Long-term increase in mesozooplankton biomass in the Sargasso Sea: Linkage to climate and implications for food web dynamics and biogeochemical cycling

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[1] Changes in zooplankton biomass and species composition over long time scales can have significant effects on biogeochemical cycling and transfer of energy to higher trophic levels. We analyzed size-fractionated mesozooplankton biomass (>200 μm) from biweekly to monthly day and night tows taken from 1994 to 2010 in the epipelagic zone at the Bermuda Atlantic Time series Study (BATS) site in the oligotrophic North Atlantic subtropical gyre. During this 17-year period total mesozooplankton biomass increased 61% overall, although a few short-term downturns occurred over the course of the time series. The overall increase was higher in the nighttime compared to daytime, resulting in an increase in calculated diel vertical migrator biomass. The largest seasonal increase in total biomass was in the late-winter to spring (February–April). Associated with the larger increase in late-winter/spring biomass was a shift in the timing of annual peak biomass during the latter half of the time series (from March/April to a distinct March peak for all size fractions combined, and April to March for the 2–5 mm size fractions). Zooplankton biomass was positively correlated with sea-surface temperature, water column stratification, and primary production, and negatively correlated with mean temperature between 300 and 600 m. Significant correlations exist between multidecadal climate indices–the North Atlantic Oscillation plus three different Pacific Ocean climate indices, and BATS zooplankton biomass, indicating connections between patterns in climate forcing and ecosystem response. Resultant changes in biogeochemical cycling include an increase in the magnitude of both active carbon flux by diel vertical migration and passive carbon flux of fecal pellets as components of the export flux. The most likely mechanism driving the zooplankton biomass increase is bottom-up control by smaller phytoplankton, which has also increased in biomass and production at BATS, translating up the microbial food web into mesozooplankton. Decreases in top-down control or expansion of the range of tropical species northward as a result of warming may also play a role.

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1. Introduction

[2] Changes in zooplankton communities are important indicators of the effects of climate change on pelagic ecosystems [*Hays et al.*, 2005; *Richardson*, 2008]. Zooplankton have relatively short life cycles (weeks to months for most species, <1 year), which makes their populations tightly coupled to environmental change [*Mackas et al.*, 2001; *Hays et al.*, 2005; *Hooff and Peterson*, 2006]. Given their central role in food webs as consumers of primary production and prey for fish and higher trophic levels, changes in zooplankton populations have the potential to alter ecosystem structure [*Fernández de Puelles and Molinero*, 2008]. In addition, changes in zooplankton biomass and species composition over long time scales can have significant effects on ecosystem function, as zooplankton also play a key role in biogeochemical cycling [*Roman et al.*, 2002; *Steinberg et al.*, 2008; *Hannides et al.*, 2009].

[3] Long-term zooplankton time series show clearly that zooplankton populations are changing in terms of their community composition, abundance, and biomass; distribution of individual species; and in the timing of important life-cycle events (phenology) [*Richardson*, 2008]. For example, in the tropical Atlantic, there has been a nearly 10-fold decrease in mesozooplankton biomass from the 1950s to 2000 [*Piontkovski and Castellani*, 2009]. A

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significant long-term increase in mesozooplankton biomass from 1994 to 2005 has been documented in the North Pacific subtropical gyre (NPSG) [*Sheridan and Landry*, 2004; *Hannides et al.*, 2009]. In the California Current ecosystem off Southern California *Lavaniegos and Ohman* [2007], extending the earlier analyses of *Roemmich and McGowan* [1995], show a decline in displacement volume of mesozooplankton from 1951 to 2005 concurrent with an increase in water column stratification. Interestingly, carbon (C) biomass did not show a significant decline, which was attributed to a long-term decline in the abundance of pelagic tunicates (mostly salps) that have high volume to C ratios. Change in long-term, large-scale distribution of zooplankton is illustrated by the northward expansion (~10° latitude) of multiple copepod species in response to oceanic warming and changes in hydrography [*Beaugrand et al.*, 2002; *Beaugrand and Ibanez*, 2004]. Long-term studies also indicate that earlier timing in peak zooplankton biomass, tied to oceanic warming, has occurred for a variety of taxa in the Central North Sea [*Edwards and Richardson*, 2004], for *Neocalanus plumchrus* copepods in the Subarctic Pacific [*Mackas et al.*, 1998], and for ctenophores in Atlantic coastal estuaries [*Costello et al.*, 2006; *Condon and Steinberg*, 2008]. Some of the above and other changes have been linked to decadal climate oscillations such as the North Atlantic Oscillation [*Beaugrand et al.*, 2002; *Lynam et al.*, 2004; *Piontkovski et al.*, 2006] or the Pacific Decadal Oscillation [*Peterson and Schwing*, 2003; *Chiba et al.*, 2006].

[4] The implications of long-term changes in zooplankton communities on transfer of energy to higher trophic levels and biogeochemical cycling are not well known. Through their feeding, metabolism, and migration behavior, zooplankton play a significant role in biogeochemical cycling [*Small et al.*, 1989; *Buitenhuis et al.*, 2006; *Hannides et al.*, 2009]. Changes in zooplankton biomass or species composition over time can thus lead to increases or decreases in removal of primary production and fecal pellet export, remineralization of nutrients, and active transport via diel vertical migration (DVM) of C and nutrients to depth. For example, many species of zooplankton (and fish) that are resident in the mesopelagic zone during the day migrate into surface waters at night to feed, and descend again before dawn. By metabolizing food at depth that they have ingested at the surface, zooplankton actively transport a substantial amount of C and nutrients to depth [e.g., *Longhurst et al.*, 1990; *Steinberg et al.*, 2000]. The above noted increase in mesozooplankton in the NPSG has led to an increase in diel vertical migrant-mediated fluxes of phosphorus (P) from surface waters, and is suggested to be an important mechanism for enhancing P-limitation of the NPSG [*Hannides et al.*, 2009].

[5] Several recent studies have examined long-term changes in biogeochemistry at the Bermuda Atlantic Time-series Study (BATS) site in the oligotrophic North Atlantic subtropical gyre, including net primary production [*Saba et al.*, 2010], carbon export [*Lomas et al.*, 2010], and biogenic silica cycling [*Krause et al.*, 2009]. In this study we examine long-term changes in mesozooplankton biomass at BATS, and explore possible mechanisms driving a zooplankton biomass increase. We discuss these results in the context of other long-term changes reported from BATS and other zooplankton time series, and the implications of these changes for biogeochemical cycling and food web dynamics.

2. Methods

2.1. Zooplankton Collection and Biomass Analyses

[6] We analyzed a 17-year time series of size-fractionated biomass of mesozooplankton (>200 μm) from biweekly to monthly day and night tows taken in the top 200 m at the Bermuda Atlantic Time-series Study (BATS) site in the oligotrophic North Atlantic subtropical gyre (31°40′N, 64°10′W) (see *Steinberg et al.* [2001] for an overview of BATS hydrography and biogeochemistry). Sampling for mesozooplankton at BATS began in April, 1994 and is ongoing. The methods have been previously reported in an early analysis of the zooplankton time series covering the period 1994–1998 [*Madin et al.*, 2001]; thus we briefly summarize here. Mesozooplankton were collected with a rectangular frame (0.8 x 1.2 m) net with 202 μm mesh. Two replicate double oblique tows through the euphotic zone at a ship speed of ~1 nm h^{-1} were made during the day (between about 0900 and 1500 h) and at night (between about 2000 and 0200 h) on each BATS cruise. The targeted maximum net depth was between 150–200 m and absolute depth was recorded with a Vemco Minilog recorder (with the exception of the first year of the time series, when net depth was estimated from the wire out and its angle). The volume of water filtered by the net (m^3) was measured with a General Oceanics flowmeter. We did not correct the net nominal mouth area (0.96 m^2) to an effective mouth area based on the angle of the net mouth as reported by *Madin et al.* [2001] (as the correction was only a 2% decrease in calculated volume filtered, and not easily applied to the entire time series). In addition, a systematic error in the calculation of volume filtered, resulting in a 17% decrease in biomass values previously reported by *Madin et al.* [2001], was corrected for data reported here (and in the online BATS database: http://bats.bios.edu/).

[7] Samples from the tows were split immediately on board. One half-split was fractionated by wet sieving through nested sieves with mesh sizes of 5.0, 2.0, 1.0, 0.5 and 0.2 mm, with individual fractions transferred to pre-weighed disks of 0.2 mm nitex netting and frozen for subsequent wet and dry weight (mg) analyses [*Landry et al.*, 2001; *Madin et al.*, 2001; *Hannides et al.*, 2009]. Dry weight biomass was converted to C biomass using the equation: C = 0.36 x dry weight [*Madin et al.*, 2001]. The other half-split was preserved in 4% buffered formaldehyde for taxonomic analysis (not reported here).

[8] Depth-integrated biomass [0–150 m] (mg C or dry wt. m^{-2}) was calculated by multiplying biomass per volume (mg C or dry wt. m^{-3}) by 150 m. The biomass of diel vertical migrators (migrant biomass) was defined as the 0–150 m integrated mean night biomass minus day biomass for each cruise. Depth-integrated biomass values are presented as cruise or monthly averages, or as monthly or annual anomalies. Integrated biomass versus time statistics were based on the linear regression of natural log-transformed biomass. Changes in biomass were calculated after de-transforming (using the exponential function) the regression model. Actual data values are shown in the plots. For each

month in the time series, the biomass anomaly (A'_m) was calculated using the formula:

$$A'_m = \log_{10}[\bar{A}_m / \bar{A}_i]$$

where $\bar{A}_m$ is the average biomass for year/month m, and $\bar{A}_i$ is the climatological mean for calendar month i. Annual biomass anomalies were then calculated as the average of A'_m for each year [O'Brien et al., 2008].

