Temporal variability of zooplankton biomass from ADCP backscatter time series data at the Bermuda Testbed Mooring site

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Abstract

Temporal variability of acoustically estimated zooplankton biomass at the Bermuda Testbed Mooring (BTM) site in the Sargasso Sea (at 31°43'N, 64°10'W) is described for time scales from less than an hour to the seasonal cycle primarily using data obtained between August 1996 and November 2000, and from May 10 to November 13, 2003. Concurrent high frequency BTM observations of meteorological, physical, and bio-optical variables are used to interpret processes contributing to the zooplankton variability. Zooplankton biomass estimates are derived from regressions of backscatter intensity data measured with an upward looking 153-kHz acoustic Doppler current profiler (ADCP) and zooplankton net tow data collected near the BTM site as part of the Bermuda Atlantic Time-series Study (BATS). Our data show clear event-scale variations. Peaks are associated with annual spring blooms involving mixed layer shoaling and in some cases passages of mesoscale eddy features. Biomass peaks are often coincident with maxima seen in BTM chlorophyll fluorescence measurements (inferred phytoplankton biomass). Some storm events do not appear to manifest in significant perturbations of zooplankton distributions; however, Hurricane Fabian (2003) greatly impacted these distributions. Estimates of zooplankton biomass and relative vertical velocity show the vertical structure of daily migration patterns. Seasonal variations in migration patterns are also evident, with diel changes in zooplankton biomass most pronounced in spring and least pronounced in winter. In summary, our high temporal resolution time series of estimated zooplankton biomass in the open ocean provide information on scales inaccessible through conventional monthly ship-based sampling. These data have implications for upper ocean ecology and the vertical transport of carbon and nitrogen through the diel migration of zooplankton.

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Keywords: ADCP backscatter; Zooplankton biomass; Mesoscale and storm events; Diel and seasonal cycles

1. Introduction

Knowledge of variability in zooplankton biomass is important for understanding the effects of climate change on ecosystems. In addition, zooplankton
contribute to transport of carbon and nitrogen to the deep sea via production of fecal pellets and active transport by diel vertical migration, important components of the biological pump (Longhurst et al., 1990; Steinberg et al., 2000, 2002; Al-Mutairi and Landry, 2001). High resolution measurements of zooplankton biomass on diel, seasonal, and interannual time scales can help constrain both the effects of climate or shorter term physical effects on zooplankton communities and the influence of zooplankton on carbon and nutrient cycling in the sea. Zooplankton collections in the oceanic region off Bermuda have been made since 1938 (Moore, 1949), providing rich data sets for studying zooplankton biomass, species composition, feeding, grazing, metabolism, and vertical migration on diel, seasonal, and interannual time scales. In particular, time-series studies of zooplankton seasonal dynamics off Bermuda date back several decades (Menzel and Ryther, 1961; Deevey, 1971; Deevey and Brooks, 1971, 1977), as do other zooplankton studies (e.g., Moore, 1949, 1950; Sutcliffe, 1960; Beers, 1966). For example, the ZOOSWAT project compared zooplankton data collected during the spring-bloom period (March/April) with the sum-

船上采样方法。不幸地，这些数据集不提供高时间分辨率（少于1小时的样本间隔）信息对延长的时期而言，且因此不能捕获影响过程的时间尺度分钟到周。重要的是，与间歇性事件和小尺度特征有关的变量在时间尺度少于几周不能被求解到，或者有月与偶数采样，但船采样可能有被遮挡的气象条件和高海状态。

使用关系在由声学回波强度得到从声学多普勒流速仪（ADCPs）和浮游动物生物量的净收集到的浮游动物样本，ADCPs的使用有助于描述变化在浮游动物生物量和浮游动物迁徙的分布。
with a deep-water platform for testing new instrumentation; (2) interdisciplinary BTM data are used for scientific studies, particularly in conjunction with other nearly co-located research programs including the Ocean Flux Program (OFP; e.g., Conte et al., 2001) and the US JGOFS BATS (e.g., Michaels and Knap, 1996; Steinberg et al., 2001); and (3) nearly continuous bio-optical time-series data are obtained for calibration, validation, and algorithm development for ocean color satellites (Dickey et al., 1998a, 2001). The BTM site is located at the northern edge of a transition region between relatively eutrophic waters to the north and more oligotrophic subtropical waters to the south. A weak surface front and energetic sub-mesoscale and mesoscale features are often present and can affect local biology (e.g., McNeil et al., 1999). Here the term “mesoscale” refers to features with horizontal scales on the order of 100–200 km that pass the mooring on a time scale of roughly a month and “sub-mesoscale” as features on the order of 10–100 km that pass the mooring on a time scale of less than a month (Dickey et al., 2001). The periodic variability of the region of the BTM site is dominated by the seasonal cycle (e.g., Michaels and Knap, 1996; Dickey et al., 1998a, 2001; Steinberg et al., 2001) and secondarily the diel cycle. The mixed layer depth and phytoplankton concentrations vary seasonally (and to a lesser degree diurnally), but their respective timing and intensities vary interannually. Synoptic scale weather patterns typically pass every few days. Several accounts of physical, bio-optical, and biogeochemical variability measured at the BTM site are presented in Dickey et al. (1998a,b, 2001), McGillivray et al. (1998), McNeil et al. (1999), Zedler et al. (2002), and Conte et al. (2003).

2.2. Data collection

Measurements made from the BTM include: surface meteorology and optics along with subsurface currents, temperature, salinity, and bio-optical and chemical variables. An RDI 153-kHz ADCP has been deployed from the BTM to obtain current and acoustic backscatter intensity (for estimating zooplankton biomass) data since late August of 1996. These measurements provide important high frequency information required for studying periodic and episodic processes. The BTM enables collection of nearly continuous data during periods of inclement weather and large sea states (even hurricane passages) when traditional ship-based sampling is not possible and provides otherwise inaccessible data in the important temporal spectral range of minutes to several years. Previous studies based on BTM measurements in the past decade have concerned physical and biogeochemical variability (e.g., Dickey et al., 1998a,b, 2001; McNeil et al., 1999; Zedler et al., 2002; Conte et al., 2003). Observations of zooplankton biomass as estimated from an ADCP deployed on the BTM are now providing concurrent and long-term biological information about zooplankton with high vertical spatial and temporal resolution, and facilitate studies of physical and biological interactions.

The mooring configuration for the present study (see www.opl.ucsb.edu/btm/methods.html) included temperature sensors at several depths from 2 to 750 m (3.75-min sampling interval), conductivity sensors (for salinity determinations) at one or two depths (3.75-min sampling interval), and fluorometers for estimating chlorophyll-a (chl-a) at several depths (3.75-min sampling interval). An upward-looking 153-kHz Blue Water broadband ADCP manufactured by RD Instruments, Inc. of San Diego, CA (RDI, 1995) was moored at depth (in range of 200–212 m) and provided horizontal and vertical currents and acoustic backscatter intensity (for estimating zooplankton biomass) from roughly 20–200 m (Table 1). The ADCP was configured to collect data in 68 vertical bins, each with a bin size of 3 m, and at a sampling time interval of 7.5 or 15 min. The ADCP beam angle is 20° from the system’s vertical axis for each of the instrument’s four transducers and the acoustic transmission beam spreads at an angle of approximately 4°. This results in a 7.5-m-diameter bin for each beam at 72-m depth, with a horizontal surface area of 44.2 m².

