Does predation control the diapausing stock of Calanus finmarchicus in the Gulf of Maine?

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ABSTRACT

The variability of zooplankton populations is controlled by external and internal forcing, with the former being principally large-scale changes in circulation, and the latter being driven by in situ growth, competition, and predation. Assessing the relative importance of these forcings is challenging and requires analyses of multifaceted observational data. As part of the U.S. GLOBEC Georges Bank program, a series of cruises were conducted in fall 1997, 1998, and 1999 to survey diapausing populations of *Calanus finmarchicus* and their predators in Wilkinson, Jordan, and Georges Basins of the Gulf of Maine. Station and underway sampling were conducted using net (1m^2 MOCNESS) and bioacoustic (BIOMAPER-II) systems, respectively, to acquire vertically stratified data for zooplankton biomass, taxonomic, size, and life-stage composition, together with associated environmental data. The results show that the autumn diapausing *C. finmarchicus* abundance was much lower in 1998 than in 1997 or 1999, even though the overall zooplankton biomass levels were comparable between the three years. The size frequency distribution of the diapausing individuals had a bi-modal pattern in 1997 and 1999, but a single mode in 1998, indicating the demise of an early cohort of the diapausing stock. The relative biomass and computed energy demand of potential invertebrate predators (euphausiids, decapods, medusae, and siphonophores) was found to be higher in 1998 and could account for the missing *C. finmarchicus* cohort. Evidence collected from this study supports the hypothesis that local predation has the potential to control the diapausing stock of *C. finmarchicus* in the Gulf of Maine.

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1. INTRODUCTION

The copepod *Calanus finmarchicus* is a one of the keystone species in the plankton of the northern Atlantic Ocean because of its high spring and summer abundance and biomass in the open ocean as well as on continental shelves and because of its importance as prey for higher trophic levels (Wishner et al, 1995; Sundby, 2000; Heath et al., 2004; Melle, et al., 2014; Suca et al. 2021; Kristiansen et al. 2021; Skjoldal et al. 2021)). The main population centers within its biogeographic range are in the Norwegian and Labrador Seas, with marginal populations derived from these sources (Heath et al. 2004; Speirs et al. 2005, 2006). Future projections of the species in a warming climate indicate a poleward shift of the main population centers and marked reduction of the population on the NW Atlantic shelf (Reygondeau and Beaugrand 2011; Grieve et al. 2017). Within the Gulf of Maine (GoM) / Georges Bank (GB) system, *C. finmarchicus* dominates zooplankton secondary production during spring and early summer, both on GB and in the GoM proper (Bigelow, 1914, 1926; Davis, 1987a; Meise and O'Reilly, 1996; Durbin, 1997; Durbin et al., 1997, 2003; Runge et al., 2006). The shallow Georges Bank *C. finmarchicus* population has been hypothesized to arise from diapausing populations in the deep basins of the Gulf of Maine. Processes that regulate the survivorship of *C. finmarchicus* from the diapausing populations may provide a seeding source of this species to Georges Bank, where growth and fertility are enhanced due to higher, but still limiting, food levels (Davis 1987a; Campbell et al., 2001). To quantify this seeding potential, information is needed about what processes regulate the abundance and mortality of the diapausing *C. finmarchicus* populations in the Gulf of Maine. Also needed is information about how physical processes in the Gulf of Maine interact with the seasonal and diel vertical migration (DVM) behaviors of *C. finmarchicus* in seeding Georges Bank with new recruits each year. More broadly, knowledge of the mechanisms controlling the diapause stock is important for a better understanding of how the population in NW Atlantic will respond to climate variability and change (Greene et al., 2013; Runge et al., 2015).

Substantial variation in *C. finmarchicus* abundance over the past several decades has been observed from MARMAP-ECOMON bongo net surveys (Meise and O'Reilly, 1996, Ji et al., 2021) and Continuous Plankton Recorder surveys (Conversi, et al., 2001, Greene and Pershing 2000, 2003; Pershing et al., 2005; Greene et al., 2013; Meyer-Gutbrod et al., 2021). The underlying physical-biological mechanisms linking the climate variability and the observed variation of *C. finmarchicus* abundance have not been fully resolved (Greene et al., 2013). Broadly speaking, the variation could be caused by one or more environmental forcings that are responsible for changes in either the internal production within the Gulf of Maine or exchange processes with external populations (Greene et al. 2004; Pershing et al., 2009). These two forcings are not mutually exclusive. Rather, they can reinforce or balance one another. The internal production term could be further divided into two major parts - population growth and mortality loss, while the exchange term could be influenced by the upstream Scotian Shelf Water, Labrador Current, or Slope Water. Multiple hypotheses have been proposed over the last several decades to assess the predominance of certain drivers, and these hypotheses need to be continuously tested using newly available methodology and datasets.

Fluctuations in the surface *C. finmarchicus* CPR data collected nearly continuously since the 1960s have been linked to remote forcing associated with decadal-scale shifts in the Arctic climate system as well as with interannual variability in the North Atlantic Oscillation (NAO - Hurrell and Deser (2009); Greene et al., 2013). The Data from the Continuous Plankton Recorder (CPR) during the 1990s showed surface abundance of late-stage *C. finmarchicus* in the Gulf of Maine were depressed, reportedly coinciding with an ecosystem regime shift associated with the arrival of negative salinity anomalies from the Arctic Ocean (Greene et al., 2012; 2013). This lower abundance, however, was not evident in the integrated tow data (0-200m) from ECOMON surveys (Ji et al, 2021). GLOBEC MOCNESS data from 1998 showed that the abundances of diapausing *C. finmarchicus* in the Gulf of Maine was low, hypothetically linked to a dramatic drop in the NAO Index and a subsequent shift in the NW Atlantic's coupled Slope Water system (Greene et al., 2003). However, the underlying causal mechanisms remain unclear (Greene et al., 2003; 2004; Ji, 2011). Greene et al. (2003; 2004) speculated that extension of the Labrador Slope Water adjacent to the outer shelf and its subsequent incursion into the GoM during strongly negative NAO years could be blocking upstream sources of *C. finmarchicus* from entering the Gulf. An alternative hypothesis is that with the incursion of Labrador Slope Water, conditions conducive to enhanced invertebrate predator populations reduced the *C. finmarchicus* diapause stock through predation.

Although during the past few decades the dominant pattern has been for the NAO to be in a positive phase, during the winter of 1995-1996 there was a substantial shift to the negative phase (Bersch, 2002). A consequence of this shift was the increased flow of colder, fresher seawater from the outer Labrador Current around the Grand Banks and into the Slope Water in 1997 (Drinkwater et al., 1998, 1999; Pershing et al., 2001; Mountain, 2012). By early 1998 some Labrador Slope Water entered the GoM (Pershing et al., 2001; Townsend et al. 2015). This change of water mass property has been hypothesized to be associated with a significant shift in the *C. finmarchicus* supply into the GoM, thus affecting the population size inside the entire Gulf (Pershing et al., 2001; Greene et al., 2003, 2004). However, both Labrador Slope Water and Warm Slope Water (WSW) (Drinkwater et al. 2003; Mountain 2012) have at least an order of magnitude lower *C. finmarchicus* abundance than the GoM (Miller et al., 1991; Head and Pepin 2008), thus potentially diluting the GoM population regardless of NAO phase.

Long-term CPR and ECOMON survey data demonstrate that there is a strong relationship between decadal-scale regime shifts in the northwest Atlantic and *C. finmarchicus* abundance in the GoM from one decade to the next (Greene et al., 2013; Meyer-Gutbrod et al., 2021). Nevertheless, recent survey data analyses of survey data and modeling studies indicate that the seasonal and interannual variability of *C. finmarchicus* in GoM is rarely determined by size of diapause stock nor by lateral exchange with adjacent water masses, but rather by internal population dynamics within the GoM itself (Ji et al. 2021). These findings are in agreement with earlier studies (Fish and Johnson, 1937; Redfield, 1941; Mullin, 1963). While size of the diapause stock may rarely influence *C. finmarchicus* abundance in the GoM from one year to the next, it is likely that the GoM population cannot sustain itself over the long run without seeding from upstream waters (Miller et al., 1998; Saumweber and Durbin, 2006; Greene et al., 2013). Therefore, understanding what processes control size of the diapause stock during anomalous years may be critical for understanding how this population may survive in the future of rapid climate change (Runge et al., 2015).

As part of the U.S. Global Ocean Ecosystem Dynamics Program (GLOBEC), diapausing *C.*

finmarchicus in the GoM deep basins were sampled in the fall to examine the population abundance, distribution, and stage structure in relation to the hydrography and zooplankton community composition. There were five cruises to the GoM with one conducted in the fall of 1997 (Oct), two in 1998 (Oct and Dec), and two in 1999 (Oct and Dec). Thus, the periods before, during, and after the Labrador Slope Water incursion occurred were sampled. The objective of this paper is to examine the year to year variability in the *C. finmarchicus* in light of this event and to assess the likelihood that increased predation, rather than supply processes, led to the inter-annual variations in *C. finmarchicus* abundance observed.

2. METHODS

Broad-scale surveys were conducted to estimate spatial and temporal changes in the distribution of the diapausing *Calanus* populations in Wilkinson, Jordan, and Georges Basins aboard either R/V *Endeavor* or R/V *Oceanus*. Included were fixed-station studies to collect 1-m^2 Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS - Wiebe et al., 1985) samples to examine diel changes in the vertical distributions and small-scale patchiness of predators and prey, and video and acoustic surveys using the BIo-Optical Multi-frequency Acoustical and Physical Environmental Recorder (BIOMAPER-II; Wiebe et al., 2002) to examine the scale-dependent spatial coupling of predators and prey in the deep basins.

The five Gulf of Maine cruises were laid out as a series of tracklines traversing the three major basins in the Gulf of Maine (Figure 1; Table 1) and took ten to twelve days to complete. On EN307, the first cruise, work began in Georges Basin and then proceeded to Jordan Basin followed by Wilkinson. For the other four cruises, work began in Wilkinson Basin and ended in Georges Basin. In addition to the along-track data collection, time was allotted each day for a CTD cast between 1000 and 1400 hours and one or two MOCNESS tows. One or more tows were taken in each basin on each cruise, with a total of 21 tows analyzed (Figure 2; Table 2). In addition to the Gulf of Maine samples, samples collected with a MOCNESS in the upper 800 to 1000 m of the Slope Water south of New England on a time-series set of cruises in 1981 and 1982 (Miller et al., 1991) were re-examined to obtain information on *Calanus finmarchicus* lengths and to present the vertical data and environmental data in the context of the Gulf of Maine *Calanus finmarchicus* data.

2.1 Gear.

2.1.1 MOCNESS.

A standard 1-m^2 MOCNESS was used to collect zooplankton for comparison with the acoustic backscattering data (Wiebe et al., 1985) and Video Plankton Recorder (VPR) data (see Benfield et al., 2003). This MOCNESS carried nine nets (335 μm mesh) and sampled eight depth-specific strata. The system was equipped with a modified TSK flowmeter and SeaBird temperature and salinity sensors, which were mounted facing forward on the frame. A SeaTech fluorometer was often mounted on the top portion of the frame. The MOCNESS was launched and recovered from the stern so that acoustic data could be obtained concurrently from the BIOMAPER-II (Wiebe et al., 2002), which was being towed off the starboard quarter of the vessel. All MOCNESS tows were conducted with ship speeds of 1.5 - 2.5 knots. The nets began collecting samples quantitatively from approximately 10 m above the sea floor to the surface. The zero net was open from the surface to the maximum depth of tow, then sampling strata for nets 1 through 8 commenced while the MOCNESS was hauled back to the surface (Net tow type 17, Wiebe et al., 2015). The depth intervals sampled were dependent on water depth. Generally, intervals of 25 m were sampled near the bottom and the surface, and remaining intervals ranged from 25 to 75 m. The down cast (net 0) was fished at a wire speed of 15 m/minute, and the up cast (nets 1-8) was hauled in at a speed of between 5 and 15 m/minute. Approximately 100 to 300 cubic meters of water were filtered for each of nets 1 through 8. Samples were often split prior to preservation with a box splitter (Motoda, 1959), with half the catch preserved in alcohol for genetic analyses and the other half preserved in buffered formalin for biovolume measurement, species identifications, and silhouette analyses (Davis and Wiebe 1985). Data were also collected in 1981 and 1982 with MOCNESS in a time-series in the Slope Water south of New England. Only temperature and depth were measured on MOCNESS. Samples were processed as described above. Some data from this time series were reported by Miller el al., (1991).

2.1.2 BIOMAPER-II.

BIOMAPER-II is a towed system capable of conducting quantitative surveys of the spatial distribution of coastal and oceanic plankton/nekton. The system consisted of a multi-frequency sonar produced by Hydroacoustic Technology Inc (HTI), a Video Plankton Recorder (VPR - Davis et al., 1992, 2004; Benfield et al., 2003), and an environmental sensor package (CTD, fluorometer, transmissometer). The acoustic system collected backscatter data from a total of ten echosounders (five pairs of transducers with center frequencies of 43 kHz, 120 kHz, 200 kHz, 420 kHz, and 1 MHz), half of which were mounted on the top of the tow-body looking upward, while the other half look downward. This arrangement enabled acoustic scattering data to be collected for much of the water column.

The acoustic frequencies were chosen to bracket the transition from the Rayleigh to geometric scattering regions for the target species under investigation. Echo integration was conducted at 12-second intervals, except on the first cruise (EN307) when the integration period was 30-s, to provide volume-backscattering data at all five frequencies. Split-beam data were collected at the four lower frequencies. All raw acoustic data were recorded on digital audio tape, while the processing for echo integration was carried out in real time.