2.2. Comparison With Environmental Parameters and Climate Indices

[9] Regression and correlation analyses were performed on the time series of zooplankton biomass versus several environmental parameters measured at BATS as well as versus North Atlantic and North Pacific decadal climate indices. Before performing analyses, data were first averaged by month. Then each time series was seasonally detrended by computing a 12-month centered moving average. Time series of environmental parameters at BATS were extracted from the BATS project website (http://bats.bios.edu/). Sea-surface temperature was the shallowest (<10 m) CTD temperature reading reported, and the mean 300–600 m temperature was the average CTD temperature between 300 and 600 m. Water column stratification index was calculated as the difference in potential density between the surface and 200 m [Steinberg et al., 2001; Krause et al., 2009]. Primary production was measured by dawn to dusk in situ ^{14}C tracer incubations, and calculated from the mean light bottle value (n = 3) minus the dark bottle value (n = 1), for each incubation depth, integrated to a depth of 140 m [Knap et al., 1997; Lomas et al., 2010; Saba et al., 2010].

[10] We used a method similar to Saba et al. [2010] for comparison of time series of the North Atlantic Oscillation index (NAO) (http://www.cpc.noaa.gov/products/precip/CWlink/pna/nao.shtml), Multivariate El Niño Southern Oscillation index (MEI) (http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/), North Pacific Gyre Oscillation index (NPGO) (http://eros.eas.gatech.edu/npgo/), and Pacific Decadal Oscillation Index (PDO) (http://jisao.washington.edu/pdo/) to the BATS zooplankton biomass time series. These climate indices are seasonally adjusted [e.g., Hurrell, 1995; Zhang et al., 1997]. Correlation analyses were conducted between the 12-month, centered moving average of each climate index and the 12-month, centered moving average of the time series of zooplankton biomass in monthly anomaly form (A'_m, see above).

2.3. Determination of Active Transport by Diel Vertical Migration and of Fecal Pellet Flux

[11] Downward active flux of respiratory CO_2 by migrant zooplankton (mg C m^{-2} d^{-1}) was calculated as by Al Mutairi and Landry [2001] using respiration rates calculated from the empirical allometric relationships of Ikeda [1985]. Migrants were assumed to reside below the mixed layer 12 h during the day, with equal time spent in the surface waters at night, and the average temperature experienced by migrants at depth during the day for each cruise was applied (average temperature between 300 and 600 m = 17.0°C, range = 15.1–18.2°C, n = 223) [Dam et al., 1995; Steinberg et al., 2000; Al-Mutairi and Landry, 2001; Steinberg et al., 2008; Hannides et al., 2009]. Downward active flux of dissolved organic carbon (DOC) excreted by

migrant zooplankton (mg C m^{-2} d^{-1}) was calculated as 31% of downward active flux of CO_2 (Steinberg et al. [2000]; equal to excretion of 1% of migrator C d^{-1} excreted as DOC). Downward active flux of POC egested as fecal pellets by migrant zooplankton (mg C m^{-2} d^{-1}) was also calculated as 31% of downward active flux of CO_2 (equal to egestion of 1% of migrator C d^{-1} as POC; calculated from Schnetzer and Steinberg [2002b, Table 4] [see also Goldthwait and Steinberg, 2008]). Annual rates were determined by averaging daily rates for each year and multiplying by 365. There were no significant differences between annual rates determined in this manner and those determined by integrating active transport calculated for each individual time point over each 365-day period (p > 0.05, paired t-test). The former approach was chosen to eliminate bias from integrating over occasional > 1 month-long gaps in the time series (e.g., the time series did not begin until April, 1994, leaving a 3-month gap in the beginning of 1994). A zero net active transport was assumed in the rare cases of calculated negative active transport (i.e., total day biomass was higher than total night biomass in the top 150 m, which occurred n = 12 out of a total of n = 207 day-night pairs for the whole time series, or as in an additional n = 10 cases, total biomass was higher at night, but day biomass in one or more size classes was higher than at night, resulting in net negative active transport when respiration by all 5 size classes was summed).

[12] Fecal pellet production was calculated following the procedure of Roman et al. [2002]. Zooplankton growth rates (d^{-1}) calculated for each size class at BATS [from Roman et al., 2002, Table 2] were multiplied by the C biomass in each size class integrated to 150 m (mg C m^{-2}) to calculate zooplankton production (P, mg C m^{-2} d^{-1}). Once material is ingested (I), it is partitioned into production (P), respiration (R), and egestion (E). We assumed a gross production efficiency (P/I) of 30%, and egestion (= fecal pellet production) as E/I = 30% (i.e., 70% of ingested material was partitioned into growth and respiration, and 30% egested as feces). Note that as the ratios of P/I and E/I are the same, production rates are equal to fecal pellet production rates [Roman et al., 2002]. Annual fecal pellet production rates (mg C m^{-2} y^{-1}) were determined by averaging daily rates calculated for each individual sampling date (average rates were not derived within time periods as in the analysis by Roman et al. [2002]) and multiplying by 365 days. Annual active flux and fecal pellet flux were then compared to annual estimates of sediment trap POC flux across 150 m at BATS. Sediment trap POC flux data were extracted from the BATS program data website (see section 2.2).

3. Results

3.1. Overall Increase in Zooplankton Biomass

[13] The total biomass of mesozooplankton at BATS has increased at a rate of 10.7 mg dry wt m^{-2} y^{-1}, a 61% total increase over the 17-year period (Figure 1a). Annual biomass anomalies noticeably changed from negative to positive beginning in 2001 (Figure 1b). While the long-term increase in biomass is significant, a downturn and small negative annual biomass anomaly occurred in 2008, followed by positive anomalies again in 2009 and 2010 (Figure 1b). The increase in biomass through 2007, before
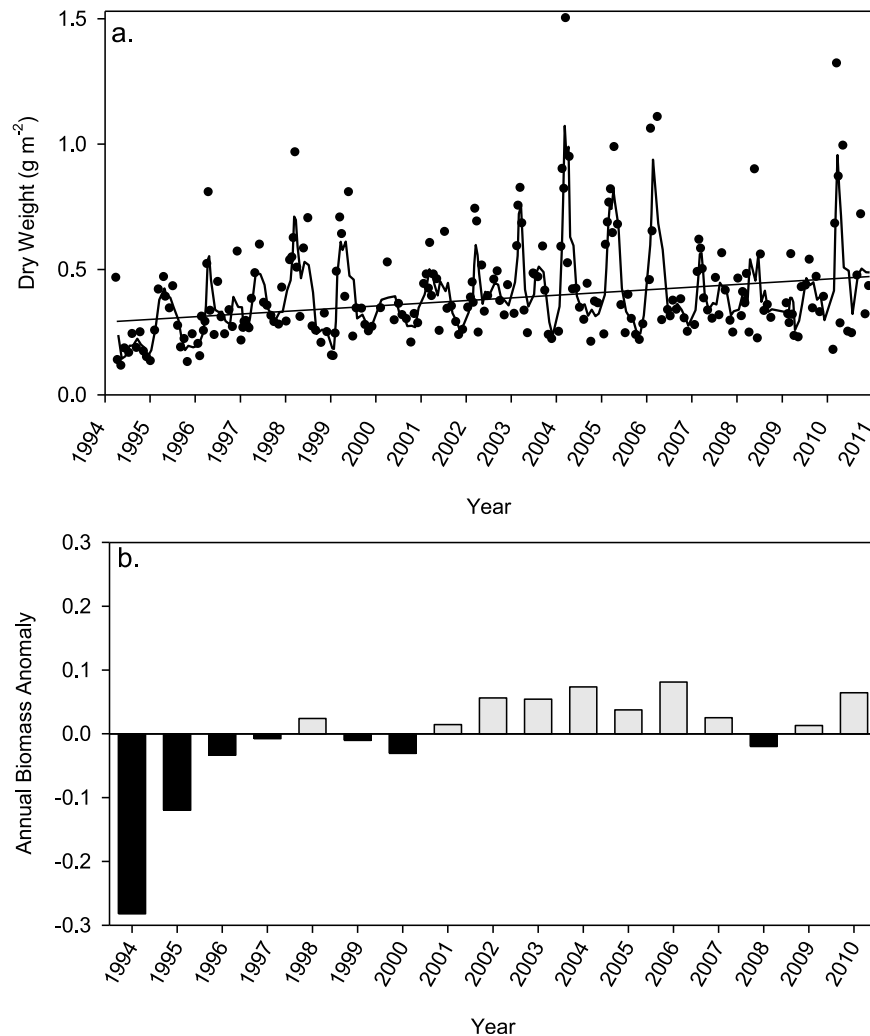
Figure 1. Long-term increase in mesozooplankton biomass at BATS, 1994–2010. (a) Increase in total integrated mesozooplankton biomass at BATS. Total mesozooplankton biomass is dry weight of all size classes combined, integrated from 0 to 150 m. Each point is the mean of day and night sample pairs for each sampling date (i.e., mean of n = 4). Solid curved line is a centered, three-point moving average. Solid straight line is the de-transformed regression for all data (see Table 1). Tick mark and labels on x axis mark January 1 of given year. (b) Annual anomaly of total mesozooplankton biomass. See Methods for calculation of anomalies.

the short downturn, was at a rate of 15.3 mg dry wt $m^{-2} y^{-1}$, a 76% increase over the 14-year period. The 1994 annual biomass anomaly starting point may be biased toward lower biomass, as 1994 does not include data for January–March, and March is a peak biomass month (see section 3.3). The largest absolute increase in biomass over time occurred in the 1 mm and 2 mm size fractions, but the largest proportional change (110% increase) occurred in the largest (>5 mm) size class (Table 1). The ratio of mesozooplankton dry weight:wet weight biomass over time for all size fractions combined, and for each size fraction separately, did not change significantly over time (mean ± 1 standard deviation, SD, for all size fractions combined = 0.2 ± 0.1).

