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# Zooplankton at the Bermuda Atlantic Time-series Study (BATS) station: diel, seasonal and interannual variation in biomass, 1994–1998

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## Abstract

Monthly zooplankton sampling was conducted at the Bermuda Atlantic Time-series Study (BATS) site from April 1994 through December 1998. Mesozooplankton were collected during the day and night in two replicate oblique tows in the top 200 m with a 1-m, 200  $\mu\text{m}$  mesh net. Subsamples were analyzed for wet, dry, carbon and nitrogen weights in five size fractions between 0.2 and  $> 5.0$  mm, and also photographed and preserved for subsequent taxonomic study. The data show a clear seasonal cycle, with maximum biomass in spring, and occasionally summer, and secondary peaks in fall and early winter. Night biomass was on average greater than day by a factor of 1.7, but was up to 3.4 times higher, indicating the importance of diel migrators at the BATS site. The increase in night over day biomass was most apparent in the larger size classes. The 4-year mean 0–200 m integrated biomass was 418  $\text{mg dw m}^{-2}$  for day samples and 659  $\text{mg m}^{-2}$  for night; mean annual values for total day and night biomass increased steadily from 1994 to 1998. These biomass values and the seasonal pattern of abundance are similar to data collected between 1957 and 1990 at Hydrostation “S” near Bermuda by previous investigators. A comparison of zooplankton biomass with primary production, phytoplankton standing stock and downward organic carbon flux at the BATS site indicated significant positive correlations with production and phytoplankton stock, but no significant relationship with flux at 200 m. © 2001 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

The Bermuda region historically has been the locale for numerous studies of hydrography, primary production, zooplankton abundance and composition, and particle flux at various depths

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(Michaels and Knap, 1996; Steinberg et al., 2001). In addition to hydrographic studies at Station S for over 45 years (Joyce and Robbins, 1996), zooplankton collections have been made at various times (Moore, 1949; Menzel and Ryther, 1961; Grice and Hart, 1962; Deevey, 1971; Deevey and Brooks, 1971; von Bodungen et al., 1982; Dam et al., 1995; Roman et al., 1993; 1995; Madin et al., 1996; Steinberg et al., 2000). Since October 1988, the US JGOFS program has supported a regular program of hydrographic and biogeochemical sampling at the Bermuda Atlantic Time-series (BATS) station, located 75 km southeast of Bermuda at 31°50'N, 64°10'W (Michaels and Knap, 1996; Steinberg et al., 2001). Regular sampling of zooplankton biomass at BATS commenced in April 1994.

The significance of zooplankton grazing, metabolism and migration for particle transformation and flux is widely recognized (e.g. Longhurst and Harrison, 1988; Longhurst et al., 1990; Michaels and Silver, 1988; Dam et al., 1995; Steinberg et al., 2000). As stated in the Joint Global Ocean Flux Study (JGOFS) Long-Range Plan: "... it should be possible to enumerate the dominant migrating species at each site and apply empirical formulae for feeding rate, defecation rate, migration depths." (US JGOFS Steering Committee, 1990). The 'empirical formulae' are determined by process studies at various times and places (e.g. Roman et al., 1993), but the biomass and species composition of zooplankton at a given site and time are essential pieces of information for application of these formulae for the determination of particle transformation and flux rates. In addition, information on seasonal and interannual variability in zooplankton biomass and species composition is crucial for testing and validation of ecosystem models, and for understanding the effects of long-term climate change on ecosystems.

The importance of zooplankton feeding and migration in the Bermuda region is especially apparent from sediment trap data, which show that fluxes near the BATS site vary seasonally, even at 3200 m, in close correlation with seasonal peaks in primary production (Deuser, 1986). This short temporal coupling between primary production and flux in deep traps implies a rapid transport mechanism, such as sinking fecal pellets. The sedimentation of fly ash (Deuser et al., 1983b) and particulate aluminum (Deuser et al., 1983a), both atmospheric inputs to the surface layers, also point to the role of particle feeding zooplankton in flux of material from the euphotic zone. However, there were few time periods for which information on production, zooplankton abundance and particle flux were available for comparison. Since the beginning of zooplankton sampling at BATS, these data have been collected simultaneously. In this paper, we report our results on zooplankton biomass at BATS from April 1994 through December 1998. Taxonomic composition of these samples is currently being analyzed and will be reported in a later paper. Similar data for zooplankton biomass (and species composition) at the JGOFS Station "Aloha" at Hawaii are reported by Landry et al. (2001).

## **2. Methods**

Zooplankton were collected at the BATS site (31°50'N, 64°10'W) with a 1-m<sup>2</sup> rectangular, 202- $\mu$ m mesh net. The net had a 4-part bridle connecting the top and bottom corners of the net frame to a spreader bar, which was attached by a 2-part bridle to the hydrowire. A depressor plate welded to the frame maintained the desired towing angle. Temperature and depth as a function of time were recorded with a Vemco Minilog recorder (between April 1994 and May 1995, the depth

recorder was not available and net depth was estimated from the wire out and its angle), and flow through the net was measured with a General Oceanics mechanical flowmeter suspended across the center of the net mouth. Volume filtered by the net was calculated from the flow-meter counts and the mouth area of the net. The nominal mouth area ( $1 \text{ m}^2$ ) was corrected to an effective mouth area based on measurements of the angle of the net frame under average towing conditions (Wiebe et al., 1985). These measurements were recorded with an electronic angle indicator and data logger during a set of test tows made in October 1998. Two replicate double oblique tows lasting approximately 30 min were made during the day (between about 0900 and 1500 h) and at night (between about 2000 and 0200 h) on each BATS cruise. Tows were made through the mixed layer, to a depth of approximately 200 m. All depth-integrated biomass data reported here are normalized to a 200 m depth by the formula

$$\text{Biomass}[0\text{--}200 \text{ m}] = \text{biomass}[0\text{--}x \text{ m}] \times 200/x,$$

where  $x$  is the actual depth of tow.

Samples from the tows were split immediately on board. One half-split was used to make a silhouette photograph of the live plankton (Ortner et al., 1979); the sample split used for the silhouette was then preserved in 5% buffered formalin. (Results from analysis of these photographs and samples will be reported separately.) The other 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 tared disks of 0.2 mm nitex netting. These were frozen for wet and dry weight analyses on shore in Bermuda. The samples were thawed, blotted on absorbent paper and weighed. Samples on the tared nitex disks were dried at  $60^\circ$  for 24 h. Wet and dry weights were determined to the nearest 0.1 mg with a Sartorius analytical balance.

For determination of C and N content as a fraction of dry weight, we took 308 subsamples of the replicate size-fractionated day and night tows from four cruises per year (January, April, July and October) from 1994 to 1998. Well-mixed aliquots of these dry samples were carefully homogenized with a mortar and pestle and combusted in a Control Equipment Corporation 240-XA Elemental Analyzer at Bermuda Biological Station for Research (BBSR). Values for C and N content were analyzed by ANOVA to determine any significant trends with size fraction, season, year or day vs. night, and appropriate values were then selected for conversion of dry weights into C weights. Data on wet weight, dry weight and CHN content were used to express zooplankton biomass in each size fraction integrated ( $\text{mg m}^{-2}$ ) over a 0–200 m depth range.

