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ORIGINAL ARTICLE

North Atlantic right whale (*Eubalaena glacialis*) and its food: (II) interannual variations in biomass of *Calanus* spp. on western North Atlantic shelves

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The North Atlantic right whale (NARW), *Eubalaena glacialis*, feeds on zooplankton, particularly copepods of the genus *Calanus*. We quantified interannual variation in anomalies of abundance and biomass of *Calanus* spp. and near-surface and near-bottom ocean temperature and salinity from 19 subregions spanning the Gulf of Maine–Georges Bank (GoM–GBK), Scotian Shelf (SS), Gulf of St. Lawrence (GSL) and Newfoundland and Labrador Shelves. We analyzed time series from 1977 to 2016 in GoM–GBK, 1982 to 2016 in southwest GSL and 1999 to 2016 in remaining areas. *Calanus finmarchicus* dominated abundance and biomass, except in the GSL where *Calanus hyperboreus* was abundant. The biomass of *Calanus* spp. declined in many subregions over years 1999–2016 and was negatively correlated with sea surface temperature in GoM–GBK and on the SS. We detected “regime shifts” to lower biomass of *Calanus* spp. in the GoM–GBK in 2010 and on the SS in 2011. In the GoM–GBK, shifts to lower biomass of *C. finmarchicus* coincided with shifts to warmer ocean temperature and with published reports of changes in spatial distribution and reduced

calving rate of NARW. We hypothesize that warming has negatively impacted population levels of *Calanus* spp. near their southern range limit, reducing the availability of prey to NARW.

KEYWORDS: *Calanus*; North Atlantic right whale; zooplankton; foraging habitat; interannual variability

INTRODUCTION

The North Atlantic right whale (NARW), *Eubalaena glacialis*, is an endangered species that resides off the east coast of North America, from Florida to Newfoundland (Winn et al., 1986; Kraus and Rolland, 2007). Calving occurs off the coast of Florida and Georgia in winter, and feeding occurs in summer and autumn in regions that include the Gulf of Maine (GoM), lower Bay of Fundy and Scotian Shelf (SS) (Baumgartner et al., 2007; Kraus and Rolland, 2007). Evidence from zooplankton community composition near feeding whales indicates dominance of late-copepodite or adult stages of the copepod, *Calanus finmarchicus*, in the diet of NARW (Kann and Wishner, 1995; Woodley and Gaskin, 1996; Baumgartner and Mate, 2003). The presence of *C. finmarchicus* in the diet has been confirmed by the analysis of feces of NARW from the SS (Stone et al., 1988).

Calanus finmarchicus is a highly abundant subarctic species with a wide geographical range in the North Atlantic (Planque et al., 1997). In the western North Atlantic, the range of *C. finmarchicus* extends from the Irminger and Labrador seas off the coast of Greenland to the northern edge of the Mid-Atlantic Bight off the coast of the USA (Conover, 1988). Two arctic species of *Calanus*, *C. hyperboreus* and *C. glacialis*, are also potential prey for NARW, but their relative importance as prey is currently unknown. The current southern range limit of *C. hyperboreus* and *C. glacialis* extends to the SS (Head and Pepin, 2010), but has extended further south to the GoM (Conover, 1988) and south of Cape Cod during cold periods in the late 1910s (Bigelow, 1926) and late 1950s/early 1960s (Mullin, 1963; Conover, 1965). *Calanus* spp. are the predominant source of biomass in the mesozooplankton community in the western North Atlantic (Sameoto and Herman, 1992; Runge et al., 1999; Head et al., 2003), and *C. finmarchicus* is among the most abundant copepod taxa on the northeast continental shelf of the USA (Kane, 2007; Friedland et al., 2013). *Calanus* spp. therefore represent a substantial source of prey in the western North Atlantic for carnivorous planktivores including NARW.

Calanus finmarchicus, *C. hyperboreus* and *C. glacialis* have different life history strategies that are strongly associated with seasonal variations in timing and duration of food (phytoplankton) availability (Falk-Peterson et al., 2009; Maps et al., 2014). A common characteristic among

these species is rapid accumulation of high-energy lipid acquired from phytoplankton in the upper water column followed by diapause for several months in deeper water. Alternation between active development and diapause in the lifecycle of *Calanus* spp. has important implications for their vertical distribution and population dynamics (Plourde et al., 2001; Plourde et al., 2003; Johnson et al., 2006; Head and Pepin, 2008) and their availability to NARW (Baumgartner and Mate, 2003; Plourde et al., n.d.).

NARW must locate and feed on dense aggregations of zooplankton to meet energy demands (Kenney et al., 1986; Baumgartner et al., 2007; Michaud and Taggart, 2007). Localized high concentrations of NARW prey are formed as a result of interactions between physical forcing and swimming, sinking or floating of prey (Epstein and Beardsley, 2001; Davies et al., 2014). NARW have been observed feeding on patches of *Calanus* spp. near the surface (Beardsley et al., 1996) or at depths between 80 and 175 m (Baumgartner and Mate, 2003). A necessary precondition to development of prey aggregations is a sufficient regional population level of prey. The number of NARW observed in foraging areas has been correlated to regional indices of abundance of *C. finmarchicus* (Pendleton et al., 2009; Pershing et al., 2009; Record et al., 2019), which suggests that population levels of prey have a positive relationship with the number and intensity of prey aggregations. Therefore, population levels of *Calanus* spp. are considered an important factor affecting suitability of foraging areas for NARW. Since direct observations of prey aggregations at the local scale are rare, the population level of prey is an important proxy for foraging conditions for NARW.

Previous studies have associated variation in abundance of *Calanus* spp. in the GoM or on the SS with that of NARW distribution (Pendleton et al., 2009; Davies et al., 2015a; Record et al., 2019) or calving rate (Greene and Pershing, 2004; Meyer-Gutbrod et al., 2015). In the 1990s, NARW abandoned Roseway Basin on the western SS when abundance of *Calanus* spp. was low, while sightings in the Grand Manan critical habitat in the Bay of Fundy increased (Patrician and Kenney, 2010; Davies et al., 2015a). During the same period, declines in population level indices of *C. finmarchicus* in the GoM (Pershing et al., 2005) and calving rate of

NARW (Meyer-Gutbrod et al., 2015) were observed. These observations suggest that in years associated with reduced food availability, alternative suitable foraging areas for NARW may have been inadequate to prevent declines in health and reproduction of NARW.

The following lines of evidence indicate that substantial changes in NARW distribution and population dynamics have been occurring since the early 2010s: (i) passive acoustic detections of NARW in the GoM and on the SS in summer–autumn declined relative to the 2000s (Davis et al., 2017); (ii) aerial and vessel-based surveys have shown dramatic declines in sightings of NARW per unit effort in the eastern GoM (Record et al., 2019); (iii) calving rate of NARW decreased (Kraus et al., 2016; Pace et al., 2017; Pettis et al., 2018); (iv) the number of opportunistic sightings of NARW in the GSL was relatively high since at least 2015 (Daoust et al., 2018); and (v) changes in the zooplankton community have been detected in the GoM (Perretti et al., 2017; Record et al., 2019), on the SS (Johnson et al., 2017; Reed et al., 2018) and in the GSL (Brosset et al., 2018). These observations suggest that NARW distribution and calving rate might have responded to changes in prey availability over a much larger spatial scale than described in previous studies focused in the GoM and on the SS (e.g. Hare and Kane, 2012; Davies et al., 2015a; Meyer-Gutbrod et al., 2015; Record et al., 2019). There is, therefore, a need to characterize variations in population levels of *Calanus* spp. across the distribution range of the NARW and investigate linkages between changes in environment and population levels of NARW prey.

In this study, we describe interannual variations *Calanus* spp. using data from sustained monitoring programs across the western North Atlantic, from the GoM to the Newfoundland and Labrador Shelves (NLS). We test the hypothesis that there has been a change in annual average abundance and biomass of late stage of *Calanus* spp. with an emphasis on comparing pre- and post-2010 periods (i.e. before and after changes in the distribution and calving rate of NARW). Quantifying the potential effects of environmental variation on population levels of *Calanus* spp. is critically important to the development of a mechanistic approach to the prediction of prey availability to higher trophic levels (Greene et al., 2013; Maps et al., 2014; Sinclair et al., 2015), including NARW. We investigate potential effects of temperature and transport by quantifying interannual variations in surface and bottom temperature and salinity and their relationship with population levels of *Calanus* spp.

METHOD

Sample collection and processing

We utilized time series of abundance (ind m^{-2}) and biomass (mg m^{-2}) of *Calanus* spp. from four ocean observing programs (Fig. 1; Table I): (i) the Fisheries and Oceans Canada (DFO) Atlantic Zone Monitoring Program (AZMP) (Therriault et al., 1998); (ii) the DFO mackerel egg production survey (“Mackerel Survey”) in the southwest GSL (swGSL) (Castonguay et al., 1998); (iii) the USA National Oceanic and Atmospheric Administration (NOAA) Marine Resources Monitoring, Assessment and Prediction and Ecosystem Monitoring surveys (data from both surveys termed “EcoMon”) in the GoM and on Georges Bank (GoM–GBK) (Richardson et al., 2010); and (iv) zooplankton monitoring in the western GoM (wGoM) (Runge et al., 2015). The AZMP survey design is comprised of stations along cross-shelf sections sampled two to three times annually and stations sampled weekly to monthly (termed “time series stations”) since 1999. Observations from AZMP were obtained from Labrador, Newfoundland and SS and slope waters and in the GSL and eastern GoM. The Mackerel Survey was sampled on a regular grid since 1982. EcoMon surveys have sampled zooplankton using a stratified random design since 1977. The strata were initially designed for groundfish surveys on the northeast continental shelf of the USA, and their boundaries were defined based on variations in bathymetry and hydrography (Grosslein, 1969). The analysis presented here only considered EcoMon data from strata in the GoM–GBK that host designated NARW habitats including Cape Cod Bay, Great South Channel and Bay of Fundy (i.e. Grand Manan basin) (Kraus and Rolland, 2007). The wGoM zooplankton collections were made at a time series station in Wilkinson Basin as well as along transects and at opportunistic stations in the coastal and Wilkinson Basin areas (Runge et al., 2015).