3.2. Day Versus Night Changes

[14] To determine if there was a change over time in the magnitude of DVM at BATS, changes in day and night biomass were compared. There was a significant increase in both

day and night biomass, however night biomass increased at a greater rate, suggesting an increase in the magnitude of DVM over time (Figure 2). Daytime mesozooplankton biomass increased at a rate of 6.6 mg dry wt $m^{-2} y^{-1}$, a 49% increase over the 17-year time series (Figure 2a and Table 1), while nighttime mesozooplankton biomass increased at a rate of 15.6 mg dry wt $m^{-2} y^{-1}$, a 73% increase over the 17-year time series (Figure 2b and Table 1). This resulted in a significant overall increase in diel migrator biomass (i.e., night-day mesozooplankton biomass in the upper 150 m) of 7.4 mg dry wt $m^{-2} y^{-1}$, a 92% increase over the time series (Figure 2c and Table 1). The mean (±1 SD) night:day biomass ratio for the time series was 1.9 ± 1.2 (range = 0.3–12.3).

3.3. Seasonal Changes

[15] The largest increase in zooplankton biomass over the time series occurred in the late winter through spring, from January/February to April (Figure 3 and Table 1).

Table 1. Rates of Increase in Mesozooplankton Biomass at BATS[a]

Parameter	Annual Slope (mg m^{-2} yr^{-1})	Overall Change (mg m^{-2})	Overall Change (%)	p-Value	r^2	n
Total	10.7	179	61	<0.0001	0.09	226
Diel Change						
Day	6.6	110	49	0.0007	0.05	219
Night	15.6	260	73	<0.0001	0.11	215
Migrator	7.4	123	92	0.0050	0.04	208
Change in Size Fractions						
0.2–0.5 mm	0.3	4	6	0.5659	0.00	226
0.5–1 mm	2.3	38	48	0.0002	0.06	226
1–2 mm	3.2	33	84	<0.0001	0.10	226
2–5 mm	2.8	47	88	<0.0001	0.07	226
>5 mm	1.3	22	110	<0.0001	0.08	226
Seasonal Change						
Winter-spring bloom	14.3	230	70	0.0041	0.09	94
Remaining year	8.6	143	53	0.0001	0.11	132

[a]Biomasss values for all parameters are mesozooplankton dry wt. integrated to 150 m April 1994 to December 2010, averaged by cruise. 'Total' includes day and night, all size fractions combined. 'Migrator' is night minus day biomass. Seasonal changes are divided into the winter-spring bloom period (January–April) and the remaining year (May–December). Statistics are based on the linear regression of natural log-transformed biomass, for data spanning the entire 17-yr. time series. 'Annual Slope' and 'Overall change' calculations are based on the de-transformed (exponential) linear regression model.

Winter-spring biomass was highest during the period from 2002 to 2007, decreased in 2008 and 2009, and increased again in 2010 (Figure 3), as also evidenced in the overall annual biomass anomalies (Figure 1b). A seasonal composite for the entire time series compared to the time period before the peak biomass (1994–2001) and during and after (2002–2010) is shown in Figure 4. The overall trend for all size classes combined was a distinct peak biomass in March (and March/April in the earlier half of the time series), with smaller secondary peaks occurring in June in the early half of the time series, and September in the latter half (Figure 4a). Differences occurred in both timing and magnitude of the peak biomass among the five size classes (Figures 4b–4f). In the 2 mm size fraction, which is mostly comprised of copepods, small amphipods, and small euphausiids, the peak shifted one month earlier in the latter half of the time series (from April to March; Figure 4e). A distinct peak occurred in May in the later half of the time series in the >5 mm fraction, which is typically comprised of larger vertical migrators (e.g., euphausiids, amphipods, sergestid shrimps, large copepods) and gelatinous zooplankton (migrating and non-migrating) (Figure 4f).

3.4. Comparison With Physical and Other Biological Changes in the Environment and With Climate Indices

[16] Zooplankton biomass was significantly and positively correlated to both sea-surface temperature (SST) (Figure 5a) and water column stratification index (Figure 5b). There was also a significant negative relationship between the mean 300–600 m temperature and zooplankton biomass (Figure 5c). Thus, warmer and more stratified surface waters, and colder water in the mesopelagic zone may lead to favorable conditions for zooplankton. There was a weaker, but significant positive relationship between integrated primary production and zooplankton biomass (Figure 5d).

[17] There were significant, although relatively weak, correlations between multidecadal climate indices and BATS zooplankton biomass anomalies (Figure 6). The zooplankton time series was initiated in 1994, just prior to when the NAO switched from largely positive to largely negative (Figure 6a). Zooplankton biomass was negatively correlated to the NAO index (r = −0.22) (Figure 6a), while positively correlated with all three Pacific Ocean climate indices, the ME (r = 0.22), NPGO (r = 0.27), and PDO (r = 0.24) (Figures 6b–6d, respectively).

3.5. Effects on Biogeochemical Cycling

[18] The effects of these long-term changes in zooplankton biomass on the biological pump were examined by quantifying annual mean changes in export processes that are mediated by zooplankton– active transport by DVM and fecal pellet production. These were then compared to passive sinking of POC measured by sediment traps. Although there were fluctuations, the annual POC flux across 150 m at BATS did not change significantly from 1994 to 2010 (Figure 7a), averaging (±1 SD) 10.2 ± 2.0 g C m^{-2} y^{-1} (note that annual mean for 2010 trap POC data excludes one extreme high outlier). Active transport by zooplankton DVM more than doubled from 1994 to 2005, decreased in 2006, and then oscillated for the subsequent four years, ending at a high in 2010 (Figure 7b). Mean annual active flux by zooplankton DVM for the time series was 1.5 ± 0.5 g C m^{-2} y^{-1}. Egestion of fecal pellets by zooplankton in the top 150 m increased by threefold from 1994 to 2004, then steadily declined over the next 4–5 years before increasing again in 2010 (Figure 7c). Mean annual egestion of fecal pellets by zooplankton in surface waters over the time series was 4.4 ± 1.0 g C m^{-2} y^{-1}.

[19] Because annual mean sediment trap POC flux across 150 m was relatively steady (but with a slight decrease) from 1994 to 2010, there was a significant increase over time in the relative importance of both active flux by DVM and flux of fecal pellets as components of the export flux (Figure 8). Active flux was on average equal to 15 ± 7% (range 5–33%) of the sinking POC flux, while fecal pellet flux was on
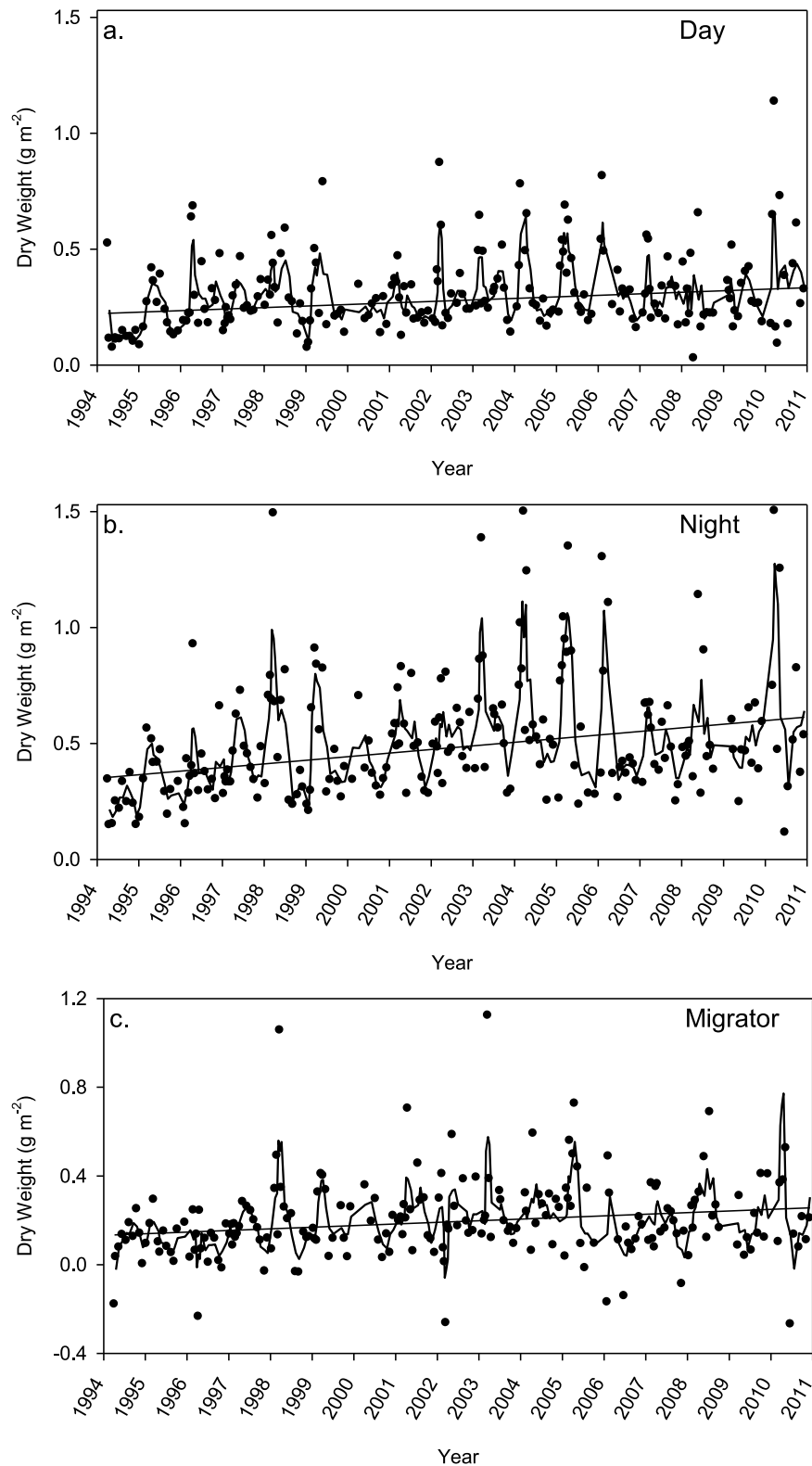
Figure 2. Day versus night comparison of mesozooplankton biomass increase over time. Mesozooplankton biomass values are dry weight of all size classes combined, integrated from 0 to 150 m. (a) Daytime mesozooplankton biomass, (b) nighttime mesozooplankton biomass, (c) increase in diel vertical migrator biomass (night minus day mesozooplankton biomass in upper 150 m). Each point for Figures 2a and 2b is usually the mean of n = 2 tows for each sampling date. See Table 1 for regression statistics. Tick mark and labels on x-axes mark January 1 of given year.
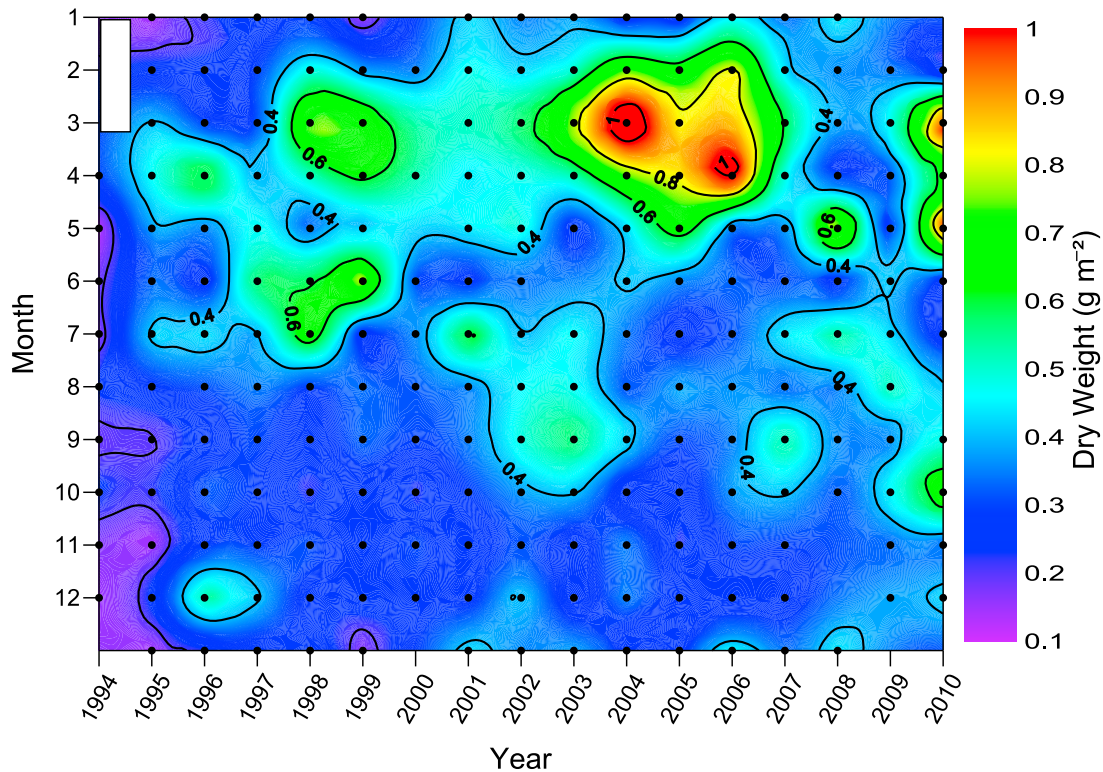
Figure 3. Seasonal and interannual changes in mesozooplankton biomass. Each point in contour plot represents total mesozooplankton dry weight biomass of all size classes combined, integrated from 0 to 150 m, and is the mean of all day and night samples taken during that year and month. Sample size ranges from n = 1–11 for each month, usually with higher sample size in the spring bloom period, January–April.

average equal to 45 ± 16% (range 28–89%) of the sinking POC flux.

4. Discussion

4.1. Possible Mechanisms for Long-Term Change in Mesozooplankton Biomass

4.1.1. Bottom-Up Control

[20] Connections between climate, physical forcing, and biological response in primary producers at BATS have been explored in prior studies [*Lomas and Bates*, 2004; *Bates*, 2007; *Krause et al.*, 2009; *Lomas et al.*, 2010; *Saba et al.*, 2010], and the present study extends these observations to consumers. Our results indicate there are significant, although weak correlations between change in BATS zooplankton biomass and climate forcing. Over the course of the BATS time series (beginning 1988) the NAO has become increasingly less positive, with a transition to a negative phase in 1996 near the start of the zooplankton time series (Figure 6a). Negative NAO phases are associated with stronger winds [*Marshall et al.*, 2001; *Bates*, 2007], and although mixed layer depth at BATS has not changed significantly as a result since 1988 [*Lomas et al.*, 2010; *Saba et al.*, 2010], the frequency of mixing in the BATS region may have increased, enhancing nutrient supply to the euphotic zone [*Lomas et al.*, 2010]. Additionally, the thickness of the underlying Subtropical Mode Water (STMW, or '18 degree water' [*Talley and Raymer*, 1982]) has been decreasing at BATS since 1997, which may also lead to an

increase in nutrient supply to the surface waters of the Sargasso Sea [*Krause et al.*, 2009]. The resultant long-term trend in increasing primary production at BATS, and the negative correlation at BATS between the NAO and both net primary production (NPP) [*Saba et al.*, 2010] and zooplankton biomass (this study), suggest bottom-up control on the mesozooplankton community. Interestingly, there was only a weak, but significant, positive correlation between primary production (and no significant correlation with Chl *a*, data not shown) and mesozooplankton biomass. This may be a result of temporal offsets in production of particles in the upper ocean and their subsequent translation into zooplankton biomass via grazing, considering the time it takes for zooplankton to progress through their growth stages after a phytoplankton bloom, making direct comparison of these measurements difficult [*Madin et al.*, 2001]. At least some vertical migrators consume mostly non-phytoplankton prey [*Schnetzer and Steinberg*, 2002a], which would also cause these temporal offsets. Significant correlations were also found between multidecadal Pacific climate indices and zooplankton biomass, suggesting teleconnections between climate forcing and ecosystem response in the two oceans. Decadal-scale Pacific and North Atlantic climate teleconnections have been previously reported [*Müller et al.*, 2008], and *Saba et al.* [2010] also found significant correlation between NPP at BATS and Pacific climate indices.

[21] Coincident with an increase in NPP at BATS is a significant increase in 0–140 m integrated Chl *a* (HPLC determined) at BATS since 1988 [*Lomas et al.*, 2010; *Saba*
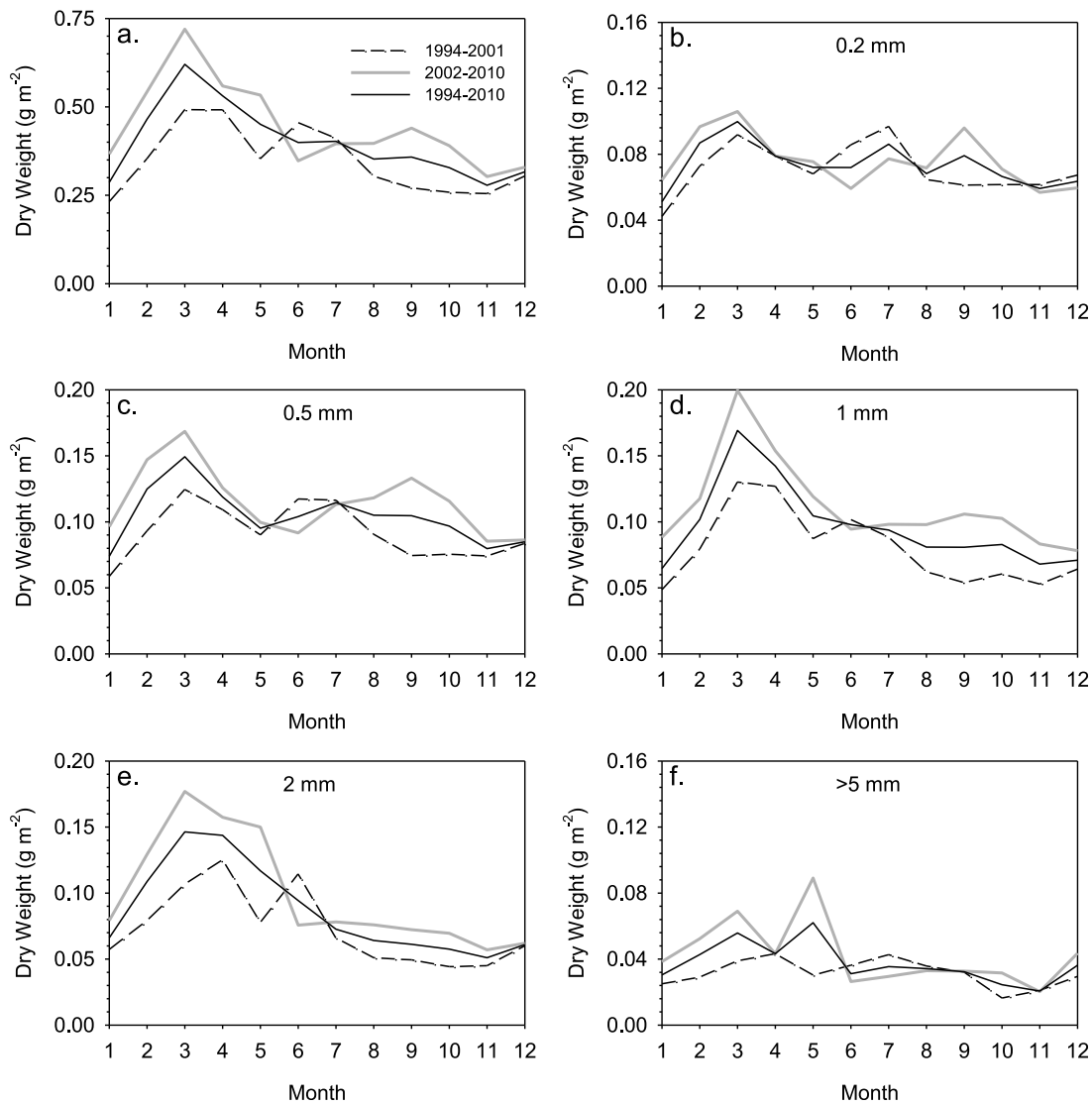
Figure 4. Seasonal composite of mesozooplankton biomass. (a) All size classes combined, (b) 0.2–0.5 mm, (c) 0.5–1 mm, (d)1–2 mm, (e) 2–5 mm, and (f) >5 mm. Each point represents total mesozooplankton biomass dry weight, integrated from 0 to 150 m, and is the mean of all day and night samples taken during that month. Composites are shown for the entire time series compared to the time period before the peak biomass (1994–2001) and during and after peak biomass (2002–2010). For a given month, n ranges from 52 to 101 for the full time series, 28–42 for the period 1994–2001, and 21–59 for the period 2002–2010.

et al., 2010]. This change in phytoplankton Chl a biomass has not been uniform across all taxa (as indicated by changes in accessory pigment biomass), which likely imparts differential bottom-up control on various zooplankton taxa via feeding preferences [Schnetzer and Steinberg, 2002a]. For the winter-spring transition period (January–April) analyzed by Lomas et al. [2010], the cyanobacteria Synechococcus increased by 64% between 1990 and 2007 (this increase was 170% between 2002 and 2007, using cell counts by flow cytometry). Furthermore, dinoflagellates and prasinophytes also significantly increased over the time period 1990–2004 analyzed by Krause et al. [2009]. Diatoms, frequently a minor (<10%) component of the total phytoplankton community at BATS [Steinberg et al., 2001], have decreased even further over time. Diatoms decreased in biomass by

113% from 1990 to 2007 based upon pigment analyses [Lomas et al., 2010] and by 40% from 1989 to 2004 based upon biogenic silica analyses [Krause et al., 2009]. Thus, evidence so far suggests that it is not the larger phytoplankton taxa that are increasing and directly providing increased food resources for mesozooplankton. Rather, increases in picophytoplankton such as Synechococcus could be fueling the microbial food web, leading to increases in protozoa (e.g., heterotrophic flagellates, ciliates, sarcodines) that make up a significant portion of mesozooplankton diet [Stoecker and Capuzzo, 1990; Fessenden and Cowles, 1994; Broglio et al., 2004], which translates into an increase in mesozooplankton biomass. The highest overall biomass increase was in the small to mid-sized (1–2 mm; mostly copepods) mesozooplankton at BATS, which
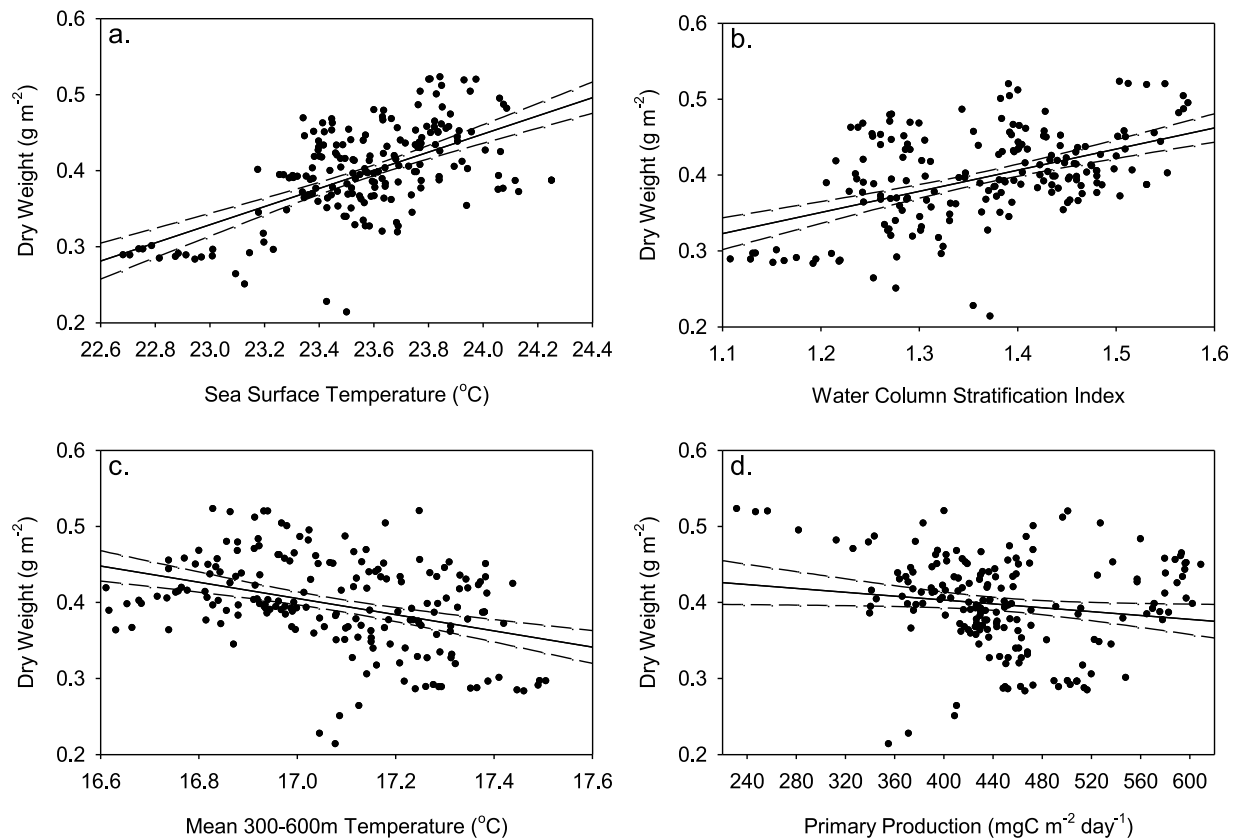
Figure 5. Changes in physical and biological parameters at BATS compared to zooplankton biomass. Data presented are 12-month moving averages in order to dampen the seasonal signal. Solid line is the least squares Model II linear regression and dashed lines are 95% confidence intervals, n = 190 for all. (a) Sea surface (<10 m) temperature (°C); ($r^2 = 0.35$, $p < 0.01$). (b) Water column stratification index, calculated as the difference in potential density between the surface and 200 m ($r^2 = 0.23$, $p < 0.01$). (c) Mean temperature 300–600 m, (°C), ($r^2 = 0.14$, $p < 0.01$). (d) Primary production (mg C m^{-2} d^{-1}), integrated 0–140 m ($r^2 = 0.02$, $p = 0.04$).

would feed more efficiently on smaller protozoans than the largest size class. The significant positive correlation between BATS zooplankton biomass with warmer and more stratified surface waters is at first counterintuitive, as warmer more stratified waters are usually associated with lower biomass. However, this trend is consistent with an increase in picophytoplankton, noted above, ultimately fueling zooplankton production, as warmer, more stratified waters favor a shift to cyanobacteria and other picophytoplankton [*Karl et al.*, 2001]. The long-term increase in mesozooplankton biomass at BATS (61% over 17 years, an increase of 3.6% yr^{-1}) is coincident with increased mesozooplankton at HOT station ALOHA in the North Pacific Subtropical Gyre (NPSG) (5% yr^{-1} for the period 1994–2002), using the same methods [*Sheridan and Landry*, 2004; *Hannides et al.*, 2009]. The smaller (0.5–2 mm) mesozooplankton also drove this increasing biomass trend at ALOHA [*Sheridan and Landry*, 2004], suggesting similar bottom-up forcing of food web dynamics in both these subtropical gyres. However, at ALOHA, increases in chlorophyll and NPP were due to increases in pico- and nano-eukaryotes and possibly diatoms, not specifically cyanobacteria [*Bidigare et al.*, 2009].

[22] While increases in the smaller zooplankton size fractions may be explained in part by increases in picophytoplankton, the larger size fractions, which comprise vertical migrators, have also increased over time. These larger zooplankton may be taking advantage of an increase in small copepod prey [e.g., *Schnetzer and Steinberg*, 2002a]. The significant decrease in 300–600 m temperature from the beginning of the zooplankton times series in 1994 to 2010 may impart a metabolic advantage to vertical migrators at their daytime residence depths in the latter part of the time series, resulting in more energy available for growth and reproduction, compared to migrators earlier in the time series that experienced warmer deep temperatures (although see *Dawidowicz and Loose* [1992], showing for freshwater cladocera a positive correlation between mean temperature experienced by migrating individuals and growth rate in laboratory experiments). Increases in available food at depth may also play a role. Suspended POC concentration in the upper mesopelagic zone (integrated 150–500 m) at BATS doubled from 1994 to 2006, increasing from 2.3 to 4.7 gC m^{-2}, respectively ($p < 0.05$, $r^2 = 0.27$, n = 45, Linear regression, data from online BATS database). These observations may in sum account for the long-term increase in
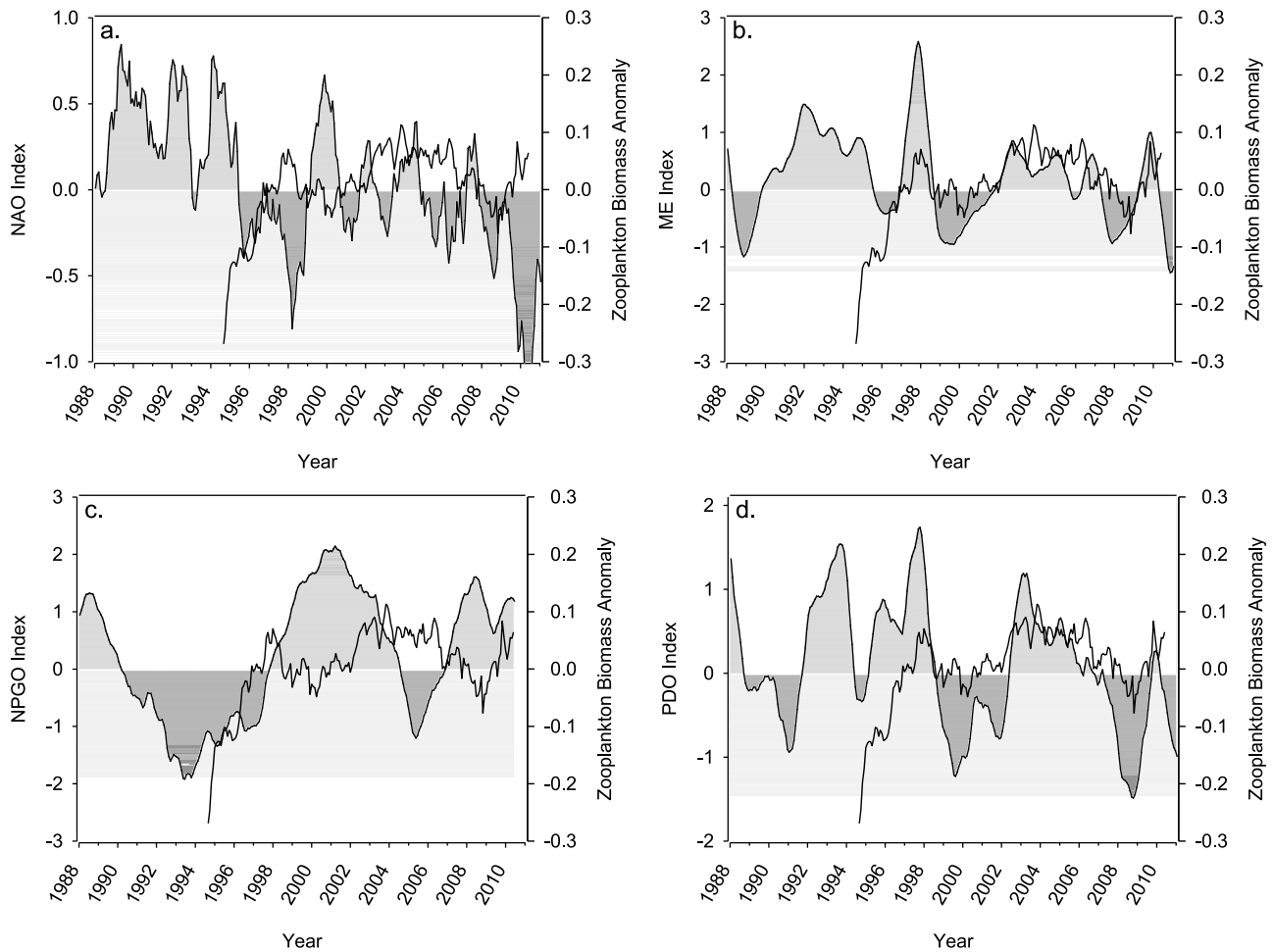
Figure 6. Multidecadal climate indices compared to BATS zooplankton biomass anomaly. (a) North Atlantic Oscillation index (NAO), correlation coefficient, $r = -0.22$; (b) multivariate El Niño Southern Oscillation index (MEI), $r = 0.22$; (c) North Pacific Gyre Oscillation index (NPGO), $r = 0.27$; (d) Pacific Decadal Oscillation index (PDO), $r = 0.24$. All multidecadal climate indices and the BATS biomass anomaly are presented as 12-month moving averages to smooth the time series (seasonality is already removed in the anomaly calculations–see methods). To provide further context for the zooplankton biomass (sampling of which commenced in 1994) data, multidecadal climate indices are presented from 1988, the start of the BATS sampling program. Correlations were significant for all comparisons ($p < 0.01$).

BATS vertical migrator biomass (this increase is discussed further in section 4.2.1).

[23] Evidence for bottom-up control of long-term changes, both increases and decreases, in open-ocean mesozooplankton communities exists elsewhere, including the NPSG discussed above and the tropical Atlantic. *Sheridan and Landry* [2004] suggest that the increase in zooplankton biomass at Station ALOHA in the NPSG is linked to the increasing role of input of new nutrients via N fixation over time [*Karl*, 1999; *Dore et al.*, 2002], which has led to increases in ecosystem productivity. Changes in stratification in the NPSG due to ENSO may also play a role [*Sheridan and Landry*, 2004]. Similarly, a nearly 10-fold decrease in mesozooplankton biomass over a 50-year period (1950–2000) in the tropical North Atlantic (23°N to 23°S) has been attributed to decreases in primary production in the tropical North Atlantic due to a thinning of the mixed layer as a result of surface-ocean warming [*Piontkovski and Castellani*, 2009]. These findings suggest that food webs

may respond in a predictable manner to climate forcing, facilitating their inclusion in global ecosystem models.

4.1.2. Top-Down Control

[24] Another possible mechanism for changing mesozooplankton biomass is top-down control by mesozooplankton predators, including: the larger carnivorous gelatinous zooplankton; crustacean micronekton such as sergestid and other decapod shrimps, and mysids; planktivorous fish such as myctophids; and seabirds. Although there are no published data for the Sargasso Sea, long-term studies of jellyfish (i.e., scyphomedusae) and ctenophores in many regions around the world indicate increases in abundance [*Purcell*, 2005; *Link and Ford*, 2006; *Lynam et al.*, 2006], which would be expected to lead to a decrease in mesozooplankton, opposite the dominant long-term trend we observe at BATS. However, long-term studies also indicate decadal-scale oscillations of gelatinous zooplankton tied to climate variability [*Purcell*, 2005; *Purcell and Decker*, 2005; *Brodeur et al.*, 2008], which can lead to oscillations in mesozooplankton.
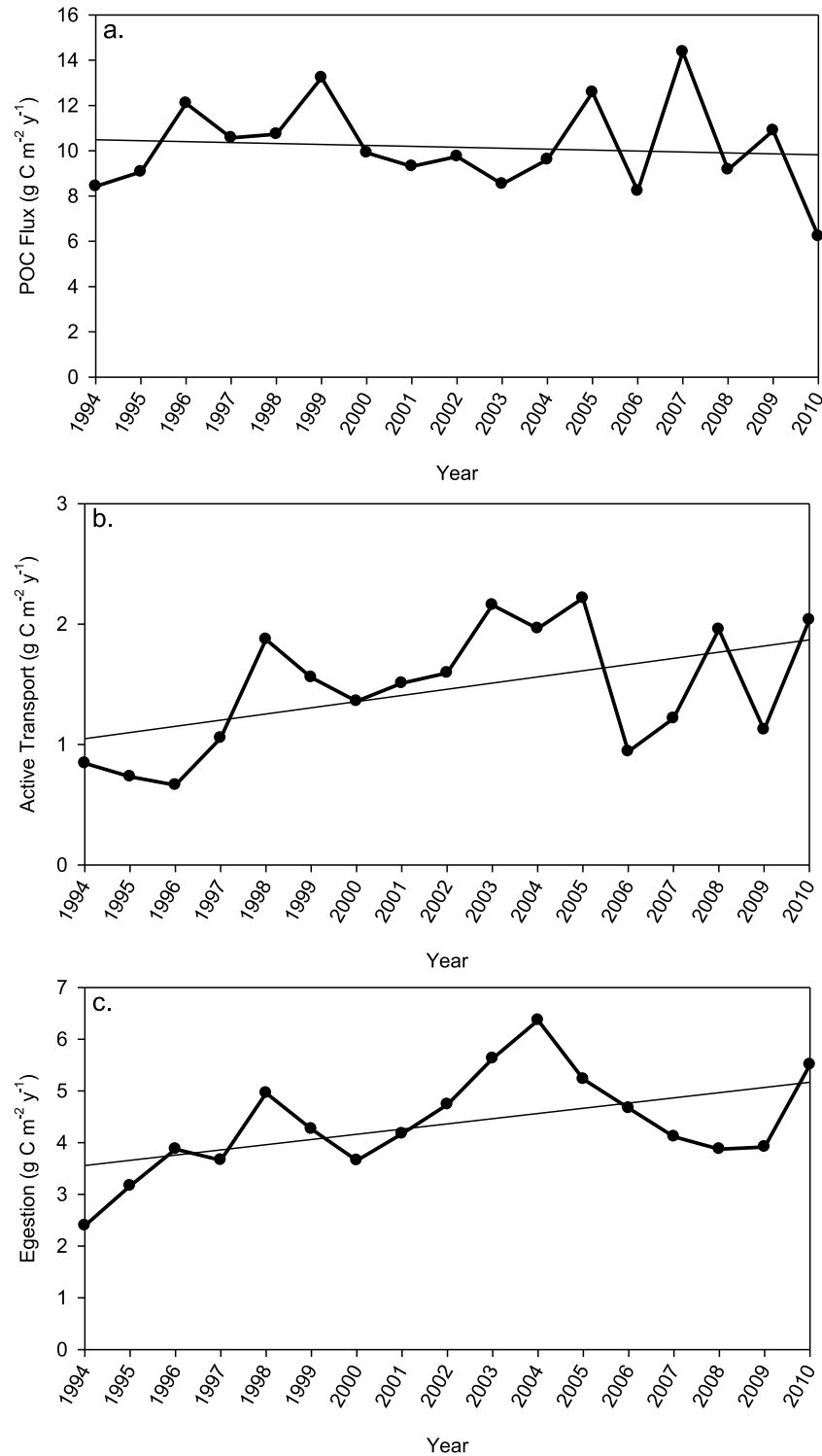
Figure 7. Changes in annual sinking POC flux, active transport by diel vertical migrators, and zooplankton fecal pellet production at BATS. The least squares Model II linear regression line is shown. (a) Sinking POC flux across 150 m as measured by sediment traps ($r^2 = 0.02$, $p > 0.05$; note that the annual mean for 2010 excludes one extreme high outlier). (b) Active vertical flux across 150 m of CO_2 respiration + DOC excretion + POC egestion as fecal pellets at depth by diel vertical migrators ($r^2 = 0.25$, $p < 0.05$). (c) Egestion of fecal pellets by zooplankton in the top 150 m ($r^2 = 0.27$, $p < 0.05$).
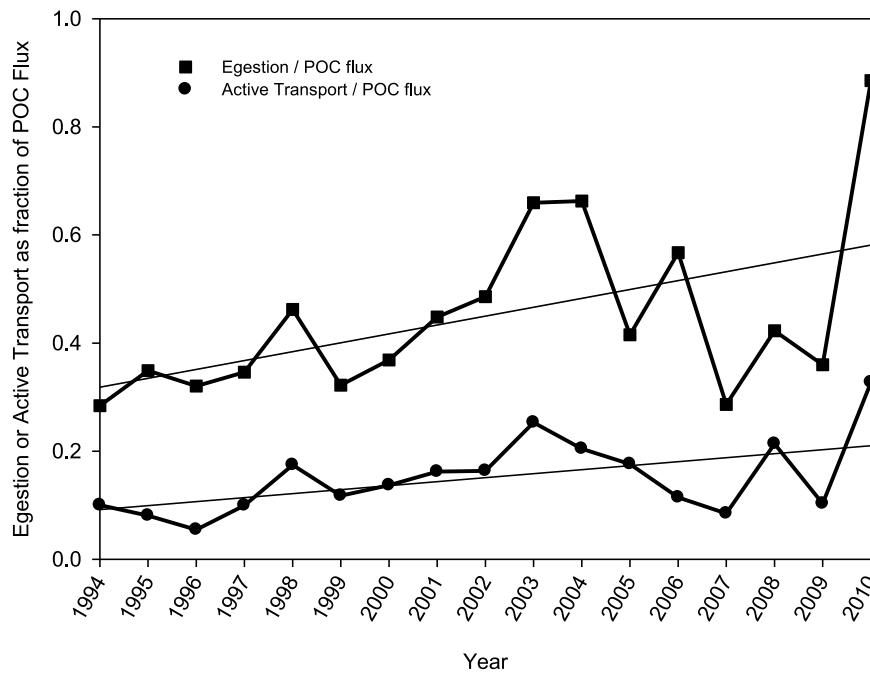
Figure 8.   Annual active transport by diel vertical migrators and egestion of fecal pellets shown as a fraction of the annual sinking POC flux measured by sediment traps. The least squares Model II linear regression line is shown. Active vertical flux (circles) across 150 m of CO_2 respiration + DOC excretion + POC egestion as fecal pellets at depth by diel vertical migrators/ sinking POC flux across 150 m measured by sediment traps ($r^2 = 0.28$, $p < 0.05$). Egestion of fecal pellets (squares) by zooplankton in the top 150 m/ 150 m sediment trap POC flux ($r^2 = 0.26$, $p < 0.05$). See Figure 7 regarding exclusion of outlier from 2010 trap POC flux.

The lack of a significant trend in the ratio of dry to wet weight biomass in our data suggests that there is no broad, taxonomic-scale change in total gelatinous zooplankton, which with our sampling gear includes both mainly herbivores (e.g., larvaceans, salps, and thecosome pteropods) and carnivores (e.g., siphonophores, chaetognaths, heteropods, and smaller medusae and ctenophores), but we cannot yet rule out long-term changes in specific groups.

[25] Control of mesozooplankton by crustacean micronekton and fish in the Sargasso Sea is also poorly known. In the oligotrophic Gulf of Mexico, the diet of mesopelagic decapod shrimps, mysids, and myctophid fish, the majority of which are diel migrators feeding in the epipelagic zone at night, is largely comprised of mesozooplankton [*Hopkins et al.*, 1994; *Hopkins and Sutton*, 1998]. However, estimates of predation impact upon the mesozooplankton community by shrimps plus mysids (1% of zooplankton standing stock, and 18% of daily zooplankton production) and myctophids (0.4% and 8%, respectively) are low [*Hopkins et al.*, 1994]. Thus, the study concluded that larger gelatinous zooplankton or other carnivorous zooplankton may account for the majority of the predation on mesozooplankton, at least in low latitude assemblages [*Hopkins et al.*, 1994]. In the eastern subtropical Atlantic significant shorter-term oscillations in predation pressure on epipelagic mesozooplankton are related to changing DVM behavior of their micronekton predators over the lunar cycle [*Hernández-León et al.*, 2002]. Time series of higher trophic-level predators from the western Sargasso Sea, and estimates of their feeding rates, are sorely needed to help decipher long-term patterns further down the food web.

[26] Whatever the combination of bottom-up versus top-down control on mesozooplankton, there are undoubtedly consequences throughout the food web of an increase in mesozooplankton biomass. For example, *Sheridan and Landry* [2004] suggest that increased mesozooplankton in the NPSG will lead to increases in grazing pressure on >5 μm protists in the microbial loop, which could release some grazing pressure on bacteria in this tightly coupled system, where changes in one end of the food web rapidly translate to the other.

4.1.3.   Range Expansion of Tropical Species Northward

[27] In interpreting the 50-year decreasing trend in mesozooplankton biomass in the tropical North Atlantic, *Piontkovski and Castellani* [2009] suggest that there may be a widening of the distributional range of tropical mesozooplankton "due to the expansion of the tropical belt," as a result of warming of surface waters. Thus, climate conditions are becoming unfavorable to the growth and reproduction of tropical species in the tropics leading to a decrease in their biomass, and more favorable further northward. If the range of Atlantic tropical species is indeed expanding northward into the subtropical BATS region, this could result in an increase in biomass at BATS. However, the question remains as to what extent the range of subtropical species is also in turn expanding northward, and shrinking in the south, as shown for some species of copepods from the Continuous Plankton Recorder surveys in the North Atlantic [*Beaugrand*

et al., 2002], possibly counteracting any increase at BATS due to increased favorable growth conditions for tropical species. Species-level identifications have been completed for several of the major taxonomic groups of zooplankton at BATS for the period 1995–2000 (http://www.iobis.org/). We analyzed the calanoid copepod data set (the most diverse, with ∼171 species) to test whether their diversity increased over time. The correlations between time and species richness, evenness, and the Shannon diversity index [*Pielou*, 1975] for calanoids over the 5-year period were positive, but non-significant (r^2 = 0.002, 0.034, and 0.038, respectively; p = 0.70, 0.07, and 0.06, respectively; Linear regression, n = 94), however this may be too short a time span to detect significant change.

4.2. Consequent Changes in the Biological Pump and Biogeochemical Cycling

4.2.1. Active Transport by DVM

[28] The increase in diel vertical migrator biomass over time has led to an overall significant increase in mean annual active transport of C, which has approximately doubled over the entire record. Active transport has also become an increasingly important component of the biological pump over time when compared to passive sinking of POC measured by sediment traps at BATS. *Hannides et al.* [2009] report that migrant zooplankton biomass at Station ALOHA during the period 1994–2006 has also increased significantly, leading to an increase in active transport of C, N, and P. Using their reported values of mean active C flux at ALOHA (3.7 mg C m^{-2} d^{-1} respiration, plus 1.2 mg C m^{-2} d^{-1} excretion of DOC) and assuming active fecal pellet flux equal to active flux of excreted DOC (1.2 mg C m^{-2} d^{-1}; see section 2.3), and multiplying by 365 d yr^{-1} to obtain an annual rate, we calculate a mean annual active C flux by migrators at ALOHA of 2.2 g C m^{-2} y^{-1}, 50% more that at BATS (1.5 g C m^{-2} y^{-1}). A causitive mechanism for higher mesozooplankton biomass and higher derived rates at HOT station ALOHA versus BATS has been speculated to be greater decoupling of phytoplankton production and mesozooplankton production at BATS due to comparatively deeper winter mixing at BATS, and more episodic input of nutrients at BATS during the stratified period via mesoscale eddies [*Roman et al.*, 2002]. This is in comparison to permanent stratification and fewer episodic increases in primary production at HOT resulting in more efficient trophic transfer at HOT [*Roman et al.*, 2002]. In a study of mesozooplankton in mesoscale eddies during summer in the Sargasso Sea, however, *Goldthwait and Steinberg* [2008] found increased mesozooplankton biomass, and enhanced active transport in the center or periphery of eddies (4.0–6.1 mg C m^{-2} d^{-1}) compared to the BATS summer mean (3.5 mg C m^{-2} d^{-1}). This suggests that mesozooplankton are able to respond to episodic nutrient input by eddy upwelling which enhances phytoplankton biomass [*McGillicuddy et al.*, 2007], and the export of C by active transport is increased as a result.

4.2.2. Mesopelagic Flux Attenuation

[29] That there has been an increase in migrating biomass at BATS suggests there may be a long-term increase in overall mesopelagic mesozooplankton biomass in the Sargasso Sea (i.e., it is not, at least solely, a consequence of increase in DVM behavior). This is consistent with documented changes in mesopelagic POC flux attenuation at BATS and also has consequences for the biological pump. *Lomas et al.* [2010] report a decade-long (1997–2007) increase in the winter-spring period (January–April) 150 m POC flux at BATS. However, winter-spring 300 m POC flux has not increased, and as a result the attenuation of sinking POC in the upper mesopelagic zone (between 150 and 300 m) at BATS has doubled over this same time frame. The increase in mesopelagic POC attenuation coincides with an increase in 200–300 m apparent oxygen utilization (AOU) at BATS, suggesting that metabolic activity of mesopelagic bacteria and/or zooplankton have increased over time [*Lomas et al.*, 2010]. Indeed, an approximation of increased respiration due to increased mesozooplankton biomass can account for a large fraction of the increase in AOU during the winter-spring period [*Lomas et al.*, 2010]. The increased mesopelagic zooplankton metabolic C demand may be partially met by consumption and respiration of sinking particles, and by consumption of surface-derived POC during diel vertical migrations that is subsequently respired at depth [*Steinberg et al.*, 2008].

[30] Has mesopelagic zooplankton biomass increased? While mesopelagic zooplankton biomass and taxonomic composition near and at BATS has been reported as part of recent studies of mesoscale eddies in the Sargasso Sea [*Goldthwait and Steinberg*, 2008; *Eden et al.*, 2009], there are limited historical data of mesopelagic zooplankton biomass at BATS with comparable gear [*Menzel and Ryther*, 1961; *Deevey*, 1971] with which to rigorously examine any long-term, sub-euphotic zone increases in zooplankton biomass. We can at least compare the two endpoints represented by these data sets. *Goldthwait and Steinberg* [2008] sampled mesopelagic zooplankton during summer in 2004 and 2005 using a 150 μm mesh, 1-m^2 MOCNESS. Using these data (EDDIES project; http://bcodmo.org/data), we calculate an overall mean (±1 SD) integrated 200–500 m daytime mesopelagic biomass (all size classes combined) of 0.15 ± 0.06 g dry wt. m^{-2} for all tows (n = 16) taken inside and outside of mesoscale eddies in the Sargasso Sea near Bermuda, and at BATS (the mean biomass was the same for the subset of tows taken only outside eddies and at BATS, n = 5). *Menzel and Ryther* [1961] sampled mesozooplankton 24 km SE of Bermuda (Station "S") during the day between 1957 and 1960. Using their data from opening closing net tows using a (coarser) 366 μm mesh net from June and August (from their Table 1), we calculate a mean integrated 200–500 m daytime mesopelagic biomass of 0.29 g dry wt m^{-2}, higher than present-day values. However, differences in net mesh sizes between the two studies prevents any firm conclusions.

4.2.3. Fecal Pellet Flux

[31] The significant decade-long increase in winter-spring 150 m POC flux measured by sediment traps at BATS between 1997 and 2007 [*Lomas et al.*, 2010] could be caused in part by increases in epipelagic mesozooplankton biomass translating into increases in fecal pellet flux. The potential, annual-averaged contribution of zooplankton fecal pellets to export tripled over the first 11-years of the zooplankton time series (1994–2004), but then steadily declined for 5 years, until increasing again in 2010. The decline in fecal pellet production in 2005 appears several years before total mesozooplankton biomass declined (in 2008;

Figure 1b), which is likely a result of an earlier decline in the smaller size classes (annual anomalies for the 0.2–0.5 mm size class went negative in 2005, while larger size class anomalies remained positive; data not shown), which have the highest growth rates [*Roman et al.*, 2002, Table 2], make up the largest proportion of the mesozooplankton biomass, and thus exert proportionally more control on fecal pellet export in our calculations.

[32] The potential annual contribution of fecal pellets to C flux was about threefold that of active transport by DVM, and appears to be a relatively more important component of the export flux when compared to sediment traps for the entire time series (Figure 7). However, we do not account for any consumption and remineralization or fragmentation of fecal pellets produced in the upper 150 m, which would decrease fecal pellet export [*Noji et al.*, 1991; *Poulsen and Kiørboe*, 2005]. *Goldthwait and Steinberg* [2008] measured zooplankton fecal pellet POC flux by analyzing fecal pellets in sediment traps deployed at 150 m inside and outside of mesoscale eddies in the Sargasso Sea and at BATS during the summer (June–August). Fecal pellet POC flux was on the order of 0.7–2 mg C m^{-2} d^{-1}, lower compared to the mean estimated from egestion rates over the entire BATS time series (June–August only) in the present study of 11.5 mg C m^{-2} d^{-1}, which suggests remineralization in the epipelagic zone. However, estimates of fecal pellet fluxes from analysis of sediment trap material may be conservative as pellets can break up in traps rendering them unrecognizable, or making it impractical to measure pellet size for use in volume to carbon conversions [*Goldthwait and Steinberg*, 2008; *Wilson et al.*, 2008]. Thus the relative importance of DVM and fecal pellet flux as carbon export mechanisms into the upper mesopelagic zone may be more equivalent than depicted in Figure 7.

5. Conclusions

[33] While there is seasonal and interannual variability in zooplankton biomass at BATS, this study indicates that over most of the time series there is a significant long-term biomass increase. Interestingly, this increase mirrors that of zooplankton biomass in the North Pacific subtropical gyre, where net primary production has also increased [*Sheridan and Landry*, 2004; *Saba et al.*, 2010]. This scenario is not what is predicted for increasingly stratified subtropical oceans in which nutrient exchange is limited and production declines [e.g., *Behrenfeld et al.*, 2006; *Doney*, 2006]. However, it is possible that for a period of time climate warming has increased primary and secondary production at BATS, and that at some future date the trend will reverse. Whether the recent, but temporary, downturn in zooplankton biomass at BATS is foretelling of a switch, remains to be seen. The most likely mechanism driving the long-term zooplankton biomass increase is bottom-up control by pico-phytoplankton, which have also increased at BATS, translating up the microbial food web into mesozooplankton. Decrease in top-down control by mesozooplankton predators or expansion of the range of tropical species northward as a result of warming may also play a role, and data with which to test these mechanisms at BATS are needed. The associated increasing importance of DVM and fecal pellet flux in the biological pump may affect the structure and functioning of the

mesopelagic food web, and could also affect food supply to the benthos, ultimately impacting deep-sea benthic communities [*Billett et al.*, 2001; *Smith et al.*, 2002; *Ruhl and Smith.*, 2004]. Future effort should be placed in better characterizing changes in individual zooplankton taxa in the epipelagic community, and at least establishing a reasonable baseline for mesopelagic zooplankton biomass to which future studies can be compared. Coupled with process studies examining grazing and metabolic rates, our ability to predict how changing zooplankton community structure affects biogeochemistry in the subtropical gyres will be enhanced.

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