### 3. Results

Table 1 summarizes data for all tows made at the BATS site between April 1994 and December 1998. Tows lasted from 21 to 71 min (mean = 37, s.d. = 8.7); volume filtered ranged from 134 to  $1484 \text{ m}^3$  (mean = 580, s.d. = 221). The mean depth of 510 tows on which the time depth recorder was used was 195.7 m (s.d. = 30.8, range = 115–292). The complete data set, including wet and dry weight biomass for individual tows and size fractions is available on CD-rom in this volume and at [<http://www.bbsr.edu> — follow links to BATS data]. Measurements of the net angle made in October 1998 indicated a mean deviation of  $10^\circ$  from a vertical ( $0^\circ$ ) angle of the net frame. Using the formulae of Wiebe et al. (1985) we calculated that this net angle results in a 2% decrease in

Table 1

Summary of total mesozooplankton biomass on BATS cruises from April 1994 to December 1998. Cruise numbers followed by “A” are bloom cruises. Temperature is mean value for 0–200 m; total day and night biomass values are means of replicate tows, all size fractions combined. N.A. indicates data missing for technical reasons

Cruise #	Date	Temp (°C)	Mean biomass (mg dw m <sup>-2</sup> )	
			Day	Night
BATS 66A	4/6/94	19.58	704	385
BATS 67	4/18/94	20.04	82	198
BATS 68	5/17/94	20.05	123	249
BATS 69	6/13/94	20.09	190	410
BATS 70	7/18/94	20.22	182	358
BATS 71	8/15/94	20.59	240	547
BATS 72	9/20/94	21.81	199	405
BATS 73	10/19/94	20.86	200	611
BATS 74	11/14/94	20.59	165	394
BATS 75	12/9/94	20.58	197	200
BATS 76	1/11/95	20.12	140	294
BATS 77	2/14/95	19.20	265	566
BATS 78	3/16/95	18.99	520	925
BATS 79A	4/27/95	19.35	684	849
BATS 80	5/10/95	18.71	593	682
BATS 81	6/12/95	19.57	439	685
BATS 82	7/11/95	19.32	640	772
BATS 83	8/18/95	20.77	320	476
BATS 84	9/12/95	21.39	296	316
BATS 85	10/10/95	21.04	231	543
BATS 86	11/6/95	21.21	211	n.a.
BATS 87	12/15/95	20.80	237	547
BATS 88	1/30/96	19.23	311	364
BATS 89	2/14/96	18.96	n.a.	248
BATS89A	2/27/96	19.07	307	708
BATS 90	3/15/96	19.35	364	465
BATS 90A	3/27/96	19.19	364	585
BATS 91	4/9/96	19.01	241	659
BATS 91A	4/22/96	18.69	1123	761
BATS 92	5/6/96	19.26	490	602
BATS 93	6/10/96	19.90	291	461
BATS 94	7/8/96	20.15	727	741
BATS 95	8/5/96	21.00	390	618
BATS 96	9/2/96	21.03	296	489
BATS 97	10/8/96	21.14	536	563
BATS 98	11/5/96	20.16	453	426
BATS 99	12/11/96	21.31	785	1082
BATS 100	1/13/97	20.23	239	463
BATS 100A	1/27/97	19.77	289	580
BATS 101	2/6/97	19.92	403	544
BATS 101A	2/20/97	19.83	329	629
BATS 102	3/4/97	19.88	346	544

Table 1 (continued)

Cruise #	Date	Temp (°C)	Mean biomass (mg dw m <sup>-2</sup> )	
			Day	Night
BATS 102A	3/18/97	19.81	318	544
BATS 103	4/8/97	20.31	485	762
BATS 104	5/5/97	20.08	560	1023
BATS 105	6/11/97	19.85	764	1192
BATS 106	7/15/97	20.35	398	796
BATS 107	8/11/97	21.89	416	744
BATS 108	9/11/97	21.79	377	647
BATS 109	10/6/97	20.92	384	562
BATS 110	11/11/97	21.26	480	430
BATS 111	12/9/97	20.84	600	794
BATS 112	1/12/98	20.51	419	532
BATS 113	2/11/98	19.72	596	1157
BATS 113A	2/28/98	19.43	492	1297
BATS 114	3/9/98	19.19	625	1169
BATS 114A	3/25/98	19.54	716	2448
BATS 115	4/7/98	19.45	544	1112
BATS 116	5/4/98	19.58	294	716
BATS 117	6/2/98	19.51	785	1121
BATS 118	7/8/98	20.23	965	1338
BATS 119	8/10/98	20.69	470	415
BATS 120	9/8/98	22.78	445	386
BATS 121	10/22/98	21.93	217	454
BATS 122	11/18/98	22.70	430	704
BATS 123	12/7/98	20.98	304	509

effective mouth area of the net, and hence a 2% decrease in the calculated volume filtered (mouth area × distance traveled). Values for volumes filtered were decreased by this factor prior to calculation of zooplankton biomass.

The relationships among biomass values expressed as wet weight, dry weight, carbon weight and C:N ratio are given in Table 2 for all samples, day vs night samples, and the five size fractions. The mean ratio of DW/WW for all samples is 0.19, (s.d. = 0.07), identical to the mean value reported previously for other oceanic zooplankton (Omori, 1969). Slightly higher values are seen for the smallest size category, dominated by small copepods, and slightly lower values for the two largest size categories, which include chaetognaths and gelatinous organisms with higher water content. On several occasions in 1994–1997 we obtained much higher values for DW/WW, but believe that these unusual peaks were the result of errors in processing some samples. High DW/WW ratios could be due either to overestimates of dry weight or underestimates of wet weight. Sources of error that we have been able to identify from examination of sample log books include on some occasions failure to store dried samples in a dessicator prior to weighing, which led to increased weight from absorption of moisture, and at other times prolonged storage in air of wet-weight samples, leading to loss of weight from evaporation. Although the variation in the taxonomic

Table 2

Relationships among zooplankton biomass measurements for all replicate samples, day vs. night samples, and each size fraction (day and night combined). Size fractions in mm

Biomass ratio	All	Day	Night	0.2–0.5	0.5–1.0	1.0–2.0	2.0–5.0	> 5.0
Dry weight/wet weight, mean	0.19	0.19	0.19	0.22	0.19	0.19	0.18	0.18
s.d.	0.07	0.07	0.06	0.11	0.07	0.07	0.07	0.11
N	234	108	118	107	114	115	121	113
C weight/dry weight, mean	0.36	0.36	0.37	0.35	0.38	0.38	0.37	0.34
s.d.	0.06	0.06	0.06	0.06	0.05	0.06	0.06	0.06
N	309	156	152	63	63	63	62	59
C:N ratio	5.1	5.1	5.1	5.4	5.1	5.1	4.9	5.0
s.d.	0.4	0.5	0.4	0.5	0.2	0.3	0.3	0.4
N	309	157	152	64	61	63	62	59

composition of the samples also may have an effect on the DW/WW ratios, it is very unlikely that any zooplankton have DW/WW ratios in excess of 0.4 (Omori, 1969). We considered values for DW/WW  $\geq 0.4$  to be anomalous, and omitted them from calculation of the mean values given in Table 2.