We analyzed time series from 19 subregions (Fig. 1) that spanned the following regions: GoM–GBK (Prince 5, east GoM, west GoM and Georges Bank), SS (Louisbourg, Halifax Line, Halifax 2 and Browns Bank), southern GSL (Shediac Valley, south GSL and swGSL), west–east GSL (Rimouski, west GSL and east GSL) and NLS (Seal Island, Bonavista, Station 27, Flemish Cap and Southeast Grand Banks). Abundance and biomass of *Calanus* spp. were analyzed from all subregions, except the swGSL (Mackerel Survey), in which only biomass was analyzed. We separated the GSL into southern and west–east regions because of substantial differences in bottom depth and environmental characteristics among regions. Each AZMP section and time series station

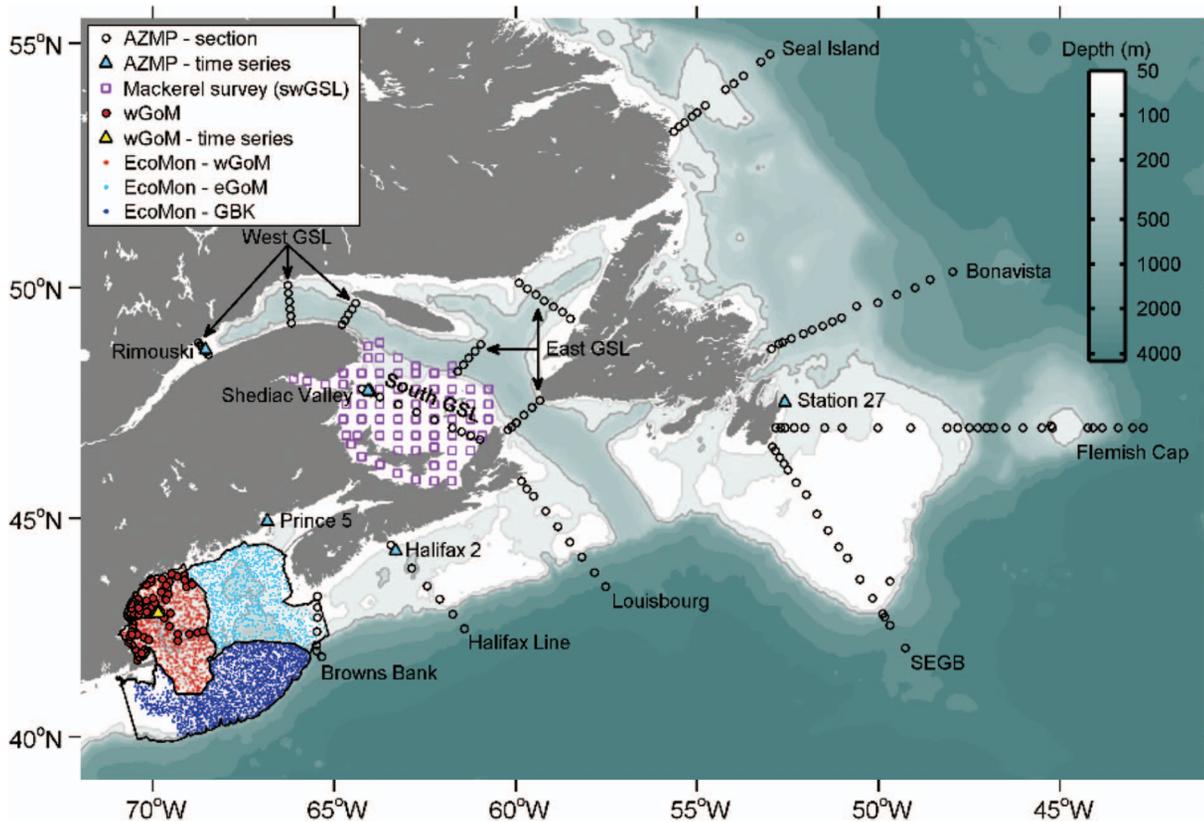


Fig. 1. Sampling locations from four ocean observing programs: Atlantic Zone Monitoring Program (AZMP), Mackerel Survey, Marine Resource Monitoring, Assessment and Prediction, and Ecosystem Monitoring (EcoMon) and western Gulf of Maine (wGoM). The scatter of EcoMon sampling sites is due to a stratified random sampling design. This map was created using the package “M_Map” v 1.4h (<https://www.eoas.ubc.ca/~rich/map.html>) in MATLAB R2013a.

Table I: Sampling methodology and analysis methods used in the Atlantic Zone Monitoring Program (AZMP), western Gulf of Maine (wGoM), Marine Resources Monitoring, Assessment and Prediction and Ecosystem Monitoring (EcoMon) and Mackerel Survey

Sample program	Region	Gear	Sample analysis	Years
AZMP	NLS, GSL, SS	Ring; 202 μ m	Taxonomy	1999–2016
wGoM	GoM–GBK	Ring; 202 μ m	Taxonomy	2002–2016
EcoMon	GoM–GBK	Bongo; 333 μ m	Taxonomy	1977–2016
Mackerel Survey	Southern GSL	Bongo; 333 μ m	Taxonomy	1982, 1985, 1987, 1990, 1993, 1996, 1999, 2003
			Dry weight	1983, 1984, 1986, 1988, 1989, 1991, 1992, 1994, 1998, 2000, 2001, 2002, 2004, 2005
			ZooImage	2006–2016

Sampling covered the Labrador and Newfoundland shelves (NLS), Gulf of Saint Lawrence (GSL), Scotian Shelf (SS) and Gulf of Maine-Georges Bank (GoM–GBK) regions (Fig. 1). In all sampling programs, taxa were identified and enumerated manually (Taxonomy). In the Mackerel Survey, biomass estimates were also derived from direct measurements of zooplankton dry weight (dry weight) image classification (ZooImage; Grosjean and Denis, 2012).

were defined as a subregion, except the west GSL and east GSL subregions, each of which consisted of three small sections (Fig. 1). Within the GoM–GBK, the west GoM, east GoM and Georges Bank subregions were defined by union of EcoMon strata (Grosslein,

1969), with one central GoM stratum split between the west and east GoM subregions. Data from the wGoM observing program were used to supplement coverage from EcoMon in the west GoM subregion (Fig. 1).

In each observing program, we obtained data from the initial year of sampling to 2016 (Table I). Within each year, the timing of sample collection varied among subregions and among years within each subregion (Fig. S1). Samples were almost always collected in at least two seasons within each year, except in the swGSL subregion (Mackerel Survey). In the swGSL, sampling was conducted in June–early July during the seasonal peak in biomass of *Calanus* spp. in the southern GSL, as demonstrated by the seasonal climatology in the Shediac Valley subregion (Devine et al., 2017). We define “seasons” as winter (December through February), spring (March through May), summer (June through August) and autumn (September through November).

In AZMP and wGoM sampling programs, zooplankton were collected with a 0.75-m diameter ring net (202- μ m mesh) towed vertically from a depth of \sim 5 m above bottom or maximum depth of 1000 m to the surface (Mitchell et al., 2002). In the EcoMon survey, a 0.61-m bongo frame equipped with 333- μ m mesh nets and a flowmeter was towed obliquely from 5 m above bottom or a maximum depth of 200 m to the surface. In the Mackerel Survey, oblique plankton tows (with flowmeter) were conducted using the same methodology as EcoMon, except the maximum sampling depth was usually 50 m. However, at bottom depths $>$ 50 m, the maximum sampling depth in the Mackerel Survey ranged from 10–100 s of meters (Fig. S2). All samples were preserved in 4 or 5% formalin.

Samples collected in AZMP, EcoMon and wGoM programs were analyzed taxonomically with species- and stage-specific abundances of *Calanus* spp. estimated from counts of individuals in subsamples (Mitchell et al., 2002; Kane, 2007). In the Mackerel Survey, from 1982 to 2006, samples were sieved at different mesh sizes (333, 500, 710 and 1000 μ m) to obtain size fractions (e.g. Runge et al., 1999), and abundance of *Calanus* spp. or dry weight of zooplankton was quantified from the $>$ 1000 μ m size fraction. In eight of these years, species- and stage-specific abundances were estimated from counts. In remaining years (prior to 2006), we used zooplankton dry weight as an estimate of *Calanus* spp. biomass (Table I), which we justify below in the subsection “Derivation of biomass”. From 2006 to 2016, abundance of *C. finmarchicus*+*C. glacialis* and *C. hyperboreus* was quantified from scanned images of preserved subsamples using an image classification software, ZooImage (Grosjean and Denis, 2012).

At locations where the sample depth was substantially shallower than bottom depth (termed “partial-water-column samples”), the abundance or biomass measurements would be underestimated. Partial-water-column samples only occurred at stations over deep basins in

the EcoMon surveys but frequently occurred in the Mackerel Survey (Fig. S2). To correct for underestimation of biomass and abundance from partial-water-column samples, we constructed generalized additive models (GAMs) that predicted the proportion of total biomass or abundance (i.e. integrated from bottom to surface) actually sampled by the plankton net (Table S1; Fig. S3; Fig. S4). The GAMs were constructed using vertically stratified abundance data and accounted for variation in biomass due to region, taxa and the life cycle status of *Calanus* spp. (i.e. timing of diapause). An estimate of biomass or abundance present in the entire water column was then made by dividing the underestimated value by the GAM prediction. Thus, we obtained a correction factor from the GAMs that we used to adjust abundance and biomass from partial-water-column samples. A detailed description of the methods used for these adjustments is provided as supplementary materials.

Near-surface and near-bottom seawater temperature and salinity (SST, SSS, BT and BS, respectively) were obtained from conductivity, temperature, depth or expendable bathythermograph casts, which were usually paired with plankton sampling efforts. Near-surface temperature and salinity were derived by averaging values within the upper 5 m of the water column, whereas near-bottom metrics represent the value within \geq 90% of the bottom depth, with the exception of the swGSL (\geq 80% of bottom depth). In the southern GSL, the near-bottom temperature and salinity are typically representative of the cold intermediate layer.

We carried out data processing and analyses using R (R Core Team, 2019) unless specified otherwise.

Derivation of biomass

For each species of *Calanus*, we restricted our analysis to the combined abundance and biomass of the fourth and fifth copepodite and adult stages (CIV–CVI). We only considered these late stages for two reasons. First, the mesh size of the plankton net used in the Mackerel Survey and EcoMon (333 μ m) did not sample all earlier stages efficiently; therefore, considering only late stages provides better comparability between these observing programs and AZMP and wGoM. Second, only late stages of *Calanus* spp. are considered a primary source of food for NARW (Baumgartner and Mate, 2003; Michaud and Taggart, 2011; Davies et al., 2013), and these stages are probably retained on the baleen of NARW with high efficiency (Mayo et al., 2001).

In cases where abundance was measured, we derived biomass (mg m^{-2}) from stage-specific abundance (individuals m^{-2}) and estimates of individual dry weight

Table II: IDW ($\mu\text{g ind}^{-1}$) of stages CIV, CV and CVI, used for calculation of dry weight of *Calanus* spp. in the Gulf of Maine-Georges Bank (GoM-GBK), Scotian Shelf (SS) and Gulf of St. Lawrence (GSL)

Taxon	CIV	CV	CVI	CIV-CVI	Measured	Applied	Source
<i>C. finmarchicus</i>	69	195	261	–	SS	GoM-GBK, SS	HH2004
<i>C. hyperboreus</i>	304	1145	2761	–	SS	GoM-GBK, SS	HH2004
<i>C. glacialis</i>	227	514	637	–	SS	All regions	HH2004
<i>C. finmarchicus</i>	96	333	347	–	GSL	GSL,NLS	P2019
<i>C. hyperboreus</i>	421	1390	2450	–	GSL	GSL,NLS	P2019
<i>C. finmarchicus/C. glacialis</i>	–	–	–	297	GSL	southwest GSL	P2019
<i>C. hyperboreus</i>	–	–	–	1725	GSL	southwest GSL	P2019

The IDWs represent averages over autumn and spring seasons from Head and Harris (2004; HH2004; autumn, October; spring, April and May) and Plourde et al. (n.d.; P2019; autumn, September and November; spring, March and May). An IDW for combined stages CIV-CVI (Plourde et al., n.d.) was used for the swGSL in June.