The software to acquire the data, which was provided by HTI, enabled the simultaneous acquisition of data on five frequencies each with two transducers (one up-looking and one down-looking). The range allocated for each transducer was dependent on frequency with the lowest frequencies given the longest range and the highest frequency the shortest range (i.e. 43 kHz = 200 m, 120 kHz = 200 m, 200 kHz = 149 m, 420 kHz = 100 m, 1000 kHz = 35 m). The vertical resolution at all frequencies after echo-integration was 0.5 m. A ping cycle for all frequencies and transducers took about 2.5 seconds with a firing sequence of down-looking 43, 120, 200, 420, 1000 kHz and then up-looking 43, 120, 200, 420, 1000 kHz. Target strength measurements were also collected on the lower four frequencies out to 20 meters from the surface of the split beam transducers.

2.2 Sample Processing.

MOCNESS: The formalin preserved fractions of the MOCNESS samples were processed using three different techniques. Displacement volumes from the Gulf of Maine and Slope Water were measured using the standard CalCOFI procedure described by Alhstrom (1958). Working in a fume hood, the sample and preserving fluid were poured into a volumetric cylinder and the total volume in cubic centimeters (cc) was recorded. If large animals (> 0.5 cc) were present they were selectively removed and their displacement volumes were measured separately. The contents of the original cylinder were then poured through a fine mesh sieve into an identical cylinder thus straining out the plankton and the volume again recorded. The difference between the reading with the plankton (with or without large animals) is the biovolume estimate.

2.2.1 *Calanus finmarchicus* Counts and Size Measurements.

Counts of *Calanus finmarchicus* adults and copepodid stages in aliquots of the samples were made with a binocular microscope. *Calanus hyperboreous* and *C. glacialis* were present in low numbers, but not counted. Depending on the abundance of *C. finmarchicus* in the samples, splits ranged from 1/256 to ½ of the entire sample. All *C. finmarchicus* were counted and staged from copepodite C1 to adult C6. (Note that stages C1-C2 were under-sampled by the 0.335mm mesh net, Anderson and Warren, 1991). Approximately 100 individuals were removed for staging and length measurement. For stages that were not abundant, all individuals encountered in the split were removed for measurement. For the Slope Water samples, the abundances had previously been determined (Miller et al., 1991), so ~30 animals were removed for each abundant stage and all specimens for rare stages were collected from a sub-sample. (This amounted to none or only a few in some cases.) The animals were placed in a Petri dish and scanned on an Epson Expression scanner at 1200 dpi and the prosome lengths (head + thorax) were measured using Matlab-based digitizer software (Little and Copley, 2003). Prosome lengths were measured from the tip of the head to the base of the urosome (as opposed to the distal end of the 5th thoracic segment). Only *C. finmarchicus* size data of the CVs from 550 to 400 m in October and December 1981 collected in the Slope Water are presented below for comparison with the October and December Gulf of Maine data.

For each basin, data were pooled together for different years and months if there was more than one tow. For example, there were two tows during October 1997 in the Wilkinson Basin. All the prosome length measurements for the individuals collected by these two tows were used in the ANOVA and GMM calculations. Samples collected by MOCNESS tows that had mid-depths deeper than 100 m and 150 m were used in the analyses to make sure they were diapausing individuals.

A 2-way ANOVA (Analysis of variance; a Matlab Mathworks® toolbox called ‘anovan’ used for N-way analysis of variance) for all basins and all years in October 1997, 1998, and 1999 was done to examine the size differences in C5s between the years and the basins. ANOVA was used because there were unequal number of size observations for the basins and years. A second 2-way ANOVA was done on the December 1998 and 1999 size data to see if a similar pattern in size differences between the years and the basins occurred. Finally, a 3-way ANOVA was done for all basins (WB, JB, GB), both months

(Oct, Dec), and two years (98 and 99) to examine differences in C5 size between months as well as basins and years.

A Gaussian Mixture Model (GMM) was used to parse the size structure of C5 individuals living deeper than 150 m into cohorts (data from below 100 m was also used and did not result in a change in results). The estimation was done using the GMM function *fitgmdist* from Mathworks® Matlab version R2020a, with an assumption that the prosome lengths from each cohort have a Gaussian distribution. The total number of cohorts for each basin was not predetermined. Instead, the Akaike information criterion (AIC) was used to choose the best fitting GMM over varying numbers of cohorts as long as they are less than 6 (theoretically the maximum number of cohorts should not exceed 3 in the Gulf of Maine). The cohorts identified ranged between one and two.

2.2.2 Estimates of Carbon Requirements in the Water Column.

A silhouette photograph was made from each sample (or a split of a sample) of selected tows to assess the contributions of the major zooplankton taxonomic groups in terms of their numerical abundance, length frequency distribution, and estimated wet weight (Davis and Wiebe, 1985; Lavery et al., 2007). The photographs (8x10”) were scanned to 1200 dpi. The silhouette procedure and a description of the software used is given by Little and Copley, 2003. In most cases animals were identified to a taxonomic group such as copepod or euphausiid, although some were classified more specifically, e.g. *Limacina retroversa* (shelled pteropods), *Clione limacina* (naked pteropod). In the case of siphonophores, which often fall apart upon capture in the nets, pneumatophores, bracts, and nectophores were counted and measured separately.

The silhouette data were used to calculate invertebrate predation impact on *C. finmarchicus* in the Gulf of Maine for each of the tows listed in Table 2 except for EN330 MOC1. For each measured individual, the length data were converted into wet weight using taxa specific equations developed by Davis and Wiebe (1985) and subsequent additions for taxa not considered originally. Wet weights were converted to carbon weights based on taxa specific conversion factors also given by Davis and Wiebe (1985) and others. The taxa-specific data were converted to abundance and standing stock of carbon based on the aliquot size, number of photographic cells measured (counted), and volume filtered by the net.

Estimated carbon requirement of each animal in a sample was based on the individual carbon estimate and the average water temperature for that sample. Using the equation by Ikeda (1985):

$$\ln(y) = a0 + a1 * \ln(x1) + a2 * x2$$

where $x1$ is body mass in mg carbon units, $x2$ is temperature in ^{o} C, $a2$ is related to Q10 by Q10= exp(10*$a2$), and y = oxygen consumption in μl O_2/individual/hr. $a0$, $a1$, and $a2$ are constants given by Ikeda et al. (2000) in their Table 10.2 - Note the equation 1 is mistyped in Ikeda et al., (2000).

Conversion of oxygen consumption to carbon was done using:

$$\text{mgC/individual/hr} = \text{ml } O_2\text{/individual/hr} * RQ * 12/22.4.$$

where 12/22.4 is the weight (12 g) of carbon in 1 mole (22.4 1) of carbon dioxide and RQ = 0.97. As noted by Ikeda et al., (2000), the carbon requirement can be used as an index of minimum food requirement when assimilation efficiency and growth are not considered. See Ikeda et al., (2000) for more details.

In the computation, small copepods, *Limacina*, crustacean larvae, cyphonautes, ostracods, and salps were considered competitors of *C. finmarchicus*, and large copepods, decapods, euphausiids, amphipods, chaetognaths, siphonophores, medusae, polychaets, and fish larvae were considered its invertebrate predators (we acknowledge that other fish predators may have been present, but we have no data on other predators in our data set).

In summary, length measurements of taxa in a sample were measured and converted to carbon. Then using the temperature for the tow/sample, the O_2 consumption for each individual was computed. The O_2 consumption was then converted to a carbon food requirement. The standing stock of the taxa as competitors and predators, and the food requirement of predators, in terms of carbon estimated for each depth strata sampled and for the entire water column, then were calculated and compared to the carbon in *C. finmarchicus*. Days to consume *C. finmarchicus* was calculated by dividing *C. finmarchicus* (mgC/m2) by the predator carbon (mgC/m2/day).

2.2.3 Acoustics.

Volume backscattering strength, S_v (where $S_v = 10\log10(s_v)$ in units of decibels, and s_v is the observed volume backscattering coefficient), is a measure of the intensity of emitted sound that is scattered back to the source per cubic meter. All transducers were acoustically calibrated by the manufacturer (Hydroacoustic Technologies Inc., Seattle, WA, USA) each year for source level, receive sensitivity, as well as transmit and receive beam patterns (Supporting Information Appendix A). An in-situ calibration also was performed prior to some cruises with a 38 mm tungsten carbide (6% cobalt) standard target, following established practices (Foote *et al.*, 1987).

Acoustic data from the up- and down-looking transducers were combined to provide a nearly continuous vertical acoustic record extending from the surface to at least 200 m, and at most 350 m, depending on the position of the BIOMAPER-II along its towyo path. This acoustic record then was edited using custom MATLAB-based routines to remove unwanted returns from the surface bubble layer and the bottom. Noise spikes also were manually removed based on visual scrutiny. Measurements of integrated backscattering were separated by day and night, and data for an hour at dawn and dusk were excluded from this analysis to eliminate possible bias from diel vertical migration. The data were used to produce average day and night profiles for each basin starting at 20 m and extending down to 200 m in 10 m intervals. This depth range was chosen since the surface bubble layer sometimes obscured measurements shallower than 20 m and all three basins had acoustic data to 200 m. In addition to mean values, 0th (minimum), 10th, 25th, 50th (median), 75th, 90th, and 100th (maximum) percentiles were computed. The total integrated S_V (dB) values per m^2 for each basin were also computed for each cruise. For EN307 in Jordan Basin, none of the surveying was done during daylight.

3. RESULTS

3.1 *Calanus finmarchicus* Abundance and Size in the Gulf of Maine.

For *Calanus finmarchicus,* autumn and winter is normally the period when the population is in diapause well below the surface throughout the North Atlantic (Hirche, 1996; Heath et al., 2004). This deep diapausing stock was true for the Gulf of Maine, with most of the *C. finmarchicus* population found below 100 m on all five cruises (Figure 3). Maximum concentration was seldom in the bottom net, but was instead at some intermediate depth. In spite of the expectation that the population should have been absent from the surface waters, there were always *C. finmarchicus* present there. Most individuals throughout the water column were C5 copepodids. The percentages varied between 77 and 95%, except for a single tow (Georges Basin, October 1998) which had 45.6% C5s and 38.8% C4s. Females and males were present in small numbers (Table 3) at times occurring in the upper 50 m. C4s were also present in all tows, often occurring at depth, but sometimes also in significant numbers in the upper 50 meters. C3s were present in all but four of the twenty-one tows, occurring mostly in the upper 50 m. On the four tows where C2s occurred, they were also in surface waters.

The depth distribution properties of the *C. finmarchicus* population were determined from plots of the cumulative frequency distribution of individuals from the surface to the maximum depth of tow. The 17, 50, and 83 centiles were used to determine the central depth distribution instead of 50 to75% to match what was done by Heath et al., 2004 and the relationship of the bulk of the population to temperature and salinity properties determined from sensors on the MOCNESS in a manner similar to that described by Heath et al., 2004. The center of distribution of the population generally fell between 100 and 200 m (Figure 4). Only in Georges Basin did the center occur between 200 and 250 m (October 1997 and 1998, and December 1999). The depth range of the central 66% of the population (17th to 83rd percentile) was usually less than 100 m and occasionally as narrow as 50 m.

The range of temperatures and salinities corresponding to the depth ranges inhabited by the core of the population was 7 to 8 ^{o}C and 33.3 to 35 PSU in 1997 and somewhat lower in 1998 (6 to 7.5 ^{o}C and 32.6 to 34.9 PSU) coinciding with the influx of colder fresher Labrador Slope Water into the Gulf of Maine (Townsend et al., 2015). In October and December1999, *C. finmarchicus* experienced much warmer and saline conditions (7.5 to 9.7 ^{o}C; 33.8 to 35.1 PSU) with the exception of those residing in Wilkinson Basin in October 1999. There they experienced slightly lower temperatures and saline conditions similar to those present in 1998 (5 to 6.5 ^{o}C; 32.7 to 33.8 PSU). Thus, the central portion of the population experienced substantial variation in temperature and salinity while maintaining a fairly steady depth distribution (Figure 4).

The 2-way ANOVA for October revealed significant differences in *C. finmarchicus* C5 size between years and basins (Table 4). A multiple comparison test (Matlab multcompare) showed that the C5s were significantly smaller in Georges Basin than either Jordan or Wilkinson Basin ($p < 0.05$), but in the latter two, they C5s were not significantly different in size ($p > 0.05$). In 1998, C5s were significantly smaller than 1997 or 1999 ($p<0.01$, Table 4). In the December case, 1998 had significantly ($p<0.01$) smaller C5s than in 1999, and the basins were significantly different from each other with GB having the smallest

C5s, WB intermediate in C5 size, and JB having the largest C5s ($p < 0.05$). The three-way ANOVA that included months (Oct, Dec), years (1998, 1999), and basins (WB, JB, GB), showed significant size differences ($p<0.01$) existed between all three parameters. A multiple comparison test revealed that December C5s were significantly smaller than in October ($p < 0.05$). The C5s were significantly smaller in 1998 than in 1999, and GB had significantly smaller *C5s* than either WB or JB ($p < 0.05$), which were not different (Table 4).

GMM analysis of the size frequency distribution of the C5 individuals below 150 m depth in October and December showed a multimodal pattern in 1997 and 1999, but a single mode in 1998 (Figure 5 A, B). The modes are indicated by the red lines on each plot. The single mode in both October and December of 1998 indicates the demise of an early cohort of the diapausing stock.

3.2 Vertical Distribution of Biovolume and Taxa.

The vertical distribution of zooplankton biovolume varied substantially between basins and between sampling times (Figure 6). Highest values can occur in all depth levels - surface waters, intermediate depth range, and in the deepest sampled depth. A part of the inconsistency could be related to diel vertical migration (Baumgartner et al., 2011). For Wilkinson Basin, which had day/night tow pairs on four of the five cruises, surface values were lower during the day than at night on three of them, indicating some diel vertical migration.