<table>
<thead>
<tr>
<th>Deployment</th>
<th>Time period</th>
<th>Depth range (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>May 3, 1997–July 30, 1997</td>
<td>20.5–203.5</td>
</tr>
<tr>
<td>8</td>
<td>August 8, 1997–November 20, 1997</td>
<td>20.5–203.5</td>
</tr>
<tr>
<td>9</td>
<td>November 26, 1997–March 31, 1998</td>
<td>21.5–201.5</td>
</tr>
<tr>
<td>10</td>
<td>November 11, 1998–March 19, 1999</td>
<td>18.5–195.5</td>
</tr>
<tr>
<td>11</td>
<td>April 1, 1999–July 21, 1999</td>
<td>19.5–196.5</td>
</tr>
<tr>
<td>12</td>
<td>July 29, 1999–November 6, 1999</td>
<td>20.5–197.5</td>
</tr>
<tr>
<td>13</td>
<td>December 5, 1999–May 27, 2000</td>
<td>19.5–196.5</td>
</tr>
<tr>
<td>14</td>
<td>June 1, 2000–November 29, 2000</td>
<td>20.5–197.5</td>
</tr>
<tr>
<td>18</td>
<td>May 10–November 13, 2003</td>
<td>20.5–191.5</td>
</tr>
</tbody>
</table>
and with a sampling volume for each beam of 133 m$^3$ with a 3-m bin size (Gilboy et al., 2000). ADCP measurements made from August 21, 1996 (BTM Deployment 6) to November 29, 2000 (BTM Deployment 14) and from May 10 to November 13, 2003 (BTM Deployment 18) are used in this study. Specific BTM deployments used for the present time-series measurements are summarized by deployment period in Table 1. The time series are not continuous for several reasons: (1) new instruments were added during the program, (2) data gaps of several days exist between mooring recoveries and redeployments, and (3) occasional delays in mooring redeployments were caused by weather and sea-state conditions and ship-related problems.

To our knowledge, most previous ADCP zooplankton estimates have relied upon narrowband ADCPs to measure acoustic backscatter. The narrowband system’s automatic gain control (AGC) output is strongly temperature dependent and many studies have been unable to determine absolute backscatter intensity since output signal strength was unknown. Broadband ADCPs (BBADCPs) have an advantage over narrowband ADCPs of having much lower random fluctuations for both current and backscatter estimations. The BBADCP also enables higher resolution along the profile with little reduction of scatter estimations. The BBADCP, which are required for absolute backscatter data (Deines, 1999). The received signal strength indicator (RSSI) outputs of BBADCPs are not temperature dependent; moreover, the ADCP manufacturer, RDI, provides transmit power data for the BBADCP, which are required for absolute backscatter estimations. The BBADCP also enables higher resolution along the profile with little reduction of velocity precision (Gilboy et al., 2000).

An important aspect of the present study is the collection of zooplankton samples, which were obtained at the BATS site (31°50′N, 64°10′W) near the BTM site with a 1-m$^2$ rectangular, 202-μm mesh net beginning in 1994 (Madin et al., 2001). Size-fractionated biomass (wet and dry weight (DW)) was determined from each tow by wet sieving through nested sieves with mesh sizes of 5.0, 2.0, 1.0, 0.5 and 0.2 mm. Two replicate double oblique tows were made from the surface to approximately 200 m during the day (between about 0900 and 1500 h) and at night (between about 2000 and 0200 h) during BATS cruises (Madin et al., 2001).

### 2.3. Estimation of zooplankton biomass from acoustic backscatter data

The echo intensity (counts) recorded by the BBADCP was converted to a backscatter coefficient, $S_v$, by use of the following equation given by Deines (1999):

$$S_v = C + 10 \log_{10}((T_x + 273.16)R^2) - L_{DBM} - P_{DBW} + 2xR + K_c(E - E_x),$$

where $S_v$ is the backscattering strength in dB re (4πm)$^{-1}$. $C$ is an empirical constant required to account for some of the relevant phenomena affecting echo intensity that cannot be measured independently. $T_x$ is temperature of the transducer (°C) and $R$ is range along the beam (slant range) to the scatterers (m). $L_{DBM}$ is $10\log_{10}$ (transmit pulse length, meters) and $P_{DBW}$ is $10\log_{10}$ (transmit power, Watts). $x$ is the sound absorption coefficient of water (dB m$^{-1}$), as calculated using the method of Francois and Garrison (1982), and the factor $2xR$ is calculated by the method given by Deines (1999). $K_c$ is the conversion factor for echo intensity (dB count$^{-1}$) and the values of $C$, $P_{DBW}$ and $K_c$ are provided by the manufacturer. Echo intensity ($E$) is derived from the RSSI of the receivers; its real-time reference level is denoted $E_r$ and a typical value is 40 counts. In practice, we assume that $E_r$ is equivalent to the lowest value of $E$ measured in the water column during the entire data collection period. There is no laboratory calibration for $E_r$; instead, we use the minimum of counts for each beam when the ADCP is sampling in the ocean. The $E_r$ values we used for each beam were 39, 37, 43, and 33 for beams 1 through 4, respectively.

To obtain absolute backscatter data, transmit power must be estimated. In general, this power is proportional to the input voltage (Deines, 1999). Our 153-kHz Broadband ADCP has a high power module (with constant power) that removes this dependence upon input voltage. If backscatter intensity of one specified beam exceeded the mean value of the other three beams by 5 db for a given bin, then data for that bin were discarded for averaging purposes. This process eliminates large scatterers (such as fish) from the data. A minimum ‘percent good’ of 25% was selected for quality control. The low RSSI values for bin 1 in Deployments 6, 7, 10, 11, 12, 13 and 14 may be due to the hardware’s Low Pass Filter time constant, which may be too long. The high bin 1 (deepest bin, closest to BBADCP) RSSI values for Deployments 8 and 9 may be due to ringing or a hard target in front of the transducer (Steve Maier, personal communication). Thus, bin 1 ADCP backscatter intensity data for all deployments were omitted. The acoustic
signal generally decreases with distance from a transducer. But in the near surface layer, measurements are contaminated by the lobe effect and air bubbles, and the signal becomes stronger. The mean profiles of intensity were calculated and then the averaged cutoff bin was determined. Typically, bins 61–63 (nearest ocean surface) and shallower bin data were unusable; thus, data within about 20 m (18.5–21.5 m) of the ocean surface were omitted from our analyses. In a few cases, erroneous values, likely caused by air bubbles (produced by strong winds and wave breaking) at depths greater than that of the averaged cutoff bin were also omitted and extrapolation was employed.

The relationship between zooplankton biomass and acoustic backscatter intensity was established by comparing biomass obtained from net tows and ensemble ADCP data.