(IDW; $\text{mg individual}^{-1}$). We could not resolve variability in IDW at the spatial and temporal scales of sampling because estimates from the western North Atlantic are sparsely distributed in space and time. We therefore used constant stage-specific estimates of IDW for each species of *Calanus*, which we calculated by averaging measurements by Head and Harris (2004) and Plourde et al. (n.d.) over spring and autumn seasons (Table II). This method was used in all subregions except swGSL, wherein an average IDW for stages CIV-CVI in June (Plourde et al., n.d.) was applied to the abundance data from the Mackerel Survey (Table II). We investigated the potential effect of variation in IDW on our results by examining (i) the natural range of seasonal and interannual variability in IDW of stage CV of *C. finmarchicus* from two sites in the GSL and (ii) the potential effect of temperature variability on biomass. This analysis is described further below in the section “Influence of variations in individual biomass of *C. finmarchicus*”.

Regarding the Mackerel Survey, a subset of samples from this sampling program was used to evaluate the relationship between estimates of biomass predicted by abundance and IDW of *Calanus* spp. and total zooplankton dry weight. A regression analysis indicated a near 1:1 relationship, reflecting the dominance of *Calanus* spp. in the $>1000 \mu\text{m}$ size fraction of the samples (Plourde, unpublished results). There is, therefore, strong justification for the use of zooplankton dry weight to estimate *Calanus* spp. biomass in selected years from the Mackerel Survey time series in the swGSL (Table I). Late stages of *Calanus* spp. were retained in the $>1000 \mu\text{m}$ size fraction, with the exception of stage CIV of *C. finmarchicus/glacialis*, which was retained at an efficiency $\sim 55\%$ (Plourde, unpublished results). This underrepresentation likely did not have a strong effect of biomass estimates, since the IDWs of stage CIV of *C. finmarchicus* and *C. glacialis* are less than half of that of stages CV or CVI (Table II), and stage CIV of *C. finmarchicus* is typically not abundant in June

when samples were obtained from the Mackerel Survey (Blais et al., 2018).

Climatological spatial pattern in abundance and biomass

We described the spatial pattern in abundance and biomass of *Calanus* spp. among subregions, using mean values over years 1999–2016. The mean was calculated hierarchically to reduce potential bias from unbalanced sampling design on $\log(x+1)$ transformed data. Within each year, averaging was first conducted on data by month for AZMP time series stations, by station for AZMP sections or by strata for wGoM and EcoMon sampling. The AZMP sections and wGoM and EcoMon data were subsequently averaged by season. Data from all sampling programs were then averaged by year to obtain an annual mean and averaged again over the years 1999–2016 to obtain an overall mean. In the swGSL subregion, abundance data of *C. finmarchicus* + *C. glacialis* and *C. hyperboreus* are only available for years 1999, 2003 and 2006–2016 (since 1999); therefore, estimates of taxon-specific mean abundance and biomass was based on only those years.

Interannual variations in abundance and biomass

Interannual variations in abundance and biomass of *Calanus* spp. and in hydrographic variables were characterized using normalized annual anomalies (i.e. Z -scores). We first obtained annual estimates of each variable by averaging predictions from general linear models (Table III) to obtain “least-squares means” (Searle et al., 1980) following Pepin et al. (2015). This procedure was implemented to reduce the influence of imbalances in sampling effort among years within month, season, station or stratum, due to missing data (Table III). *Calanus*

Table III: Linear models used for derivation of annual estimates of abundance and biomass of *Calanus* spp. (i.e. y) for each sample type

Sample type	Model
AZMP fixed stations	$\log(y + 1) = \alpha + \beta \text{Year} + \gamma \text{Month} + \varepsilon$
AZMP sections	$\log(y + 1) = \alpha + \beta \text{Year} + \gamma \text{Season} + \delta \text{Station} + \varepsilon$
Mackerel Survey	$\log(y + 1) = \alpha + \beta \text{Year} + \delta \text{Station} + \varepsilon$
EcoMon + wGoM	$\log(y + 1) = \alpha + \beta \text{Year} + \gamma \text{Season} + \delta \text{Strata} + \varepsilon$

spp. abundance and biomass values were $\log(x + 1)$ transformed prior to analysis to reduce skew in the distribution of observations, while untransformed values were used for the hydrographic variables. In the case of the GoM–GBK, where a stratified random sampling design was used, annual values of hydrographic variables were estimated as the mean of area-weighted averages obtained from the EcoMon surveys.

All annual anomalies were calculated with reference to the mean and standard deviation (SD) over years 1999 through 2010. Anomalies were calculated over years 1977–2016 for the EcoMon surveys, 1982–2016 for the Mackerel Survey and 1999–2016 for all data sources. Regarding the 1999–2016 period, we also obtained cumulative anomalies by summing anomalies across subregions in the following regions: GoM–GBK, SS, southern GSL, west–east GSL and NLS. Cumulative anomalies provide a simplified view of temporal variability at the regional scale.

We used sequential t -test analysis of regime shifts (STARS) to identify potential interannual “regimes” in annual anomalies (Rodionov, 2004). This analysis was implemented using an add-in for Microsoft Excel (National Oceanic and Atmospheric Administration, 2006). Use of this method requires specification of the minimum regime length, l . Regime lengths $< l$ can be detected but require a greater magnitude in shift in comparison to those $\geq l$ (Rodionov, 2004). The longest zooplankton time series in our data set is from the GoM–GBK, where shifts in the mesozooplankton community appear to occur on time scales of ~ 10 years since the late 1970s (Hare and Kane, 2012; Perretti et al., 2017). We therefore used $l = 7$, as this value was < 10 years and also large enough to facilitate detection of shifts within our time series. Outliers were weighted using a Huber’s weight parameter of 3 (National Oceanic and Atmospheric Administration, 2006), and red noise was filtered from the data using the “inverse proportionality with four corrections” (i.e. IP4) pre-whitening method prior to analysis (Rodionov, 2006). We conducted the

STARS analysis on annual anomalies for each subregion, as well as for cumulative anomalies summed over subregions within each region. We assessed the significance of regime shifts at $\alpha = 0.1$, which is consistent with our use of STARS as a quantitative tool to explore time variation in annual anomalies. Regime shifts detected near the end of the time series should be interpreted with caution if the number of years after the shift is $< l$ because these shifts are not fully substantiated by data at this time.

We examined relationships between anomalies of species-specific abundance or biomass of *Calanus* spp. and hydrographic variables using Pearson correlation coefficients. We analyzed correlations between cumulative and subregion-specific anomalies for the 1999–2016 and 1977–2016 periods, respectively. We evaluated statistical significance of the correlation coefficients after correcting for multiple comparisons using a false discovery rate of 0.1 (Benjamini and Hochberg, 1995). We did not correct P -values for autocorrelation, which was minimal in cumulative anomalies over years 1999–2016, with significant autocorrelation observed in only 24% of *Calanus* spp. and hydrographic time series. In years 1977–2016, significant autocorrelation was absent in all time series from the swGSL subregion, but was present in 73% of the time series in the GoM, including all time series from the west GoM subregion. Therefore, the statistical significance of correlations from GoM subregions in the 1977–2016 period should be interpreted with caution.

Influence of variations in individual biomass of *C. finmarchicus*

Temperature variation can affect the size of crustacean zooplankton due to a decoupling of rates of development and growth (Forster and Hirst, 2012). We carried out a sensitivity analysis to provide a simple quantitative demonstration of the relative impact of (i) observed declines in abundance of late stage *C. finmarchicus* and (ii) a hypothetical decrease in IDW due to warming. We used abundance data from the Rimouski, Shediac Valley and Halifax 2 subregions for this analysis because these stations were sampled at a relatively high temporal frequency and are locations where persistent declines in abundance have been observed in the 2010s. At each station, we calculated the change in biomass of late stage *C. finmarchicus* (after observed transitions to persistent negative anomalies) that corresponded with an increase in 0–50 m averaged ocean temperature by one SD relative to the climatological average. Both temperature and abundance data were restricted to months of the year in which *C. finmarchicus* is actively developing in the upper water column (i.e. not in diapause; Table IV).

Table IV: The potential effect of a hypothetical temperature (0–50 m depth average) increase of 1 SD, on stage-specific IDW of *C. finmarchicus* and total biomass of combined stages (bold) in years after an observed decline in abundance at Rimouski, Shediac Valley and Halifax 2 subregions (see Fig. 8)

Subregion	Averaging period	Temperature, mean ± SD (°C)	Stage	% Decrease in dry weight
Rimouski	April–July	2.54 ± 0.54	CIV	5.4
			CV	5.6
			CVI	2.0
			CIV–CVI	4.1
Shediac Valley	April–July	3.70 ± 1.64	CIV	16.4
			CV	16.9
			CVI	6.0
			CIV–CVI	13.2
Halifax 2	March–June	2.63 ± 0.96	CIV	13.3
			CV	16.8
			CVI	4.7
			CIV–CVI	14.2

For each of stages CIV, CV and CVI of *C. finmarchicus*, we calculated the temperature-driven reduction in the IDW, ΔIDW_T , using published stage-specific linear relationships between temperature and carbon weight individual⁻¹ (Campbell et al., 2001). We converted carbon weight individual⁻¹ to IDW using dry weight to carbon weight ratios of 1.8 (CV) or 2 (CIV and CVI; Plourde, unpublished results). Next, we subtracted ΔIDW_T from the initial IDW (Table II) to obtain a temperature-penalized IDW. We then used the penalized IDW to convert abundance to biomass and computed the average penalized biomass of late stage *C. finmarchicus* over years after the shift to low abundance identified following the procedure for AZMP time series stations outline in the above section: “Climatological spatial pattern in abundance and biomass”. The ratio of temperature-penalized biomass to observed biomass was then used as a coarse indicator of the potential effect of a shift in temperature on average biomass, compared to the effect of a shift in only abundance.

Seasonal and interannual variations in IDW of stage CV of *C. finmarchicus* were estimated from measurements of prosome length (PL) from the Rimouski subregion and southern GSL (swGSL and south GSL subregions, combined) during 1993–2016 (Plourde, unpublished results). We converted PL to IDW using the following relationship (Plourde, unpublished results), which was derived using a small subset ($n = 111$) of PL data in the west GSL subregion:

$$IDW = 0.0062e^{1.5342(PL)}, \quad (\text{Eq. 1})$$

where IDW is measured in mg and PL is measured in mm.

RESULTS

Spatial variation in abundance and biomass climatology (1999–2016)

The total abundance of late stage *Calanus* spp. was highest in subregions of the west–east GSL (east GSL, west GLS and Rimouski), northern NLS (Seal Island and Bonavista) and GoM (west and east GoM; Fig. 2). *Calanus finmarchicus* was generally abundant across all regions, *C. hyperboreus* was most abundant in the west–east GSL and on the northern NLS and was present at lower abundance on the SS (Louisbourg, Halifax Line and Halifax 2) and southern NLS (Station 27, Flemish Cap and SEGB). *Calanus glacialis* was the least abundant of the three species, with highest abundance on the northern NLS and west–east GSL and low abundance in the southern NLS, southern GSL (Shediac Valley and South GSL) and on the SS. In the GoM-GBK, observations of *C. hyperboreus* were very rare, and there were no confirmed records of *C. glacialis*. The biomass of *Calanus* spp. was highest in the west–east GSL, and *C. hyperboreus* was frequently a strong contributor to biomass throughout the GSL, especially in the west–east GSL (Fig. 2). Estimates of *Calanus* spp. biomass in the swGSL, following correction for partial-water-column sampling (Supplement), were strongly influenced by *C. hyperboreus* (Fig. 2). Outside of the GSL, *C. finmarchicus* was the dominant contributor to biomass, but the biomass contribution from *C. hyperboreus* in the northern NLS was substantial.

Interannual variability, 1999–2016

Abundance anomalies varied in sign and magnitude both spatially and interannually for the three species. In general, positive anomalies were more frequent in the 2000s, whereas negative anomalies were frequent in the 1999–2000 period, and were usually strong and persistent in

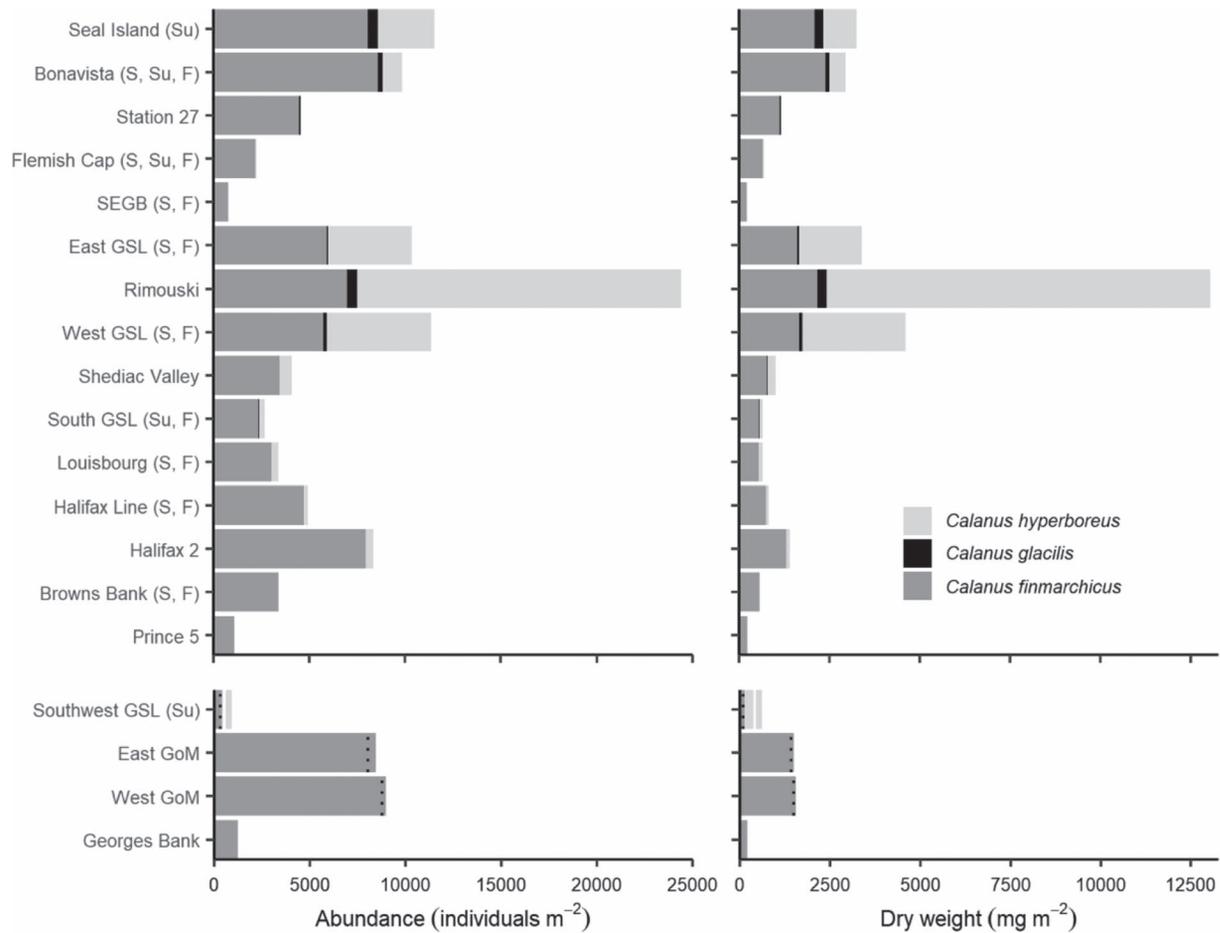


Fig. 2. The contribution of *C. finmarchicus*, *C. hyperboreus* and *C. glacialis* late-copepodite stages (CIV–CVI) to climatological estimates of abundance (individuals m⁻²; left panel) and biomass (mg m⁻²; right panel) of *Calanus* spp. in each subregion from 1999 to 2016. Season(s) targeted for sampling in each subregion is indicated in parentheses (S, spring; Su, summer; F, autumn), unless sampled throughout the year (AZMP time series stations; EcoMon + wGoM sampling). In the bottom panels, vertical lines indicate values of abundance and biomass of *C. finmarchicus* (broken black lines) and *C. hyperboreus* (solid white line) that have not been corrected for partial-water-column samples.

the GSL, on the SS and in the GoM–GBK, in the 2010s (Fig. 3). Notable exceptions to the pattern of strong negative anomalies in the 2010s were the persistence of positive or near-zero abundance anomalies of *C. finmarchicus* in the Halifax line and Prince 5 subregions, *C. glacialis* in the west GSL subregion and *C. hyperboreus* in the Rimouski and west GSL subregions in the 2010s (Fig. 3). The timing of transitions from sustained positive to negative anomalies varied among species and subregions and appeared to occur later in subregions to the northeast, with the exception of the GSL.

An analysis of cumulative anomalies indicated shifts to lower abundance of all species of *Calanus* in the late 2000s or early 2010s in many regions (Fig. 3). Shifts to lower abundance of *C. finmarchicus* occurred in GoM–GBK in 2010, on the SS in 2011 and in the west–east GSL and on the NLS in 2013. Shifts to lower abundance of *C. hyperboreus* occurred on the SS in 2012 and in the

southern GSL in 2015. Shifts to lower abundance of *C. glacialis* occurred on the SS and in the southern GSL in 2010 and in the west–east GSL in 2015. The only shift to higher abundance occurred for *C. hyperboreus* in the west–east GSL in 2012. In general, variations in biomass of *Calanus* spp. (Fig. 4) were similar to those of abundance of *C. finmarchicus* on the SS, in the GoM–GBK and in the southern GSL, while interannual variations in biomass in the west–east GSL and on the NLS did not closely resemble those of either of the two dominant *Calanus* species.

In the context of temperatures observed since the 1980s, 1999–2016 was a warm period (Hebert et al., 2018), but there was spatial and interannual variability in both surface and bottom temperatures within this period. The strongest and most persistent positive anomalies of near sea surface temperature (SST) occurred in the GoM–GBK and on the SS in the 2010s (Fig. 5). Widespread positive SST anomalies occurred in 2006,

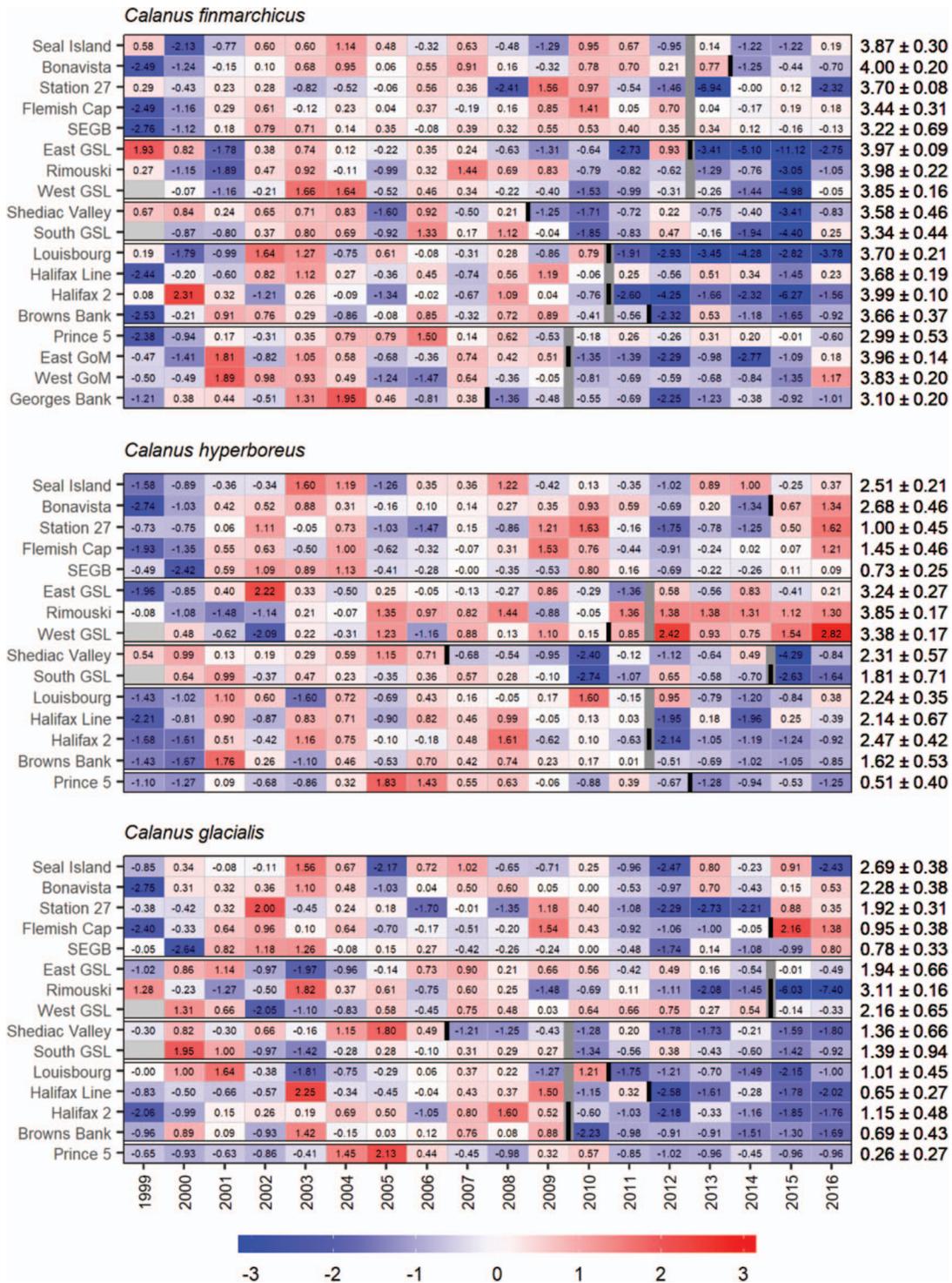


Fig. 3. Annual abundance anomaly scorecards for *C. finmarchicus*, *C. hyperboreus* and *C. glacialis*. For each species, subregions are grouped into Labrador and Newfoundland Shelves, west–east GSL, southern GSL, Scotian Shelf and Gulf of Maine–Georges Bank regions (top to bottom). Values in each cell are normalized anomalies from the climatological mean $\log(x + 1)$ abundance (individuals m^{-2}) averaged over years 1999–2010; climatological means and SDs are listed at the right of each panel. Red (blue) cells indicate higher (lower) than normal abundances. A blank cell indicates missing data. Vertical lines indicate the timing of shifts in anomalies identified from STARS. Black lines indicate subregion-specific shifts, and gray lines indicate shifts in cumulative anomalies within region.

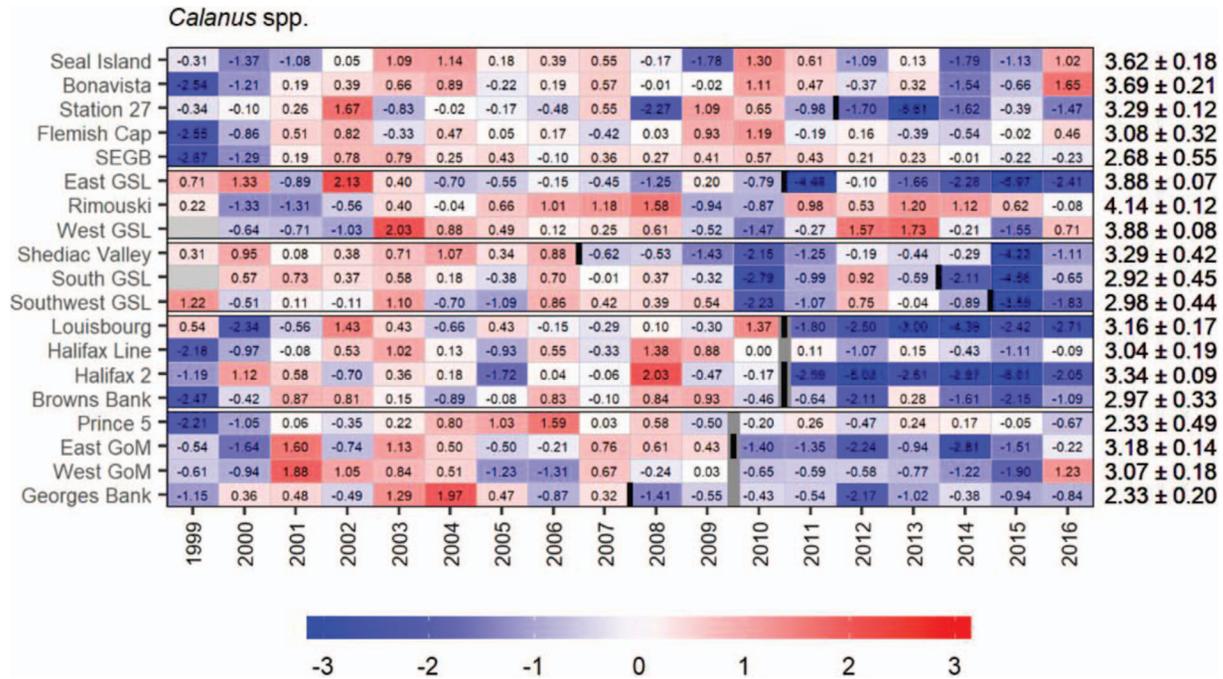


Fig. 4. Annual biomass anomaly scorecard for *Calanus* spp. (species combined). Subregions are grouped into Labrador and Newfoundland Shelves, west–east GSL, southern GSL, Scotian Shelf and Gulf of Maine–Georges Bank regions (top to bottom). Values in each cell are normalized anomalies from the mean $\log(x + 1)$ transformed biomass (mg m^{-2}) averaged over years 1999–2010; climatological means and SDs are listed at the right of each panel. Red (blue) cells indicate higher (lower) than normal biomass. A blank cell indicates missing data. Vertical lines indicate the timing of shifts in anomalies identified from STARS. Black lines indicate sub-region-specific shifts, and gray lines indicate shifts in cumulative anomalies within region.

and negative SST anomalies occurred in the early 2000s. Negative SST anomalies in the NLS and the west GSL subregion occurred in the 2010s. Patterns of anomalies of BT anomalies were generally consistent with those of SST but were more variable than those of SST among subregions on the SS and were primarily strong and positive in the deep subregions in the west–east GSL in the 2010s (Fig. 5). Shifts to higher SST and BT occurred in GoM–GBK in 2010 and on the SS in 2012. Shifts to higher BT occurred in the west–east GSL in 2015 (Fig. 5).

Positive anomalies of sea surface salinity (SSS) frequently occurred in the GoM–GBK in the late 1990s, early 2000s and 2010s (Fig. 5). Negative anomalies of SSS frequently occurred on the SS (except the Browns Bank subregion), in the west–east GSL and on the NLS in the 2010s. Positive anomalies of bottom salinity (BS) were strong and persistent in the GoM–GBK, on the SS and to a lesser extent in the west–east GSL in the 2010s. The east GSL, SEGB and Bonavista subregions exhibited a stable pattern of primarily weak positive anomalies throughout the 2000s and 2010s. In 2012, regime shifts to higher SSS and BS occurred in GoM–GBK and shifts to lower SSS occurred on the NLS. A shift to higher SSS occurred in SS in 2014 (Fig. 5).

With respect to cumulative anomalies of abundance of *Calanus* spp. and those of environmental variables, *C. finmarchicus* was significantly correlated (i) negatively with SST for the GoM–GBK and for the SS, and with BT for the GoM–GBK and west–east GSL; and (ii) positively with SSS for the NLS (Table V). Abundance of *C. hyperboreus* was significantly correlated positively with BT for the west–east GSL and SSS for the NLS (Table V). Abundance of *C. glacialis* was significantly correlated (i) negatively with SST for the SS and (ii) negatively with BT for the SS and west–east GSL and (iii) positively with SSS for the NLS (Table V). Correlations between cumulative biomass anomalies of *Calanus* spp. and hydrographic variables exhibited the same patterns as for *C. finmarchicus*, except that there was no significant correlation with BT for the west–east GSL (Table V).

Interannual variability, 1977–2016

In the 1977–2016 period, interannual variations in anomalies of biomass of *Calanus* spp. are presented along with a schematic timeline indicating alternating periods of high and low calving rate and presence of NARW in the GoM or on the SS (Fig 6A). In the swGSL subregion, *Calanus* spp. biomass anomalies were

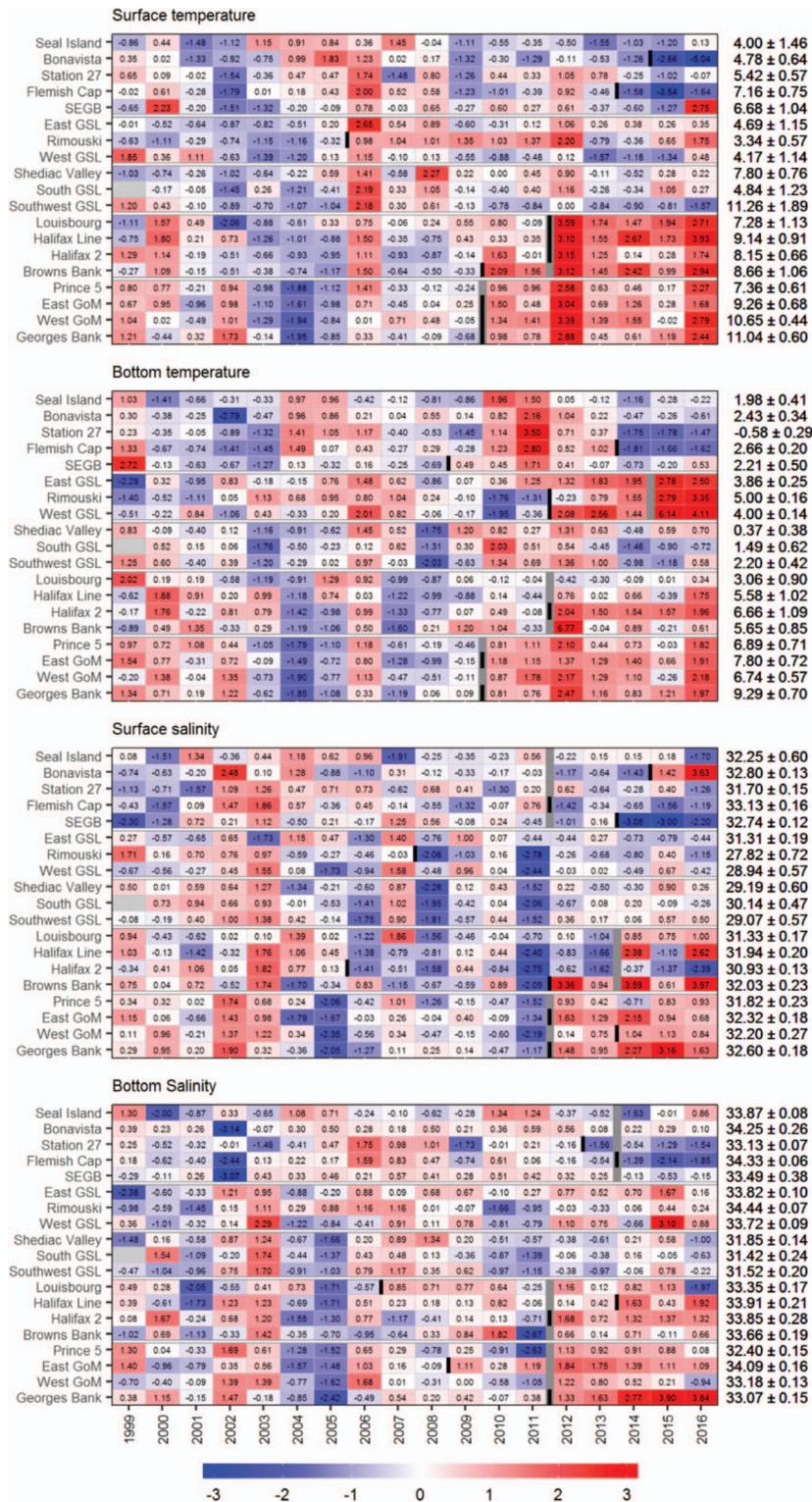


Table V: Pearson correlation coefficients from relationships between cumulative annual anomalies (i.e. anomalies summed over regions Newfoundland and Labrador Shelves [NLS], west-east GSL, southern GSL, Scotian Shelf [SS] and Gulf of Maine–Georges Bank [GoM–GBK]) of abundance of each species of *Calanus* (*C. finmarchicus*, *C. hyperboreus* and *C. glacialis*) or biomass of *Calanus* spp. and hydrographic variables (near sea surface temperature, SST; bottom temperature, BT; sea surface salinity, SSS; bottom salinity, BS) over years 1999–2016