The contribution of *C. finmarchicus* to the zooplankton biovolume measurements varied between years. A regression analysis of the vertical distribution of zooplankton biovolume versus *Calanus finmarchicus* wet weight (as computed from individual lengths determined by stage during counting individuals in each net) was conducted (Figure 7). If the depth distribution for the total water column sampled is compared, the relationship between these two variables is slightly positive for 1997, slightly negatively related for 1998, and more strongly positively related in 1999. Only the 1999 relationship is significant ($p<0.01$), however. If only samples deeper than 100 m are considered, the relationships are stronger and positively significant in 1997 and 1999. Although the regression is not significant with our sample size ($p = 0.41$, $n = 28$), the apparent negative relationship for 1998 suggests that, as other components of the invertebrate biomass increased, *C. finmarchicus* did not change significantly. Based on the silhouette data, euphausiids and medusae (*Calanus* predators) dominated the biomass in 1998 as described below.

3.3 Vertical Distribution from Acoustic Backscattering Data.

The high frequency volume backscattering data provided the most complete coverage of the Gulf of Maine basins on the cruises (Figure 1). Although the backscattering data did not measure the distribution of the biomass of the zooplankton and micronekton directly, the composition of organisms and their scattering characteristics, in addition to biomass, influence total backscattering, so overall patterns in the acoustics data can augment the interpretations of the net tow data. The vertical distribution of the 200 kHz volume backscattering integrated in 10 m bins from 20 m to 200 m (Figure 8) were similar to the vertical patterns observed at 120 and 420 kHz (not shown). The observations at 200 kHz were chosen for presentation as a balance between water column coverage (i.e., sampling to greater ranges than at 420 kHz) and optimizing for small zooplankton (i.e., better than 43 and 120 kHz).

Water column-integrated day and night volume backscattering values for each basin were essentially the same during all cruises, so there was no significant day/night bias (Table 5; p = 0.9 – 1-way Anova). There were, however, clear day/night shifts in some of the vertical profiles of volume backscattering (Figure 8). During the day, depths below 100 m generally had larger Sv and surface values were lower. The reverse generally occurred at night. The differences were most evident in 1999 (both October and December) and much less apparent in December of 1998 when the changes between day and night in Wilkinson and Georges Basin were small.

3.4 Vertically Integrated Abundance Patterns for the Three Years.

The abundance of *C. finmarchicus* was an order of magnitude lower in 1998 than it was in 1997 or 1999. The water column-integrated numbers of *C. finmarchicus* during the three years ranged from 15,686 to 86,341 per m^2 in 1997, 2,168 to 6,962 per m^2 in 1998, and 14,119 to 85,359 per m^2 in 1999 (Figure 3). Georges Basin usually had the lowest numbers per m^2 for each sampling period and it also had the smallest C5s for all three years (Figure 3). There was not a substantial difference in the abundance between the October and December in 1998 and 1999. The dramatic drop in the abundance during 1998 compared to 1997 and 1999, however, was statistically significant ($p < 0.001$- 1-way Anovan. The drop was Gulf-wide with the lowest values recorded in Georges Basin.

The integrated values of biovolume, total numbers of copepods from the silhouette analysis, and integrated volume backscattering data did not show the dramatic drop that the *Calanus finmarchicus* abundance showed (Figures 6, 7, 8). There was a not a significant drop in the integrated biovolume during 1998 compared to 1997 and 1999 ($p > 0.1$ - Wilcoxon test) that paralleled that observed significant drop in the *C. finmarchicus* abundance data (Figure 9).

The major zooplankton taxonomic groups in terms of their numerical abundance and estimated wet weight biomass (as determined by silhouette analysis) were copepods (2 categories < 2.5 mm and >= 2.5 mm), euphausiids, decapod shrimp, pteropods (*Limacina* sp), medusa, siphonophores, and salps. Numerous other categories that were not as abundant were combined into the other category (Figure 10). In 1997 and 1999, copepods were dominant. In contrast, in 1998, there were fewer copepods, and predators dominated, including euphausiids, decapods, medusae, and siphonophores (Figure 10). There was significantly higher percent biomass of predators in 1998 than in 1997 or 1999 (p = 0.014 1-way Anovan test). The pteropod, *Limacina retroversa,* was also very abundant, especially in Georges and Jordan Basin.

3.5 Comparison of the GoM *Calanus* Distributions to those in Slope Water.

Diapausing *C. finmarchicus* were present below 400 m in the Slope Water from June until March 1980-81 (Figure 3 in Miller et al., 1991 – Figures 12, 13). This pattern was very different from what was observed in the Gulf of Maine, where the C5s leave diapause and begin molting to adult in January (Davis 1987b; Lynch et al. 1998). The size of *C. finmarchicus* C5s in the Slope Water was slightly larger than those in the Gulf of Maine (Figure 6) and much lower in abundance. The diapausing depth of

C. finmarchicus in the Slope Water (>400m) was well below the sill depth of the Northeast Channel (~230 m).

4. DISCUSSION

The motivation for studying the GoM diapause stock of *Calanus finmarchicus* during the GLOBEC years (1995 to 1999) was to examine the hypothesis that processes regulating the survivorship and supply of *C. finmarchicus* from diapausing stocks in the deep basins of the Gulf of Maine determine its annual production on Georges Bank (Clarke et al. 1943; Davis 1987a; GLOBEC 1992). The cruises in fall of 1997, 1998, and 1999 were designed to determine what processes regulate the abundance and survivorship of these diapausing *Calanus* stocks.

Following the abrupt drop in the NAO index in 1996, the Labrador Current intensified, making a larger than usual contribution to the Slope Water during 1998 and replacing the warm Slope Water that typically occurs there and in the GoM (Pershing et al., 2001; Mountain, 2012; Townsend et al. 2015). It apparently entered the GoM in 1998. It was hypothesized that the low abundance of diapausing *C. finmarchicus* in the deep basins during fall 1998 was due to a reduction in its supply to the Gulf of Maine (Greene and Pershing, 2000, Pershing et al., 2001). Since both Labrador Slope Water and Warm Slope Water have an order of magnitude lower abundance of *C. finmarchicus* than the GoM, differences between these “sources” is not a viable explanation, as both inflows would reduce the diapause stock. While a disruption of advective supply from the Western Scotian Shelf has been hypothesized (Greene et al., 2013), we have seen no data that can be directly attributed to *C. finmchicus* CVs advected into the GoM from the Scotion Shelf Water in the fall. In this paper, we examine an alternative hypothesis - that enhanced invertebrate predation reduced the *C. finmarchicus* population in the GoM before and during fall of 1998. We examine this hypothesis by analyzing the size structure of diapausing individuals and the energy demand of potential predators in the years before, during, and after 1998.

4.1 C. finmarchicus Diapause Depth in the Gulf of Maine.

Previous modeling has suggested that a significant number of diapausing *C. finmarchicus* C5s must reside below 200 m in the deep basins of the Gulf of Maine in order to produce the observed population in the GoM in the spring time (Lynch et al., 1998). They indicated that the numbers of the unmeasured deep population had to be similar to that measured by the MARMAP surveys in the GoM (which had a maximum sampling depth of 200m, Meise and O'Reilly (1996). Our sampling to just above the bottom in the GoM basins showed that most of the diapausing C5s occurred between 100 and 200 m (Figure 3), not next to the bottom and thus not in support of the Lynch et al. (1998) contention. Field data from Head and Pepin (2008) also showed that in some inshore areas of the Canadian NW Atlantic Continental Shelf, highest abundance of diapausing *C. finmarchicus* were below 100 m, but well above the bottom (i.e. Cabot Strait), which they attributed to possible predator avoidance.

4.2 Comparison with Slope Water and Other Parts of the North Atlantic.

Bigelow (1926) described the GoM as a "*Calanus* community". Its high abundance in this region equals or exceeds that in other regions of the North Atlantic (Melle et al., 2014). Abundance of *C. finmarchicus* in the deep basins of the GoM ranged from 15,666 to 86,341/ m^2 in fall 1997, and from 14,119 to 85,359 / m^2 in fall 1999. In contrast, the *C. finmarchicus* abundance ranged between 2,168 to 6,962 /m^2 in the fall of 1998 (Figure 3). Except for Georges Basin in which the central portion of the population was in 200 to 250 m depths, the central portion of *C. finmarchicus* in the other basins was between 100 and 200 m. Temperatures were above 6 ^oC up to 9 ^oC and salinities ranged from 33 to 35 PSU (Figure 4). In the Slope Water time series, *C. finmarchicus* was primarily at the surface during the period of the spring bloom in March through early June (Figure 12). The rest of the year, C5s were diapausing at depth. The values of *C. finmarchicus* ranged from 500 to 23,000 /m^2 (Figure 12) and the diapausing population was found below 400 m and in temperatures below 6 ^oC (Figure 13). Salinities (not measured on the tows) experienced by *C. finmarchicus* would normally range from 34.8 to 35 PSU for *Calanus* at these depths. In an earlier study, Mullin (1963) found high abundance of *C. finmarchicus* in Wilkinson Basin that ranged from ~3,000 /m^2 in early spring (March 1962) to 41,000 /m^2 in June 1963.

In other portions of its range in Northern Atlantic and Norwegian Sea, Heath et al. (2004) reported abundances of stage C4-C5 *C. finmarchicus* ranging from >15,000 /m^2 in the Labrador Sea, northern Irminger Basin, northern Iceland Basin, Faroe-Shetland Channel/eastern Norwegian Sea, and Norwegian Trench of the eastern North Sea. The Faroe-Shetland Channel and Norwegian Sea had abundances >40,000 /m^2. The depths of the diapausing *C. finmarchicus* in the North Atlantic are below 500 m to around 1500 m with temperatures ranging around 4 ^oC down to 0 ^oC and salinities were below 35 PSU, except in the Rockall Basin and Norwegian Trench where temperature were around 8 ^oC and salinities above 35 PSU. These latter regions also had much lower *C. finmarchicus* abundances. In the Labrador Sea, Head and Pepin (2008) reported abundances of *C. finmarchicus* > 600 m down to 2000 m between 9,000 and 20,000 /m^2 in winter 2002. Higher abundances (> 30,000 /m^2) occurred southwest of the tail of the Grand Bank and in Cabot Strait region (~46,000 /m^2). In the Slope Water off the Western Scotian Shelf, the abundances (4,000-21,000 /m^2) were similar to those in the Slope Water south of New England (Miller et al., 1991; Figure 12). At two stations in the shallow water regions of the Grand Banks and Flemish Cap, very high abundances of late-stage (C4-C6 stages of *C. finmarchicus* occurred (> 100,000 /m^2) in ring net tows. Similar high abundance of *C. finmarchicus* C5s (mixed with *C. helogolandicus*) were noted by Halvorsen et al., (2003) in the waters of the Norwegian Sea west of Trompso in the Trompso Basin in the Norwegian Sea. They ranged from 70,000 to 150,000 /m^2 and were mainly diapausing at depths of 700 to 1200 m. The *C. finmarchicus* abundances in the Gulf of Maine in Fall 1997 and Fall 1999 were as high or higher than those found elsewhere in the North Atlantic.

4.3 Physiological Consequences of Diapausing at Warm Temperatures.

Most diapausing *C. finmarchicus* reside between 100 and 200 m in the GoM, with salinities between 33 and 35 PSU, and temperatures well above 6 ^oC. Current physiological models predict short diapause (<90 days) at these temperatures due to early depletion of lipid reserves (Saumweber and Durbin, 2006; Ingvarsdottir et al, 1999; Jónasdóttir, 1999). One consequence of a short diapause period is an early end of diapause and return to the surface before the spring bloom (Saumweber and Durbin, 2006; Johnson et al., 2008). Head and Pepin (2008) also noted that diapausing *C. finmarchicus* were found in high concentrations in a wide range of temperatures ranging from 2 to 9 ºC and were uncertain of the effects on the populations residing in high temperatures. Exiting diapause early could result in higher predation risk and reduced survivorship.

4.4 Enhanced Predation Being Important in 1998.

The silhouette data and the derived total *C. finmarchicus* carbon and predator carbon consumption rates suggested that invertebrate predators as defined in the Methods could have had a major impact on the *C. finmarchicus* population (Table 6). There were substantial differences fall estimates of predator consumption of *C. finmarchicus* in some or all of the GoM basins especially in December of 1998 (OC334 - Figure 11). The fall 1998 estimates of the time to consume *Calanus* was significantly lower than in 1997 and 1999 (p = .0211 – one way Anovan). By contrast the competitors of *C. finmarchicus* had lower biomass and overall consumption rates in 1998 than other years, so that competition is an unlikely cause of the *Calanus* decline. In addition, *Calanus* biomass was relatively lower than that of its competitors in 1998, suggesting that *Calanus* may have been the preferred prey of the invertebrate predators.

Durbin et al., (1995) found deep diel vertical migration of the *C. finmarchicus* population in the 1988 SCOPEX study site in the southern portion of the Wilkinson Basin, but essentially none in the following year, and suggested that the diel migration was likely to be in response to the variable presence of predators. Baumgartner et al. (2011) found similarly variable diel vertical migration in the southwestern Gulf of Maine and attributed the observed variability to *C. finmarchicus* feeding history (i.e., lipid accumulation) and predation. Based on the acoustics data presented in Figure 8, DVM was stronger in 1997 and 1999, and almost non-existent in 1998. The implication is that enhanced predation reduced the numbers of *C. finmarchicus* in 1998 and caused a decline in DVM in 1998. In addition, the single mode in the size distribution in 1998 (Figure 5) indicates the demise of an early cohort of the diapausing stock.

