t isopycnal (26 to 26.2), and not necessarily at it. However, they provide a reasonable starting point for developing buoyancy models that are valid for copepods diapausing on the continental shelf as well as over the continental slope.

5. Conclusions

We sought to address three objectives in this study. First, in quantifying the magnitude of interannual variation in *Calanus* energy density from year to year, we discovered that depth-integrated energy density in the deep diapausing copepod layer can vary by an order of magnitude among years. All other metrics defining the copepod layer (average energy, thickness, maximum energy) were statistically lower in 2008 than in either 2007 or 2009. Second, we explored whether there were general physical-biological oceanographic mechanisms operating among years, and discovered that both the magnitude of Calanus energy density and vertical thickness of the deep copepod layer varied positively with water mass density among years. Third, we sought to determine whether there are years when the west to east southern margin of Roseway Basin is a measurably richer or poorer copepod habitat, and we found that the margin was a richer, higher density habitat during 2007 and 2009 compared to 2008. We thus conclude that there is measurable interannual variation in the deep copepod layer among years in Roseway Basin, and we have provided some new insights into the physical drivers that explain the variation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.jmarsys.2015.06.001.

References

- AZMP (Atlantic Zone Monitoring Program) Monitoring Group, 2008. Physical, chemical and biological status of the environment. Atlantic Zone Monitoring Program Annual Bulletin. Fisheries and Oceans Canada. 1916-6362 (Available online at: http://www. meds-sdmm.dfo-mpo.gc.ca/zmp/main_zmp_e.html).
- Baumgartner, M.F., Cole, T.V.N., Clapham, P.J., Mate, B.R., 2003. North Atlantic right whale habitat in the lower Bay of Fundy and on the southwest Scotian Shelf during 1999– 2001. Mar. Ecol. Prog. Ser. 264, 137–154.
- Baumgartner, M.F., Mayo, C.A., Kenney, R.D., 2007. Enormous carnivores, microscopic food and a restaurant that's hard to find. In: Krauss, S.D., Rolland, R. (Eds.), The urban whale: North Atlantic right whales at a crossroads. Harvard University Press (543 pp.).
- Brown, M.W., Brault, S., Hamilton, P.K., Kenney, R.D., Knowlton, A.R., Marx, M.K., Mayo, C.A., Slay, C.K., Kraus, S.D., 2001. Sighting heterogeneity of right whales in the western North Atlantic 1980–1992. J. Cetacean Res. Manag. Spec. Issue 2, 245–250.
- Campbell, R.W., 2008. Overwintering habitat of *Calanus finmarchicus* in the North Atlantic inferred from autonomous profiling floats. Deep-Sea Res. I 55, 630–645.
- Campbell, R.W., Dower, J.F., 2003. Role of lipids in the maintenance of neutral buoyancy by zooplankton. Mar. Ecol. Prog. Ser. 263, 93–99.
- Davies, K.T.A., Ryan, A., Taggart, C.T., 2012. Measured and inferred gross energy content in diapausing *Calanus* spp. in a Scotian Shelf basin. J. Plankton Res. 34, 614–625.
- Davies, K.T.A., Ross, T., Taggart, C.T., 2013. Tidal and subtidal currents affect deep aggregations of right whale prey, *Calanus* spp., along a shelf-basin margin. Mar. Ecol. Prog. Ser. 479, 263–282.
- Davies, K.T.A., Taggart, C.T., Smedbol, R.K., 2014. Water mass structure defines the diapausing copepod distribution in a right whale habitat on the Scotian Shelf. Mar. Ecol. Prog. Ser. 497, 69–85.
- Galbraith, P.S., Pettipas, R.G., Chassé, J., Gilbert, D., Larouche, P., Pettigrew, B., Gosselin, A., Devine, L., Lafleur, C., 2010. Physical oceanographic conditions in the Gulf of St. Lawrence in 2009. Fisheries and Oceans Canada CSAS Res. Doc. 2009/014 (73 pp.).
- Greene, C.H., Pershing, A.J., 2004. Climate and the conservation biology of North Atlantic right whales: the right whale at the wrong time? Front. Ecol. Environ. 2, 29–34.
- Greene, C.H., Meyer-Gutbrod, E., Monger, B.C., McGarry, L.P., Pershing, A.J., Belkin, I.M., Fratantoni, P.S., Mountain, D.G., Pickart, R.S., Proshutinsky, A., Ji, R., Bisagni, J.J., Hakkinen, S.M.A., Haidvogel, D.B., Wang, J., Head, E., Smith, P., Conversi, A., 2013. Remote climate forcing of decadal-scale regime shifts in Northwest Atlantic shelf ecosystems. Limnol. Oceanogr. 58, 803–816.
- Hannah, C.G., Shore, J.A., Loder, J.W., Naimie, C.E., 2001. Seasonal circulation on the western and central Scotian Shelf, J. Phys. Oceanogr. 31, 591–615.
- Harrison, G., Johnson, C., Head, E., Pauley, K., Maass, H., Kennedy, M., Porter, C., Soukhovtsev, V., 2008. Optical, chemical and biological oceanographic conditions in the Maritimes region in 2007. Fisheries and Oceans Canada Can. Sci. Adv. Sec. Res. Doc. 2008/044 (66 pp.).
- Harrison, G., Johnson, C., Head, E., Spry, J., Pauley, K., Maass, H., Kennedy, M., Porter, C., Soukhovtsev, V., 2009. Optical, chemical, and biological oceanographic conditions in the Maritimes Region in 2008. Fisheries and Oceans Canada CSAS Res. Doc. 2009/ 054 (61 pp.).

- Head, E.J.H., Harris, L.R., Petrie, B., 1999. Distribution of *Calanus* spp. on and around the Nova Scotia shelf in April: evidence for an offshore source of *Calanus finmarchicus* to the central and western regions. Can. J. Fish. Aquat. Sci. 56, 2463–2476.
- Herman, A.W., 1988. Simultaneous measurement of zooplankton and light attenuance with a new optical plankton counter. Cont. Shelf Res. 8, 205–221.
- Herman, A.W., 1992. Design and calibration of a new optical plankton counter capable of sizing small zooplankton. Deep-Sea Res. 39, 395–415.
- Herman, A.W., Sameoto, D.D., Shunian, C., Mitchell, M.R., Petrie, B., Cochrane, N., 1991. Sources of zooplankton on the Nova Scotia shelf and their aggregation within deep basins. Cont. Shelf Res. 11, 211–238.
- Hirche, H.J., 1996. Diapause in the marine copepod *Calanus finmarchicus* a review. Ophelia 44, 129–143.
- Hirche, H.J., 1983. Overwintering of Calanus finmarchicus and Calanus helgolandicus. Mar. Ecol. Prog. Ser. 11, 281–290.
- Johnson, C., Harrison, G., Head, E., Spry, J., Pauley, K., Maass, H., Kennedy, M., Porter, C., Yashayaeva, I., Casault, B., 2012. Optical, chemical and biological oceanographic conditions in the maritimes in 2009 and 2010. Can. Sci. Advis. Secret. 2012/012.
- Kenney, R.D., Hyman, M.A.M., Owen, R.E., Scott, G.P., Winn, H.E., 1986. Estimation of prey densities required by North Atlantic right whales. Mar. Mamm. Sci. 2, 1–13.
- Kogeler, J.W., Falk-Petersen, S., Kristensen, A., Petterson, F., Dalen, J., 1987. Density and sound speed contrasts in sub-Arctic zooplankton. Polar Biol. 7, 231–235.
- Kraus, S.D., Rolland, R.M., 2007. Right whales in the urban ocean. In: Kraus, S.D., Rolland, R. (Eds.), The urban whale: North Atlantic right whales at the crossroads. Harvard University Press, pp. 1–38 (543 pp.).
- Legendre, P., Borcard, D., 2008. Statistical comparison of univariate tests of homogeneity of variances. J. Stat. Comput. Simul. 514, 1–22.
- Legendre, P., Legendre, L., 2012. Numerical Ecology. 3rd ed. Elsevier Science BV, Amsterdam (998 pp.).
- McLaren, I.A., Head, E., Sameoto, D.D., 2011. Life cycles and seasonal distributions of Calanus finmarchicus on the central Scotian Shelf. Can. J. Fish. Aquat. Sci. 58, 659–670.
- Michaud, J., Taggart, C.T., 2007. Lipid and gross energy content of North Atlantic right whale food, *Calanus finmarchicus*, in the Bay of Fundy. Endanger. Species Res. 3, 77–94. Michaud, J., Taggart, C.T., 2011. Spatial variation in right whale food, *Calanus finmarchicus*,
- in the Bay of Fundy. Endanger. Species Res. 15, 179–194. Murison, L.D., Gaskin, D.E., 1989. The distribution of right whales and zooplankton in the
- Bay of Fundy, Canada. Can. J. Zool. 67, 1411–1420.
- Patrician, M.R., Kenney, R.D., 2010. Using the continuous plankton recorder to investigate the absence of North Atlantic right whales (*Eubalaena glacialis*) from the Roseway Basin. J. Plankton Res. 32, 1685–1695.

- Petrie, B., Pettipas, R.G., Petrie, W.M., Soukhovtsev, V., 2008. Physical oceanographic conditions on the Scotian Shelf and in the Gulf of Maine during 2007. Fisheries and Oceans Canada Can. Sci. Adv. Sec. Res. Doc. 2008/017 (47 pp.).
- Pond, D.W., Tarling, G.A., 2011. Phase transitions of wax esters adjust buoyancy in diapausing Calanoides acutus. Limnol. Oceanogr. 56, 1310–1318.
- Sameoto, D.D., Herman, A.W., 1990. Life cycle and distribution of *Calanus finmarchicus* in deep basins on the Nova Scotia shelf and seasonal changes in *Calanus* spp. Mar. Ecol. Prog. Ser. 66, 225–237.
- Sameoto, D.D., Jaroszynski, L.O., Fraser, W.B., 1980. BIONESS, a new design in multiple net zooplankton samplers. Can. J. Fish. Aquat. Sci. 37, 722–724.
- Sartoris, F.J., Thomas, D.N., Cornils, A., Schnack-Schiel, S.B., 2010. Buoyancy and diapause in Antarctic copepods: The role of ammonium accumulation. Limnol. Oceanogr. 55, 1860–1864.
- Sprules, W.G., Jin, E.H., Herman, A.W., Stockwell, J.D., 1998. Calibration of an optical plankton counter for use in fresh water. Limnol. Oceanogr. 43, 726–733.
- Taggart, C.T., Thompson, K., Maillet, G., Lochmann, S., Griffin, D., 1996. Abundance distribution of larval cod (*Cadus morhua*) and zooplankton in a gyre-like water mass on the Scotian Shelf. In: Watanabe, Yoshiro, Yamashita, Yoh, Oozeki, Yoshioki (Eds.), Proceedings of international workshop: Survival strategies in early life stages of marine resources. Yokohama, Japan. A.A. Balkema Publishers, Brookfield, VT (USA), pp. 155–173.
- Tremblay, M.J., Roff, J.C., 1983. Community gradients in the Scotian Shelf zooplankton. Can. J. Fish. Aquat. Sci. 40, 598–611.
- Vanderlaan, A.S.M., Taggart, C.T., Serdynska, A.R., Kenney, R.D., Brown, M.W., 2008. Reducing the risk of lethal encounters: vessels and right whales in the Bay of Fundy and on the Scotian Shelf. Endanger. Species Res. 4, 283–297.
- Visser, A.W., Jonasdottir, S.H., 1999. Lipids, buoyancy and the seasonal vertical migration of *Calanus finmarchicus*. Fish. Oceanogr. 8, 100–106.
- Woodley, T.H., Gaskin, D.E., 1996. Environmental characteristics of North Atlantic right and fin whale habitat in the lower Bay of Fundy, Canada. Can. J. Zool. 74, 75–84.
- Yayanos, A.A., Benson, A.A., Nevenzel, J.C., 1978. The pressure-volume-temperature (PVT) properties of a lipid mixture from a marine copepod, *Calanus plumchrus*: implications for buoyancy and sound scattering. Deep-Sea Res. I 25, 257–268.
- Zakardjian, B.A., Sheng, J., Runge, J.A., McLaren, I.A., Plourde, S., Thompson, K.R., Gratton, Y., 2003, Effects of temperature and circulation on the population dynamics of *Calanus finmarchicus* in the Gulf of St. Lawrence and Scotian Shelf: Study with a coupled three-dimensional hydrodynamic, stage-based life history model. J. Geophys. Res. 108 (C11), 8016.