Taxa	Region	SST	BT	SSS	BS
<i>C. finmarchicus</i>	NLS	–0.01	0.13	0.63	0.21
	West–east GSL	0.04	–0.60	0.15	–0.22
	Southern GSL	0.06	–0.16	–0.18	0.29
	SS	–0.63	–0.39	–0.17	–0.21
	GoM–GBK	–0.70	–0.68	–0.20	–0.43
<i>C. hyperboreus</i>	NLS	–0.41	–0.19	0.57	–0.18
	West–east GSL	0.37	0.64	–0.20	0.45
	Southern GSL	–0.11	–0.29	–0.07	0.16
	SS	–0.40	–0.47	–0.37	–0.38
<i>C. glacialis</i>	NLS	–0.45	–0.47	0.58	–0.38
	West–east GSL	0.06	–0.74	–0.04	–0.46
	Southern GSL	–0.17	–0.08	–0.11	–0.07
	SS	–0.74	–0.55	–0.18	–0.33
<i>Calanus</i> spp. biomass	NLS	0.04	–0.03	0.68	0.07
	West–east GSL	–0.01	–0.25	0.18	0.12
	Southern GSL	0.01	0	–0.03	0.25
	SS	–0.65	–0.47	–0.25	–0.26
	GoM–GBK	–0.70	–0.69	–0.28	–0.48

Significant correlation coefficients are indicated in bold.

characterized by primarily negative anomalies in the 1980s, early 1990s and 2010s. While both positive and negative anomalies occurred in the 2000s, there were more positive anomalies in this decade than in any other decade of the time series (Fig. 6A). In subregions of the GoM–GBK, interannual patterns in anomalies of biomass were generally consistent with those in the swGSL subregion. However, strong negative anomalies, which occurred at swGSL and west GoM subregions in the late 1980s and 1990s, were not observed in the east GoM and Georges Bank subregions during this time period. The analysis of cumulative anomalies in the GoM–GBK indicated shifts to higher and lower biomass of *Calanus* spp. 2001 and 2010, respectively (Fig. 6A).

Anomalies of SST were primarily negative in GoM–GBK from 1977 through 1998, followed by a variable period from 1999 to 2009 and primarily positive anomalies from 2010 to 2016 (Fig. 6B). In the swGSL subregion, anomalies of SST were also primarily negative in the 1980s, though not as strong as the west and east GoM subregions, and persistent negative anomalies occurred in the 2010s. Anomalies of BT in the GoM–GBK and swGSL subregion were characterized by short-term (2–5 years) variability. The only periods with persistently positive anomalies of BT occurred in the 1990s in the west GoM subregion and from 2011 to 2016 throughout the GoM–GBK (Fig. 6B). Anomalies of SSS and BS in the GoM–GBK were primarily positive in the late 1970s, early 1980s and 2010s and negative in the late 1980s and 1990s. Neg-

ative anomalies of BS were stronger than those of SSS in the late 1980s and 1990s (Fig. 6B). In the swGSL, negative anomalies of SSS and BS were also observed in the 1990s; however, interannual variation was not consistent among salinity metrics in this region in the 2000s and 2010s.

Anomalies of biomass of *Calanus* spp. were significantly negatively correlated with all environmental metrics in the Georges Bank subregion and with SST and BT in the east GoM subregion (Table VI). Anomalies of biomass of *Calanus* spp. were significantly positively correlated with SST and BS in the west GoM subregion and with BT in the swGSL subregion (Table VI).

Variability in IDW of *C. finmarchicus*

IDWs derived from PL were slightly greater in the Rimouski subregion compared to southern GSL (Fig. 7). IDWs used to derive biomass from abundance of stage CV of *C. finmarchicus* (Table II) were consistent with mean IDWs measured in the Rimouski subregion but slightly greater than IDWs measured from the south GSL (Fig. 7).

A hypothetical 1 SD increase in 0–50 m average temperature over the growing season of *C. finmarchicus* resulted in a decrease in IDW that varied between 2 and 17%, depending on subregion and stage (Fig. 8; Table IV). In the Rimouski subregion, where both mean and SD of temperature were lowest, the effect on biomass of *C. finmarchicus* of this hypothetical upward shift in temperature was 4% of the abundance-driven effect, while it was

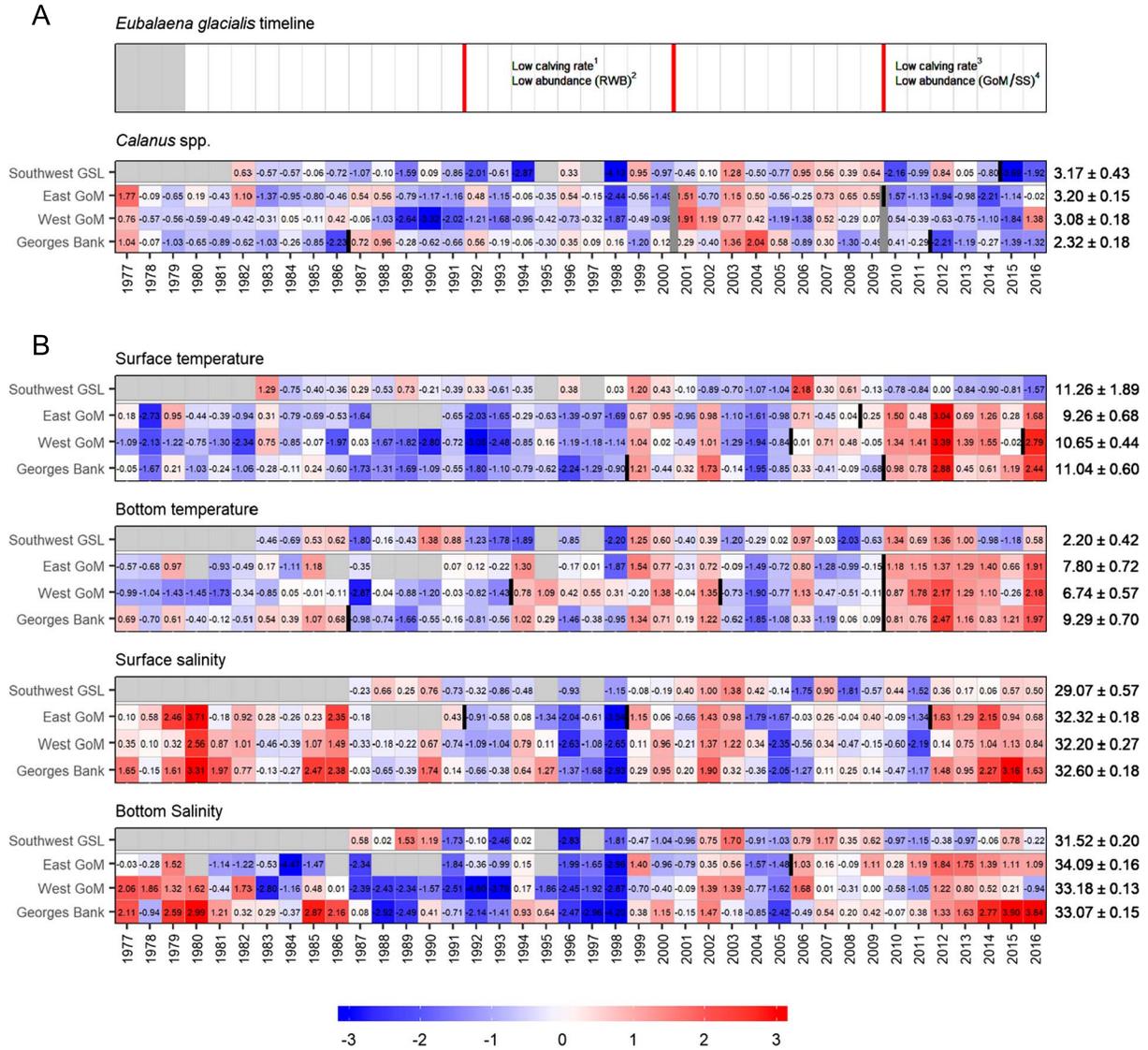


Fig. 6. (A, top panel) Schematic timeline indicating alternating periods of high and low calving rate and abundance of *Eubalaena glacialis* in the GoM or on the SS (¹Meyer-Gutbrod et al., 2015; ²Davies et al., 2015a; ³Kraus et al., 2016; ⁴Davis et al., 2017). Gray cells indicate no data on calving rate. (A, bottom panel) Scorecard of annual anomalies of $\log(x + 1)$ transformed biomass (mg m^{-2}) of *Calanus* spp. from the swGSL and east, west and Georges Bank subregions (top to bottom). Values in each cell are anomalies from the mean $\log(x + 1)$ transformed biomass, calculated over years 1999–2010. (B) Scorecards of annual anomalies of sea surface and bottom temperature and salinity from the same subregions in (A). For all scorecards, climatological mean and SDs are listed at the right, and red (blue) cells indicate higher (lower) than normal values. A blank gray cell indicates missing data. Vertical lines indicate the timing of shifts in anomalies. Black lines indicate subregion-specific shifts, and gray lines indicate shifts in regional cumulative anomalies. Cumulative anomalies were not evaluated from times series of temperature and salinity due to missing data in years that differed among subregions.

13–14% in the Shediac Valley and Halifax 2 subregions (Fig. 8; Table IV).

DISCUSSION

Our analysis characterizes regional and interannual variation in the *Calanus* species complex of the western North Atlantic shelf system, reflecting spatial and temporal vari-

ations in population levels of potential prey prey available to NARW. Around 2010, the abundance of *C. finmarchicus*, a key prey for NARW, declined in the GoM and on the SS, which coincided with a shift in the distribution of NARW (Davis et al., 2017). In the eastern GoM, the post-2010 decline in population levels of *C. finmarchicus* has been associated with a decrease in sightings per unit effort of NARW (Record et al., 2019). These observations

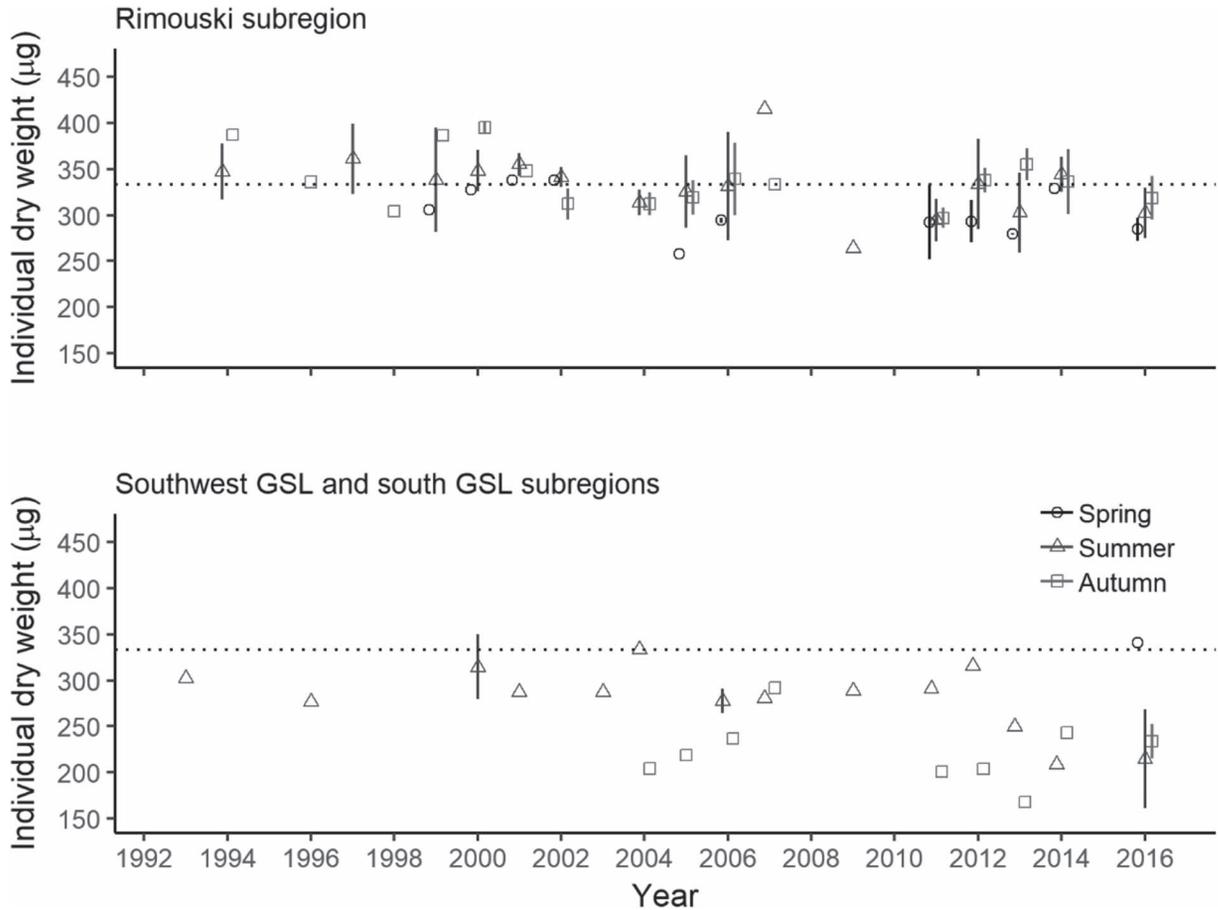


Fig. 7. Time series of IDW of stage CV of *C. finmarchicus* (mean \pm 1 SD) from the Rimouski subregion (upper panel) and southwest GSL and south GSL subregions (lower panel). The mean and SD within each season (spring, summer and autumn) were calculated from data averaged by month. In each year, points with no error bars indicate data from only 1 month within each season. The broken horizontal line indicates the constant IDW used to convert abundance to dry weight in the current study (Table II).

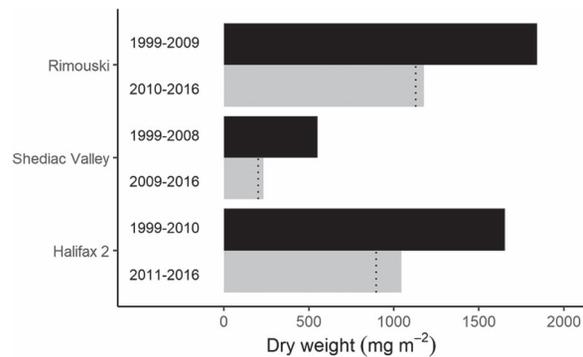


Fig. 8. Mean biomass of *C. finmarchicus* at Rimouski, Shediac Valley and Halifax 2 subregions during active development in years of high (black) and low (gray) abundance (see Fig. 3), which are indicated to the left of each bar. Broken vertical lines indicate the potential effect of a hypothetical temperature increase of 1 SD from the climatological mean 0–50 m depth average temperature (years 1999–2010) on biomass in the low abundance period (Table IV).

are consistent with the hypothesis that interannual and regional variability of population levels of *Calanus* spp. influence the spatial distribution of NARW in known foraging areas (Pendleton et al., 2009; Davies et al., 2015a, Record et al., 2019).

Calanus hyperboreus and *C. glacialis* are also potential prey for NARW in shelf areas upstream (i.e. north and east) of the SS. The larger of these two species, *C. hyperboreus*, makes a substantial contribution to *Calanus* spp. late-stage biomass in the GSL and on the NLS. The relatively deep subregions of the west–east GSL (Rimouski, west GSL and east GSL) provide habitat for diapausing *Calanus* spp. (Krumhansl et al., 2018) and represent the current southern reproductive range limit of *C. hyperboreus* (Sameoto and Herman, 1992). In contrast to *C. finmarchicus*, in the 2010s, the abundance of *C. hyperboreus* increased in the west–east GSL. The co-occurrence of three *Calanus* species on the shelves to the north and east of the SS provides potential for resilience to changes in biomass

Table VI: Pearson correlation coefficients from relationships between annual anomalies of biomass of *Calanus* spp. and hydrographic variables (near sea surface temperature, SST; bottom temperature, BT; surface salinity, SSS; and bottom salinity, BS) from 1977–2016 (west GoM, east GoM and Georges Bank) or 1982–2016 (southwest GSL)

Subregion	SST	BT	SSS	BS
southwest GSL	0.27 (32)	0.37 (32)	0.09 (28)	0.19 (28)
East GoM	-0.39 (37)	-0.34 (34)	-0.01 (37)	-0.05 (34)
West GoM	0.32 (40)	0.11 (40)	0.25 (40)	0.38 (40)
Georges Bank	-0.56 (40)	-0.66 (40)	-0.46 (40)	-0.50 (40)

Sample size is indicated in parentheses, and significant correlation coefficients are indicated in bold.

of *Calanus* spp. because the three species may respond differently to environmental variation.

Interannual variation in *Calanus* spp. across the western North Atlantic shelf system

The abundance and biomass of late-stage *Calanus* spp. have declined in many subregions of the western North Atlantic since the late 2000s. Persistent shifts to negative cumulative anomalies of biomass of *Calanus* spp. were detected in the GoM–GBK in 2010 and on the SS in 2011, driven primarily by changes in abundance of *C. finmarchicus*. The timing of these shifts to lower biomass of *Calanus* spp. occurred within 1 year of shifts to strong positive anomalies of SST and BT. Populations of *C. finmarchicus* at the southern end of their range may be particularly vulnerable to subsurface ocean warming. Elevated temperatures can increase metabolic rates of diapausing copepods, thus increasing risk of emergence from diapause well before the spring bloom, a mismatch with their food source and mortality (Maps et al., 2014). High SST can also reduce egg hatching success of *C. finmarchicus*, as has been observed in the GoM when temperatures exceed 19°C during the phytoplankton bloom in autumn (Preziosi and Runge, 2014).

While temperature-driven changes in seasonal production timing could cause apparent changes in abundance levels in annually repeated observations, the similarity in temporal patterns between subregions sampled in only one or two seasons (Mackerel Survey and AZMP sections) and those sampled throughout the year (AZMP time series stations) suggest that interannual variations presented here reflect overall changes in annual population levels, rather than changes in phenology. For years 1999–2016, there appears to be no clear interannual trend in phenology of stages CIV–CVI of *C. finmarchicus* in the Halifax 2 subregion (Johnson, unpublished results); however, a trend toward earlier timing in production of *C. finmarchicus* has been observed in the Rimouski subregion (Blais et al., 2018). Nevertheless, changes in phenology in the Rimouski subregion likely would not

have a major influence on stage composition of CIV–CVI in spring and should not affect stage composition in autumn because most individuals are in diapause (Blais et al., 2018).

Surface and subsurface temperatures have been rapidly warming in the GoM, associated with the position of the Gulf Stream (Pershing et al., 2015; Record et al., 2019). Species distribution models that use SST or BT as explanatory variables indicate that population centers of *C. finmarchicus* in the north Atlantic have shifted north (Chust et al., 2014) and predict declines in abundance of *C. finmarchicus* near its southern range limit in response to climate change projections (Reygondeau and Beaugrand, 2011; Grieve et al., 2017). The negative correlation between cumulative anomalies of abundance of *C. finmarchicus* and those of SST and BT in GoM–GBK since 1999 is consistent with predictions from these studies as well as results from other correlation analyses (Licandro et al., 2001; Kane, 2007). Increases in SST and BT and declines in abundance of each species of *Calanus* have also been observed on the SS since 1999 (Reed et al., 2018), which is consistent with our observations of interannual variation in these variables and the negative correlation between cumulative anomalies of *Calanus* spp. (abundance and biomass) and those of SST on the SS.

Associations between population levels of *C. finmarchicus* and temperature may also be a due to an indirect effect of changes in ocean circulation and transport of *Calanus* spp. For example, a strong effect of advective transport on densities of *Calanus* spp. has been inferred from interannual and spatial variation in abundance of *Calanus* spp. and seawater temperature or density on the SS (Head et al., 1999; Patrician and Kenney, 2010; Davies et al., 2015b). In the 2010s, a negative association between subsurface ocean temperature and abundance of *C. finmarchicus* in the interior of the GoM has been attributed to a reduced supply of diapausing copepods from the Northeast Channel and enhanced mortality due to subsurface warming (Record et al., 2019). Transport of *C. finmarchicus* has also been hypothesized to affect population levels on the western side of the GoM due

to variation in supply of high concentrations of this species in the Maine Coastal Current (MCC), which is rich in phytoplankton and relatively cool in comparison to interior areas of the GoM in spring and summer (Runge et al., 2015; Ji et al., 2017). In our study, the west GoM subregion covered the domain of the MCC and interior areas, and the abundance of late stages of *C. finmarchicus* declined in this subregion during the period of warm SST and BT in the 2010s. Contrasting correlations between anomalies of abundance of *C. finmarchicus* and those of SST between east and west GoM subregions over years 1977–2016 indicate spatial differences in the relationships of abundance indices of *Calanus* and temperature between west and east GoM subregions.

In the 1977–2016 period, low abundances of *C. finmarchicus* in the GoM–GBK during the 1990s, relative to the 2000s, are consistent with previous analyses of zooplankton from the EcoMon data set by Kane (2007) and Perretti et al. (2017). Hydrographic conditions associated with low population levels of *Calanus* spp. in the GoM were not consistent in the 1977–2016 period. Previous studies have suggested that the southwestward extent of cool and fresh Labrador slope water was negatively associated with population levels of *Calanus* spp. in the GoM (Greene et al., 2013). Alternatively, in the 2010s, positive salinity anomalies in the GoM have been associated with reduced strength of equatorward currents on the SS (Feng et al., 2016), suggesting reduced connectivity between the GoM and SS. Non-stationary interannual relationships between abundance indices of *C. finmarchicus* and environmental variables in the GoM (Hare and Kane, 2012) likely reflect the complexity of *Calanus* population dynamics, which integrate interactions among the seasonal timing of transitions between developmental phases of active development and diapause, phytoplankton production patterns, vertical migration behavior and shelf circulation (e.g. Runge et al., 2015; Ji et al., 2017).

In the west–east GSL, *C. finmarchicus*/*C. glacialis* and *C. hyperboreus* abundances were strongly correlated with BT in opposing directions. In the Rimouski subregion, the abundance of *C. hyperboreus* has actually increased since the early 1990s, despite warming and an increase in contribution of smaller copepods species to the zooplankton community (Plourde et al., 2015; Brosset et al., 2018). Differences in population dynamics of *C. finmarchicus*/*C. glacialis* and *C. hyperboreus* may be linked to the interaction between life history strategy and environmental conditions, including temperature. In contrast to *C. finmarchicus*/*C. glacialis*, *C. hyperboreus* enters diapause at a larger size and relies solely on energy reserves to produce eggs, which can develop to feeding nauplii prior to the spring bloom (Hirche and Niehoff, 1996;

Falk-Peterson et al., 2009). Therefore, abundance of *C. hyperboreus* may be less affected by a relatively warm BT during diapause and a possible mismatch between timing of emergence from diapause and phytoplankton food availability (Maps et al., 2014). In addition, *C. hyperboreus* is characterized by a relatively long period of diapause at depths >200 m in the GSL (Plourde et al., 2003); therefore, this species is less likely to be exposed to adverse conditions near the surface including losses from the GSL from net outward advection (Koutitonsky and Bugen, 1991). The persistence of strong positive anomalies of abundance of *C. hyperboreus* in the west–east GSL may indicate that biomass of *Calanus* spp. is more resilient to the range of observed environmental variation in the GSL in comparison to the GoM and SS.

The west–east GSL has been hypothesized to be an important contributor of *Calanus* spp. to its adjacent regions including the eastern SS (Sameoto and Herman, 1992; Head et al., 1999) and southern GSL (de Lafontaine, 1994). Biophysical modeling exercises have indicated that transport of actively developing *Calanus* spp. from the Laurentian Channel in spring and summer is the dominant mechanism of supply of individuals to the southern GSL (Zakardjian et al., 2003; Maps et al., 2011; Brennan et al., 2019). Despite this strong potential for connectivity, the biological oceanography and zooplankton community of the southern GSL is distinct from the neighboring west–east GSL (de Lafontaine, 1991). In shallow waters (e.g. <100 m) of the southern GSL, *Calanus* spp. are considered to be vulnerable to predation by pelagic fishes (de Lafontaine, 1991) and do not have optimal habitat for diapause. These pressures are consistent with the large differences in multi-annual averages of abundance of *Calanus* spp. between west–east and southern GSL regions and may also contribute to spatial differences in interannual patterns of abundance and biomass. For example, temporal patterns in annual anomalies of abundance of *C. finmarchicus* were similar between west–east and south GSL regions, but this was not the case for *C. hyperboreus*.

Our observation of primarily negative anomalies of abundance for each species of *Calanus* on the NLS in the late 1990s and early 2000s and positive anomalies in the mid-late 2000s is generally consistent with previous reports of higher abundance in the 2000s than the 1990s (Head and Sameoto, 2007). In this region, the abundance of *C. glacialis* was negatively correlated with BT, consistent with a previous study on habitat characteristics of this species in Canadian waters (Albouy-Boyer et al., 2016). Furthermore, we found that all three species of *Calanus* were positively correlated with SSS. A positive correlation between anomalies of SSS and abundance of *C. finmarchicus* and *C. hyperboreus* is consistent with population

centers located in slope waters (Falk-Peterson et al., 2009) that are typically characterized by higher SSS. However, *C. glacialis* is typically more abundant in shelf waters (Head et al., 2003; Falk-Peterson et al., 2009), which is not consistent with this interpretation. Alternatively, variations in SSS could reflect the presence or absence of sea ice, which in turn, could affect the timing of the spring bloom, and the success of *Calanus* spp. in a particular year.

Biomass variability

The most important food-related metric for NARW is energy density (Michaud and Taggart, 2007; McKinstry et al., 2013). We have used biomass of *Calanus* spp. as a coarse proxy for energy available to NARW and calculated biomass of prey from abundance using species- and stage-specific IDW conversions that were constant in time. We did not account for variability in biomass, lipid or energy content of individuals of *Calanus* spp. that occurs at the spatial and temporal scales of our sampling resolution (e.g. Miller et al., 2000; Michaud and Taggart, 2007; McKinstry et al., 2013). Our analysis of IDW of stage CV of *C. finmarchicus* in the GSL indicates that we overestimated levels of biomass of *Calanus* spp. in the southern GSL (south GSL, Shediac Valley and swGSL subregions). Furthermore, interannual variation in IDW of this stage in summer and autumn seasons, quantified as the coefficient of variation (σ/μ), was slightly lower in the Rimouski subregion ($\sigma/\mu_{\text{autumn}} = 0.09$, $\sigma/\mu_{\text{summer}} = 0.10$) in comparison to subregions in the southern GSL ($\sigma/\mu_{\text{autumn}} = 0.16$, $\sigma/\mu_{\text{summer}} = 0.12$) and Grand Manan Basin ($\sigma/\mu_{\text{autumn}} = 0.19$, $\sigma/\mu_{\text{summer}} = 0.13$; calculated from McKinstry et al., 2013, Table 2). Our sensitivity analysis indicated that the potential effect of IDW (temperature) from hypothetical “regime shifts” in temperature contributed to <20% of variation in biomass of late stage *Calanus* spp., with the remainder being attributed to variation in abundance.

Implications for NARW

The timing of declines in biomass of *Calanus* spp. in GoM–GBK and on SS is consistent with the interpretation that, in the 2010s, a reduction in prey availability contributed to changes in the distribution of NARW (Davis et al., 2017; Record et al., 2019) and a decline in calving rate (Kraus et al., 2016; Pace et al., 2017; Pettis et al., 2018). A similar pattern occurred in the 1990s, when population levels of *Calanus* spp. dramatically declined in the west GoM subregion and in Roseway Basin on the western SS, concurrent with declines in observations of NARW in these areas (Patrician and Kenney, 2010; Davies et al., 2015a), and reduced calv-

ing rate (Greene and Pershing, 2004; Meyer-Gutbrod et al., 2015).

Relatively large numbers of NARW have been observed in the southern GSL (Shediac Valley, south GSL and swGSL subregions) since dedicated whale survey efforts were undertaken in 2015 (Daoust et al., 2018; Meyer-Gutbrod et al., 2018), despite the relatively low population levels of *Calanus* spp. in this region and their general decline since the late 2000s. Whether more NARW have used this area since 2010, when the abundance of *C. finmarchicus* declined in traditional foraging areas, is unknown given the lack of survey effort in the southern GSL prior to 2015. The biomass of *Calanus* spp. is generally higher in the west–east GSL compared to the southern GSL, and the deep (>200 m) bathymetry may provide a refuge from predation by NARW. Advective transport of *Calanus* spp. from this region is likely a major contributor to the abundance of NARW prey in the southern GSL (Brennan et al., 2019). The climatological abundance and biomass of *Calanus* spp. in the southern GSL was highest at Shediac Valley, where NARW have been frequently observed (Daoust et al., 2018; DFO, unpublished results).

In our study, annual and climatological estimates of prey abundance and biomass from all subregions represent population levels averaged across vertical and horizontal space and do not account for mechanisms that locally concentrate prey. One potential explanation for the presence of NARW in the southern GSL, despite relatively low population levels of *Calanus* spp., is that the potential for aggregation of prey may be greater in this area. In the southern GSL, *Calanus* spp. are accessible to NARW throughout the water column because of the relatively shallow bathymetry, which may contribute to the aggregation of diapausing *Calanus* spp. near the bottom (Krumhansl et al., 2018; Plourde et al., n.d.). Taking the vertical dimension of prey biomass into consideration, Plourde et al. (n.d.) identified the southern GSL as a potentially important foraging area for NARW.

In the NLS, the direct importance of population dynamics of *Calanus* spp. to NARW is unclear. Although NARW have been observed off the coast of Newfoundland (Winn et al., 1986), no specific foraging areas have been identified in this region. Regardless, the NLS may be an important source of *Calanus* spp. to the GSL, via transport of individuals through the Strait of Bell Isle and Cabot Strait.

CONCLUSION

Population levels of *Calanus* spp. have been lower than the long-term average since the late 2000s or early 2010s

in many areas of the GoM, SS and GSL. These declines in NARW prey have corresponded with observations of fewer NARW in their traditional summer–fall foraging areas in the GoM (Davis et al., 2017; Record et al., 2019) and lower NARW calving rates (Kraus et al., 2016). The southern GSL has been identified as a potentially important foraging area for NARW (Plourde et al., n.d.), and large numbers of NARW have been reported in this area in the 2010s despite relatively low levels of abundance and biomass of *Calanus* spp. Our analysis of interannual and regional variability of population levels of *Calanus* spp. provides no conclusive explanation for the increased presence of NARW in southern GSL. However, *C. hyperboreus* abundances have generally increased in adjacent waters of the western and eastern GSL, which are sources of *Calanus* spp. to the southern GSL (Brennan et al., 2019). The combination of advective supply and shallow bottom depths, which deny *Calanus* a refuge in deep water from NARW predation and potentially concentrate *Calanus* spp. at near-bottom depths accessible to NARW may provide conditions favorable for foraging by NARW in the southern GSL (Plourde et al., n.d.), even during periods of low abundance and biomass.

In the GoM–GBK and SS, *Calanus* spp. were negatively correlated with temperature, and post-2010 declines in population levels of *Calanus* spp. coincided with a shift to warmer temperatures. In the eastern GoM, temperature may be a proxy for changing sources of advective supply of *Calanus* spp. (Record et al., 2019). In addition, temperature may directly impact *Calanus* spp. through its influence on timing of emergence from diapause (Maps et al., 2014) and egg hatching success (Preziosi and Runge, 2014). Increasing temperature could also reduce the size of individuals (Campbell et al., 2001; Forster and Hirst, 2012) and presumably energy content, reducing the quality of prey for NARW.

If the quantity and quality of *C. finmarchicus* continue to decline in traditional foraging areas in the GoM–GBK and western SS, NARW will need to find alternate suitable foraging areas either in the GSL and NLS or elsewhere in the North Atlantic. The presence of multiple species of *Calanus* in the GSL and NLS, each with different life history characteristics (Falk-Peterson et al., 2009; Maps et al., 2014), may help buffer negative effects of environmental change on the abundance of *Calanus* spp. However, travel to potential habitats farther north may impose an additional energetic cost to NARW, and a change in their distribution may expose them to risk of injury or mortality (Meyer-Gutbrod et al., 2018). Estimates of historical NARW population levels prior to 1700 were in the thousands (Reeves et al., 2007). Evidence that the current low population of NARW, about 430

individuals (Pettis et al., 2018), may be exceeding its carrying capacity in traditional foraging areas highlights the potential broader ecosystem implications of population declines of *Calanus* spp.

SUPPLEMENTARY DATA

Supplementary data can be found at *Journal of Plankton Research* online.

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