In a comparison of mortality rates of *Calanus finmarchicus* in five locations in the North Atlantic (Georges Banks, the northern North Sea, Ocean Station M, Lurefjorden, and Sørfjorden), Ohman et al. (2004) found that the observed mortality rates were appreciably higher than those determined in mesocosms with few predators. They concluded that natural populations experience significantly higher mortality than might be expected due to physiological shortcomings alone. Ohman et al. (2004) also concluded that *"In those situations where the predator field has been well characterized, regional variations are clearly relatable to different types of predators with different prey selection characteristics. We expect that such differences in predator fields underlie the remaining geographic variations, although this issue requires direct quantitative test. Just as local variations in the primary production cycle can generate different rates of population increase, spatial differences in the rates, patterns, and causal agents of mortality will influence the dynamics of Calanus finmarchicus in different sectors of the Atlantic."*

A recent study that applied model-based scaling and sensitivity analyses to the MARMAP and the EcoMon regional plankton dataset collected over the last four decades (1977-2017) revealed that interannual variability of the *C. finmarchicus* population in the GoM was driven by both internal population dynamics and external exchanges, with the relative importance of each driver depending on the season (Ji et al., 2021). The internal dynamics could be the dominant driver for the spring growing season across all three basins; while the role of the external exchange is basin-dependent. For example, Georges Basin could be more influenced by a Slope Water intrusion than the other two basins due to its proximity to the Slope Water, suggesting a Gulf-wide decline of diapausing stock could be caused by drivers other than Slope Water intrusion. Our data support the hypothesis that predators in the Gulf of Maine strongly influence the mortality of *Calanus finmarchicus,* agreeing with previous studies on predatory control of copepod populations on Georges Bank (Davis, 1984), in Disko Bay, Greenland (Banas et al., 2021), southwest of Iceland (Gislason et al., 2007), in Norwegian fjords (Bageon et al., 2001; Eiane et al., 2002), and in the Barents Sea (Kvile et al., 2021). The estimates of days to consume resident *C. finmarchicus* in the GoM suggest that increased predation caused the low abundances of *C. finmarchicus* adults observed in 1998 (Figure 11; Table 6). A significantly higher percent biomass of predators occurred in 1998, especially euphausiids and medusae (Figure 10). Thus, predation loss rather than advective supply provides a viable explanation for the low abundance of diapausing *C. finmarchicus* in the GoM in 1998.

5. CONCLUSIONS

1) Diapausing populations of *Calanus* in the Gulf of Maine had abundances per m^2 in 1997 and 1999 that are among the highest observed in the North Atlantic Ocean.

2) The *C. finmarchicus* population in the Gulf of Maine lives at shallower depths and warmer temperatures than the population in the adjacent Slope Water.

3) There was a significant and marked decline in the abundance of diapausing *C. finmarchicus* in the Gulf of Maine during the fall of 1998, relative to 1997 and 1999.

4) The lower abundance of GoM *C. finmarchicus* in 1998 was coincident with the lagged hydrographic effects of the 1995-1996 negative NAO, which dramatically altered the NW Atlantic's coupled Slope Water system. However, both Labrador Slope Water and Warm Slope Water have an order of magnitude lower *C. finmarchicus* abundance than the GOM, eliminating supply from these sources as a viable explanation for the lower abundances observed in 1998.

5) Total water column biovolumes and acoustic backscattering were similar among years due to a marked proportional increase in invertebrate predators of *C. finmarchicus* in 1998. Estimated predation rates associated with these invertebrate predators could account for the reduction of the 1998 *C. finmarchicus* diapause stock to the observed levels as spring C. finmarchicus production was similar between years.

6) In general, predation can play a key role in copepod population dynamics and should be examined more closely in future studies.

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Figure Legends

Figure 1. Distribution of cruise tracklines in the Gulf of Maine along which BIOMAPER-II acoustic, optical, and environmental data were collected in fall of 1997, 1998, and 1999. The bold red lines indicate where BIOMAPER-II was being towyo'd. WB- Wilkinson Basin, JB- Jordan Basin, and GB - Georges Basin.

Figure 2. Distribution of 1-m^2 MOCNESS tows taken on the fall cruises to the Gulf of Maine in 1997, 1998, and 1999 (indicated by the numbers and symbols). The circled tows are those that have been processed.

Figure 3. The vertical distribution (individuals/m^3) of *Calanus finmarchicus* collected in the three major basins in Gulf of Maine during the fall of 1997, 1998, and 1999 as stacked horizonal bars with the various copepodid stages indicated by the colors. WB- Wilkinson Basin, JB- Jordan Basin, and GB - Georges Basin. Bottom depth indicated by diamond on each vertical plot. Total (vertically integrated) abundance individuals/m^2 also is given for each profile. Day and Night tows indicated by N and D in the Cruise tow number at the top of each plot.

Figure 4. The distribution of the central 66% portion (17th to 83rd percentile) of *Calanus finmarchicus* sampled in the Gulf of Maine in 1997, 1998, and 1999 as a function of depth, temperature, and salinity measured with the MOCNESS sensors. The dotted lines provide a context for viewing relationship between depth, temperature, and salinity. WB- Wilkinson Basin, JB- Jordan Basin, and GB - Georges Basin.

Figure 5, *Calanus finmarchicus* C5 size distribution in 1997, 1998, 1999 taken from samples below 150 m. Cohorts were decomposed using a Gaussian Mixture Model (GMM). μ is the mean of a probability distribution, σ is the standard deviation of the Probability Distribution Function (PDF), and p is the

Component Proportion, n is the number of observations. The red line on the plots demarks the modes. WB- Wilkinson Basin, JB- Jordan Basin, and GB - Georges Basin.

Figure 5A. October size distribution of *Calanus finmarchicus* C5s (1997, 1998, 1999)

Figure 5B. December size distribution of *Calanus finmarchicus* C5s (1998, 1999).

Figure 6. The vertical distribution of MOCNESS zooplankton biovolumes collected in the three major basins in Gulf of Maine during the fall of 1997, 1998, and 1999. WB- Wilkinson Basin, JB- Jordan Basin, and GB - Georges Basin. Total integrated biovolumes as cubic centimeters (cc) per m^2 are given for each profile. Day and Night tows indicated by N and D in the Cruise tow number at the top of each plot. The line with the double-sided arrow distinguishes October data from December data.

Figure 7. The relationship between total zooplankton biovolume and the wet weight of *Calanus finmarchicus* by years for all MOCNESS tow depths and only those greater than 100 and 150 meters. *C. finmarchicus* wet weights determined from a length to ww relationship.

Figure 8. The day/night vertical distribution of volume backscattering at 200 kHz in the three major basins in Gulf of Maine during the fall of 1997, 1998, and 1999. WB- Wilkinson Basin, JB- Jordan Basin, and GB - Georges Basin. Each plot gives median backscattering in 10 m depth bins between 20 and 200 m, and the error bars on that show the 25th and 75th percentiles. Day is blue; night is red. The line with the double-sided arrow distinguishes October data from December data.

Figure 9 Time-series changes in integrated values of a) *Calanus finmarchicus*, b) total biovolumes, c) average volume backscatter at 200 kHz, d) silhouette total copepod counts, and e) biomass of *Calanus* (square) and total copepods (triangle) based on length to wet weight relationships. The individual symbols in each plot represent integrated values for a MOCNESS tow, except for the volume backscattering (SV) where individual symbols represent the mean from a particular tow.

Figure 10. The percent composition of zooplankton taxa based on silhouette data for each MOCNESS net that were integrated for the water column. The minor contributors to both abundance and biomass are grouped as “others”.

Figure 11. Predation pressure on *C. finmarchicus* in the GoM based on estimates of the carbon in *C. finmarchicus*, invertebrate competitors and predators based on Silhouette analysis of the MOCNESS samples and Ikeda’s 1985 model of oxygen uptake as a function of individual length and temperature. Note: the half-year increments on the X-axis are given as .5.

Figure 12. The vertical distribution of *Calanus finmarchicus* collected in the Northwest Atlantic Slope Water during 1981 and 1982 south of New England. Total integrated numbers per m^2 are given for each profile. Most vertical profiles published by Miller et al., (1991) as cumulative percents as a function of depth by stage.

Figure 13. The distribution of the central portion (17th to 83rd percentile) of the *Calanus finmarchicus* population sampled in the North Atlantic Slope Water in 1981 and 1982 as a function of depth and temperature. The numbers above the month designations are the year-days when the tows were taken. Note there are two May values and two October values in 1981 and two March values in 1982. Environmental data not published by Miller et al., (1991) as presented herein.

Table 1. Information about each cruise used in this paper. The Tracklines are illustrated on Figure 1.

Ship/Cruise	Cruise Dates	BIOMAPER-II Trackline distance
R/V Endeavor 307	7-17 October 1997	1017.1km; 549.2nm
R/V Oceanus 332	19-28 October 1998	558.6km; 301.6nm
R/V Oceanus 334	3-13 December 1998	929.6km; 502.0nm
R/V Endeavor 330	16-24 October 1999	1085.6km; 586.2nm
R/V Endeavor 331	4-14 December 1999	876.3km; 473.1nm

Table 2. MOCNESS tow information (21 tows). Bottom depth estimated using etopo1 data. WB-Wilkinson Basin; JB-Jordan Basin; GB-Georges Basin.

Cruise	Day/Month/Year	Basin	Time In*	Time Out*	Lat In	Lon In	Lat Out	Lon Out	Max Depth of Tow (m)	Bottom Depth (m)
En307m9_N	16/Oct/1997	WB	289.898600	289.942789	42.48	-68.75	42.51	-68.77	180	185.4
En307m7_D	14/Oct/1997	WB	287.619500	287.676898	42.40	-68.82	42.41	-68.74	190	205.75
En307m4_N	12/Oct/1997	JB	285.048600	285.098345	43.52	-67.89	43.55	-67.89	240	245.17
En307m3_N	10/Oct/1997	GB	284.151430	284.206481	42.42	-67.00	42.44	-67.05	344	363.05
Oc332m1_N	22/Oct/1998	WB	295.808700	295.860160	42.60	-69.76	42.63	-69.75	175	235.75
Oc332m2_D	23/Oct/1998	WB	296.586280	296.635660	42.38	-69.07	42.37	-69.01	200	212.91
Oc332m3_D	24/Oct/1998	JB	297.617100	297.663870	43.78	-67.60	43.75	-67.63	225	231.25
Oc332m4_N	24/Oct/1998	JB	297.960200	298.012190	43.28	-67.83	43.25	-67.84	230	234
Oc332m6_N	26/Oct/1998	GB	299.854100	299.908320	42.30	-66.89	42.32	-66.84	280	290.9
Oc334m1_N	04/Dec/1998	WB	338.963180	339.027770	42.39	-69.13	42.39	-69.07	215	223.7
Oc334m3_N	06/Dec/1998	JB	343.006940	343.063190	43.35	-67.99	43.39	-67.97	235	240.15
Oc334m5_D	06/Dec/1998	GB	343.629830	343.703660	42.34	-67.66	42.34	-67.57	223	241.43
En330m1_D	17/Oct/1999	WB	290.607000	290.634010	42.25	-69.25	42.26	-69.28	195	206.25
En330m2_N	18/Oct/1999	WB	294.01597	294.0806	42.42	-69.82	42.42	-69.80	241	246.75
En330m4_D	20/Oct/1999	JB	294.66597	294.71458	43.51	-67.17	43.53	-67.22	208	200.7
En330m5_N	22/Oct/1999	JB	295.00903	295.05278	43.64	-67.51	43.61	-67.52	215	223.11
En330m6_N	24/Oct/1999	GB	297.84236	297.90763	42.32	-67.60	42.33	-67.68	240	257.65
En331m2_N	04/Dec/1999	WB	338.95694	339.001380	42.27	-69.31	42.26	-69.35	200	211.3
En331m5_N	06/Dec/1999	JB	340.91319	340.95764	43.83	-67.72	43.80	-67.70	225	213.82
En331m4_D	06/Dec/1999	JB	340.51458	340.562500	43.32	-68.00	43.28	-68.01	211	235.6
En331m6_N	08/Dec/1999	GB	343.90138	343.968056	42.50	-67.08	42.49	-67.03	200	333.8

*- Year-day.Time in fractions of a day.

Table 3. Percent of *Calanus finmarchicus* in stages C2 to C6 in MOCNESS tows based on integrated counts from all eight nets. Cruise WB = Wilkinson Basin; JB = Jordan Basin; GB = Georges Basin.

Cruise	Month/Year	Basin	female	male	C5	C4	C3	C2
En307m9	Oct/1997	WB	4.87	0.03	81.69	13.26	0.16	0.00
En307m7	Oct/1997	WB	2.27	0.16	88.29	4.10	3.52	1.66
En307m4	Oct/1997	JB	1.77	0.22	77.55	20.46	0.00	0.00
En307m3	Oct/1997	GB	2.28	0.23	88.79	8.61	0.09	0.00
Oc332m1	Oct/1998	WB	3.09	0.55	70.97	24.00	1.39	0.00
Oc332m2	Oct/1998	WB	5.19	1.67	78.27	14.66	0.22	0.00
Oc332m3	Oct/1998	JB	2.01	0.79	65.67	27.84	3.51	0.18
Oc332m4	Oct/1998	JB	6.31	1.39	78.33	13.97	0.00	0.00
Oc332m6	Oct/1998	GB	1.67	0.27	45.55	38.78	13.72	0.00
Oc334m1	Dec/1998	WB	1.69	0.58	79.05	18.22	0.45	0.00
Oc334m3	Dec/1998	JB	2.20	0.79	80.98	15.37	0.63	0.03
Oc334m5	Dec/1998	GB	6.90	2.19	77.22	13.69	0.00	0.00
En330m1	Oct/1999	WB	1.43	0.18	84.61	13.77	0.00	0.00
En330m2	Oct/1999	WB	1.92	0.16	85.07	12.72	0.11	0.01
En330m4	Oct/1999	JB	1.24	0.21	93.53	5.01	0.00	0.00
En330m5	Oct/1999	JB	1.74	0.09	90.15	8.01	0.02	0.00
En330m6	Oct/1999	GB	3.11	0.28	82.91	13.68	0.02	0.00
En331m2	Dec/1999	WB	3.84	1.98	86.25	7.81	0.12	0.00
En331m5	Dec/1999	JB	1.32	0.80	93.81	4.06	0.01	0.00
En331m4	Dec/1999	JB	1.83	1.02	95.30	1.84	0.01	0.00
En331m6	Dec/1999	GB	1.96	0.47	89.96	7.59	0.01	0.00

Table 4. *Calanus finmarchicus* C5 statistics (Mean size, Standard deviation, and number of observation) by basin, months, and years. Slope Water C5 values are included for comparison with the Gulf of Maine values. Wilkinson basin = WB, Jordan basin = JB, Georges basin = GB, Slope Water = SW.