Zooplankton biomass data used for regression with ADCP data were the sum total DW per unit volume filtered for all size fractions of the individual tows taken from September 2, 1996 to November 14, 2000. For each of the concurrent zooplankton sampling time periods, ADCP backscatter intensity data were averaged over the depths of nominally 20 m to the deepest zooplankton sampling depth. This latter depth is typically 200 m, but can vary from 75 to 292 m and thus introduces some error. We performed individual calibrations for data collected during each separate deployment as well as for the ensemble of deployments (Table 2). The relationship between zooplankton biomass and ADCP data was weak or not statistically significant for a few deployments (see $r^2$ and $p$ values, respectively, in Table 2). Possible reasons for the weaker relationships for some deployments include: locations of zooplankton net tow sampling were too far away from the BTM (i.e., beyond reasonable coherence length scale—spatial patchiness); maximum net tow sampling depths were not always close to the depth range of the ADCP; and relatively fewer tows were taken during some BTM deployments.

Because the slope and intercept for the ensemble (overall) calibration are similar to most of those of the individual deployments (Table 2), we applied the following ensemble calibration formula to all of the data (see Fig. 1 for regression calibration curve)

$$\text{Log}(\text{DW}/4\pi) = 0.0313 \times S_v + 2.0631$$

($r^2 = 0.25$, $p < 0.05$, $n = 156$),

(2)

where DW is total DW of zooplankton biomass per unit volume, $S_v$ is the backscattering strength in dB re $(4\pi m)^{-1}$. Although the $r^2$ value for the regression formula is low, the relationship between zooplankton DW and ADCP backscatter intensity is highly significant. Further, the purpose of this study is to examine variability in zooplankton as related to environmental and biological conditions rather than establishing quantitative estimates of zooplankton populations. Future studies will need to be mindful of the need for specially designed calibrations.

2.4. Estimation of vertical velocity using ADCP data

The ADCP measures the speed of scattering particles suspended in water, rather than the water

<table>
<thead>
<tr>
<th>Deployment no.</th>
<th>ADCP time periods</th>
<th>Net tow time periods</th>
<th>Symbols in Fig. 1</th>
<th>Log(DW/4π) = $A \times S_v + B$</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>08/21–96–01/10/97</td>
<td>09/02/96–12/14/96</td>
<td>Dot</td>
<td>$r^2 = 0.6504$, $p = 0.00161$, $A = 0.0363$, $B = 2.4945$, $n = 16$</td>
</tr>
<tr>
<td>7</td>
<td>05/03–97–07/30/97</td>
<td>05/05/97–07/15/97</td>
<td>Circle</td>
<td>$r^2 = 0.3823$, $p = 0.032108$, $A = 0.0282$, $B = 1.9632$, $n = 12$</td>
</tr>
<tr>
<td>8</td>
<td>08/08–97–11/20/97</td>
<td>08/11/97–01/14/97</td>
<td>Plus</td>
<td>$r^2 = 0.6007$, $p = 0.000421$, $A = 0.0330$, $B = 2.1306$, $n = 16$</td>
</tr>
<tr>
<td>9</td>
<td>11/26–97–03/31/98</td>
<td>12/09/97–03/25/98</td>
<td>x-mark</td>
<td>$r^2 = 0.0803$, $p = 0.179610$, $A = 0.0198$, $B = 1.1963$, $n = 24$</td>
</tr>
<tr>
<td>10</td>
<td>11/11–98–03/19/99</td>
<td>11/18/98–02/24/99</td>
<td>Square</td>
<td>$r^2 = 0.5536$, $p = 0.000331$, $A = 0.0688$, $B = 5.0825$, $n = 24$</td>
</tr>
<tr>
<td>11</td>
<td>04/01–99–07/21/99</td>
<td>04/07/99–07/06/99</td>
<td>Star</td>
<td>$r^2 = 0.1753$, $p = 0.066156$, $A = 0.0233$, $B = 1.4958$, $n = 20$</td>
</tr>
<tr>
<td>12</td>
<td>07/29–99–11/06/99</td>
<td>08/03/99–10/12/99</td>
<td>Diamond</td>
<td>$r^2 = 0.6923$, $p = 0.002805$, $A = 0.0317$, $B = 2.0181$, $n = 10$</td>
</tr>
<tr>
<td>13</td>
<td>12/05–99–05/27/00</td>
<td>12/08/99–04/11/00</td>
<td>Triangle</td>
<td>$r^2 = 0.1856$, $p = 0.213930$, $A = 0.0252$, $B = 1.5714$, $n = 10$</td>
</tr>
<tr>
<td>14</td>
<td>06/01–00–11/29/00</td>
<td>06/06/00–11/14/00</td>
<td>Pentagram</td>
<td>$r^2 = 0.6576$, $p = 0.000015$, $A = 0.0358$, $B = 2.4257$, $n = 24$</td>
</tr>
<tr>
<td>Overall</td>
<td></td>
<td></td>
<td></td>
<td>$r^2 = 0.2454$, $p = 4.9029e–011$, $A = 0.0313$, $B = 2.0631$, $n = 156$</td>
</tr>
</tbody>
</table>

Correlation coefficient ($r^2$) and significance level ($p$) are given for the regression (see Methods for explanation of variables in regression equation); $n$ is number of samples used in the regression.
itself. If vertical water velocities are small, the vertical velocity measured by the ADCP can be interpreted as the vertical swimming velocity of the scattering organisms (Heywood, 1996; Luo et al., 2000). Because of surface waves, the mooring buoy moves vertically, and the vertical velocity measured by the ADCP is not truly an absolute velocity of scattering organisms. To ascertain migration velocity, we define one bin (or in some cases the averages of several bins) near the surface for reference and then subtract its value from each bin in the same profile (Luo et al., 2000). This approach minimizes biases introduced by vertical buoy motions.

2.5. Statistical methods

The ADCPs depth varied somewhat for different deployments (Table 1), and the top bin used for the analyses (i.e., cut off bin) also varied with sea state. For consistency, depth bins for zooplankton biomass and backscatter intensity as recorded by the ADCP were interpolated to enable statistical analyses of data for depths between 22 and 190 m. Spectra were computed for current speeds and zooplankton biomass using 1024-point fast Fourier transforms (FFTs) tapered with a Hanning window, zero overlap. The 95% confidence intervals were calculated for the spectra. In order to calculate cross-correlations between zooplankton biomass, chl-\(a\), and temperature, daily averages were computed using the high-resolution time series data and then a high-pass filter (30 days) was applied to remove low-frequency variability (61 days of data were used for each computation). Cross-correlations were then computed to investigate relationships between zooplankton biomass and environmental parameters.

3. Results

The results of our analyses are subdivided in order to focus on some of the more important processes and their respective scales as follows: seasonal cycles and spring blooms, mesoscale eddies, wind events, and variability in diel vertical migration.
3.1. Seasonal cycles and blooms

Seasonal cycles in temperature typical of a mid-latitude open ocean site are evident in our temperature records (Fig. 2). Solar insolation cycles and upper ocean thermodynamic responses to heating and cooling cycles and events as well as wind forcing all combine to produce sequences of spring warming and mixed layer shoaling, and late fall-winter cooling and mixed layer deepening (e.g., Dickey et al., 1998a, 2001). Superimposed on this typical upper ocean seasonal temperature pattern are occasional major deviations caused by episodic wind events including tropical storms and hurricanes and passages of eddies.

Seasonal patterns in phytoplankton populations are well documented and spring phytoplankton blooms are evident. These patterns and blooms result from the interplay of upper ocean dynamics, solar insolation and surface heat flux variations, and the changing availability of plant nutrients and light (e.g. Dickey et al., 2001; Steinberg et al., 2001). In general, zooplankton concentrations tend to roughly track phytoplankton concentrations and both are impacted by the natural seasonal cycles of the upper ocean dynamics listed above and by episodic events—described below. Daily averaged, depth-integrated (22–190 m) zooplankton biomass anomaly estimated using ADCP backscatter data along with concurrent temperature, chlorophyll fluorescence (in relative units), and current measurements from late August 1996 through late November 2000 are shown in Fig. 2a–t. Since variability in the biomass of zooplankton is the primary focus of this study, zooplankton biomass anomalies were computed as the difference between the instantaneous biomass values and the mean for the time series of August 1996–November 2000 (Zooplankton Biomass panels in Fig. 2); note that the mean depth-integrated, daily averaged value of 497 mg dw m⁻² of the zooplankton biomass is shown on the right of each of the relevant panels for reference. During this time period, depth-integrated daily zooplankton biomass fluctuated from 343 to 700 mg dw m⁻² (Table 3). Our data show strong event-scale variations (or fluctuations), in depth-integrated (22–190 m) zooplankton biomass. Zooplankton biomass peaks (shown as anomalies in Fig. 2) occur throughout the time series. These peaks are sometimes associated with spring phytoplankton blooms or in some cases passages of mesoscale features as discussed later.

The seasonal patterns of chl-a and zooplankton biomass do not display the rather smooth regularity of upper ocean temperatures and are not necessarily in phase with each other. Rather, episodes of increased levels of phytoplankton and zooplankton, which are sometimes associated with spring shoaling of the mixed layer, occur for periods of a few to several weeks at a time. Further, the onset of such blooms vary interannually. For example, the time series of chl-a fluorescence at 77 m show strong evidence of a spring phytoplankton bloom in mid-May to mid-June, 1997 (Fig. 2g). The chl-a fluorescence started to rapidly increase around May 15, 1997; during this time ADCP-estimated daily averaged, depth-integrated zooplankton biomass increased significantly and reached its maximum of 700 mg dw m⁻². Zooplankton biomass concentrations with relatively high values (greater than 6 mg dw m⁻³) extended to ~110–120 m during the nights of May 17–19, 1997 (Fig. 3b). In mid-February to late March 1998, daily averaged, depth-integrated zooplankton biomass was relatively high (Fig. 2f); during the period of March 3–22, 1998, significant increases in zooplankton biomass concentrations also extended much deeper as indicated in Fig. 3b. This episode may have been related to incipient springtime shoaling of the mixed layer (see Fig. 2e temperature data). Unfortunately, chl-a data were not available for this time period. From late February to March 1999, the time series of chl-a at 72 m shows strong evidence of a bloom (Fig. 2k). Chl-a fluorescence started to increase rapidly around February 16 and more than doubled in magnitude on February 24. Zooplankton biomass increased significantly during this period and reached its peak value of 647 mg dw m⁻² on February 22 (Fig. 2j). This bloom was likely due to the onset of stratification that followed deep mixing, which penetrated as deeply as 100 m depth as shown in the stack plot of temperature in Fig. 2i. In March 2000 there were also elevated levels of zooplankton biomass; these too may be related to an incipient spring bloom (unfortunately, no chlorophyll records are available). Finally, an extended summertime increase in zooplankton biomass, July–August, 2000 (Figs. 2r and 3e) was not coincident with an increase in chl-a.

As mentioned above, higher zooplankton biomass values for at least some blooms appeared to extend deeper into the water column during biomass peaks, as illustrated by the black line in Fig. 3 (indicating the maximum depth where biomass
Fig. 2. (a)-(t) Time series of daily averaged temperature at several depths; daily averaged, depth-integrated (22–190 m) zooplankton biomass anomaly (in mg dw m\(^{-2}\)) estimated using ADCP backscatter intensity data; chlorophyll-\(a\) fluorescence (in relative units) at specific depths; and horizontal current speed measured by the ADCP at about 45 and 150 m. Years are indicated in each panel. The color bar scale indicates depths of temperature measurements. The mean depth-integrated, daily averaged value of 497 mg dw m\(^{-2}\) of the zooplankton biomass is shown on the right of each of the relevant panels for reference.
Fig. 2. (Continued)
values remain at least 3 mg dw m$^{-3}$). We tested this notion and whether deeper zooplankton values may have increased disproportionately during the peaks by calculating the depth at which about 50% of the integrated zooplankton biomass (using 24-h averaged data) was above that depth ($D_{50}$). We separated the $D_{50}$ data set for the whole time series into “peak” (>1 standard deviation above the mean integrated biomass, $n = 172$) and “non-peak” (all other data, $n = 970$) categories. The mean (±1 standard deviation) $D_{50}$ during biomass peaks was 90 m (±7 m), slightly but significantly lower than during non-peaks which had a $D_{50}$ of 84 m (±7 m) (Wilcoxon Two-Sample Test, $p < 0.0001$), indicating the biomass distribution was marginally deeper during biomass peaks.

The statistical relationships between the phytoplankton and zooplankton time series for segments of one of the spring bloom periods are described next. Fig. 4a shows 30-day, high pass filtered time series of zooplankton biomass concentrations and chlorophyll fluorescence during the spring bloom of
Fig. 3. Contours of zooplankton biomass estimated from ADCP backscatter intensity (using 1-h averaged data) during Deployment 6–14 (1996–2000). The black line is the maximum depth where biomass values remain at least 3 mg dw m$^{-3}$ (using 24-h averaged data).
May–June 1997 (Deployment 7). Zooplankton biomass and chlorophyll fluorescence matched very well during the period of days 143–172 (May 23–June 21) as indicated in Fig. 4b, which shows that the cross-correlation between zooplankton biomass (76 m) and chlorophyll fluorescence (77 m) is positive with the maximum correlation of 0.89 at near 0 day time lag. Note that in the inset notation used for the cross-correlation vs. time lag plots, $r_{\text{max/\text{lag}}}$ values indicate a maximum correlation coefficient and days phase lag, and $r_{\text{min/\text{lag}}}$ denotes the minimum correlation coefficient (negative values) and days phase lag. Negative phase lag values indicate that either chl-$a$ or temperature lags behind zooplankton biomass concentration (given in DW per unit volume) in these plots. A similar analysis was applied to temperature and zooplankton biomass as indicated in Fig. 4c. There was an inverse relation (i.e., high negative correlation or min value in Fig. 4c) between zooplankton biomass and temperature with a maximum negative correlation of $-0.79$ at near 0 lag (Fig. 4d). When comparing the time series and cross-correlation/time lag plots it is evident that cool and likely relatively nutrient-rich waters coincide with both the elevated chl-$a$ and zooplankton biomass.

In order to examine the seasonal variability in zooplankton biomass, the ADCP-derived depth-integrated zooplankton biomass data were averaged for each month of the year. That is, all depth-integrated zooplankton data collected from August 1996 through November 2000 were binned by month to produce the seasonal composite shown in Fig. 5.

Our BTM data are overlayed with a similar analysis by Madin et al., 2001 for BATS net tow data collected between April 1994 and December 1998 (Fig. 5). For the BTM, monthly averaged,
daytime depth-integrated zooplankton biomass data shown were collected from 10 a.m. to 2 p.m. and nighttime data were collected from 10 p.m. to 2 a.m., all in local time. The largest monthly average depth-integrated zooplankton biomass values occurred in March for both day and night samples, with a secondary maximum occurring in July. This is similar to the results of Madin et al. (2001), however their net data show a daytime biomass peak in April as well. The large standard deviations are not surprising considering the high frequency variability associated with episodic events. The nighttime BTM mean values are roughly 150 mg dw m$^{-2}$ greater than the daytime values, and the Madin et al. (2001) mean nighttime values are greater than the BTM from February through July, while the daytime values are generally well within the standard deviations of the two separate time series.

### 3.2. Eddies

Mesoscale eddy features have been suggested as playing an important role for new production and phytoplankton dynamics near Bermuda (e.g., Jenkins, 1988; McGillicuddy et al., 1998; McNeil et al., 1999) and may influence zooplankton populations as well.

A major mode eddy (second baroclinic mode) passed the BTM site in 1994 and exhibited some of the highest concentrations of chl-a recorded at the site. Unfortunately, an ADCP was yet be deployed from the BTM mooring and hence we do not have a concurrent zooplankton data set. Nonetheless, the data under consideration here indicate the passages of at least two other mesoscale features.

During the period of October 26, 1996–January 4, 1997 (Deployment 6), the physical conditions at the BTM site were characterized by relatively high wind stress (Dickey et al., 2001; Conte et al., 2003), monotonic cooling of near-surface waters, highly variable temperature at depths of 7–154 m with major warming (by ~4 °C) first at 71 m and about a month later at 154 m, deepening of the mixed layer from about 50 to >175 m (Fig. 2a), directional changes in currents, and currents with magnitudes of up to 50 cm s$^{-1}$ (Fig. 2d). In late November and December 1996, the BTM sampling showed evi-
a) Dep. 6 DW and Chl, 30 days high-pass filter

b) DW vs Chl

C) Dep. 6 DW & Temp, 30 days high-pass filter
d) DW vs Temp

e) Dep. 10 DW & Chl, 30 days high-pass filter
f) DW vs Chl

G) Dep. 10 DW & Temp, 30 days high-pass filter
h) DW vs Temp
dance of significantly elevated concentrations of phytoplankton, which were apparently associated with the passage of a warm mesoscale eddy as evidenced by both subsurface temperature and currents (Figs. 2a and d). The feature was characterized by anti-cyclonic rotation of currents and a thick, warm, low salinity isothermal layer > 180 m in depth. Within the feature, sensors on the BTM mooring recorded roughly 50% increases in chl-α. The daily averaged ADCP estimates of 22–190 m integrated zooplankton biomass increased significantly when the feature arrived at the BTM site and peaked (648 mg dw m$^{-2}$) on December 13–14 when the central portion of the feature appeared to be nearly centered upon the mooring (Fig. 2b). This was confirmed by zooplankton net tow data. Within the feature, integrated zooplankton biomass in the upper 200 m averaged 785 mg dw m$^{-2}$ at midday and 1082 mg dw m$^{-2}$ at night (Madin et al., 2001). Interestingly, at about the same time, the Oceanic Flux Program (OFP) sediment traps recorded an abrupt, factor of 2.5, increase in mass flux at 3200 m depth during the eddy’s passage (Conte et al., 2001). Cross-correlational methods were used to examine effects of this eddy in a manner similar to that used to explain spring blooms in the previous section. Filtered time series shown in Fig. 6a indicate that zooplankton biomass (46 m) and chlorophyll fluorescence (45 m) tracked each other (maximum correlation coefficient of 0.87 shown in Fig. 6b) with chlorophyll lagging zooplankton concentrations by about 2 days. There was also a positive relationship between zooplankton biomass and temperature with maximum correlation of 0.51 at 1 day lag (Figs. 6c and d).

During Deployment 10 (November 11, 1998–March 19, 1999), current vectors show clear evidence of a strong, cold mesoscale cyclonic eddy with horizontal size 314 km$^2$ from December 26, 1998 to February 4, 1999. Stack plots of temperature show that temperatures between depths of 150 and 250 m decreased significantly during this period, indicating a cold eddy with counter-clockwise current rotation (Figs. 2i and l). Surprisingly, chl-α fluorescence and zooplankton biomass did not change significantly during the passage of this strong eddy. One possible explanation for this is the presence of a shallow mixed layer and a strong thermocline, which could have restricted injection of nutrients into the surface layer and led to depletion of nutrient that were trapped in the mixed layer. Interestingly, elevated values of both chl-a and depth-integrated zooplankton biomass do appear toward the end of February as the edge of the eddy passes over the BTM. We can speculate that either eddy edge effects or possibly incipient springtime stratification or both may have contributed to the large increases in both zooplankton and phytoplankton biomass (Figs. 2j and k). Again, by applying cross-correlational methods for this eddy feature, it was found that the correlation between zooplankton biomass concentration (73 m) and chlorophyll fluorescence (72 m), calculated from January 2 to 31, 1999, is positive with the maximum correlation of 0.79 at 0 lag (Figs. 5e and f). Zooplankton biomass and temperature were also inversely related with a maximum negative correlation of −0.70 at −2 days lag (Figs. 5g and h). While other mesoscale eddies of varying strength passed the site during the period of our study (e.g., see October 1997; late June 1999; October 2000), none of these appear to have exhibited appreciable biomass signals.

### 3.3. Wind events

The Bermuda region is often impacted by tropical storms and hurricanes. Specifically, 153 tropical storms and hurricanes have tracked within a square roughly 400 km on side centered on the BTM site since 1851, and 15 have passed through this area between 1995 and 2005. The physical effects of extreme storms on the upper ocean have been reasonably well documented at the BTM site and are characterized by rapid mixed layer deepening, cooling of the near surface layer, warming of waters below the cooling depths, large horizontal currents peaked near the local inertial period, large vertical oscillations in the thermocline near the inertial
zooplankton biomass variability (due to diel vertical migration) of the upper ocean, such as shown in the ADCP acoustic backscatter data. The depth-integrated zooplankton biomass as estimated from the ADCP acoustic backscatter data indicate a significant decrease as shown in Figs. 7c and f. Interestingly, zooplankton biomass distribution extended deeper into the water column after the hurricane; meanwhile, the depth-integrated zooplankton biomass decreased.

3.4. Diurnal variability and diel vertical migration

Physical variability of the upper ocean is often characterized by energy peaks associated with semi-diurnal (~12.5 h period, or frequency of 0.16 cpd) and diurnal (~24 h period or frequency of 0.1 cpd) tides, diurnal cycles of heating and cooling, and mixed layer depth shoaling and deepening associated with the daily solar insolation cycle. In addition, wind events, especially major storms and hurricanes, produce currents near the local inertial period, which is 22.8 h (inertial frequency is 0.0438 cph or 1.05 cpd) at the BTM site. Phytoplankton populations can also exhibit diel rhythms. These various processes contribute to elevated power spectra values in physical and biological variables as discussed in detail with respect to the BTM site by Dickey et al. (2001). The elevation of energy in the range of periods of 22–25 h is illustrated for ADCP current power spectra shown in Fig. 8 for individual BTM Deployments 7 (May 4–July 29, 1997), 8 (August 9–November 19, 1997), and 9 (November 27, 1997–May 30, 1998). The spectra are computed for four depths: 45, 75, 150, and 190 m. Seasonal and depth differences are apparent in these individual spectra. However, the most important result for this study is the clear elevation of energy in the vicinity of the diurnal and near-inertial periods.

Likewise, the power spectra for zooplankton biomass (Fig. 9) indicate a clear diurnal peak in zooplankton biomass variability (due to diel vertical migration, and Ekman pumping (e.g., Dickey et al., 1998a, b, 2001; Zedler et al., 2002). Phytoplankton concentrations are now thought to increase in the wakes of many hurricanes, as shown by extensive analyses of satellite ocean color data (e.g., Babin et al., 2004). In regard to the present study, we pose the question, “Do tropical storms and hurricanes affect zooplankton abundance?”

During the first half of Deployment 6 (approx. August–October 1996), three hurricanes, Edouard, Hortense, and Lili, passed into the region of the BTM. The eye of Edouard passed 570 km to the west of the BTM on August 31, 1996 while Hortense and Lili passed 530 km to the west on September 13, 1996 and 170 km to the southeast on October 20, 1996, respectively. All three hurricanes are evident in time series of winds. However, the hurricanes generated oceanic responses to different degrees. Hurricane Lili excited the strongest oceanic signals at the BTM location, while the response to Hurricane Hortense was weaker but still evident in relative humidity, short wave radiation, radiance and irradiance data. Hurricane Edouard did not generate a significant response. When Hurricane Lili passed, barometric pressure dropped by about 30 mb from 291 to 295 (October 17–21). This hurricane also excited strong inertial oscillations in the upper ocean, as shown in horizontal currents. Chl-a fluorescence levels at 45 and 73 m (Fig. 2c) were generally low during the passages of these three storms and showed no significant effect of the atmospheric disturbances. Zooplankton biomass was likewise apparently not impacted by these hurricane passages as indicated by integrated zooplankton biomass time series (Fig. 2b) or the vertical distributions of concentrations of zooplankton biomass (Fig. 3a). Similar results were found for Hurricane Gert which passed within about 160 km of the BTM on September 21, 1999.

Although the physical effects of the hurricanes described thus far were apparently insufficient to significantly affect the local phytoplankton and zooplankton distributions and abundances, data collected in 2003 are especially interesting in regard to hurricane effects on phytoplankton and zooplankton. The eye of Hurricane Fabian passed within 100 km and to the west of the BTM. Time series of wind speed are shown in Fig. 7a.

Direct measurements from the BTM’s anemometer were available only through September 5, 2003 when the instrument stopped collecting data. Quikscat satellite wind data are shown as a dashed curve for the remainder of the period. Peak winds reached 34 m s⁻¹ at the BTM site. The mixed layer deepened from about 20 to 50 m with the passage and surface waters cooled by over 3 °C as shown in Fig. 7b. Vertical oscillations of the seasonal thermocline near the local inertial period (near 22.8 h) are evident as well. Near-inertial currents reaching well over 100 cm s⁻¹ were produced in the upper layer (Fig. 7c). Chlorophyll fluorescence increased after passage of the hurricane. The 35 m chlorophyll fluorescence record appears to have subsequently become erroneous, likely because of biofouling. The zooplankton biomass as estimated from the ADCP acoustic backscatter data indicate a significant decrease as shown in Figs. 7e and f. Interestingly, zooplankton biomass distribution extended deeper into the water column after the hurricane; meanwhile, the depth-integrated zooplankton biomass decreased.
Fig. 7. Time-series of wind, temperature, fluorescence, zooplankton biomass and zooplankton biomass anomaly during the period of hurricane Fabian: (a) wind speed, solid line-from BTM, dash line-from Quikscat; (b) 2-h averaged temperature at depth 1, 8, 11, 18, 21, 35, 46, 56, 72, 101, 151 and 201 m; (c) 2-h averaged fluorescence at 11 and 35 m; (d) 2-h averaged current at 36 and 150 m; (e) contour of zooplankton biomass estimated from ADCP; and (f) 1-day averaged and depth-integrated zooplankton biomass anomaly.
migration), which is depth dependent (analogous to the current power spectra in Fig. 8). The diurnal peak in zooplankton biomass variability occurs down to roughly 150 m for the organisms observable with our ADCP system. Interestingly, a smaller semidiurnal peak is evident in the zooplankton power spectra as well (of which the cause is unclear).

To further examine seasonal differences in diel variability of zooplankton, the daily cycle of zooplankton biomass and vertical movement velocity (relative to 34–43 m depth) was computed using data collected during each of four specified 14-day intervals. Data used for this analysis cover an approximate annual cycle (Deployments 7–9 encompassing May 3, 1997 through March 31, 1998) during four seasons (spring, summer, fall, and winter). All data were registered to a 24-h cycle in order to compute time series for examining diel variability. Specifically, data collected from midnight to 15 min after midnight were ensemble
averaged (14 realizations since 14 days of data were used for the calculation) to produce a single mean value for this interval. This procedure was repeated for every ensuing 15-min interval including the final ensemble averaging period prior to the next day’s midnight. The ensemble averaged diel cycle data for zooplankton biomass concentrations and relative vertical velocity, both with respect to depth, are presented in Fig. 10a–i for each of the representative seasons. Analogous depth-integrated zooplankton biomass ensemble time series for each of the seasons are shown in Fig. 11.

During the spring, biomass is generally high in the upper layer and decreases with depth (Fig. 10a). During the night, the highest average biomass is 5.7 mg dw m$^{-3}$ at 22 m and values greater than 5 mg dw m$^{-3}$ occasionally extend to 94 m. Interestingly, there is a relatively high biomass ($>4.8$ mg dw m$^{-3}$) thin layer (22–31 m) near the surface during the day from 8:00 to 17:00 local time.
Fig. 10. The daily cycle of zooplankton biomass and relative vertical velocity (relative to 34–43 m depth) computed using an ensemble average of 14-day time series show zooplankton biomass vertical distributions and daily migration patterns in the spring (May 16–29, 1997), summer (August 16–29, 1997), fall (November 1–14, 1997) and winter (February 10–23, 1998). Negative and positive relative velocity indicates downward and upward movement, respectively.
Fig. 10. (Continued)
Depth-integrated zooplankton biomass is highest at night; it ranges from roughly 650 to 680 mg dw m$^{-2}$ (Fig. 11). Relative vertical velocity contour plots show strong diel migration signals at sunrise and sunset (Fig. 10b). Downward velocity has a maximum value of 5.4 cm s$^{-1}$ at 163 m at about 4:45 (dawn), while upward velocity has a maximum value of 5.0 cm s$^{-1}$ at 169 m at about 19:45 (dusk). Downward velocities have large values at depths greater than about 100 m, while upward velocities have large values at depths greater than about 120 m.

In the summer, <100 m nighttime zooplankton biomass is generally lower than in the spring (Fig. 10c). Also, there appears to be one or two subsurface maxima in zooplankton biomass. The nighttime depths where zooplankton biomass falls to values less than about 4 mg dw m$^{-3}$ are roughly near 120 m for both the spring and summer periods. The daytime zooplankton concentrations are considerably lower during the summer than the fall (compare Figs. 10c and e). Diel migration signals for the summer period are clear, but migration speeds are somewhat slower than in the spring period (compare Figs. 10b and d).

In the fall, there is a persistent, strong subsurface maximum layer with high zooplankton biomass (greater than 5 mg dw m$^{-3}$) between ~60 and ~80 m during the nighttime (Fig. 10c). A subsurface maximum in zooplankton biomass also appears during the daytime in the fall (Fig. 10e). The nighttime depth-integrated zooplankton biomass for the fall is comparable to that observed during the springtime.

In the winter, diel migration is still evident, though less pronounced than for the other seasons (Fig. 10h); biomass is lower in the upper layer at night, and differences between zooplankton biomass during night and day are relatively small compared with the other seasons. There is little vertical structure in zooplankton biomass, which appears to persist at relatively high values at somewhat deeper depths than for the other seasons (Fig. 10g). This is likely related to deeper wintertime mixed layer depths.

Our high temporal resolution, long-term time series allows us to examine the modulation of diel migration and acoustic backscatter as depicted in Fig. 12 as contour plots of acoustic backscatter and relative vertical velocity with hour of day (ordinate)
Fig. 12. Backscatter intensity and relative vertical velocity (relative to 34–43 m depth) averaged between 121 and 190 m depths from May 4, 1997 through March 30, 1998 show seasonal variations in diel migration. The top panel shows backscatter intensity. The bottom panel shows relative vertical velocity; negative values indicate downward motion, and positive values represent upward motion; black lines represent sunrise and sunset times (in hours).
versus day of the year (abscissa). Shown in the figure are averaged values over the depth interval of 121–190 m for backscatter intensity and relative vertical velocity (the latter relative to 34–43 m depth) from May 4, 1997 through March 30, 1998 (Deployments 7–9). These time series clearly show seasonal variations of the diel migration and zooplankton biomass (Fig. 12). Specifically, day length modulates the timing of the migration. The timing of migration clearly changes with the seasonal light progression, with ascents earlier in the evening (backscatter intensity increases), and descents later (backscatter intensity decreases) in the morning in winter compared to summer (Fig. 12).

Fig. 13 shows the timing of peak downward and upward migration velocity relative to the times of sunrise and sunset. The difference in minutes between the time of the peak vertical velocity between 4:00–7:00 and 17:00–20:00 and the time of sunrise/sunset was calculated; negative values indicate that migration preceded sunrise/sunset. Data used for this figure were from May 4, 1997 through March 30, 1998.
sunrise and sunset. Backscatter intensity begins to decrease before sunrise and begins to increase after sunset. Most downward movements begin about 40 min before sunrise (Fig. 13a) and upward movements begin about a half an hour after sunset (Fig. 13b).

4. Discussion and conclusions

The use of ADCPs for estimating zooplankton biomass has several attractive aspects. For example, ADCPs are increasingly being used for physical current measurements and thus provide enhanced opportunities to study zooplankton via the recording of acoustic backscatter data. The availability of broadband ADCPs is a positive development as well. The vertical and temporal resolution of the ADCPs is excellent and provides biological oceanographers with data on essentially the same time and space scales as the physical data, affords the possibility of decade-long sampling, and enables climatic studies with continuous measurements.

There remain some inherent constraints for the ADCP method. Our ADCP sampling intervals are either 7.5 or 15 min. With a migratory speed of 5 cm s\(^{-1}\), the depth range of a migrator moving during the sampling intervals would be 22.5 and 45 m. Also, our ping intervals are either 36 or 73 s, so the depth ranges of migrators moving during these ping intervals are approximately 1.8 and 3.7 m, respectively. Thus, any specified scattering organism may be in different depth bins for different pings. Long ping intervals and sampling intervals may explain in part why we cannot clearly see migration at a deeper depth.

Another important problem is sampling only a limited size range of organisms. Generally, ADCPs measure objects in the size range of millimeters to a few centimeters. The minimum length of organisms detected by a 153-kHz ADCP has been reported to be about 1 mm (Luo et al., 2000). The most likely acoustic scatterers to be detected by a 153-kHz ADCP are copepods, euphausiids and amphipods (Fischer and Visbeck, 1993; Roe and Griffiths, 1993; Heywood, 1996; Rippeth and Simpson, 1998). For our Bermuda site, Madin et al. (2001) found that the smaller size classes (0.2–1.0 mm) constituted the highest proportion of the biomass during the day and the increase in nighttime biomass is mostly due to increases in the biomass of larger size organisms (84% of the migrating biomass > 1.0 mm in the upper 200 m, and 56% > 2.0 mm). Steinberg et al. (2000) observed that the dominant migratory species at the BATS site include large copepods such as Pleuromamma spp. and Euchirella messinessis (2–6.5 mm). Other dominant migrators included euphausiids 12–23 mm), hyperiid amphipods (6–20 mm), and sargostid shrimps 5–30 mm) (Steinberg et al., 2000), and a variety of gelatinous taxa such as siphonophores and salps. Although, we likely sampled a fairly high percentage of relevant zooplankton with our ADCP data, some organisms are clearly unsampled or undersampled. On the other hand, as pointed out by Ashjian et al. (2002), some organisms that are not collected by net tows, such as fish, fast swimming euphausiids, and siphonophores, may contribute substantially to acoustic backscatter measurements (also see Wiebe and Greene, 1994; Holliday and Pieper, 1995; Stanton et al., 1993, 1994).

The calibration issue has been addressed in the present work by utilization of concurrent zooplankton net tow data. However, this approach is not without problems. As indicated earlier, it is difficult to do net tows near the ADCP and spatial variations (patchiness) can introduce large sampling discrepancies. Also, the net tow data represent integrals and thus valuable vertical distributional data are not obtained, and the calibration relationships are not particularly strong. In this context, some may prefer to only report the ADCP data in relative backscatter units. However, we feel that there is merit in attempting to use these data as proxies for zooplankton biomass at this well-sampled time-series site, and at least for establishing zooplankton variability, particularly because our seasonal, depth-integrated zooplankton biomass time series results appear to be in reasonable agreement with the net tow results of Madin et al. (2001) obtained near our site in a similar time frame (Fig. 5).

Future studies can benefit from more intense calibration efforts that could include not only net tow data, but also lowered multi-frequency acoustic, optical, video, and holographic camera systems. These systems would provide increased vertical resolution and organism identification capabilities. Optimally, future deep-sea moorings may be capable of profiling such suites of instruments in the upper ocean. Already, coastal versions are being utilized. The problem of distinguishing vertical water motion opposed to zooplankton migratory motion is very challenging as noted by Fischer and
Visbeck (1993) and will require new ideas and technologies.

4.1. Seasonal variability in zooplankton biomass

The seasonal variability of zooplankton biomass has rarely been studied using high temporal resolution data sets and thus our results provide some new insights. Our study indicates the mean seasonal signal results from the integrated effects of many episodic events as well as the periodic physical forcing at the annual cycle driven by solar insolation. Cool and likely nutrient rich waters along with shoaling mixed layers and increased light exposure contribute to spring blooms as evidenced in both elevated chl-a and zooplankton biomass. The lack of a significant lag in time between phytoplankton and zooplankton spring blooms is somewhat surprising. However, it appears that these were locally realized springtime blooms in that the temperature and current records during the blooms do not indicate significant eddy or advective features that could explain the results. Thus the cross-correlation analyses indicated a tight coupling between increases in phytoplankton and zooplankton, and both the phytoplankton and zooplankton blooms appear as pulses that eventually are manifested in monthly averaged increases in the springtime.

The nearly continuous sampling afforded by the ADCP technique is effective for making good seasonal estimates, especially because of the degree of short-term variability in the biology that cannot be adequately sampled using traditional ship-based net tows, which can generally be done only for a few days per month and not during inclement ocean conditions. Nevertheless, our seasonal composite data comparison with that of Madin et al. (2001) indicates that the net tow data approximate the seasonal cycle—with a high spring, and a second, smaller summer biomass peak—quite well. The nighttime net tow measured biomass was, however, higher than the BTM estimated biomass. There are several likely explanations for the observed differences between the two data sets: the methodologies were quite different (ADCP acoustics vs. net tows), sampling was nearly continuous with the ADCP opposed to once per month for the net tows, the depths of integration for the ADCP were about 22–190 m whereas the net tows sampled from 0 to 200 m, and the organisms sampled with the ADCP are from a selected size class whereas the net tow data include organisms ranging over a much broader size range. The latter two differences likely account for the smaller values of depth-integrated zooplankton biomass observed at night by the ADCP method, as the larger diel migrators are less likely to be detected by the ADCP than sampled by the net. Thus we conclude that while the monthly net sampling represents the seasonal cycle in zooplankton biomass well, the episodic changes that make up the seasonal signal are best captured by the ADCP.

4.2. Effects of eddies

Mesoscale eddies are of special interest for upper ocean ecology and biogeochemistry (e.g., review by Lewis, 2002) and have been suggested as playing an important role for new production and phytoplankton dynamics near Bermuda (e.g., Jenkins, 1988; McGillicuddy et al., 1998; McNeil et al., 1999). For example, the influence of mesoscale features was estimated by McGillicuddy et al. (1998) using the BTM data set, shipboard observations, and a regional eddy-resolving model. They have suggested that the flux of nutrients induced by mesoscale eddies may be sufficient to balance the nutrient budget of the Sargasso Sea. Mesoscale eddies are also known to affect oceanic zooplankton communities (e.g., Wiebe et al., 1992; Piontkovski et al., 1995; Hernández-León et al., 2001) and elevated zooplankton biomass and enhanced fecal pellet flux have been found in a cold-core and a mode water eddy in the Sargasso Sea off Bermuda (Goldthwait and Steinberg, submitted). Mesoscale eddies often pass the BTM mooring site (e.g., Dickey et al., 1998a, 2001; McNeil et al., 1999; Conte et al., 2003). Previous reports have documented enhanced primary productivity associated with first and second baroclinic mode eddies. However, the present study is the first to examine a long record of eddy influence on zooplankton distributions as well. The strongest eddy to pass the BTM was likely the summer 1994 event; however, this was prior to acquisition of an ADCP. The time period of prime interest here indicates the passages of eddies. Some of these appear to reflect enhanced zooplankton as well as phytoplankton concentrations. However, others do not. This is important with respect to inferred influence of these features, as it appears not all mesoscale eddies play a significant role in modulating upper ocean plankton community structure, biogeochemistry, and carbon fluxes. Our
time series results indicate that more in situ time series data sets such as those described here along with focused process-oriented eddy experiments (e.g., recent EDDIES experiment off Bermuda and E-Flux off Hawaii), devoted to the ecology, community structure, and biogeochemistry as well as the physics of mesoscale eddies are essential for future progress.

4.3. Effects of wind events

There is increasing interest in the effects of high wind and especially hurricanes on the ocean. Our study region is ideal for such research. Because of the difficulty of sampling with ships during major wind events, moored observations are important. Early indications suggest that there are likely a variety of physical parameters, which need to be considered in determining how upper ocean biology will respond. Already, some investigators have provided evidence of induced phytoplankton blooms in the wakes of hurricanes in the North Atlantic (i.e., Babin et al., 2004). Fewer data are available to determine effects upon zooplankton. Our data sets, though rather limited for making broad conclusions, suggest that at least major hurricanes such as Hurricane Fabian may result in deeper distributions of zooplankton and possibly reduced depth-integrated zooplankton biomass. It is possible that the increased mixing distributed zooplankton deeper and also advected some of the biomass away from the sampling site. We suggest that some wind speed threshold must be reached for there to be major effects on zooplankton distributions in the upper ocean, and thus effects on zooplankton in our study were only notable during this strong hurricane in close proximity to the BTM site. Observations of more hurricane events should help to determine if this apparent phenomenon was aberrant or the norm.

4.4. Diel vertical migration patterns

The seasonal modulation of the diel vertical migration of zooplankton is very evident in our high-resolution data. In springtime, zooplankton biomass is generally high in the upper layer and decreases with depth and there is strong vertical migration at sunrise and sunset. The estimated maximum relative vertical velocity computed using an ensemble average of 14-day time series of data occurred in spring with a value of 5.4 cm s\(^{-1}\). This value is comparable to results presented by other researchers as summarized by Luo et al., 2000): 1–4 cm s\(^{-1}\) (Plueddemann and Pinkel, 1989), 3–8 cm s\(^{-1}\) (Smith et al., 1989), 2–4 cm s\(^{-1}\) (Roe and Griffiths, 1993), 2–6 cm s\(^{-1}\) (Heywood, 1996), and maximum of 10 cm s\(^{-1}\) (Luo et al., 2000). Diel migration patterns for the summer period are evident, but vertical migration speeds are slower than in the spring. In the fall, there is a persistent, strong subsurface maximum layer during the night. In winter, diel migration is less pronounced compared with the other seasons, and there is only weak structure in zooplankton biomass distribution, likely explained by deeper wintertime mixed layers.

The high-resolution nature of our sampling enabled us to examine the annual modulation of diel migration and acoustic backscatter. These data clearly illustrate how the length of daylight modulates the timing of the zooplankton migration. Migratory ascents occur earlier in the evening (backscatter intensity increases), and descents take place later in the morning in winter compared to summer. Seasonality of diel migration was also explored by Fischer and Visbeck (1993) using an ADCP in the Greenland Sea. As expected at this high latitude site, the timing and intensity of diel migration was considerably more variable over an annual cycle than in the Sargasso Sea, with diel migration dampened in mid-summer and winter and pronounced in the periods in between. The specific timing of peak downward and upward migration velocity relative to the times of sunrise and sunset was documented for the first time at our site, with most frequent downward movements beginning about 40 min before sunrise and upward movements beginning about a half an hour after sunset. Vertically migrating zooplankton play an important role in biogeochemical cycling as they can actively transport a significant amount of dissolved inorganic and organic carbon and nitrogen to the deep sea (e.g., Longhurst et al., 1990; Steinberg et al., 2000, 2002; Al-Mutairi and Landry, 2001). These high-resolution data showing diel changes in zooplankton biomass will help constrain estimates of active transport of carbon and nitrogen to the deep sea via zooplankton migration.

To conclude, long-term BTM observations with acoustic zooplankton biomass measurements will play an important role in understanding zooplankton biomass variability with episodic events (e.g., eddy passages, wind mixing) and diel zooplankton migrator patterns in the Sargasso Sea, and can facilitate studies of physical and biological interactions and biogeochemical cycling.
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