While the overall mean value for carbon as a fraction of dry weight (CW/DW) was 0.36 (s.d. = 0.06,  $n = 308$ ), there was a general decrease in the CW/DW ratio between 1994 and 1998, with significant differences between years ( $p < 0.001$ ). Variation in CW/DW ratio was not significantly correlated with season independently of year ( $p = 0.07$ ), and as a result we use three values of CW/DW in subsequent calculations of carbon biomass: 0.41 for 1994–1995, 0.36 for 1996 and 0.32 for 1997–1998. The overall mean value for C:N ratio was 5.1, but the ratios varied slightly between size fractions, most notably in the 0.2–0.5 mm category (Table 2). A value of 5.1 is probably sufficient for estimation of bulk nitrogen biomass.

Mean values from the entire time series for day and night biomass in each size category are shown in Table 3 as dry weight and carbon weight ( $\text{mg m}^{-2}$ ), along with coefficients of variation and 95% confidence limits. Variability in biomass is higher in the larger size fractions, but overall the mean coefficients of variation, reflecting all sources of error in the collection and processing of the zooplankton samples, are low (12.5–16.5 for total samples, Table 3). Fig. 1 shows wet and dry weight biomass in the five size fractions for day and night samples for each cruise between April 1994 through December 1998. Biomass was highest in spring and summer (March to August) in all years, but with peaks also in the fall of 1997 and 1998. In general, wet weight and dry weight values are correlated, differing by factors of 6 to 8. There are consistent differences between day and night biomass in almost all size categories, with night often twice the day value, and much higher in some tows. In general, night biomass was 1.5 to 2.5 times greater than day, with a maximum differential of 3.4 times in March 1998 (Fig. 2). The absolute differential between overall mean day and night biomass was  $241 \text{ mg dw m}^{-2}$ . On only 6 sample dates out of 56 was night biomass less than day. A seasonal composite of day and night biomass (Fig. 3) shows a high spring biomass with small subsequent peaks in July, October and December. Although several of these peaks are well above

Table 3

Summary of overall means for day and night zooplankton biomass in each size category, with estimates of errors. Biomass values ( $\text{mg m}^{-2}$  for 0–200 depth interval) are geometric means for each category, across 65 cruises (April 1994–December 1998). Carbon weights are calculated from dry weights using the ratios given in the text. Coefficient of variation is standard deviation of the means, expressed as a percent of the means. Confidence limits are at 95% level

Size fraction	Day			Night		
	Mean	C.V.	95% C.L.	Mean	C.V.	95% C.L.
Dry weight ( $\text{mg m}^{-2}$ )						
0.2–0.5	110	20.3	95–125	114	19.5	97–131
0.5–1.0	122	16.0	108–136	157	17.1	133–181
1.0–2.0	86	28.6	71–101	153	19.9	132–174
2.0–5.0	70	27.7	59–81	170	24.1	146–194
> 5.0	30	49.2	24–36	65	47.5	53–77
Total	418	12.5	367–469	659	15.7	573–745
Carbon ( $\text{mg m}^{-2}$ )						
0.2–0.5	39	20.6	34–43	40	19.3	35–45
0.5–1.0	43	16.0	38–48	55	17.0	47–63
1.0–2.0	30	28.3	25–35	54	19.8	47–61
2.0–5.0	25	28.1	21–29	60	24.3	52–68
> 5.0	10	49.7	8–12	22	47.7	18–26
Total	147	12.8	129–165	231	16.5	204–258

the 5-year mean values of  $710 \text{ mg m}^{-2}$  (night) and  $454 \text{ mg m}^{-2}$  (day), their high variability renders the differences non-significant (ANOVA,  $p > 0.05$ ).

The increase in night biomass in both the wet and dry weight data is mostly due to increases in the biomass of larger organisms, particularly in the 2.0–5.0 mm size class. Averaged over the entire time series, this size class constituted 27 and 26% of the total night wet and dry biomass, respectively, as compared to 19 and 16% of the total day wet and dry biomass, respectively (Table 4). Conversely, the smaller size classes (0.2–0.5 mm, and 0.5–1.0 mm) constituted the highest proportion of the biomass in the day, with the largest discrepancy between day and night apparent in the 0.2–0.5 mm size class, which constituted 24 and 27% of total day wet and dry biomass, respectively, as compared to 15% and 18% of total night wet and dry biomass, respectively (Table 4). Subtraction of mean night minus mean day biomass in each size fraction further illustrates the contribution of the larger size classes to the migrating community, with 84% of the migrating biomass  $> 1.0 \text{ mm}$ , and 56%  $> 2.0 \text{ mm}$  (Table 4).

In Fig. 4, total zooplankton biomass (mean of day and night) is compared to integrated primary production and phytoplankton standing stock (as Chl *a*) in the top 200 m, and organic C flux collected in sediment traps at 200 m. The zooplankton carbon biomass is calculated from measured dry weights using the year-specific CW/DW values given above. Primary production, chlorophyll *a* and flux data are from the BATS program (Steinberg et al., 2001). Since these measurements were not all taken on exactly the same day during a given cruise, we have aligned all values on the dates

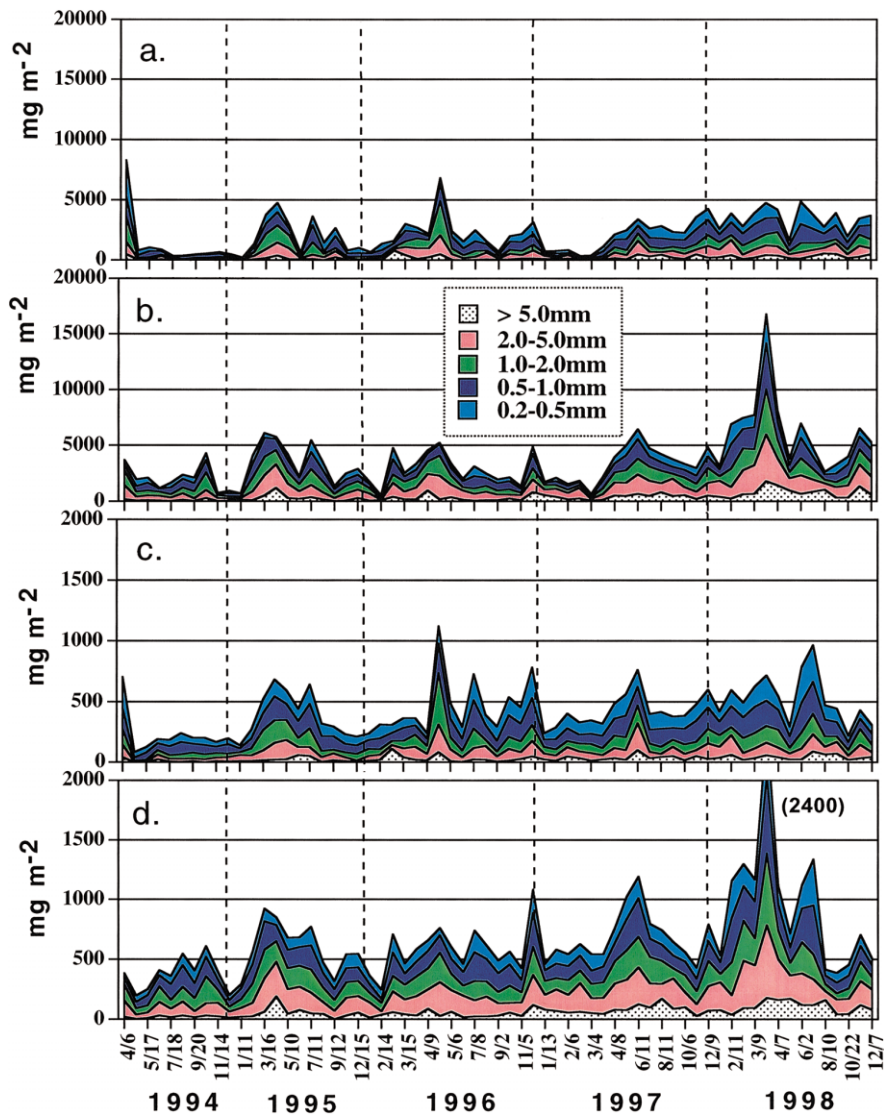


Fig. 1. Mesozooplankton biomass by size fractions for all cruises from April 1994 to December 1998, means of replicate tows. a, day wet weight; b, night wet weight; c, day dry weight; d, night dry weight. All values in  $\text{mg m}^{-2}$  for 0–200 m depth range.

when the zooplankton were sampled (usually  $\pm 2$  days). Temperatures in the top 200 m vary from  $18.5^\circ$  to about  $23^\circ\text{C}$  over this period (Table 1), with expected maxima in summer, and highest values overall from July to October, 1998. In most years the lower spring temperatures coincide with high zooplankton stocks, and high late summer and fall temperatures with lower zooplankton biomass. Primary production values fall generally between  $250$  and  $1000 \text{ mg C m}^{-2} \text{ d}^{-1}$ , phytoplankton chlorophyll *a* between  $10$  and  $60 \mu\text{g Chl } a \text{ m}^{-2}$ , zooplankton biomass from about  $100$ – $1000 \text{ mg C m}^{-2}$ , and downward flux across 200 m depth from about  $10$  to  $40 \text{ mg C m}^{-2} \text{ d}^{-1}$ .

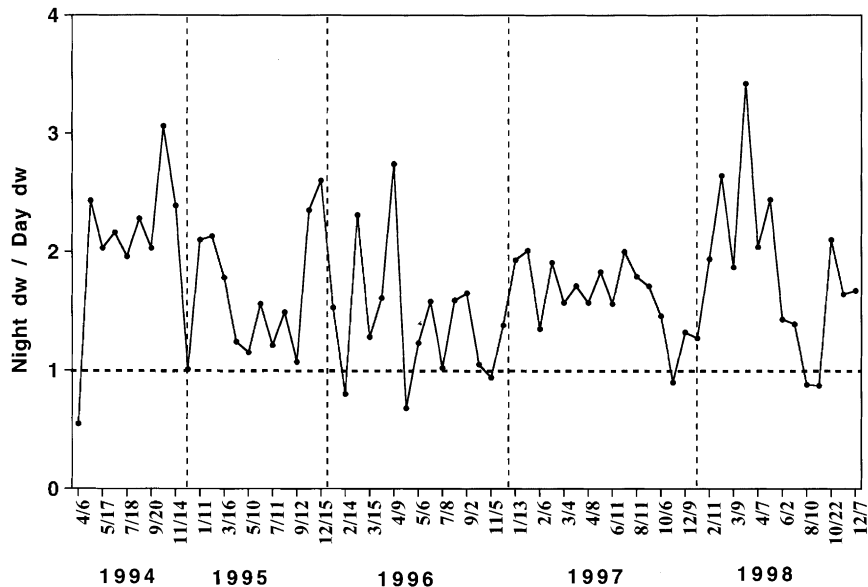


Fig. 2. Comparison of day and night dry weight biomass. Night dry weight/day dry weight ratio over time for all cruises. Values are sums of all size fractions and means of replicate tows. Horizontal dashed line indicates equality of day and night values.

The general pattern of spring and summer increase is seen in both phytoplankton and zooplankton biomass. A lag in zooplankton biomass increase following a production peak is apparent in some places in the time series (e.g., March/April 1995, February/March 1998). There are also related peaks in spring and summer (April/May 1996, July 1996), and in fall and early winter (e.g. October 1994, October to December 1995, December 1996, December 1997), but strong maxima of production are not always associated with increases in zooplankton biomass (e.g. December 1996 to March 1997). The same is generally true of the relationship between Chl *a* and zooplankton biomass, but perhaps with fewer coincident peaks than with primary production. A broad peak in integrated Chl *a* biomass occurs in February/March of each year (except 1997), with shorter increases occurring in late spring or summer. Most peaks in zooplankton biomass occur after this February/March increase. The relationship with flux at 200 m is less obvious, although there are some increases (February to March 1995, January to February 1996, December 1996, February to March 1998) that appear coincident with peaks in primary production, Chl *a*, zooplankton or all three.

Comparisons by linear regression of zooplankton biomass categories (total, day only, night only, > 2.0 mm only) with primary production revealed significant positive relationships in all cases except night biomass > 2.0 mm. The strongest relationships, between primary production and total (mean of day and night) and day biomass, are shown in Fig. 5. The regression of total biomass on primary production (Fig. 5a) is given by  $y = 0.171x + 115.8$ ;  $r^2 = 0.20$ ;  $n = 64$ ;  $p < 0.0005$ ; where  $x$  is the primary production integrated to 140 m ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) and  $y$  the mean total zooplankton biomass ( $\text{mg C m}^{-2}$ ); for day only biomass (Fig. 5b) the equation is  $y = 0.191x + 64.1$ ;  $r^2 = 0.31$ ;  $n = 65$ ;  $p < 0.0005$ ). The lack of a significant relationship with night biomass > 2.0 mm

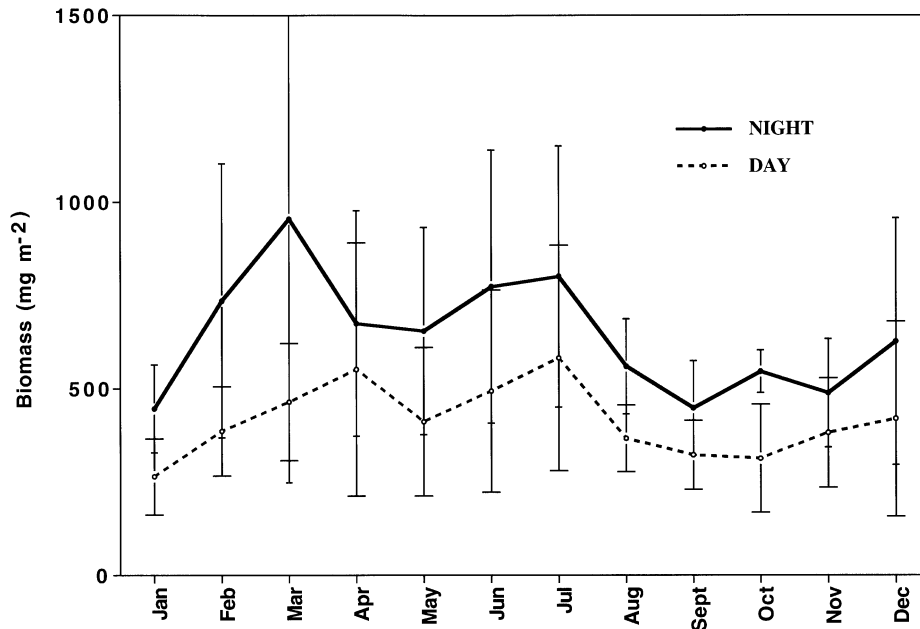


Fig. 3. Composite seasonal cycle of zooplankton biomass at BATS. Values are means of day and night dry weight ( $\text{mg m}^{-2}$ ) for each month, 1994–1998. Error bars are 1 standard deviation.

Table 4

Contribution of size fractions as a percent of total tow biomass, averaged over the entire time series

Biomass measurement	Mean percent of total tow biomass (s.d.)				
	0.2–0.5 mm	0.5–1.0 mm	1.0–2.0 mm	2.0–5.0 mm	> 5.0 mm
Day wet	24.5 (9.3)	29.4 (7.9)	19.4 (7.4)	18.9 (8.3)	7.8 (6.9)
Day dry	26.9 (6.6)	30.1 (5.4)	19.7 (5.5)	16.3 (6.1)	7.1 (5.3)
Night wet	15.2 (6.6)	23.6 (6.2)	23.5 (6.0)	27.2 (8.2)	10.4 (7.3)
Night dry	17.6 (4.9)	23.6 (5.1)	23.4 (4.8)	25.8 (6.6)	9.7 (6.2)
Night–day wet <sup>a</sup>	< 0.1	15.9	27.6	41.1	15.4
Night–day dry <sup>a</sup>	1.5	14.3	28.1	41.8	14.3

<sup>a</sup>Calculated by subtracting day mean biomass in each size fraction from night, and dividing by total mean biomass (averaged over entire time series).

is not surprising, as the growth dynamics of these larger and longer-lived vertical migrators are less likely to be closely coupled to surface production. The relationships between Chl *a* stock and zooplankton biomass were significant for total zooplankton ( $y = 2.049x + 141.5$ ;  $r^2 = 0.08$ ;  $n = 65$ ,  $p < 0.05$ ; where  $x$  is the phytoplankton biomass integrated to 200 m as  $\mu\text{g Chl } a \text{ m}^{-2}$ , and  $y$  the mean total zooplankton biomass in  $\text{mg C m}^{-2}$ ) and for day zooplankton biomass ( $y = 1.638x + 108.13$ ;  $r^2 = 0.07$ ;  $n = 65$ ;  $p < 0.05$ ). No regressions with flux at 200 m were significant.

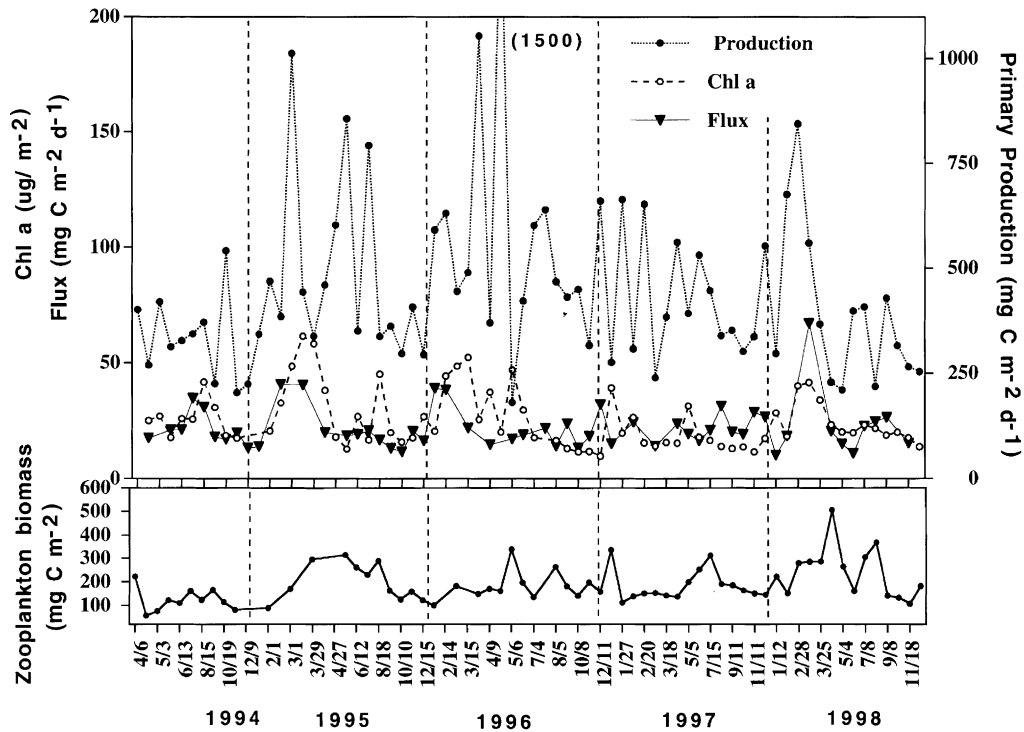


Fig. 4. Four year time series of primary production, phytoplankton standing stock, organic carbon flux (upper panel) and zooplankton biomass (lower panel) at the BATS station. Zooplankton biomass in the top 200 m ( $\text{mg C m}^{-2}$ ) is the mean of day and night replicates tows from all cruises, calculated using conversions given in text. Data for primary production ( $\text{mg C m}^{-2} \text{d}^{-1}$ ; 0–140 m integrated), phytoplankton standing stock ( $\mu\text{g Chl } a \text{ m}^{-2}$ ; 0–200 m integrated) and C flux at 200 m depth ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) are all from concurrent BATS observations (Steinberg et al., 2001).

We also tested whether a temporal lag, which often is apparent in Fig. 4, would improve the relationship between production or Chl *a* and zooplankton biomass, or between zooplankton biomass and flux. Given the integration time scales for these different measurements, the time required for zooplankton to progress through growth stages after a phytoplankton bloom, and for particles to sink from the surface waters, it may be unreasonable to expect these parameters to be synchronous. We used a cross correlation analysis described in Steinberg et al. (2001) to determine if apparent lags were statistically significant. All parameters were linearly interpolated on regular 1-week or 1-month time scales and cross correlation analysis was performed on this data set. The results indicated that zooplankton biomass followed production with a significant positive correlation with a 1-week up to a 1-month lag ( $r^2 = 0.21, 0.17, 0.15,$  and  $0.11$  for 1-week, 2-week, 3-week, and 1-month imposed lags, respectively,  $n = 68, p < 0.05$ ). No significant positive relationship was seen for zooplankton biomass following Chl *a*, although the highest correlation occurred with a 1-month imposed lag ( $r^2 = 0.09, n = 68, p > 0.05$ ). In addition, no significant positive relationship was seen for flux following zooplankton biomass, although the highest correlation occurred with a 2-week imposed lag ( $r^2 = 0.09, n = 68, p > 0.05$ ).

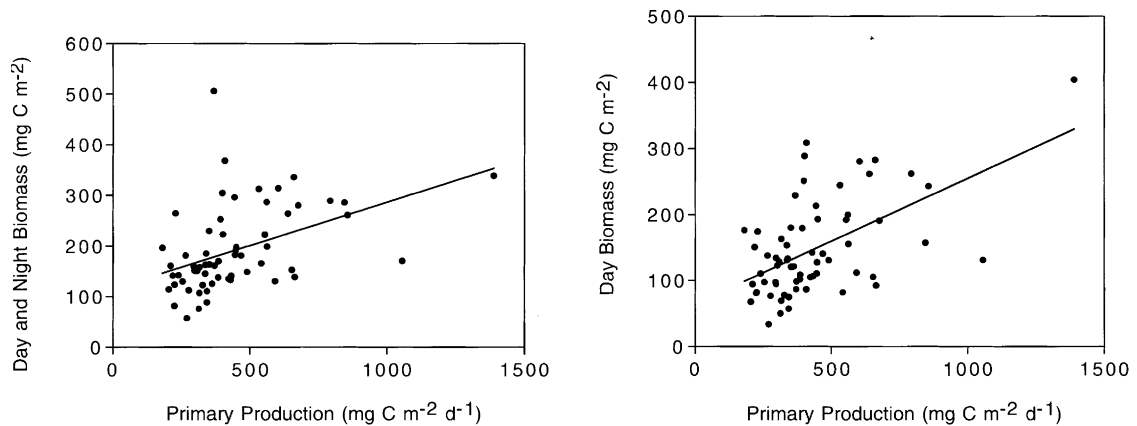


Fig. 5. Relationships between zooplankton biomass and primary production at the BATS site, 1994–1998. a, total zooplankton biomass (mean of day and night values); b, day zooplankton biomass. Both regressions are significant ( $p < 0.0005$ ), equations given in text.

## 4. Discussion

### 4.1. Comparisons with other zooplankton data from Bermuda

There have been several previous investigations of the zooplankton around Bermuda. Moore (1949) analyzed a series of net collections made between 1938 and 1940, using a closing net without a flowmeter. The data are presented only as numbers of individuals in different taxa, and cannot easily be compared to subsequent measures of biomass. A more quantitative sampling program was undertaken from November 1957 to April 1960 by Menzel and Ryther (1961), who used a 0.75-m plankton net to sample from 0 to 500 m at Station “S” 24 km southeast of Bermuda. The samples were split, with half used for measurement of displacement volume, dry weight and ash-free dry weight. Additional tows with closing nets were made during three months to determine the vertical distribution of the biomass between 0 and 2000 m. Essentially, the same methods were used in a subsequent study by Deevey (1971), who sampled from March 1961 through April 1962. Deevey determined displacement volume and dry weight, but in addition, enumerated and identified all the major taxa. Deevey and Brooks (1971) sampled again at Station “S” from July 1968 to June 1969, this time between 0 and 2000 m, using an open net from 0 to 500 m and closing nets for 500–1000, 1000–1500 and 1500–2000 m depth strata. They reported total displacement volumes and counts of various taxa from these samples. The transect study by Grice and Hart (1962) included stations to the northwest of Bermuda, but far enough from both Station “S” and the BATS site (24 and 75 km southeast of Bermuda, respectively) that we have not included them here for comparison with other results. As part of a survey of Bermuda’s marine environment, zooplankton sampling was conducted at Station “R” (7–11 km southeast of Bermuda) in the top 100 m (von Bodungen et al., 1982). These authors reported numbers of individuals and total carbon weight of the zooplankton from monthly samples taken between February 1979 and April 1980. More recently, Roman et al. (1993, 1995) reported the results of

zooplankton sampling done during the ZOOSWAT program at the BATS station. Stratified day and night samples in the top 200 m were taken using a 1 m<sup>2</sup> MOCNESS net with a 200 µm mesh; data are reported as mg C m<sup>-2</sup>.

We report two types of comparisons between our results and those obtained by previous studies. In Table 5, we summarize mean annual values for zooplankton biomass from five previous studies and our current results. The samples reported in these papers are from different depth ranges than we sampled (except Roman et al., 1993), and the zooplankton biomass is reported in various units. Table 5 gives the net mesh size used, the original sample depths, the number of tows made, the biomass data in the form originally reported, and as converted to mg dry weight m<sup>-2</sup> for 0–200 m. We first adjusted the integrated biomass data to match the 0–200 m depth range we sampled. Menzel and Ryther (1961), Deevey (1971) and Deevey and Brooks (1971) all sampled between 0 and 500 m. Although their tows were made during the day, this depth range probably encompasses the daytime depths of many of the vertical migrators that we sampled at night in the top 200 m; thus, their integrated biomass from 0 to 500 may be comparable to an average of our day and night values. To estimate the fraction of the total 0–500 m biomass between 0 and 200 m, we used data

Table 5

Comparison of zooplankton biomass data from previous and current sampling in the Bermuda region. Mean values for integrated total biomass for the time periods and depth ranges indicated, and as converted to dry weight integrated over 0–200 m. Conversions from original data format to mg dry weight m<sup>-2</sup> as described in text. *N* = number of sample dates reported

Report	Mesh (µm)	Depth range (m)	<i>N</i>	Original data	mg dry weight (0–200 m)
Menzel and Ryther (1961) Nov 1957–Apr 1960, day	366	0–500	52	1.08 g dw m <sup>-2</sup>	497
Deevey (1971) Mar 1960–Apr 1962, day	366, 203	0–500	24	1.31 g dw m <sup>-2</sup>	626
Deevey and Brooks (1971) Jul 1968–Jun 1969, day	366, 203	0–500	12	14.9 ml vol m <sup>-2</sup>	631
Von Bodungen et al. (1982) Feb 1979–Apr 1980, day	300	0–100	12	62.9 mg C m <sup>-2</sup>	245
Roman et al. (1993) Aug 1989, day and night	200	0–200	16	168 mg C m <sup>-2</sup>	466
Mar–Apr 1990, day and night	200	0–200	16	445 mg C m <sup>-2</sup>	1236
This paper					
Apr–Dec 1994	200	0–200	9 <sup>a</sup>	—	419
Jan–Dec 1995	200	0–200	12	—	475
Jan–Dec 1996	200	0–200	15	—	523
Jan–Dec 1997	200	0–200	15	—	555
Jan–Dec 1998, day and night	200	0–200	14	—	738

<sup>a</sup>Data from 9 months in 1994, but annual value normalized to 12 months for comparison with other years, see text.

from Menzel and Ryther (1961; Table 1) on the vertical distribution of biomass. They made stratified tows in June, August and February at 100-m intervals between 0 and 500 m, reporting total dry weight of zooplankton for each interval. The average fraction of biomass in the 0–200 m range was 46% of the 0–500 m range. We took 46% of values for 0–500 m integrated biomass values from Menzel and Ryther, Deevey (1971) and Deevey and Brooks (1971) to estimate the 0–200 m integrated biomass. Sampling by von Bodungen et al. (1982) at Station “R” was between 0–100 m. The mean biomass value for 100–200 m from Menzel and Ryther (1961) is 40% of the 0–100 value, so we adjusted the data of von Bodungen et al. by multiplying by 1.4. For conversion of biomass units to mg dry weight  $m^{-2}$ , we used the factors given in Table 2. Deevey and Brooks (1971) reported biomass only as displacement volume ( $ml m^{-2}$ ), but Deevey (1971) provided both volume and dry weight data. From those data, we assumed the displacement volume (ml) equals wet weight (g), and calculated a DW/WW ratio of 0.09 (less than half our values from Table 2, or those of Omori, 1969), and used this to convert displacement volume from Deevey and Brooks (1971) to dry weight. Biomass was reported by von Bodungen et al. (1982) and by Roman et al. (1993) as  $mg C m^{-2}$ . We converted this to an estimate of dry weight by dividing by 0.36 (the CW/DW ratio for all samples, Table 2).

The range of mean biomass values from previous studies is relatively small, and falls within the range of monthly values measured in the present time-series study (Table 1). Menzel and Ryther (1961), Deevey (1971) and Deevey and Brooks (1971) all sampled at Station “S” using the same equipment and protocols, and results in their papers are very similar for 1957–1960, 1960–1962, and 1968–1969. Menzel and Ryther used a coarser net (No. 2 nylon: 366  $\mu m$ ) than Deevey or Deevey and Brooks (Nos. 2 and 8 nylon: 366 and 203  $\mu m$ ), which may account for their somewhat smaller biomass values. Menzel and Ryther compared catches of the 366- and 203- $\mu m$  nets and concluded there was no significant difference, but when Deevey made the same comparison she concluded that the 203- $\mu m$  mesh net caught four times as many organisms as the 366- $\mu m$  net. Von Bodungen et al. (1982) sampled at a more inshore station, with a 300- $\mu m$  mesh; both factors might contribute to the lower values they report. Roman et al. (1993) sampled zooplankton in the 64–200- $\mu m$  and the  $> 200$ - $\mu m$  size ranges, using different nets or pumps. The total integrated zooplankton for both size ranges combined was similar for August 1989 and March–April 1990, but the proportions of the two size classes were reversed, with the  $> 200$ - $\mu m$  size class making up only 30% of the total in August, but 75% of the total in March–April. The total biomass they reported for zooplankton  $> 200$ - $\mu m$  exceeds any value we obtained, except on BATS 114A, a bloom cruise in March 1998 (Table 1).

Yearly mean values from our sampling (Table 5) reveal an increase in zooplankton biomass from 1994 to 1998. Our data for 1994 do not include the first three months of the year, which is often when peak biomass occurs. We can make a conservative correction to a full year by multiplying the 9-month mean ( $314 mg dw m^{-2}$ ) by 1.33 to adjust for the missing 3 months; this yields an estimated mean for 1994 of  $419 mg dw m^{-2}$  (Table 5). The high value for 1998 is affected by the peak in March–April of that year (Figs. 1, 2 and 4). The overall mean of all previous values given in Table 5 is  $617 mg dw m^{-2}$ . Our annual means, and the overall value of  $542 mg dw m^{-2}$  for 1994–1998, are similar to the other averages reported in Table 5. Although most of the previous samples were from daytime only, the greater depth range sampled (except von Bodungen et al., 1982) includes the daytime range of most vertical migrators and is probably comparable to our day and night mean values.

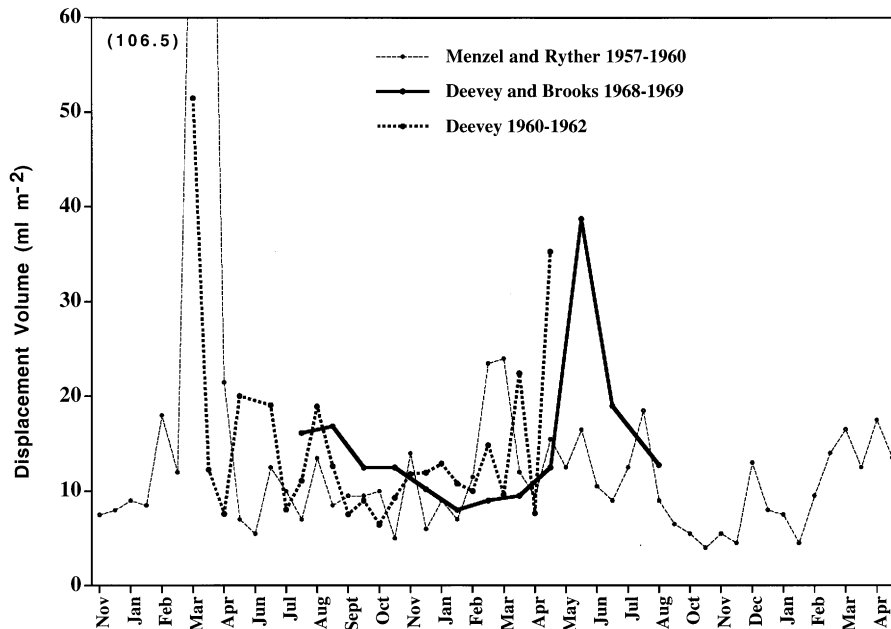


Fig. 6. Historical data on seasonal distribution of zooplankton biomass at Station “S”. All data are displacement volume ( $\text{ml m}^{-2}$ ) integrated through the 0–500 sampling depth. Data from Menzel and Ryther (1961) for November 1957 through April 1960, from Deevey (1971) for March 1960 to April 1962, from Deevey and Brooks (1971) for July 1968 to June 1969. Results from different years are aligned on a single monthly axis. These data are from daytime tows, but through a depth range which probably included daytime depths of vertical migrators (see text).

Seasonal variation in zooplankton biomass measured in previous studies is compared in Fig. 6. We have plotted data from Menzel and Ryther (1961), Deevey (1971) and Deevey and Brooks (1971) for zooplankton displacement volume (the only unit common to all three papers) in the 0–500 m depth range. Although we have not adjusted these values to 0–200 m depth, they represent a seasonal pattern of variation that is generally similar to our data (Figs. 1, 3 and 4). Biomass is highest in the spring, somewhere between March and June, and generally low in the summer and fall, although with small peaks in August 1958 and 1960, November 1958, and July and November 1959. The very high values of March–April 1958 were considered suspect by Menzel and Ryther because “... the volumes indicated by the net flow meter were exceptionally low. Without question there was a population maximum at that time but it is quite possible that gelatinous animals interfered with the turning of the meter, exaggerating the magnitude of the standing crop” (1961, p. 256). Gelatinous zooplankton such as medusae, siphonophores and salps were generally most abundant in March and April, and relatively sparse the rest of the year (Deevey, 1971, Deevey and Brooks, 1971). We also have found high densities of salps in several samples from spring and summer cruises.

#### 4.2. Relationship of zooplankton biomass to primary production and flux at BATS

Our results suggest that phasing between phytoplankton and zooplankton changes throughout the year, as well as interannually. Some phytoplankton bloom periods are quickly tracked

by (presumably) fast-growing zooplankton in these warmer subtropical waters, while other blooms are not. Peaks in zooplankton biomass generally occur during the spring bloom period, often synoptic with peaks in primary production, as shown in Fig. 4 and supported by the significant positive relationship in a regression of primary production vs. zooplankton biomass (Fig. 5). Some significant increases in zooplankton biomass also occur up to one month after primary production peaks, as shown in Fig. 4 and supported by cross-correlation analysis of lagged data. Peaks in zooplankton biomass do occur during other times of the year, but do not as obviously relate to or follow peaks in primary production. For much of the time series, increases in phytoplankton standing stock (Chl *a*) accompany increases in primary production. However, the relationship between Chl *a* and zooplankton biomass was not as strong as for primary production. The weak correlation between zooplankton biomass and carbon flux (with some peaks in downward flux even occurring before zooplankton biomass peaks, Fig. 4) is perhaps not too surprising considering the non-parallelism between zooplankton biomass and community metabolic rates (Ikeda, 1985), and the inherent spatial variability and different integration time scales of the measurements.

Significant positive correlations between zooplankton and flux have been reported (e.g., Bishop et al., 1986). As some of the larger zooplankton size classes might be expected to contribute more to downward flux, we also tested the relationship between the > 5.0-mm and > 2.0-mm size classes vs. flux, but these correlations were no stronger than with all size classes combined. Strong correlations do exist between some individual zooplankton taxa, such as salps, and flux at BATS (Steinberg and Madin, in preparation). Thus, the relationships among these parameters also will depend significantly on the community composition of the phytoplankton and zooplankton as well as their biomass. Sinking characteristics of cells, feeding and migration behavior of zooplankton, and the structure of the epipelagic food web (Michaels and Silver, 1988) will all affect the connection between production and flux. The patterns will likely be clearer upon full analysis of taxonomic composition throughout the time series.

#### 4.3. Vertical migration and significance for active transport of carbon and nutrients at BATS

The main deep scattering layer near Bermuda lies at 400–600 m in the daytime (Menzel and Ryther, 1961; Moore, 1950). Results thus far from this time-series study indicate mean zooplankton biomass in the upper 200 m on average nearly doubles at night due to vertically migrating zooplankton, similar to what has been found in short-term studies at BATS (Roman et al., 1993). Biomass in the surface waters at night increased by as much as a factor of 3.4 over day values. Migrating biomass (mean night biomass minus mean day biomass in top 200 m) at BATS averages 241 mg dw m<sup>-2</sup>, and reached 1732 mg dw m<sup>-2</sup> (March 1998) over the entire time series. This mean migrating biomass is just over half that found at Station Aloha (394 mg dw m<sup>-2</sup>; Al-Mutairi and Landry, 2001). Applying the dry weight to carbon conversions determined above (CW/DW = 0.37 for night), this corresponds to a mean migrating biomass of 89 mg C m<sup>-2</sup> and maximum of 641 mg C m<sup>-2</sup>. Dam et al. (1995) report a mean migrating biomass of mesozooplankton during the spring period of 191 mg C m<sup>-2</sup> (range 82–536) in the top 160 m during a single sampling cruise at BATS, although summer biomass of migrating mesozooplankton was lower (mean 42.4 mg C m<sup>-2</sup>; Dam, pers. comm.).

Much of this increased biomass at night was due to increases in the larger size classes. These include some of the larger copepods such as *Pleuromamma xiphias*, and *P. abdominalis* (Steinberg et al., 2000), and *Euchirella messinensis* (Schnetzer and Steinberg, in prep.). Other dominant species of migrators at BATS include euphausiids such as *Thysanopoda aequalis* and *Nematobrachion flexipes*. Steinberg et al. (2000) found *Pleuromamma* spp. copepods and the euphausiid *Thysanopoda aequalis* alone made up a substantial proportion of the biomass of zooplankton present in surface waters at night (mean = 23%, range = 4–70% for *Pleuromamma* and *Thysanopoda* combined). Other common migrators include the hyperiid amphipods *Anchylomera blossevillei* and *Scina* spp, and several species of migrating sergestid shrimps including *Sergia splendens*, *Sergestes atlanticus*, and *Sergestes vigilax* (Steinberg et al., 2000). The large migrating biomass in March 1998 was 2–3 times greater in all but the > 5.0-mm size category than the average of 10 cruises immediately preceding and following it. Taxa present included larger numbers of the euphausiid *Nematoscelis* sp. and the pteropod *Limacina* sp.

These substantial diel changes in biomass have important implications for active transport of material to depth. The downward migration of zooplankton that have been feeding in the surface waters not only releases particulate organic matter via fecal pellet production, but also dissolved inorganic and organic material via respiration and excretion below the mixed layer during the day. Vertically migrating zooplankton can actively transport a significant amount of dissolved inorganic carbon and nitrogen to deep water, which can be significant relative to the gravitational vertical export of sinking particulate organic matter measured with sediment traps (Longhurst and Harrison, 1988; Longhurst et al., 1989, 1990; Dam et al., 1995; Zhang and Dam, 1997; Le Borgne and Rodier, 1997; Steinberg et al., 2000; Al-Mutairi and Landry, 2001).

Several studies provide estimates of the magnitude of this transport in the Sargasso Sea. For example, ammonia excretion rates below the euphotic zone by migrating zooplankton are estimated at 8% of the particulate nitrogen flux in the Northern Sargasso Sea (Longhurst et al., 1989), and 13–58% of the particulate carbon flux in a range of stations in subtropical and tropical oceans (Longhurst et al., 1990). Using the same approach, Dam et al. (1995) calculated respiratory carbon flux as 18–70% of POC flux, and ammonia excretion as 17–82% of PON flux at BATS. In a subsequent study at BATS, Steinberg et al. (2000) found on average, excretion of DOC makes up 24% (range = 5–42%) of the total carbon metabolized (excreted + respired) and could represent a significant augmentation to the vertical flux that has already been documented for respiratory CO<sub>2</sub> flux by migrant zooplankton. Combined active transport of CO<sub>2</sub> and DOC by migrators at BATS is equal to a mean of 7.8% and a maximum of 38.6% of the mean sinking POC flux at 150 m, and is an even higher proportion of the sinking POC flux at deeper depths (Steinberg et al., 2000). Active DOC export by migrators is equal to a mean of 1.9% and a maximum of 13.3% of the annual DOC export by physical mixing (Carlson et al., 1994) at BATS. Al-Mutairi and Landry (2001) suggest the migrant flux at BATS may be even higher than noted above because the metabolic rates in Steinberg et al. (2000) were derived from relatively large animals and applied to the whole migrating community, without corrections for smaller animals with higher mass-specific metabolic rates. However, a majority of the migrating community at BATS is composed of organisms in the larger size fractions (84% of the night minus day biomass in the upper 200 m is > 1.0 mm, and 56% is > 2.0 mm, Table 4), thus the rates applied in Steinberg et al. (2000) are likely representative of much of the migrating community. Active transport of carbon and nutrients by vertical migrators is an important export mechanism relative to other

fluxes at BATS, and dependent on both the biomass and the species composition of the migrating community.

The collection of zooplankton at this site has continued since December 1998 as part of the BATS time-series program. Future taxonomic analysis of samples will make possible comparisons of species composition and abundance with earlier data from Moore (1949), Deevey (1971) and Deevey and Brooks (1971), all of whom included detailed species lists. Comparisons between the HOT data and earlier collections in the central Pacific have revealed significant changes in zooplankton species composition over decadal periods (Landry et al., 2001). Evidence for analagous shifts in diversity also may emerge from the BATS data. Other investigators are beginning to use the BATS zooplankton collections for ancillary studies on diel migration, carbonate flux, and stable isotope ratios. The comprehensive physical, chemical and biological data set resulting from the continuing BATS time-series study will provide a powerful context for analysis of the ecological, zoogeographic and biogeochemical roles of mesozooplankton in the subtropical Atlantic Ocean.

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