Year	WB	std	N	JB	std		GB	std	N	Basin means
1997 Oct	2.228	0.2461	344	2.351	0.2346	303	2.196	0.2240	597	2.26
1998 Oct	2.228	0.2268	264	2.160	0.2021	318	2.161	0.1894	558	2.18
1998 Dec	2.114	0.2140	220	2.117	0.2069	210	2.021	0.1666	446	2.08
1999 Oct	2.262	0.2790	570	2.248	0.2243	434	2.157	0.2002	155	2.22
1999 Dec	2.171	0.2311	227	2.257	0.2510	498	2.119	0.2242	442	2.18
Mean	2.20			2.23			2.13			
OctMeans	2.24			2.25			2.17			
DecMeans	2.14			2.19			2.07			
	SW									
1981 Oct	2.321	0.1860	29							
1981 Dec	2.224	0.1946	29							

Table 5. Mean values of 200 kHz acoustic data for depth interval 20 to 200 m. The mean S_v is expressed in dB (10*log10(s_v). There were no day data in Jordan basin. The nighttime (nt)-day differences are not significantly different at the p = 0.9 level (1-way Anova). Wilkinson basin = WB, Jordan basin = JB, Georges basin = GB.

cruise_Basin	Year_month	Night	Day	nt - day
en307_GB	1997 Oct	-64.5862	-67.7064	3.1202
en307_JB	1997 Oct	-67.4687	-	-
en307_WB	1997 Oct	-67.8637	-69.1834	1.3197
oc332_GB	1998 Oct	-70.3786	-67.7376	-2.6410
oc332_JB	1998 Oct	-66.8753	-69.2102	2.3348
oc332_WB	1998 Oct	-66.7779	-66.7122	-0.0657
oc334_GB	1998 Dec	-62.8006	-61.4028	-1.3979

oc334_JB	1998 Dec	-62.0602	-62.1371	0.0769
oc334_WB	1998 Dec	-62.4439	-62.7466	0.3027
en330_GB	1999 Oct	-68.2266	-67.2492	-0.9775
en330_JB	1999 Oct	-63.4989	-64.3849	0.886
en330_WB	1999 Oct	-67.4132	-68.0534	0.6402
en331_GB	1999 Dec	-64.6574	-65.7603	1.1029
en331_JB	1999 Dec	-65.9626	-63.5816	-2.3809
en331_WB	1999 Dec	-64.4086	-63.8081	-0.6005
			Mean Diff	1.7199

Table 6. Estimates of the carbon in *C. finmarchicus*, invertebrate competitors and predators based on Silhouette analysis of the MOCNESS samples and Ikeda's 1985 model of oxygen uptake as a function of individual length and temperature. Days to consume *C. finmarchicus* was calculated by dividing *C. finmarchicus* (mgC/m2) by the predcarb (mgC/m2/day).

Cruise	Tow	YearTime	C. fin mgC/m2	compet mgC/m2	pred mgC/m2	competcarb mgC/m2/day	predcarb mgC/m2/day	Ccompet/predcarb - days	C.fin/predcarb - days
EN307	m3	1997.778	1146.2	1406.73	1087.27	92.96	39.98	35.2	28.67
EN307	m4	1997.781	6343.81	4327.47	5159.85	264.38	229.40	18.9	27.65
EN307	m7	1997.787	864.47	1210.77	414.95	74.46	15.97	75.8	54.13
EN307	m9	1997.793	1905.18	2158.44	1140.95	132.80	38.02	56.8	50.11
OC332	m1	1998.81	565.38	731.64	415.40	45.39	11.33	64.6	49.92
OC332	m3	1998.816	591.80	1098.71	426.55	61.86	12.63	87.0	46.85
OC332	m4	1998.816	363.48	718.85	2235.87	46.84	57.50	12.5	6.32
OC332	m6	1998.822	184.28	968.63	4217.82	65.19	99.78	9.7	1.85
OC334	m1	1998.927	334.10	1477.62	2014.58	92.65	45.56	32.4	7.33
OC334	m3	1998.933	334.39	941.52	1527.02	54.74	34.69	27.1	9.64
OC334	m5	1998.94	208.84	855.08	768.02	50.76	19.49	43.9	10.72
EN330	m2	1999.796	7255.55	5524.46	4246.49	322.52	157.52	35.1	46.06
EN330	m5	1999.808	5620.50	5059.23	1716.51	317.80	60.02	84.3	93.64
EN330	m6	1999.816	2556.23	2283.32	1328.10	163.86	43.35	52.7	58.97
EN331	m2	1999.929	2972.58	1830.48	2856.44	105.45	80.80	22.7	36.79
EN331	m4	1999.933	5773.08	4443.86	2287.87	248.97	108.05	41.1	53.43
EN331	m5	1999.934	4832.81	3346.39	1510.18	204.53	65.29	51.3	74.02
EN331	m6	1999.942	1200.09	869.58	2173.68	53.94	63.31	13.7	18.96

Appendix A. Supporting Information. Calibration data for BIOMAPER-II echosounder and transducers.

EN307

	43 kHz		120 kHz		200 kHz		420 kHz		1000 kHz	
Parameter	DOWN	UP	DOWN	UP	DOWN	UP	DOWN	UP	DOWN	UP
Nominal beamwidth	6	6	3	3	3	3	3	3	3	3
Mean beam pattern factor (bav2)	9.95e-4	1.018e-3	1.95e-4	2.12e-4	2.38e-4	2.10e-4	2.86e-4	2.78e-4	2.16e-4	2.22e-4
Source level (re:1 µPA at 1 m)	223.31	223.12	228.59	228.41	227.82	227.5	226.99	227.69	218	218
Receiving Sensitivity (re: 1 V/µPa)	-151.59	-153.44	-162.28	-162.21	-168.44	-169.07	-168.34	-167.68	-182.58	-183.33
Receive gain setting	0	0	0	0	6	6	0	0	12	12
A(Integration scaling constant)	9.974e-7	1.0081e-6	1.0003e-6	1.0023e-6	1.0060e-6	9.957e-7	9.910e-7	1.0002e-6	9.975e-7	1.0097e-6
Pulse length (ms)	5	5	5	5	5	5	2.5	2.5	1.25	1.25
Chirp bandwidth (kHz)	10	10	10	10	10	10	10	10	10	10
Ping rate	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.417

OC332 & OC334

	43 kHz		120 kHz		200 kHz		420 kHz		1000 kHz	
Parameter	DOWN	UP	DOWN	UP	DOWN	UP	DOWN	UP	DOWN	UP
Nominal beamwidth	6	6	3	3	3	3	3	3	3	3
Mean beam pattern factor (bav2)	1.018e-3	9.95e-4	1.95e-4	2.12e-4	2.38e-4	2.10e-4	2.86e-4	2.78e-4	2.16e-4	2.22e-4

Source level (re:1 μPA at 1 m)	223.12	223.31	228.59	228.41	227.82	227.5	226.99	227.69	218	218
Receiving Sensitivity (re: 1 V/μPa)	-153.44	-151.59	-168.28	-168.21	-168.44	-169.07	-168.34	-167.68	-182.58	-183.33
Receive gain setting	0	0	6	6	6	6	0	0	12	12
A(Integration scaling constant)	1.0081e-6	9.974e-7	1.0003e-6	1.0023e-6	1.0060e-6	9.957e-7	9.910e-7	1.0002e-6	9.975e-7	1.0097e-6
Pulse length (ms)	5	5	5	5	5	5	5	5	5	5
Chirp bandwidth (kHz)	10	10	10	10	10	10	10	10	10	10
Ping rate	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.417

EN330 & EN331

	43 kHz		120 kHz		200 kHz		420 kHz		1000 kHz	
Parameter	DOWN	UP	DOWN	UP	DOWN	UP	DOWN	UP	DOWN	UP
Nominal beamwidth	6	6	3	3	3	3	3	3	3	3
Mean beam pattern factor (bav2)	1.140e-3	9.27e-4	2.24e-4	1.99e-4	2.22e-4	2.29e-4	2.72e-4	2.79e-4	2.79e-4	2.73e-4
Source level (re:1 μPA at 1 m)	224.32	223.07	229.44	226.94	227.22	227.53	221.5	222.12	217.27	216.96
Receiving Sensitivity (re: 1 V/μPa)	-154.01	-154.49	-162.87	-167.59	-170.57	-170.13	-170.44	-169.5	-184.92	-182.42
Receive gain setting	0	0	0	0	6	6	0	0	12	12
A(Integration scaling constant)	1.2071e-6	1.3371e-6	8.470e-7	5.0407e-6	1.9626e-6	1.2517e-6	5.5576e-6	5.6955e-6	1.6702e-6	8.962e-7

Pulse length (ms)	5	5	5	5	5	5	5	5	1.25	1.25
Chirp bandwidth (kHz)	10	10	10	10	10	10	10	10	10	10
Ping rate	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.417

Figure 1. Distribution of cruise tracklines in the Gulf of Maine along which BIOMAPER-II acoustic, optical, and environmental data were collected in fall of 1997, 1998, and 1999. The bold red lines indicate where BIOMAPER-II was being towyo'd. WB- Wilkinson Basin, JB- Jordan Basin, and GB - Georges Basin.

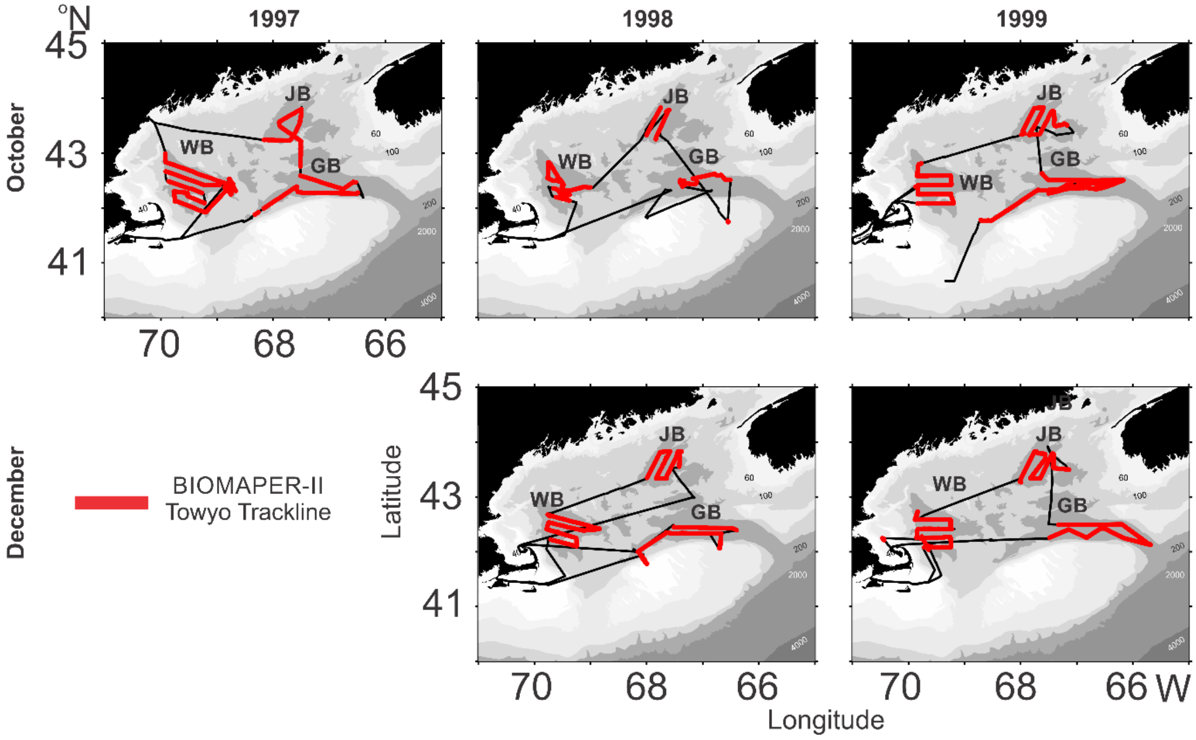


Figure 2. Distribution of 1-m^2 MOCNESS tows taken on the fall cruises to the Gulf of Maine in 1997, 1998, and 1999 (indicated by the numbers and symbols). The circled tows are those that have been processed.

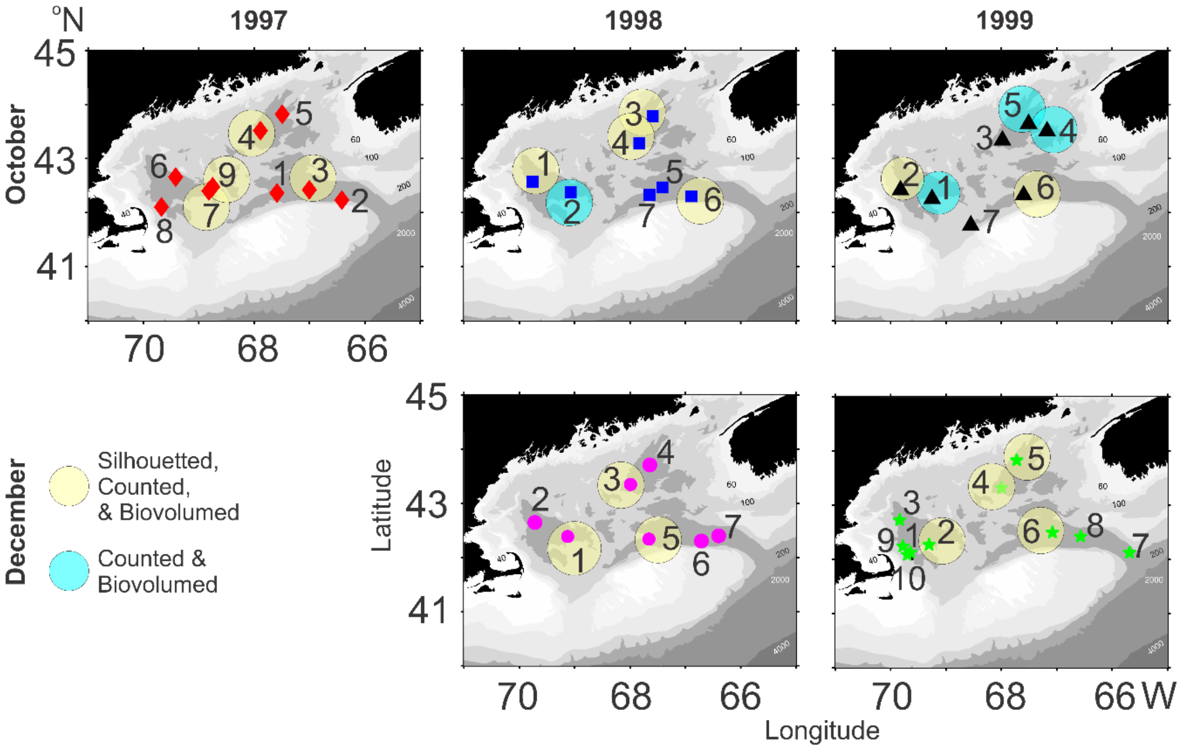


Figure 3. The vertical distribution (individuals/m^3) of *Calanus finmarchicus* collected in the three major basins in Gulf of Maine during the fall of 1997, 1998, and 1999 as stacked horizonal bars with the various copepodid stages indicated by the colors. WB- Wilkinson Basin, JB- Jordan Basin, and GB - Georges Basin. Bottom depth indicated by diamond on each vertical plot. Total (vertically integrated) abundance individuals/m^2 also is given for each profile. Day and Night tows indicated by N and D in the Cruise tow number at the top of each plot. The line with the double-sided arrow distinguishes October data from December data.

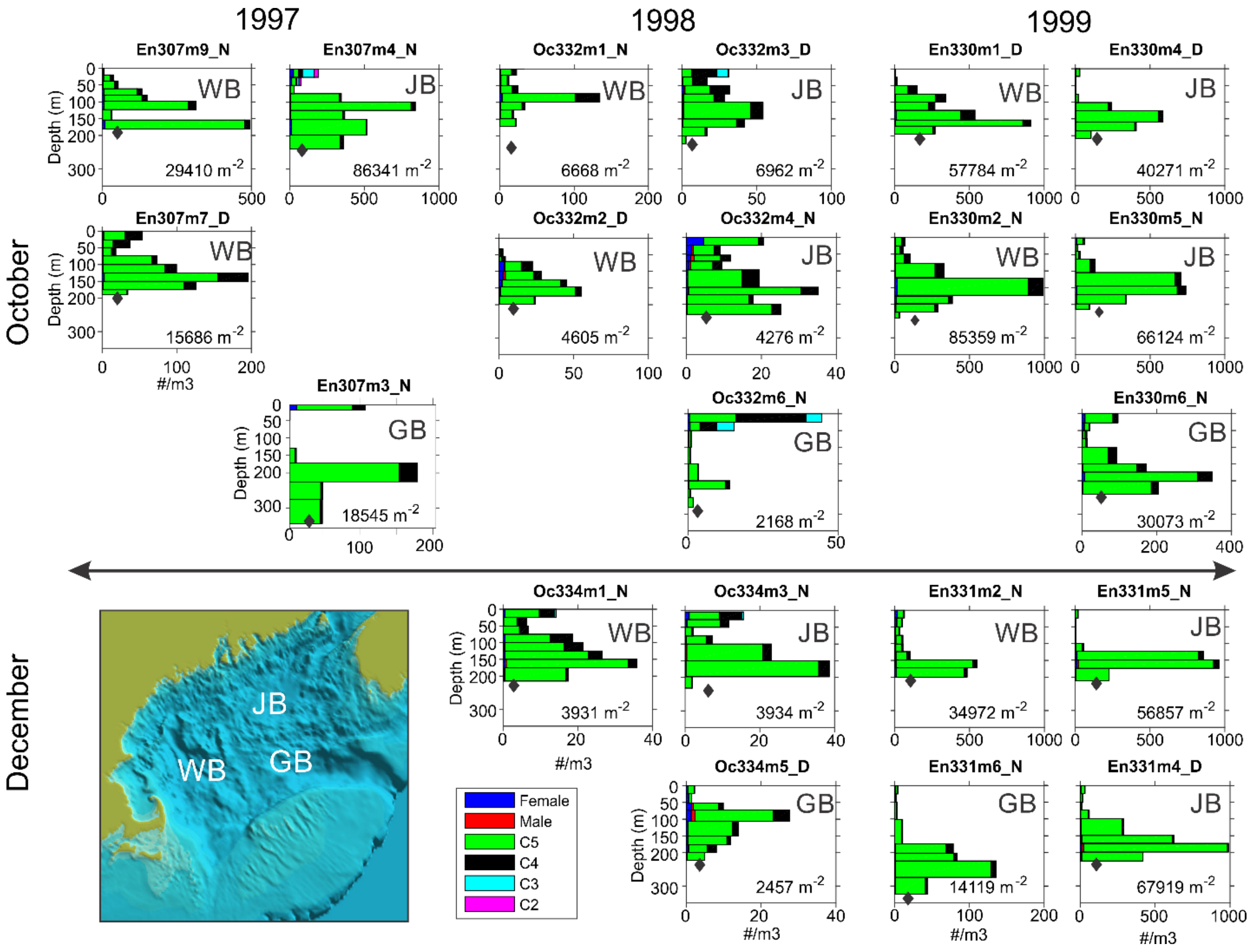


Figure 4. The distribution of the central 66% portion (17th to 83rd percentile) of *Calanus finmarchicus* sampled in the Gulf of Maine in 1997, 1998, and 1999 as a function of depth, temperature, and salinity measured with the MOCNESS sensors. The dotted lines provide a context for viewing relationship between depth, temperature, and salinity. W- Wilkinson Basin, J- Jordan Basin, and G - Georges Basin.

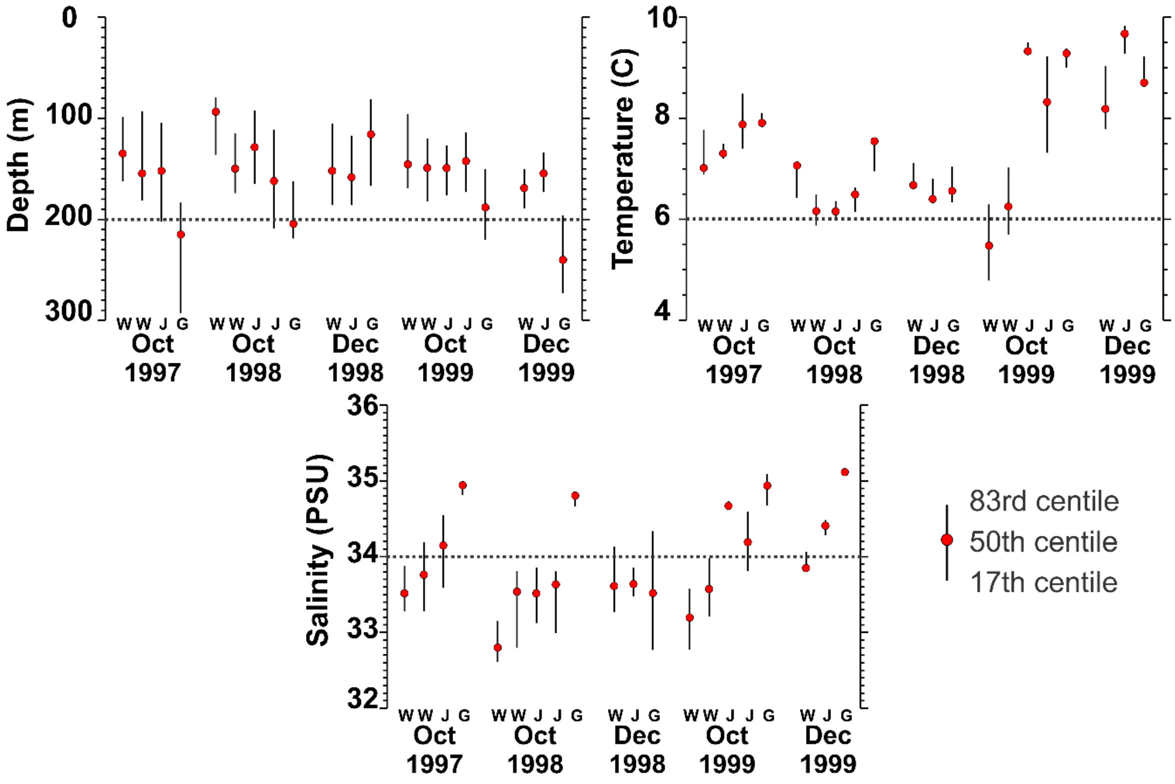


Figure 5, *Calanus finmarchicus* C5 size distribution in 1997, 1998, 1999 taken from samples below 150 m. Cohorts were decomposed using a Gaussian Mixture Model (GMM). μ is the mean of a probability distribution, σ is the standard deviation of the Probability Distribution Function (PDF), and p is the Component Proportion, n is the number of observations. The red line on the plots demarks the modes. WB- Wilkinson Basin, JB- Jordan Basin, and GB - Georges Basin.

Figure 5A. October size distribution of *Calanus finmarchicus* C5s (1997, 1998, 1999)

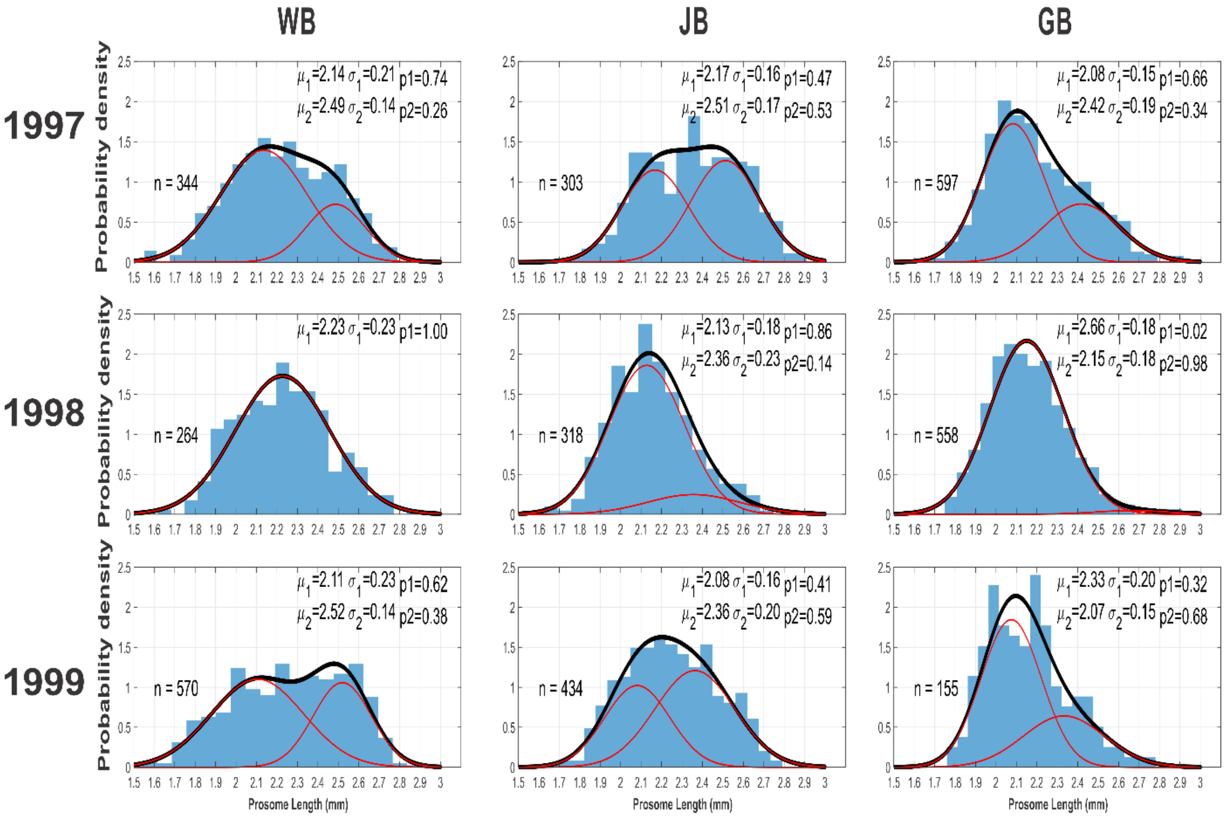


Figure 5B. December size distribution of *Calanus finmarchicus* C5s (1998, 1999).

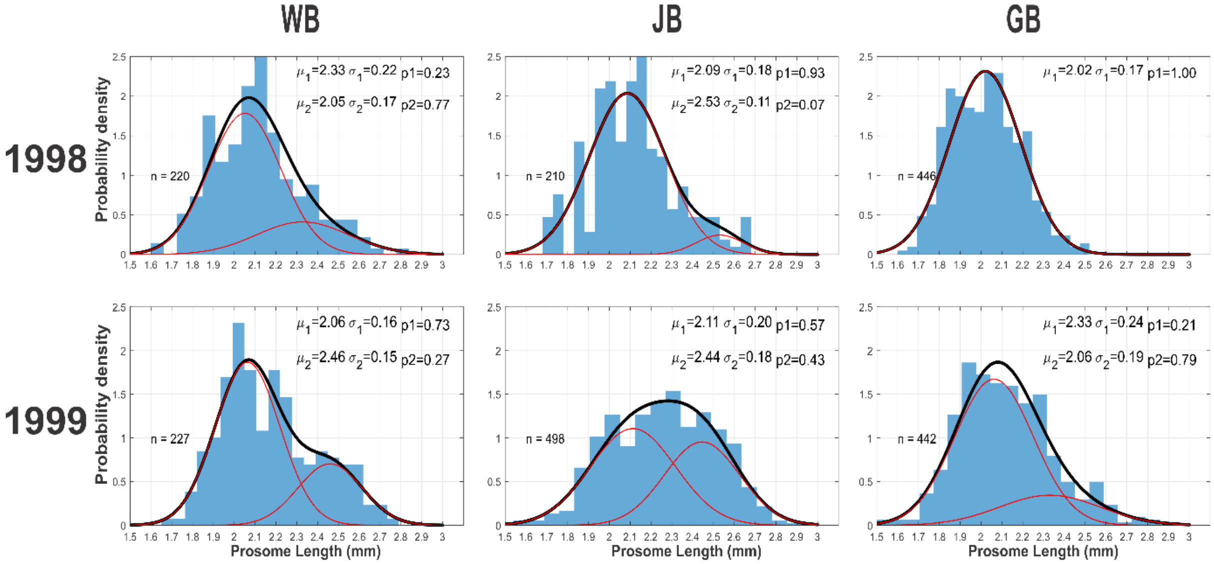


Figure 6. The vertical distribution of MOCNESS zooplankton biovolumes collected in the three major basins in Gulf of Maine during the fall of 1997, 1998, and 1999. WB- Wilkinson Basin, JB- Jordan Basin, and GB - Georges Basin. Total integrated biovolumes as cubic centimeters (cc) per m^2 are given for each profile. Day and Night tows indicated by N and D in the Cruise tow number at the top of each plot. The line with the double-sided arrow distinguishes October data from December data.

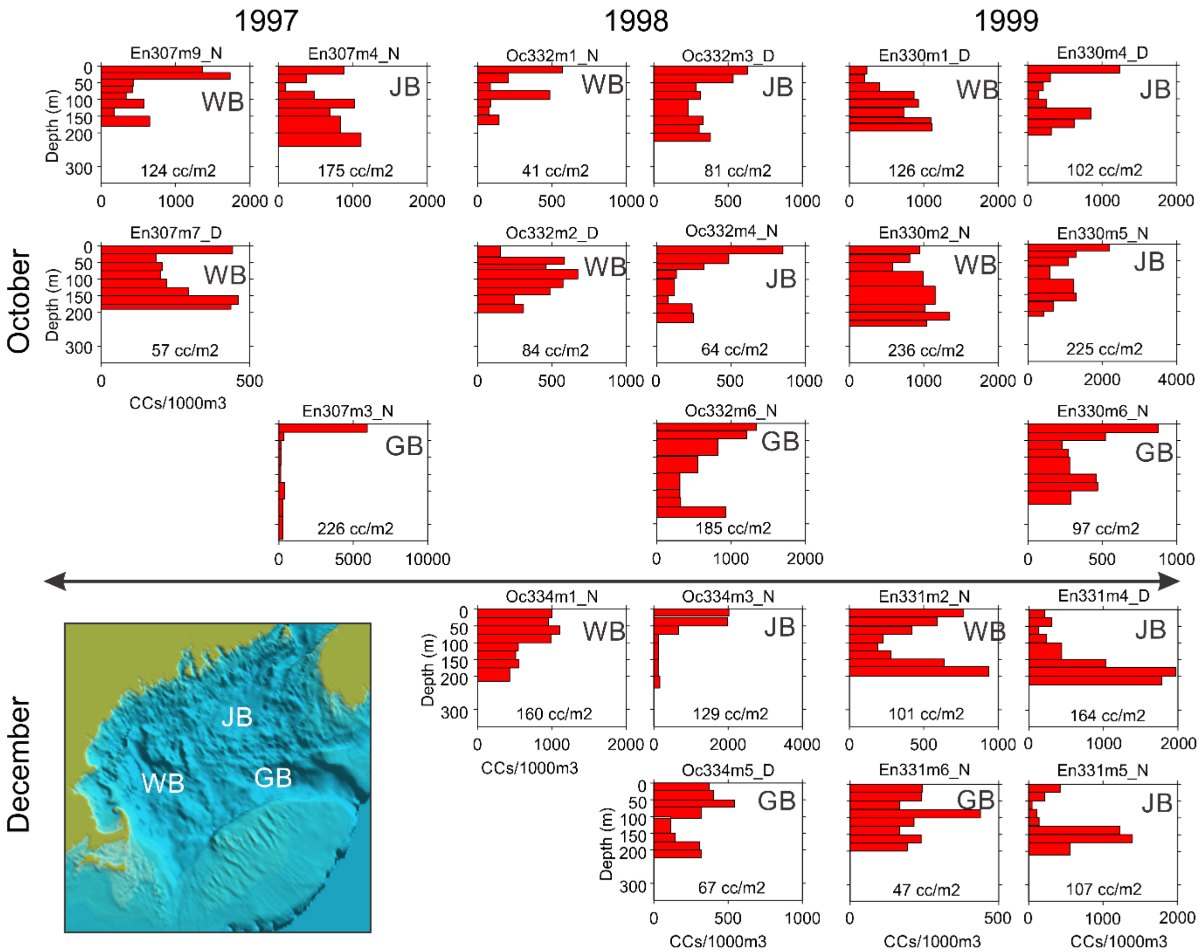


Figure 7. The relationship between total zooplankton biovolume and the wet weight of *Calanus finmarchicus* by years for all MOCNESS tow depths and only those greater than 100 and 150 meters. *C. finmarchicus* wet weights determined from a length to ww relationship.

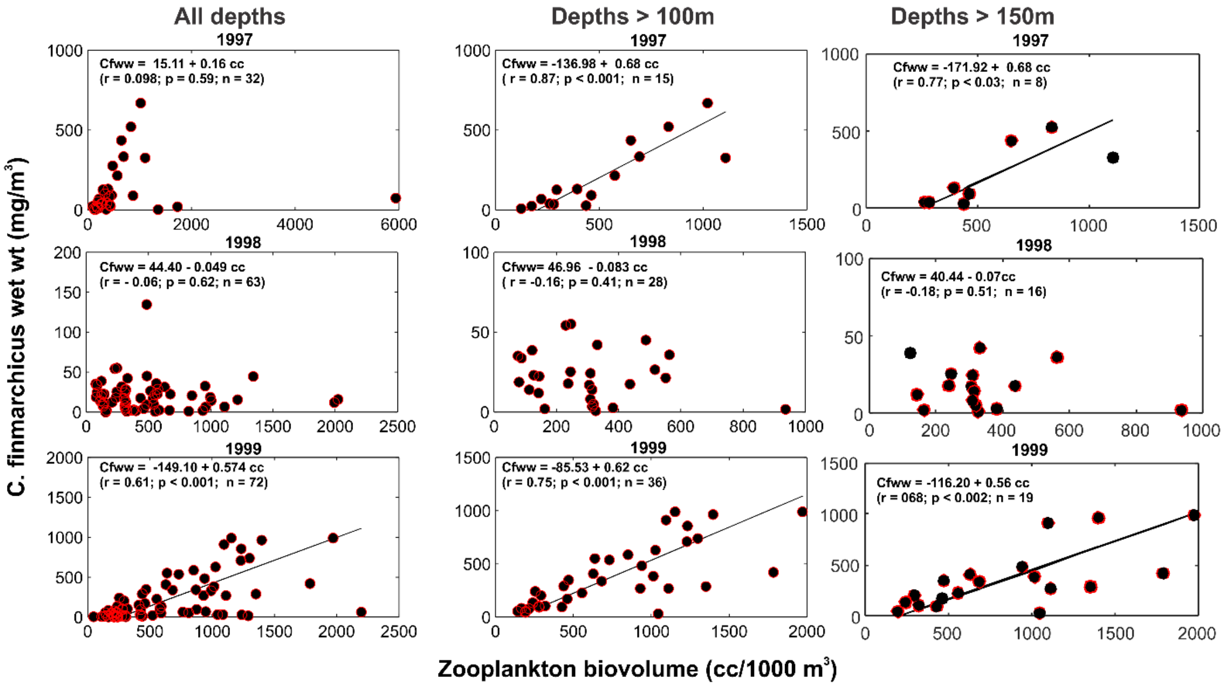


Figure 8. The day/night vertical distribution of volume backscattering at 200 kHz in the three major basins in Gulf of Maine during the fall of 1997, 1998, and 1999. WB- Wilkinson Basin, JB- Jordan Basin, and GB - Georges Basin. Each plot gives median backscattering in 10 m depth bins between 20 and 200 m, and the error bars on that show the 25th and 75th percentiles. Day is blue; night is red. The line with the double-sided arrow distinguishes October data from December data.

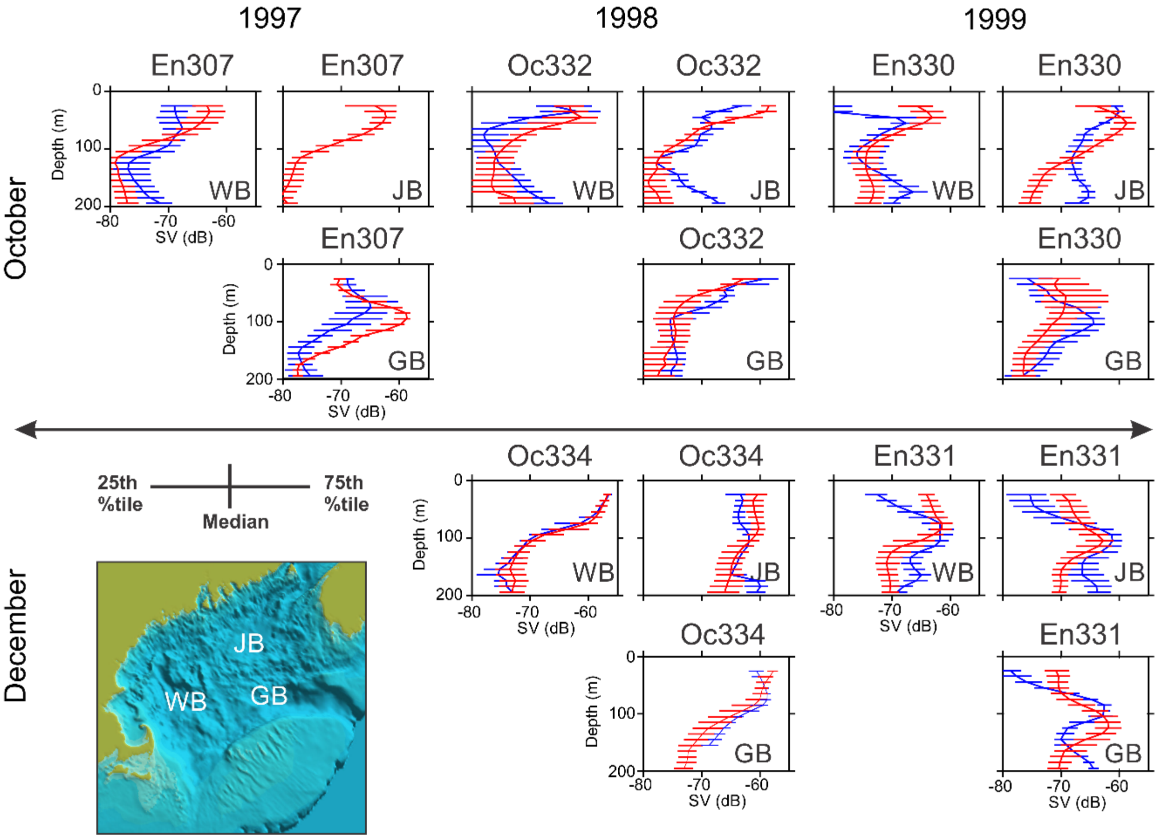


Figure 9 Time-series changes in integrated values of a) *Calanus finmarchicus* abundance, b) total biovolumes, c) average volume backscatter at 120 kHz, d) silhouette total copepod counts, and e) biomass of *Calanus* (square) and total copepods (triangle) based on length to wet weight relationships. The individual symbols in each plot represent integrated values for a MOCNESS tow, except for the volume backscattering (S_V) where individual symbols represent the mean from a particular tow..

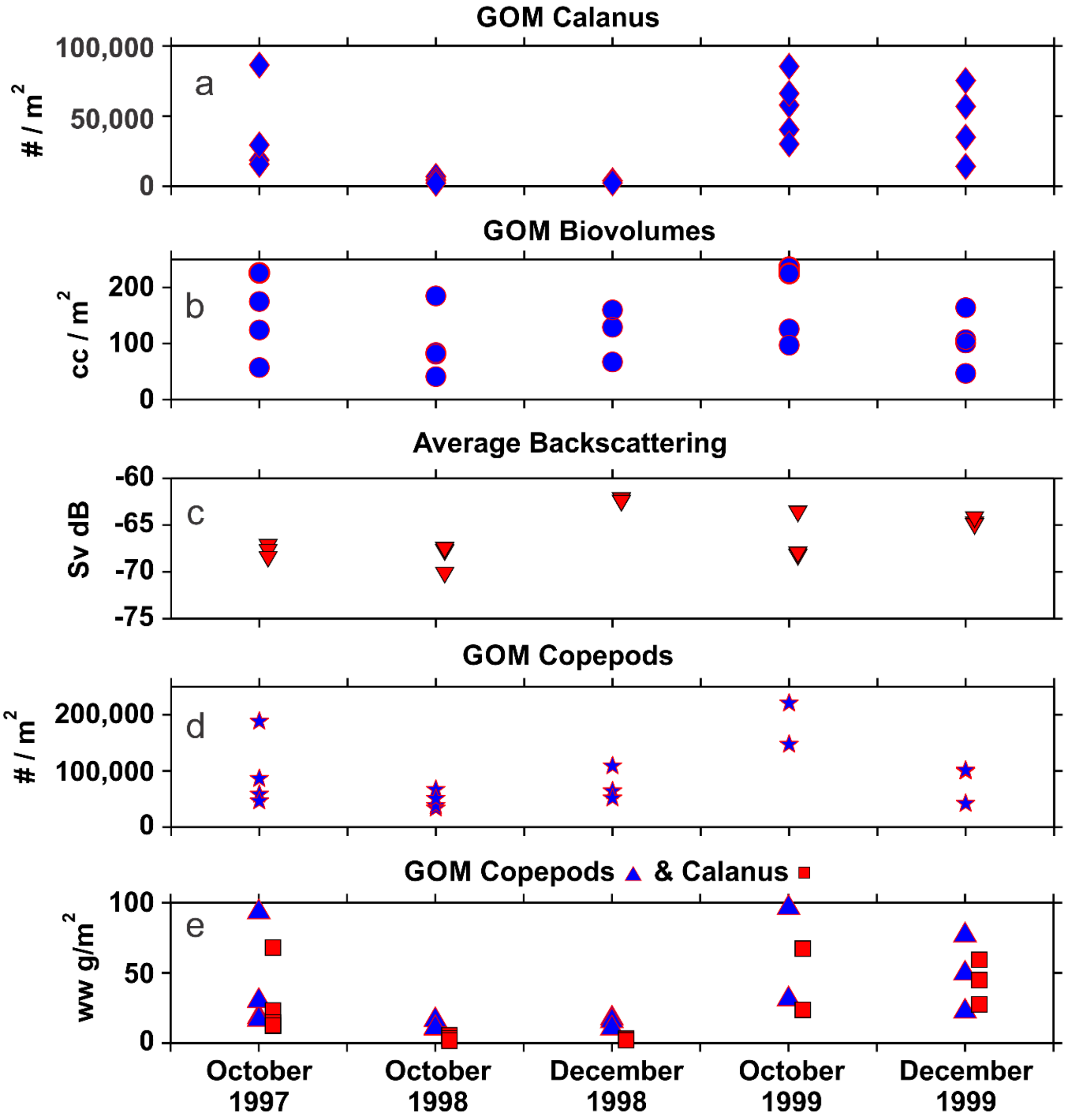


Figure 10. The percent composition of zooplankton taxa based on silhouette data for each MOCNESS net that were integrated for the water column. The minor contributors to both abundance and biomass are grouped as "others".

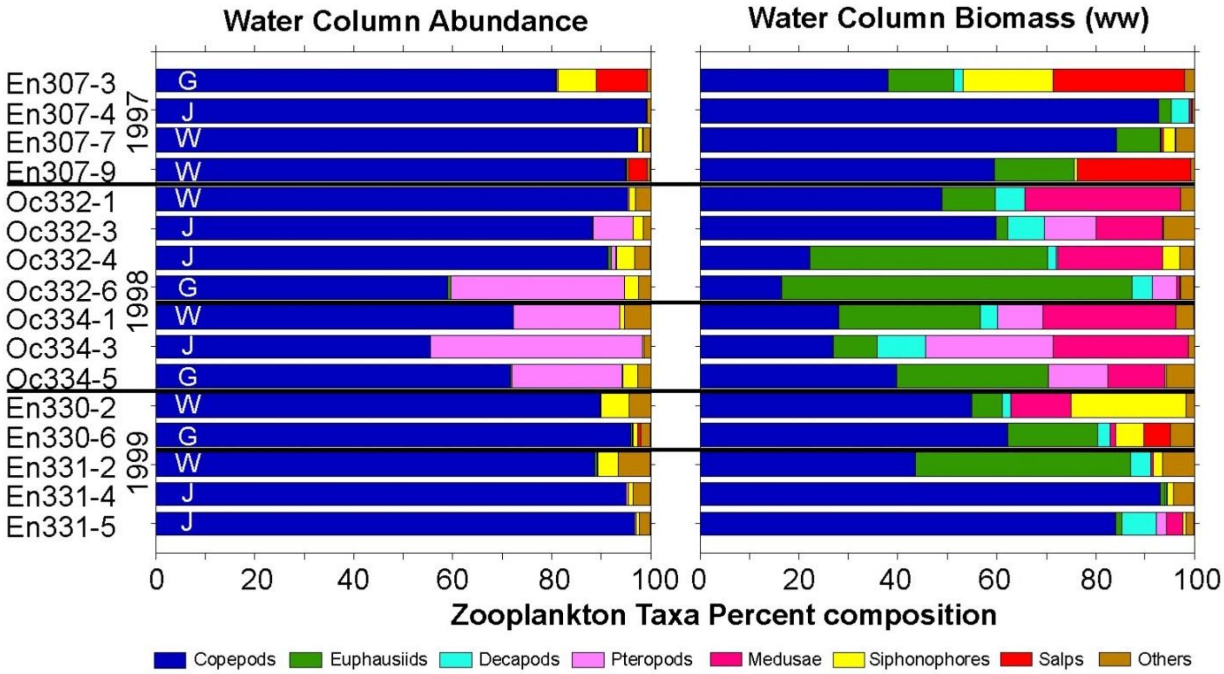


Figure 11. Predation pressure on *C. finmarchicus* in the GoM based on estimates of the carbon in *C. finmarchicus*, invertebrate competitors and predators based on Silhouette analysis of the MOCNESS samples and Ikeda's 1985 model of oxygen uptake as a function of individual length and temperature. Note: the half-year increments on the X-axis are given as .5.

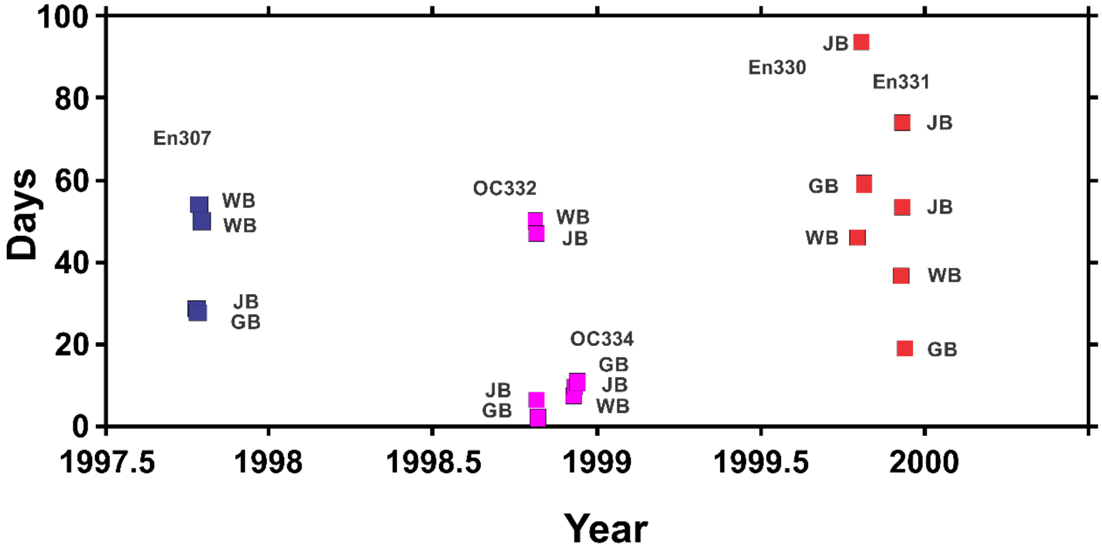


Figure 12. The vertical distribution of *Calanus finmarchicus* collected in the Northwest Atlantic Slope Water during 1981 and 1982 south of New England. Total integrated numbers per m^2 are given for each profile. Most vertical profiles published by Miller et al., (1991) as cumulative percents as a function of depth by stage.

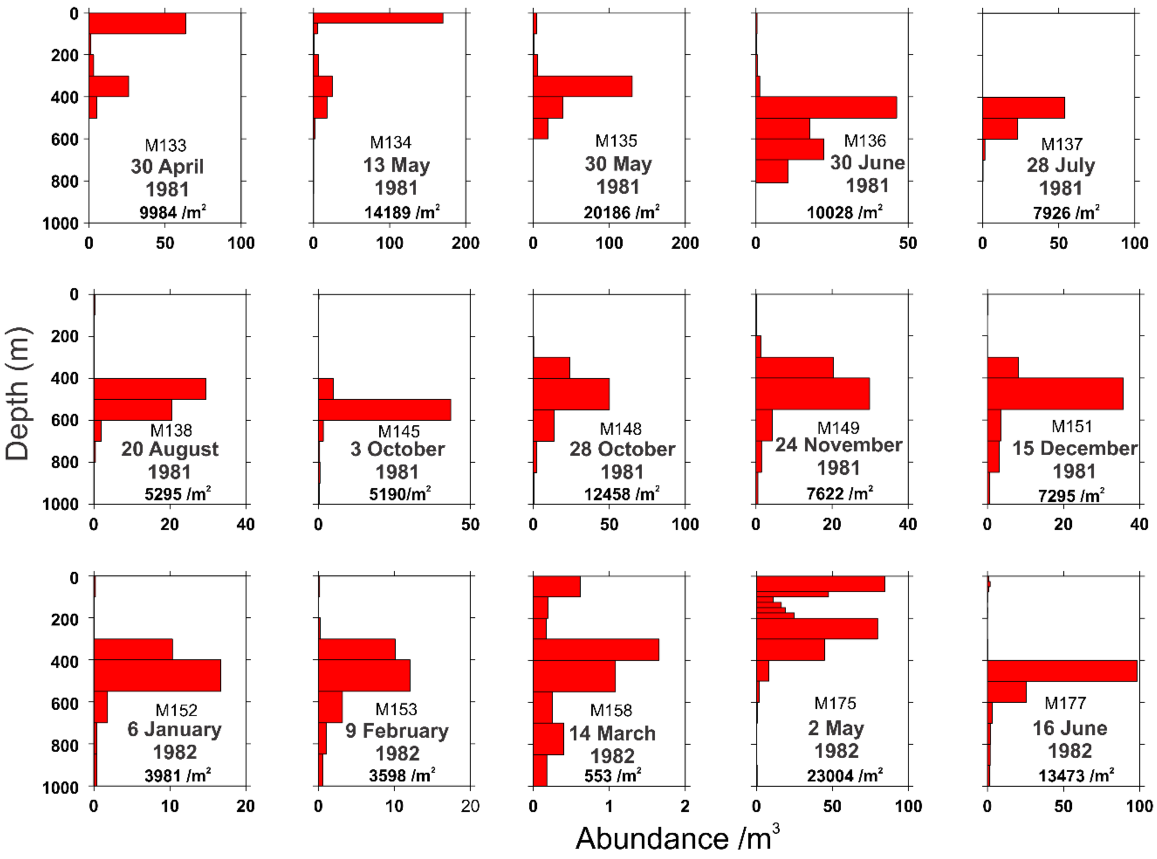
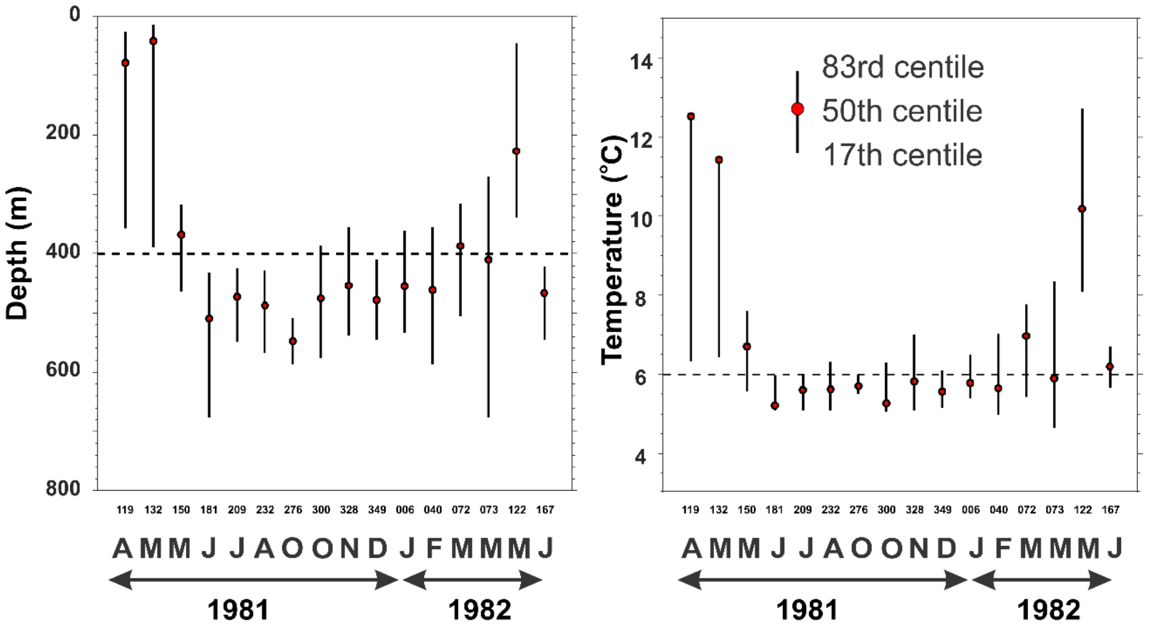


Figure 13. The distribution of the central portion (17th to 83rd percentile) of the *Calanus finmarchicus* population sampled in the North Atlantic Slope Water in 1981 and 1982 as a function of depth and temperature. The numbers above the month designations are the year-days when the tows were taken. Note there are two May values and two October values in 1981 and two March values in 1982. Environmental data not published by Miller et al., (1991) as presented herein.



Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: