

Contribution to the Theme Section 'Jellyfish blooms and ecological interactions'

# Long-term time-series study of salp population dynamics in the Sargasso Sea

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**ABSTRACT:** Salps are bloom-forming, pelagic tunicates with high grazing rates on phytoplankton, with the potential to greatly increase vertical particle flux through rapidly sinking fecal pellets. However, the frequency and causes of salp blooms are not well known. We quantified salps from day and night zooplankton net tows in the epipelagic zone of the North Atlantic subtropical gyre as part of the Bermuda Atlantic Time-series Study (BATS). Salp species and size were quantified in biweekly to monthly tows from April 1994 to November 2011. Twenty-one species of salps occurred at the BATS site over this time period, and the most common bloom-forming salps were *Thalia democratica*, *Salpa fusiformis*, *Weelia (Salpa) cylindrica*, *Cyclosalpa polae*, and *Iasis zonaria*. Five species of salps exhibited diel vertical migration, and salp abundances varied seasonally, with *T. democratica*, *S. fusiformis*, and *C. polae* blooms coincident with the spring phytoplankton bloom, and *W. cylindrica* blooms occurring more often in late summer. For *T. democratica*, mean annual biomass increased slightly over the time series and was elevated every 3 yr, and biomass increased in the presence of cyclonic mesoscale eddies. Decadal climate oscillations and biogeochemical conditions influenced multi-year trends in salp abundance and biomass. Both total salp and *T. democratica* abundance were positively correlated with primary production, total salp biomass was positively correlated with the North Pacific Gyre Oscillation, and *T. democratica* biomass was negatively correlated with the Pacific Decadal Oscillation. These salp bloom dynamics have important implications for planktonic food web interactions and biogeochemical cycling.

**KEY WORDS:** Salps · Thaliacea · Jellyfish blooms · Gelatinous zooplankton · Mesoscale eddies · *Thalia democratica* · Sargasso Sea · Atlantic Ocean

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## INTRODUCTION

Salps are gelatinous, planktonic tunicates with a life history alternating between sexual and asexual stages, enabling them to rapidly replicate, forming high-density blooms when conditions are favorable (Godeaux et al. 1998). Salps are known to form large blooms in many regions of the world's oceans, including the Sargasso Sea (Madin et al. 1996, 2001, Roman et al. 2002), Mediterranean Sea (Ménard et al. 1994), Southern Ocean (Atkinson et al. 2004, Loeb & Santora 2012), western Tasman Sea (Everett et al. 2011), southwestern Atlantic (Daponte et al. 2011), and Hauraki Gulf (Zeldis et al. 1995). Salps can feed efficiently

on small phytoplankton and bacteria (Bone et al. 2003), have some of the highest clearance rates of any zooplankton—up to several liters h<sup>-1</sup> salp<sup>-1</sup> (Harbison & McAlister 1979, Madin & Purcell 1992, Madin & Kremer 1995), and can consume over 100% of the daily primary production (PP) (Hereu et al. 2006). These high clearance rates contribute to production by salps of large, fast-sinking fecal pellets (Caron et al. 1989, Sutherland et al. 2010b), with sinking rates ranging from 42 to 2700 m d<sup>-1</sup> (Andersen 1998, Yoon et al. 2001, Phillips et al. 2009). Because of their high fecal pellet production rates, salp blooms have a significant effect on particle export (Madin 1982, Caron et al. 1989). This, coupled with sinking of dead car-

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cases (Lebrato & Jones 2009, Henschke et al. 2013, Lebrato et al. 2013), represents a fast and efficient pathway for organic matter in the surface waters to move to depth. During a salp bloom, salps can thus be major contributors to the total carbon flux from the surface to the deep sea, as demonstrated in the Mediterranean Sea (Yoon et al. 1996, Fernex et al. 1996), Sargasso Sea (Conte et al. 2001), Southern Ocean (Phillips et al. 2009), and Tasman Sea (Henschke et al. 2013).

Salp populations are sensitive to interannual or longer-term changes in the environment (Ménard et al. 1994, Licandro et al. 2006). A long-term decrease in pelagic tunicates, particularly salps, in the California Current is attributed to a long-term increase in water column density stratification, which has weakened the eddy kinetics of the region as well as the southward flow of water and the seeding populations of salps within it (Lavaniegos & Ohman 2007). Salp populations in some regions of the Southern Ocean have been increasing in abundance and expanding their range (Atkinson et al. 2004) as a result of long-term warming and decreases in sea ice (Vaughan et al. 2003, Stammerjohn et al. 2012). Variability in the Southern Ocean Antarctic Circumpolar Current Front causes fluctuations in salp abundance off the western Antarctic Peninsula (Loeb et al. 2010). Ménard et al. (1994) and Sutherland et al. (2010a) found salp abundance in the Mediterranean Sea declined in response to increases in temperature and stratification of the water column, which decreased mixing of nutrients to the surface and PP. Likewise, salp, doliolid, and pyrosome abundance in the South China Sea increased with an increase in chlorophyll *a* (chl *a*) concentration caused by coastal upwelling and injection of nutrients into surface waters by cold-core eddies in the summer (Li et al. 2011). While previous studies help us to understand salp population dynamics in coastal upwelling and continental shelf regions, very little is known about how salps respond to environmental changes in the open ocean.

The Sargasso Sea is an oligotrophic, open-ocean region of the western North Atlantic subtropical gyre, with patterns in the biogeochemistry of the region influenced by physical forcing with ties to decadal-scale climate oscillations (Saba et al. 2010, Álvarez-García et al. 2011, Wu et al. 2011). Long-term changes in regional biogeochemistry of the Sargasso Sea have been documented, including: an increase in net primary productivity correlated with the North Atlantic Oscillation (NAO) (Saba et al. 2010), increases in both shallow-water particulate organic carbon export and mesopelagic zone particle attenuation in the winter–spring period (Lomas et al.

2010), and an increase in epipelagic mesozooplankton biomass (Steinberg et al. 2012). Mesoscale eddies are an important physical feature in the Sargasso Sea also affecting ecosystem structure and biogeochemical cycling. Cyclonic (cold-core) eddies are an important periodic source of nutrient injection into the euphotic zone stimulating new PP (McGillicuddy et al. 1998, 2007), leading to changes in zooplankton community structure (Eden et al. 2009) as well as an increase in mesozooplankton biomass, enhanced fecal pellet flux, and increased carbon export by diel vertical migration (DVM) (Goldthwait & Steinberg 2008). The goals of this study are to examine seasonal, interannual, and decadal patterns in the abundance of salp species in the Sargasso Sea and to determine the physical or biogeochemical conditions that lead to these patterns.

## MATERIALS AND METHODS

### Salp collection

Mesozooplankton were collected as part of the Bermuda Atlantic Time-series Study (BATS) in the oligotrophic North Atlantic subtropical gyre (31° 40' N, 64° 10' W) (Madin et al. 2001, Steinberg et al. 2012). We identified and enumerated salps from 17 yr of the time series. Overall, 776 tows were analyzed from 238 cruises from April 6, 1994 to November 11, 2011. Mesozooplankton tows were conducted using a net with a 0.8 × 1.2 m rectangular mouth and 202 µm mesh, with replicate, double-oblique tows made during day (09:00–15:00 h) and night (20:00–02:00 h) each month (May–January) or biweekly (February–April) (Madin et al. 2001, Steinberg et al. 2012). Targeted net depth was between 150 and 200 m, and actual depth was recorded using a Vemco Minilog recorder with the exception of the first year, when depth was estimated by wire out and wire angle. Volume filtered was measured using a General Oceanics flowmeter. Tow contents were immediately split on board with one half-split size-fractionated for total mesozooplankton biomass measurements, and the other half-split preserved in 4% buffered formaldehyde for taxonomic analysis (Madin et al. 2001, Steinberg et al. 2012).

### Salp enumeration and biomass determination

Salps were analyzed from archived, preserved samples using an Olympus SZX-10 dissecting

microscope at 6–10× magnification under dark and bright field illumination. Salps from the entire half-split or quarter-split were identified to species and enumerated, and the oral–atrial length of each salp was measured. Samples in which small salps (e.g. *Thalia democratica*) were very abundant (>2000 salps per tow) were subsampled using a 10 ml Stempel pipette (2.5 cm in diameter) after removal of any large salps. This subsample, and all large salps, were enumerated. At least 40 individuals of small salps, and all large salps, were measured to determine average length. Individual salp length was measured as the oral–atrial distance using an ocular micrometer, and these lengths were used in published salp live length to carbon weight regression equations for each species to calculate salp carbon biomass (see Table 5.3 in Madin & Deibel 1998, and references therein). Total length of salps preserved in formaldehyde has been shown to decrease over time (Heron et al. 1988, Nishikawa & Terazaki 1996). However, because this animal shrinkage is minimal and our preservation times varied, we did not correct salp length; thus, our carbon biomass estimates may be conservative. Salp data are presented as total salps, *T. democratica*, *Salpa fusiformis*, *Weelia (Salpa) cylindrica*, or *Cyclosalpa polae* abundance (density; ind. m<sup>-3</sup>) or carbon biomass (mg C m<sup>-3</sup>).

### Comparison to environmental parameters and data analysis

We examined potential environmental and climatological parameters influencing salp species abundance and biomass. For these analyses, salp biomass data for total salps and the 4 most abundant species on each sampling date were averaged between replicate tows and then between night and day. Average biomass for each sampling date was then compared to environmental data extracted from the BATS website (<http://bats.bios.edu/>) including sea-surface temperature (SST), water potential density, chl *a* integrated to 140 m, and PP integrated to 140 m (Knap et al. 1997, Steinberg et al. 2001). The water-column stratification index (WCSI) was calculated as the difference in potential density between the surface and 200 m (Steinberg et al. 2012). Salp abundance was compared to the 12 mo centered moving average of the NAO ([www.cpc.noaa.gov/products/precip/CWlink/pna/nao/shtml](http://www.cpc.noaa.gov/products/precip/CWlink/pna/nao/shtml)), Multivariate El Niño Southern Oscillation (MEI) ([www.esrl.noaa.gov/psd/people/](http://www.esrl.noaa.gov/psd/people/)

klaus.wolter/MEI/), North Pacific Gyre Oscillation (NPGO) (<http://eros/eas/gatech.edu/npgo/>), and Pacific Decadal Oscillation (PDO) (<http://jisao.washington.edu/pdo/>) indices as described in Steinberg et al. (2012). Salp biomass anomaly was calculated for each month using the following formula:

$$A'_m = \log_{10} \left[ \frac{\bar{A}_m}{\bar{A}_i} \right]$$

where  $\bar{A}_m$  is the average biomass for year/month  $m$ , and  $\bar{A}_i$  is the climatological median biomass for calendar month  $i$ . Annual biomass anomalies were then calculated as the average of  $A'_m$  for each year (Steinberg et al. 2012) and included total salps, *T. democratica*, *S. fusiformis*, and total salps minus *T. democratica* and *S. fusiformis*.

The Spearman rank correlation coefficient was used to compare salp abundance and biomass with environmental parameters, climate indices, and date to analyze seasonal and long-term changes. Monthly time series from April 1994 to November 2011 were constructed, with one observation per month, by averaging within months that contained more than one observation. Months with missing data ( $n = 13$  out of 212) were assigned the median measured value of that calendar month, and the smallest non-zero observation for each species was added to all observations to eliminate zeroes. The time-series data were then natural-log transformed. After constructing the time series, each species and environmental data set was decomposed into its long-term trend (12 mo moving average), seasonal component (average of each calendar month after removing the long-term trend), and noise component (the remainder after removing both the long-term trend and seasonal component) using the time-series (ts) and decompose functions in R 2.13.0. The Spearman rank correlation coefficients were then calculated by comparing the extracted long-term trends of each variable, and the effective degrees of freedom used in calculating significance were adjusted for autocorrelation using Eq. (1) in Pyper & Peterman (1998). In order to better examine the synergistic effects of different environmental variables on salp populations, correlations of seasonal and long-term trends were also compared using principal component analysis (PCA) in JMP 11.0.0. Bloom seasonality was analyzed by comparing the median bloom frequency between 2 seasonal periods within the year (e.g. February and March vs. the other 10 months of the year), and DVM was analyzed by comparing day and night salp abundance, both using the Mann-Whitney rank sum test.

### Mesoscale eddies

To examine the role that mesoscale eddies play in salp population dynamics, mesoscale eddy data in raw form were downloaded from the Cooperative Institute for Oceanographic Satellite Studies website (<http://cioss.coas.oregonstate.edu/eddies/>) (Chelton et al. 2011). This information included weekly eddy locations, rotation direction, amplitude, radius, and rotation speed. Using ESRI ArcGIS (version 10.0), we then determined which eddies were present at the BATS sampling location during tow sampling events. Only eddies with a total lifespan of 8 wk or more were used. As eddy location was only given weekly, any eddy that overlapped the BATS sampling site within 110% of its circumference (our own estimate to include any eddy edge effect) within 6 d of the sampling date was considered present at the time of BATS sampling. The effect of eddy type and presence on salp biomass was evaluated using an ANOVA on ranks, the Bonferroni-Dunn test was used for pairwise comparisons, and correlations between salp biomass and eddy speed, amplitude, and radius were calculated using the Spearman rank correlation coefficient.

Additionally, eddy presence data were obtained from Mouriño-Carballido (2009), who determined eddy presence and type from 1993 to 2002 using both satellite altimetry and BATS hydrographic profiles. Mouriño-Carballido (2009) categorized eddy influence on the BATS site as cyclonic, anticyclonic, mode-water, none, or the frontal region between cyclonic and anticyclonic eddies. For the purposes of our study, mode-water and anticyclonic eddies were combined into one 'anticyclonic' category, and frontal regions were delineated as no eddy present. A separate analysis was completed with these categorizations over the shorter time period, using an ANOVA on ranks to determine eddy influence on salp biomass.

## RESULTS

### Species composition and seasonality

In total, 21 species of salps were identified in the time series, with *Thalia democratica*, *Salpa fusiformis*, *Weelia* (*Salpa*) *cylindrica*, and *Cyclosalpa polae* being the most common species (present

in tows from 77, 61, 21, and 16% of the 238 monthly cruises, respectively) (Fig. 1, Table 1). *Thalia democratica* was the most abundant salp species and had the highest biomass, with average abundance across all samples of the time series in day and night tows of 3.31 and 1.90 ind. m<sup>-3</sup>, respectively, and biomass of 40.8 and 30.2 µg C m<sup>-3</sup>, respectively. This was considerably higher than the second-most abundant and highest-biomass species, *S. fusiformis*, with an average abundance in day and night tows of 1.86 × 10<sup>-3</sup> and 2.56 × 10<sup>-2</sup> ind. m<sup>-3</sup>, respectively, and a biomass of 0.21 (day) and 3.39 (night) µg C m<sup>-3</sup> (Table 1). Total salp abundance and biomass was influenced mainly by *T. democratica*, although the other 20 species contributed relatively more to total biomass than abundance (Table 1), as *T. democratica* is one of the smallest salps in the region. Qualitatively, salps were highest in biomass during the spring (February–April) throughout the entire time series, with both early and late summer peaks (July–August) as well, particularly from 1999 to 2003 (Fig. 2).

Salp 'blooms' were defined as the top 10% of biomass observations within all non-zero observations for each species. The species analyzed for blooms were *T. democratica*, *S. fusiformis*, *W. cylindrica*, and *C. polae*. All of the bloom events were more than one order of magnitude greater than the median (*T. democratica* and *S. fusiformis*) or mean (*W. cylindrica* and *C. polae*; median was zero) biomass.

Salp blooms occurred regularly, with blooms of *T. democratica*, *S. fusiformis*, and *C. polae* occurring

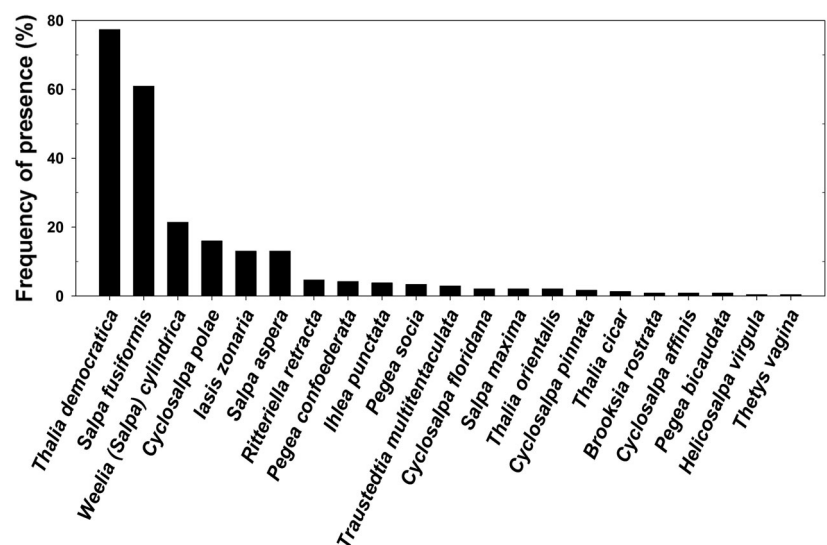


Fig. 1. Frequency of presence (as %) of each salp species in monthly cruises (n = 238). A total of 776 tows were analyzed from all cruises between April 1994 and November 2011

Table 1. Day (n = 227) and night (n = 222) biomass and abundance (mean  $\pm$  SD) for each salp species in the epipelagic zone at the Bermuda Atlantic Time-series Study (BATS) site. Mean and maximum day and night biomass and abundance are given for each species for the entire 17 yr time series. Species are listed in decreasing order of frequency of presence (see Fig. 1). See 'Materials and methods' for biomass calculations

Species	Abundance (ind. m <sup>-3</sup> )				Biomass ( $\mu$ g C m <sup>-3</sup> )			
	Day mean	Night mean	Day max.	Night max.	Day mean	Night mean	Day max.	Night max.
Total salps	3.32 $\pm$ 25.5	1.95 $\pm$ 17.5	281	221	43.1 $\pm$ 361	41.5 $\pm$ 245	4470	2630
<i>Thalia democratica</i>	3.31 $\pm$ 25.5	1.90 $\pm$ 17.5	281	221	40.8 $\pm$ 361	30.2 $\pm$ 245	4470	2630
<i>Salpa fusiformis</i>	1.86 $\pm$ 7.35 $\times 10^{-3}$	2.56 $\pm$ 7.11 $\times 10^{-2}$	0.073	0.962	0.211 $\pm$ 1.24	3.39 $\pm$ 13.6	14.1	178
<i>Weelia (Salpa) cylindrica</i>	3.44 $\pm$ 14.4 $\times 10^{-3}$	6.32 $\pm$ 30.9 $\times 10^{-3}$	0.133	0.293	0.245 $\pm$ 1.10	0.587 $\pm$ 4.40	8.45	62.6
<i>Cyclosalpa polae</i>	7.52 $\pm$ 34.3 $\times 10^{-4}$	2.98 $\pm$ 17.6 $\times 10^{-3}$	0.033	0.186	0.150 $\pm$ 0.810	0.240 $\pm$ 1.11	6.72	11.6
<i>Iasis zonaria</i>	1.37 $\pm$ 10.9 $\times 10^{-4}$	2.01 $\pm$ 7.09 $\times 10^{-3}$	0.012	0.061	0.070 $\pm$ 0.934	1.22 $\pm$ 5.23	14.0	60.6
<i>Salpa aspera</i>	4.24 $\pm$ 40.1 $\times 10^{-4}$	1.41 $\pm$ 10.3 $\times 10^{-2}$	0.054	1.44	0.034 $\pm$ 0.347	3.77 $\pm$ 15.4	4.07	136
<i>Ritteriella retracta</i>	6.09 $\pm$ 64.9 $\times 10^{-5}$	1.03 $\pm$ 7.67 $\times 10^{-3}$	0.007	0.098	0.057 $\pm$ 0.836	0.202 $\pm$ 1.29	12.6	12.6
<i>Pegea confoederata</i>	1.23 $\pm$ 11.7 $\times 10^{-3}$	1.69 $\pm$ 17.5 $\times 10^{-3}$	0.143	0.239	0.298 $\pm$ 3.11	0.242 $\pm$ 2.53	44.4	35.8
<i>Ihleia punctata</i>	4.04 $\pm$ 41.2 $\times 10^{-4}$	8.05 $\pm$ 62.3 $\times 10^{-4}$	0.053	0.071	0.035 $\pm$ 0.396	0.134 $\pm$ 1.02	5.69	12.6
<i>Pegea socia</i>	8.34 $\pm$ 83.3 $\times 10^{-4}$	2.57 $\pm$ 20.7 $\times 10^{-4}$	0.114	0.023	1.10 $\pm$ 14.1	0.148 $\pm$ 1.64	210	23.7
<i>Traustedtia multitentaculata</i>	1.84 $\pm$ 13.6 $\times 10^{-4}$	2.53 $\pm$ 27.8 $\times 10^{-4}$	0.015	0.040	0.019 $\pm$ 0.232	0.017 $\pm$ 0.200	3.45	2.90
<i>Cyclosalpa floridana</i>	8.50 $\pm$ 98.4 $\times 10^{-5}$	2.22 $\pm$ 16.9 $\times 10^{-4}$	0.014	0.016	0.002 $\pm$ 0.017	0.003 $\pm$ 0.027	0.22	0.34
<i>Salpa maxima</i>	6.42 $\pm$ 70.3 $\times 10^{-5}$	4.72 $\pm$ 69.2 $\times 10^{-3}$	0.009	1.03	0.005 $\pm$ 0.055	1.20 $\pm$ 16.7	0.78	249
<i>Thalia orientalis</i>	6.02 $\pm$ 61.3 $\times 10^{-4}$	3.22 $\pm$ 34.6 $\times 10^{-4}$	0.083	0.047	0.013 $\pm$ 0.124	0.008 $\pm$ 0.092	1.45	1.35
<i>Cyclosalpa pinnata</i>	8.32 $\pm$ 73.7 $\times 10^{-5}$	2.63 $\pm$ 39.2 $\times 10^{-5}$	0.008	0.006	0.017 $\pm$ 0.199	0.008 $\pm$ 0.120	2.93	1.79
<i>Thalia cicar</i>	2.29 $\pm$ 34.5 $\times 10^{-5}$	7.04 $\pm$ 75.2 $\times 10^{-5}$	0.005	0.009	0.001 $\pm$ 0.018	0.001 $\pm$ 0.020	0.27	0.30
<i>Brooksia rostrata</i>	3.16 $\pm$ 47.6 $\times 10^{-5}$	6.32 $\pm$ 94.1 $\times 10^{-5}$	0.007	0.014	0.000	0.014 $\pm$ 0.215	0.07	3.20
<i>Cyclosalpa affinis</i>	1.96 $\pm$ 29.6 $\times 10^{-4}$	2.86 $\pm$ 42.6 $\times 10^{-5}$	0.045	0.006	0.001 $\pm$ 0.009	0.003 $\pm$ 0.050	0.14	0.75
<i>Pegea bicaudata</i>	2.48 $\pm$ 37.4 $\times 10^{-5}$	5.33 $\pm$ 79.4 $\times 10^{-4}$	0.006	0.118	0.002 $\pm$ 0.028	0.061 $\pm$ 0.907	0.42	13.5
<i>Helicosalpa virgula</i>	0.00	1.64 $\pm$ 24.4 $\times 10^{-5}$	0.000	0.004	0.000	0.001 $\pm$ 0.016	0.00	0.24
<i>Thetyis vagina</i>	0.00	1.83 $\pm$ 27.3 $\times 10^{-5}$	0.000	0.004	0.000	0.015 $\pm$ 0.222	0.00	3.31

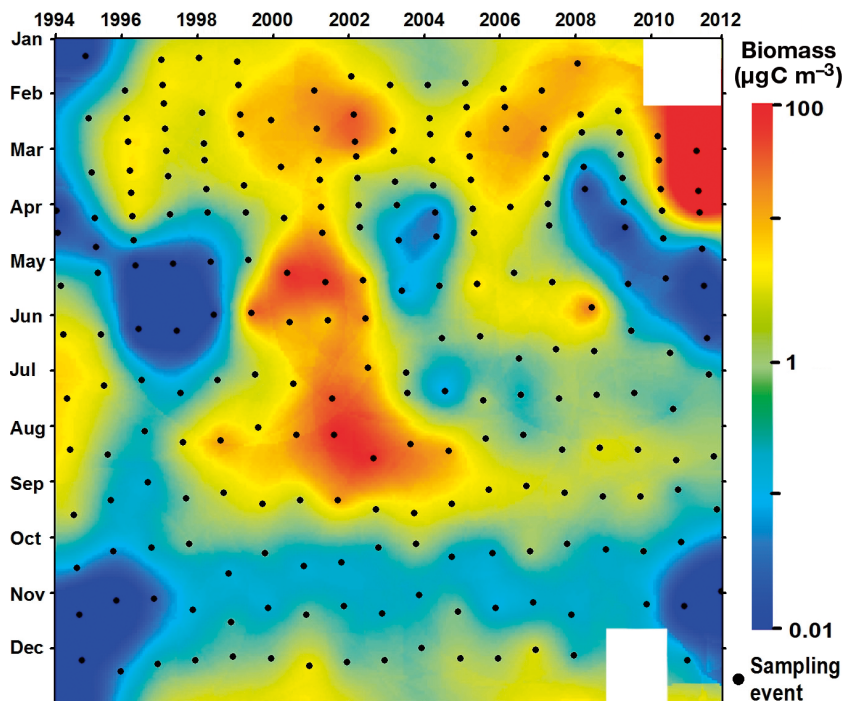


Fig. 2. Seasonal and interannual total salp biomass at the Bermuda Atlantic Time-series Study (BATS) site. Total combined (all species) salp biomass across the time series (April 1994–November 2011). Note that biomass is depicted on a log scale and areas with low temporal coverage have been whited-out

more often in February and March, with a median total of 5.5, 4, and 1 bloom, respectively, in each of those months over the time series (Fig. 3A). The occurrence of blooms in those 2 months was significantly higher than the median occurrence in the other 10 months of the year ( $p < 0.05$ ; Mann-Whitney rank sum test). *W. cylindrica* blooms occurred more commonly in late summer (median total of 1 bloom in each of July, August, and September) compared with the rest of the year ( $p = 0.002$ ). Blooms in all other species combined were evenly distributed throughout the year. Monthly averages of salp biomass with the long-term trend removed showed similar seasonal patterns with *T. democratica*, *S. fusiformis*, and *C. polae* peaking in the spring, *W. cylindrica* peaking in late summer, and all others remaining relatively constant throughout the year (Fig. 3B).

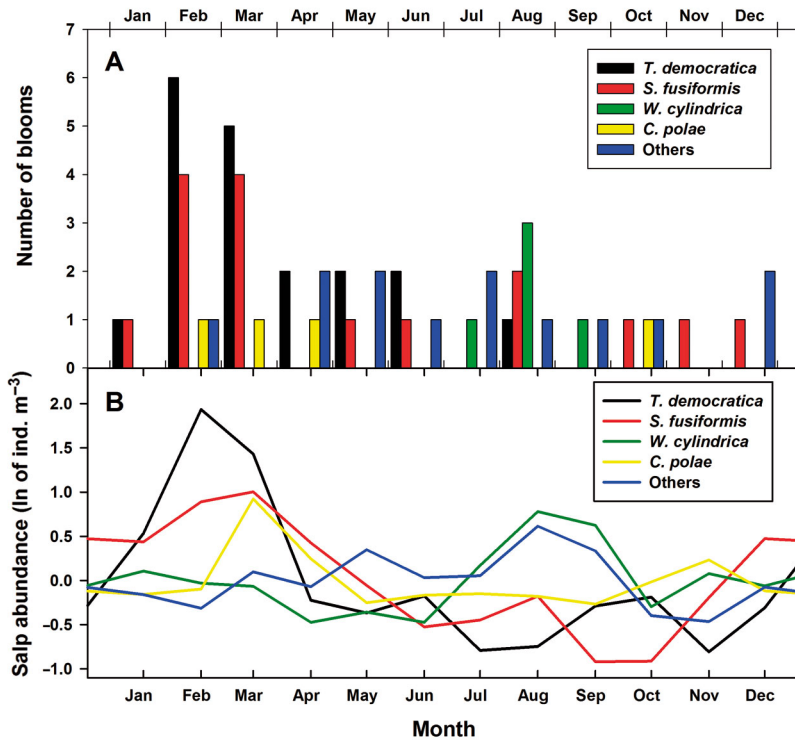


Fig. 3. Monthly distribution of (A) salp blooms and (B) average monthly abundance after removal of the long-term trend. Shown are the sums of all blooms in each month for the 4 most abundant species—*Thalia democratica*, *Salpa fusiformis*, *Weelia (Salpa) cylindrica*, and *Cyclosalpa polae*, and all other salps combined over the entire time series (April 1994–November 2011)

**Diel vertical migration**

Of the 21 salp species present, 5 exhibited a detectable pattern of DVM, with significantly higher median biomass during the night than during the day (Fig. 4). These diel vertical migrators included 2 species of *Salpa* (*S. fusiformis*,  $n = 136$ ,  $p < 0.001$ ; *S. aspera*,  $n = 30$ ,  $p < 0.001$ ), *W. cylindrica* ( $n = 48$ ,  $p = 0.030$ ), *Iasis zonaria* ( $n = 31$ ,  $p < 0.001$ ), and *Ritteriella retracta* ( $n = 11$ ,  $p = 0.002$ ). Overall, *T. democratica* did not demonstrate DVM (Fig. 4), with day median biomass ( $0.342 \mu\text{g C m}^{-3}$ ) not significantly different from night median biomass ( $0.362 \mu\text{g C m}^{-3}$ ;  $n = 165$ ,  $p = 0.899$ ). When at bloom concentrations, we did detect day–night differences in *T. democratica*, with 6 blooms (out of 33) having at least 2-fold higher biomass in surface

waters at night compared to during the day, but also 12 blooms with at least 2-fold higher biomass in the surface waters during the day than at night. For most other species, presence in tows was too infrequent or biomass likely too low for a significant difference between day and night to be detected.

**Mesoscale eddies**

A total of 56 mesoscale eddies were detected intersecting the BATS site within 6 d of a zooplankton sampling event from April 1994 to November 2011, using the Chelton and Schlax eddy data set. Of these 56 eddies, 38 were cyclonic and 18 were anticyclonic; there was no significant difference between the median amplitude, speed, and radius of the 2 eddy types (Table 2). When comparing median abundance of *T. democratica* between cyclonic, anticyclonic, and no eddies, there was a significant difference between treatments ( $p = 0.017$ ), but there were no significant differences in pairwise comparisons. However, the median biomass of *T. democ-*

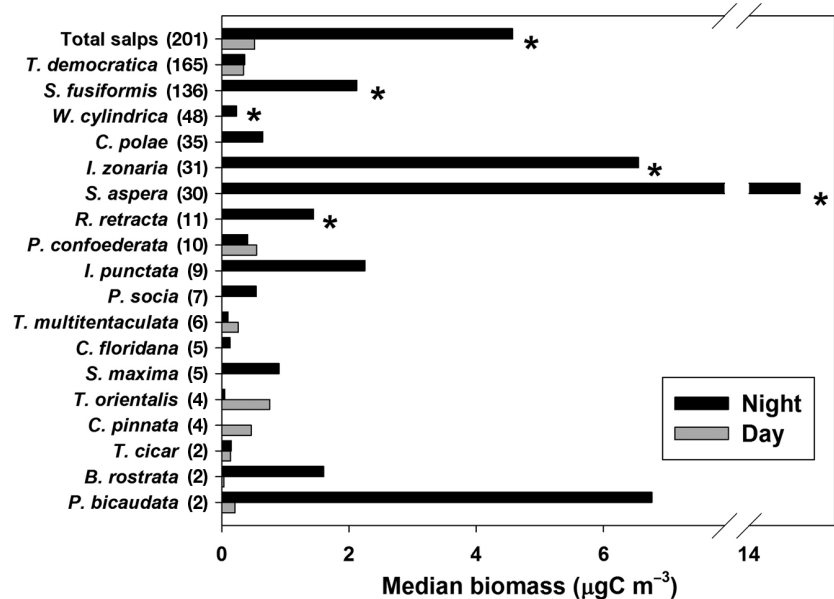


Fig. 4. Salp diel vertical migration. Day and night median biomass of total salps and 18 species of salps at the Bermuda Atlantic Time-series Study (BATS) site across the time series (April 1994–November 2011). Day and night biomasses that are significantly different (i.e. the species demonstrates diel vertical migration) are marked with an asterisk; the number of day–night observation pairs for each species is in parentheses. Full species names given in Fig. 1

*ratuca* was significantly higher within cyclonic eddies ( $0.609 \mu\text{g C m}^{-3}$ ) than within anticyclonic eddies ( $0.129 \mu\text{g C m}^{-3}$ ; Fig. 5). Within the 38 cyclonic eddies, *T. democratica* biomass was not significantly correlated with eddy rotational speed or amplitude. No significant relationships between other salp species and eddy presence, type, or attributes were found.

Table 2. Mean ( $\pm$ SD) and range for the amplitude, rotation speed, and radius of the 56 mesoscale eddies that passed through the Bermuda Atlantic Time-series Study (BATS) site within 6 d of a zooplankton sampling event. Eddies were considered to have passed through the BATS site if 110% of their circumference encompassed the BATS site. Eddy data were collected from the online database <http://cioss.coas.oregonstate.edu/eddies/> (Chelton et al. 2011)

	Cyclonic	Anticyclonic
Number	38	18
Mean amplitude (cm)	$8.0 \pm 4.4$	$8.1 \pm 2.8$
Amplitude range (cm)	1.2–16.5	4.2–14.2
Mean rotational speed ( $\text{cm s}^{-1}$ )	$17.0 \pm 6.4$	$17.5 \pm 3.8$
Rotational speed range ( $\text{cm s}^{-1}$ )	7.1–33.9	13.1–26.6
Mean radius (km)	$96 \pm 22.2$	$104 \pm 29.5$
Radius range (km)	54–148	66–159

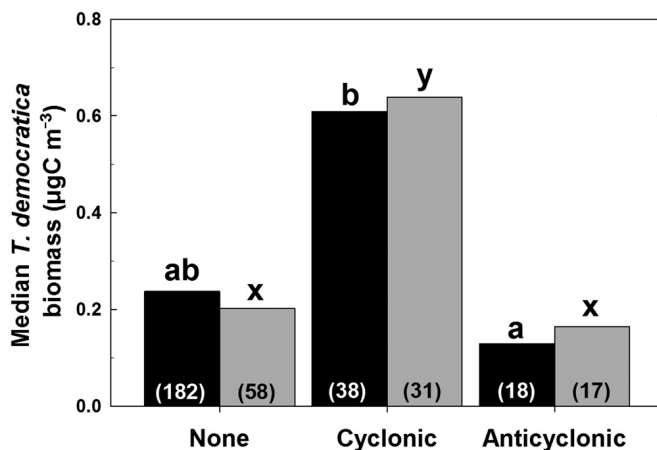


Fig. 5. Median biomass of *Thalia democratica* within cyclonic and anticyclonic eddies, and when no eddies are present, at the Bermuda Atlantic Time-series Study (BATS) site. Black bars represent salp median biomass for eddies from the Chelton and Schlax database (<http://cioss.coas.oregonstate.edu/eddies/>) that encompassed the BATS site within 110% of their circumference within 6 d of a zooplankton sampling event and represents our entire salp time series (April 1994–November 2011). Gray bars represent salp median biomass for eddies listed in Mouriño-Carballido (2009) that influenced BATS from April 1994 to December 2001. Numbers in parentheses indicate the number of eddy-influenced samples within each category. Bars with different letters are significantly different (Bonferroni-Dunn test,  $p < 0.05$ ) from other bars within that database ('a' and 'b' for Chelton and Schlax, and 'x' and 'y' for Mouriño-Carballido)

Using the Mouriño-Carballido (2009) eddy determinations, a total of 48 sampling events between April 1994 and December 2001 were eddy influenced, with 31 cyclonic eddies and 17 anticyclonic eddies. The median biomass of *T. democratica* was significantly higher within cyclonic eddies ( $0.638 \mu\text{g C m}^{-3}$ ) than within anticyclonic eddies ( $0.165 \mu\text{g C m}^{-3}$ ) or in the absence of eddies ( $0.202 \mu\text{g C m}^{-3}$ ; Fig. 5). No significant relationships between other salp species and eddy presence or type were found.

### Long-term trends

There was no significant long-term positive or negative trend in total salp biomass over the 17 yr time series; however, over the time series there were weak, but significant, increases in both *T. democratica* and *C. polae* biomass, and in WCSI (Fig. 6A, B, and C, respectively). The linear increase in WCSI is due to both a significant increase in SST and a coinciding decrease in temperature from 300 to 600 m depth ( $R^2 = 0.25$ ,  $p < 0.0001$ , for both) over the time series. The increases in salp biomass were log-linear and represented an increase of  $0.01 \mu\text{g C m}^{-3} \text{ yr}^{-1}$  for *T. democratica* and  $0.003 \mu\text{g C m}^{-3} \text{ yr}^{-1}$  for *C. polae*. Mean annual biomass anomalies for *T. democratica* (Fig. 7B) were consistently positive over the last 6 yr of the time series, and for *S. fusiformis* were strongly negative over the last 4 yr (Fig. 7C). Additionally, there was a distinct shift after 2000 ( $t = -3.413$ ,  $p = 0.004$ ) from consistently negative to positive anomalies in total salps other than *T. democratica* and *S. fusiformis* (Fig 7D).

Additionally, a cyclical pattern in *T. democratica* biomass was evident, with average annual biomass increasing by 3–7 orders of magnitude every 3 yr (Fig. 8). This cycle is supported by the spectral density of the *T. democratica* biomass long-term trend, which was highest in value at a period of 33.3 mo (Fig. 8, inset). This pattern is mostly driven by larger spring blooms of *T. democratica* during these peak years, but also by elevated biomass throughout the year, and occasional non-spring blooms.

### Environmental and climate influences

Total salp seasonality was most closely grouped with integrated PP in the PCA of seasonality in salps and environmental parameters (Fig. 9A). Additionally, *T. democratica* and *S. fusiformis* were closely grouped with PP and chl *a* concentrations. These 2 species were also seasonally negatively correlated

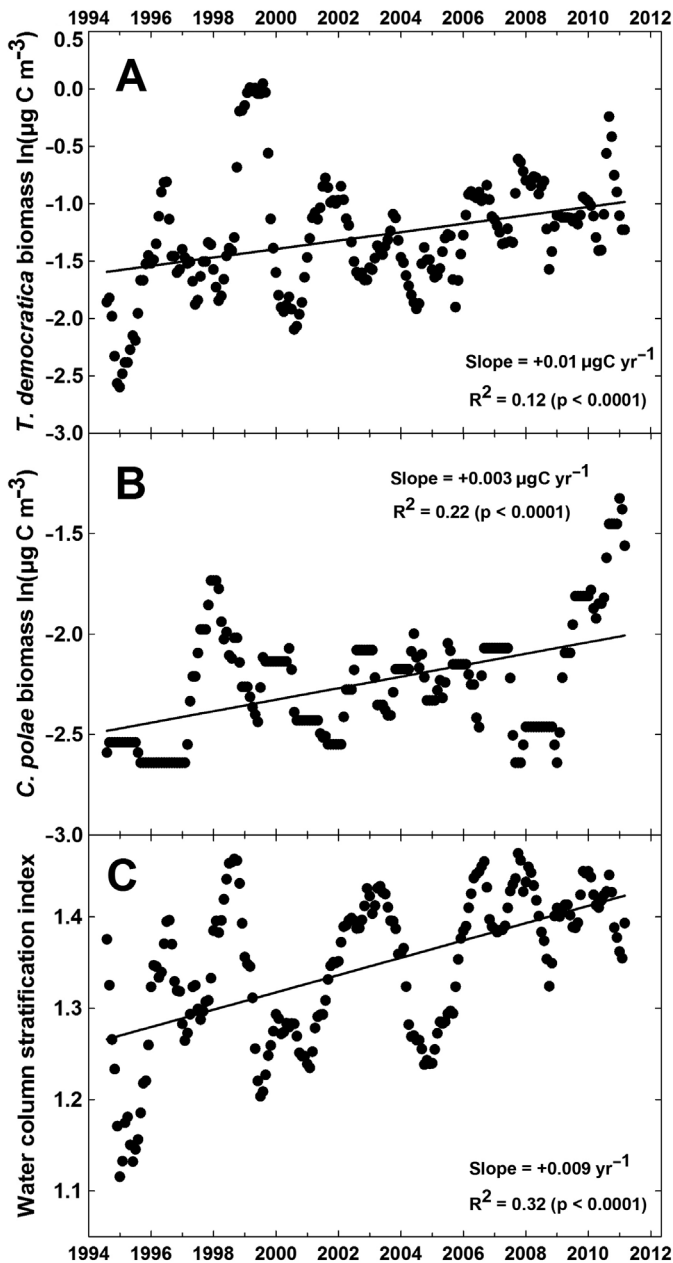


Fig. 6. Twelve month moving average of (A) *Thalia democratica* biomass, (B) *Cyclosalpa polae* biomass, and (C) the water column stratification index (WCSI) across the time series (October 1994–May 2011). Note the natural log scale for the salp biomass plots. All regressions are log-linear

with SST and the WCSI. *C. polae* was weakly negatively correlated with SST and the WCSI. *W. cylindrica* and all salps other than the 'top' (highest biomass) 4 species grouped together, and were most strongly, and negatively, correlated with 300–600 m water temperature, although this only explained a small portion of their variability.

Long-term trends in salp biomass were significantly correlated with several environmental parameters (Table 3, Fig. 9B). However, the variance explained by components 1 and 2 of the PCA (Fig. 9B) is low, suggesting a complex system poorly represented by the first 2 components alone. Both SST and the WCSI were positively correlated with *T. democratica* and *C. polae* biomass (Table 3). Additionally, *T. democratica* and *C. polae* were positively correlated with SST in the PCA (Fig. 9B). PP was negatively correlated with biomass of *S. fusiformis*, *C. polae*, and *W. cylindrica* (Table 3), but strongly positively correlated with total salp and *T. democratica* abundance (Table 3, Fig. 9B). Integrated chl *a* was negatively correlated with *W. cylindrica* and weakly so with biomass of less abundant salp species (Table 3). Chl *a* was positively correlated with *C. polae* biomass and abundance and *S. fusiformis* abundance (Table 3). Lower mesopelagic temperatures corresponded with higher biomass of total salps, *T. democratica*, *S. fusiformis*, *C. polae*, and other less abundant species (Table 3).

We compared the long-term trend of biomass of total salps, *T. democratica*, *S. fusiformis*, *W. cylindrica*, *C. polae*, and all other salp species combined with the 12 mo moving average of 4 decadal climate indices (Table 4, Fig. 10). Total salp biomass was most strongly, and positively, correlated with the NPGO (Fig. 10A). *T. democratica* was most strongly, and negatively, correlated with the PDO (Fig. 10B). *S. fusiformis* was significantly positively correlated with the PDO (Fig. 10C), while all other salps combined was most strongly positively correlated with the NPGO (Fig. 10D). Significant correlations between other salp species and climate indices can be found in Table 4.

## DISCUSSION

### Salp species composition and seasonality

We found a total of 21 species of salps present in the entire time series, compared to 16 species over 2 cruises in late summer and spring of 1989–1990 (Madin et al. 1996) and 20 species throughout the year in 1967–1972 (van Soest 1975) in the BATS region. Of the 25 salp species van Soest (1998) reported to occur throughout the northwestern Atlantic Ocean, only 4 species were not present at the BATS site: *Salpa younti*, *Brooksia bermeri*, *Cyclosalpa bakeri*, and *C. foxtoni*. The most common species at the BATS site were *Thalia democrat-*



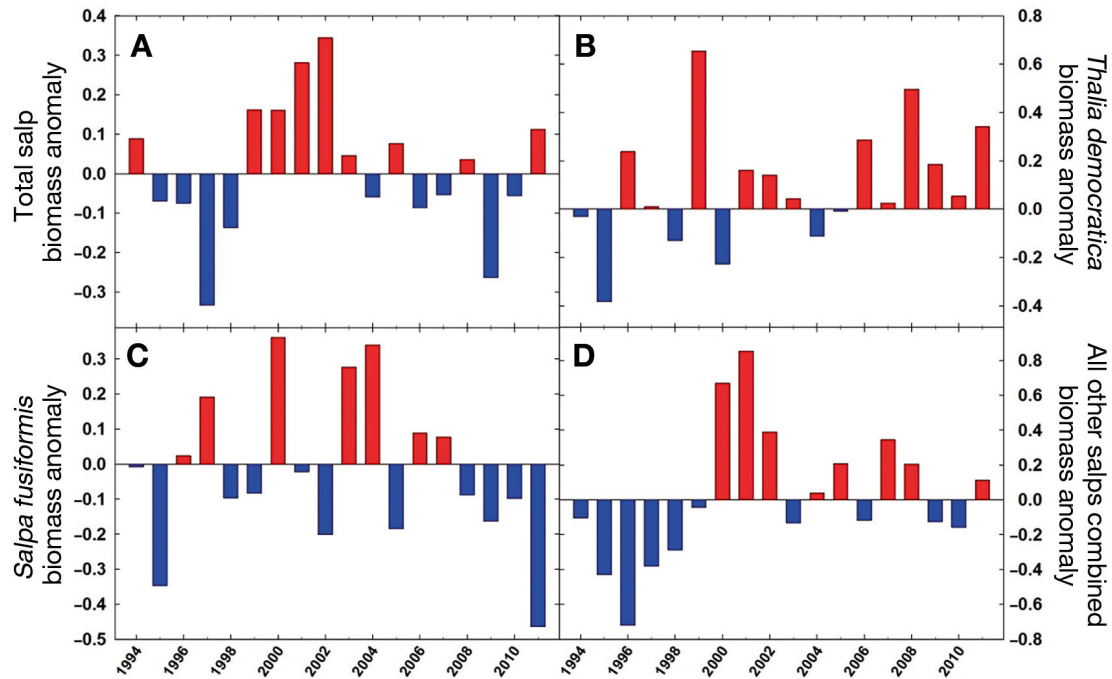


Fig. 7. Yearly average biomass anomaly for (A) total salps, (B) *Thalia democratica*, (C) *Salpa fusiformis*, and (D) total salps minus *T. democratica* and *S. fusiformis*. Red and blue bars indicate higher and lower biomass, respectively, for that year compared to the annual median of the whole time series

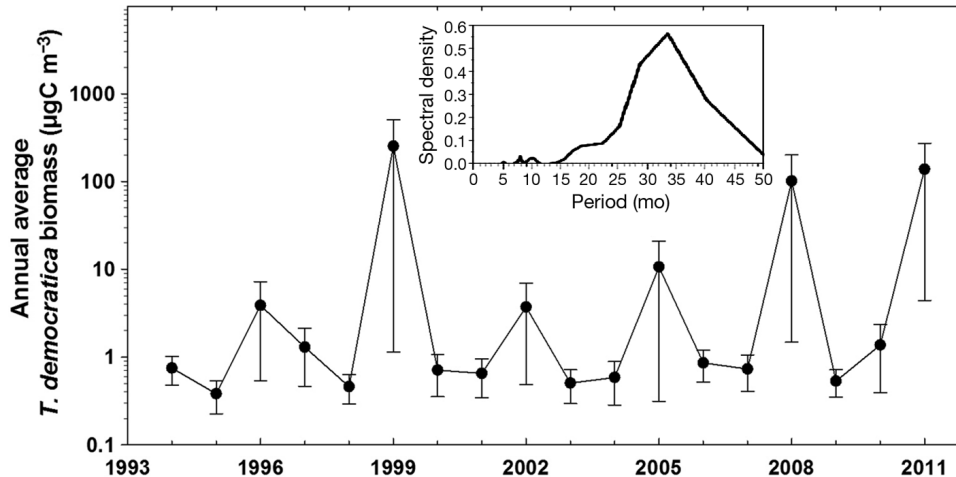


Fig. 8. Annual average biomass of *Thalia democratica*. Monthly averages were calculated first to avoid bias towards the more frequently sampled spring period, and the median monthly value of each month was used for missing data points. Error bars represent standard error. Note natural log scale and the cycle of higher average biomass every 3 yr. Inset is the calculated spectral density of the monthly time series 12 mo moving average showing the most significant periodicity

*ica* and *S. fusiformis*, with other species such as *Weelia (Salpa) cylindrica*, *C. polae*, *Iasis zonaria*, and *S. aspera* seasonally abundant. While van Soest (1975) and Madin et al. (1996) did not measure absolute abundance of salps, the relative abundances of species that they observed were similar to those we found. In the BATS time series, total salp

abundance reached as high as  $371 \text{ ind. m}^{-3}$  (during a *T. democratica* bloom), which is comparable to documented maxima of  $150 \text{ ind. m}^{-3}$  for the Bay of Bengal (Madhupratap et al. 1980),  $300 \text{ ind. m}^{-3}$  for the Agulhas Bank (Gibbons 1997), and  $100 \text{ ind. m}^{-3}$  in the South Atlantic Bight of the USA (Paffenhöfer & Lee 1987). However, this is lower than off south-

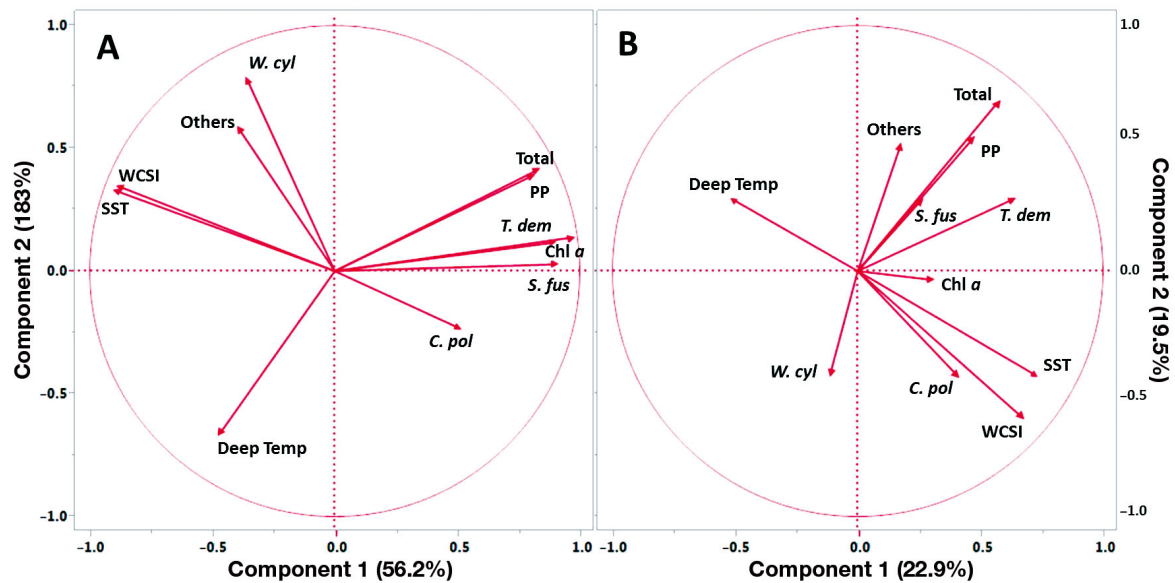


Fig. 9. Principal component analysis of salp biomass and environmental parameters for (A) seasonal averages after removing the long-term trend and (B) the long-term trend. Total: total salps; *T. dem*: *Thalia democratica*; *S. fus*: *Salpa fusiformis*; *C. pol*: *Cyclosalpa polae*; *W. cyl*: *Weelia (Salpa) cylindrica*; Others: all other salp biomass combined; PP: primary production integrated to 140 m; Chl *a*: chlorophyll *a* integrated to 140 m; WCSI: water column stratification index; SST: sea surface temperature; Deep Temp: mean temperature in mesopelagic zone from 300 to 600 m

east Australia, where abundance exceeded 2444 ind.  $m^{-3}$  for *T. democratica* in a bloom event within an eddy (Henschke et al. 2011). The second most common species, *S. fusiformis*, reached 0.96 ind.  $m^{-3}$ , which is comparable to a *S. fusiformis* maximum of 1.6 ind.  $m^{-3}$  in coastal Taiwan (Tew & Lo 2005) and 2 ind.  $m^{-3}$  in the Humboldt Current (González et al. 2000). But this is much lower than  $\sim 700$  *S. fusiformis* ind.  $m^{-3}$  found in the North Atlantic west of Ireland (Bathmann 1988) and 225 ind.  $m^{-3}$  off northwest Spain (Huskin et al. 2003).

There was a distinct seasonality in salp blooms, with 3 of the 4 most abundant species (*T. democratica*, *S. fusiformis*, and *C. polae*) blooming more commonly in February and March (spring), coinciding with the seasonal increase in primary production and chlorophyll biomass (Steinberg et al. 2001, Lomas et al. 2013). In contrast, *W. cylindrica* bloomed more frequently in late summer, suggesting that other processes are responsible for their rapid population increase. Similarly, Madin et al. (1996) found *W. cylindrica* present in August but absent in March and

Table 3. Spearman correlation coefficients for the 12 mo moving average of salp abundance (ind.  $m^{-3}$ ) and biomass ( $\mu g C m^{-3}$ ) versus environmental parameters. Not significant (NS);  $p \geq 0.05$ ;  $0.05 > p \geq 0.01$ ;  $0.01 > p \geq 0.001$ ;  $p < 0.001$

Species	Sea surface temperature	Water column stratification index	Temperature 300 to 600 m	Primary production integrated to 140 m	Chlorophyll <i>a</i> integrated to 140 m
Total salp abundance	NS	NS	NS	0.42***	NS
Total salp biomass	NS	NS	-0.23**	0.18*	NS
<i>Thalia democratica</i> abundance	NS	0.20*	-0.24**	0.32***	NS
<i>Thalia democratica</i> biomass	0.23**	0.48***	-0.43***	0.22**	NS
<i>Salpa fusiformis</i> abundance	NS	NS	-0.29***	NS	0.20*
<i>Salpa fusiformis</i> biomass	NS	NS	-0.36***	-0.19**	NS
<i>Weelia (Salpa) cylindrica</i> abundance	NS	NS	NS	-0.30***	-0.32***
<i>Weelia (Salpa) cylindrica</i> biomass	NS	NS	NS	-0.38**	-0.23***
<i>Cyclosalpa polae</i> abundance	0.34***	0.29***	NS	NS	0.20**
<i>Cyclosalpa polae</i> biomass	0.31***	0.30***	-0.16*	-0.16*	0.24***
Others combined abundance	NS	NS	NS	NS	NS
Others combined biomass	NS	NS	-0.19*	NS	-0.20*

Table 4. Spearman correlation coefficients for the 12 mo moving average of climate index anomalies versus the 12 mo moving average of salp biomass and abundance. MEI: Multivariate El Niño Southern Oscillation; NAO: North Atlantic Oscillation; NPGO: North Pacific Gyre Oscillation; PDO: Pacific Decadal Oscillation. Not significant (NS);  $p \geq 0.05$ ;  $*0.05 > p \geq 0.01$ ;  $**0.01 > p \geq 0.001$ ;  $***p < 0.001$

Species	MEI	NAO	NPGO	PDO
Total salp abundance	-0.40***	NS	0.55***	-0.37***
Total salp biomass	-0.22**	0.20**	0.57***	-0.45***
<i>Thalia democratica</i> abundance	-0.44***	NS	0.28***	-0.35***
<i>Thalia democratica</i> biomass	-0.44***	NS	0.40***	-0.54***
<i>Salpa fusiformis</i> abundance	NS	NS	NS	0.25**
<i>Salpa fusiformis</i> biomass	NS	NS	NS	0.27***
<i>Weelia (Salpa) cylindrica</i> abundance	NS	NS	NS	NS
<i>Weelia (Salpa) cylindrica</i> biomass	NS	NS	NS	NS
<i>Cyclosalpa polae</i> abundance	NS	-0.33***	0.26***	NS
<i>Cyclosalpa polae</i> biomass	NS	-0.32***	0.22**	NS
Others combined abundance	NS	0.25***	0.47***	-0.25**
Others combined biomass	NS	0.38***	0.46***	-0.27**

April, although van Soest (1975) found *W. cylindrica* present in low abundances year-round. Other salp species were more variable in their bloom seasonality and showed no overall trend.

### Environmental influences

Environmental parameters such as SST and water column stratification (which in turn influence mixing and PP) are important seasonal regulators of salp abundance at BATS. The BATS region is characterized by a spring phytoplankton bloom in January–March that follows a period of winter mixing (Steinberg et al. 2001). Abundance and biomass of 3 of the 4 most common species of salps at BATS (*T. democratica*, *S. fusiformis*, and *C. polae*) respond to this seasonal bottom-up forcing, as shown by the increase in their abundance with increasing chl *a* and PP, and the more frequent occurrence of blooms in early spring than at other times of the year. Correspondingly, seasonally lower SST and reduced stratification, typical of conditions at the onset of the spring bloom, result in higher abundance of these 3 salp species. This response of salps to the spring phytoplankton bloom is similar to that in other systems, including *T. democratica* off the southern Atlantic coast of the USA (Deibel & Paffenhöfer 2009) and in the Tasman Sea (Heron 1972), *S. fusiformis* off northwestern Spain (Huskin et al. 2003), and both *T. democratica* and *S. fusiformis* in the western Mediterranean Sea (Ménard et al. 1994). In some coastal systems, the correlation between chl *a* and salp abundance becomes negative at very high chl *a* concentrations (Zeldis et al. 1995, Liu et al.

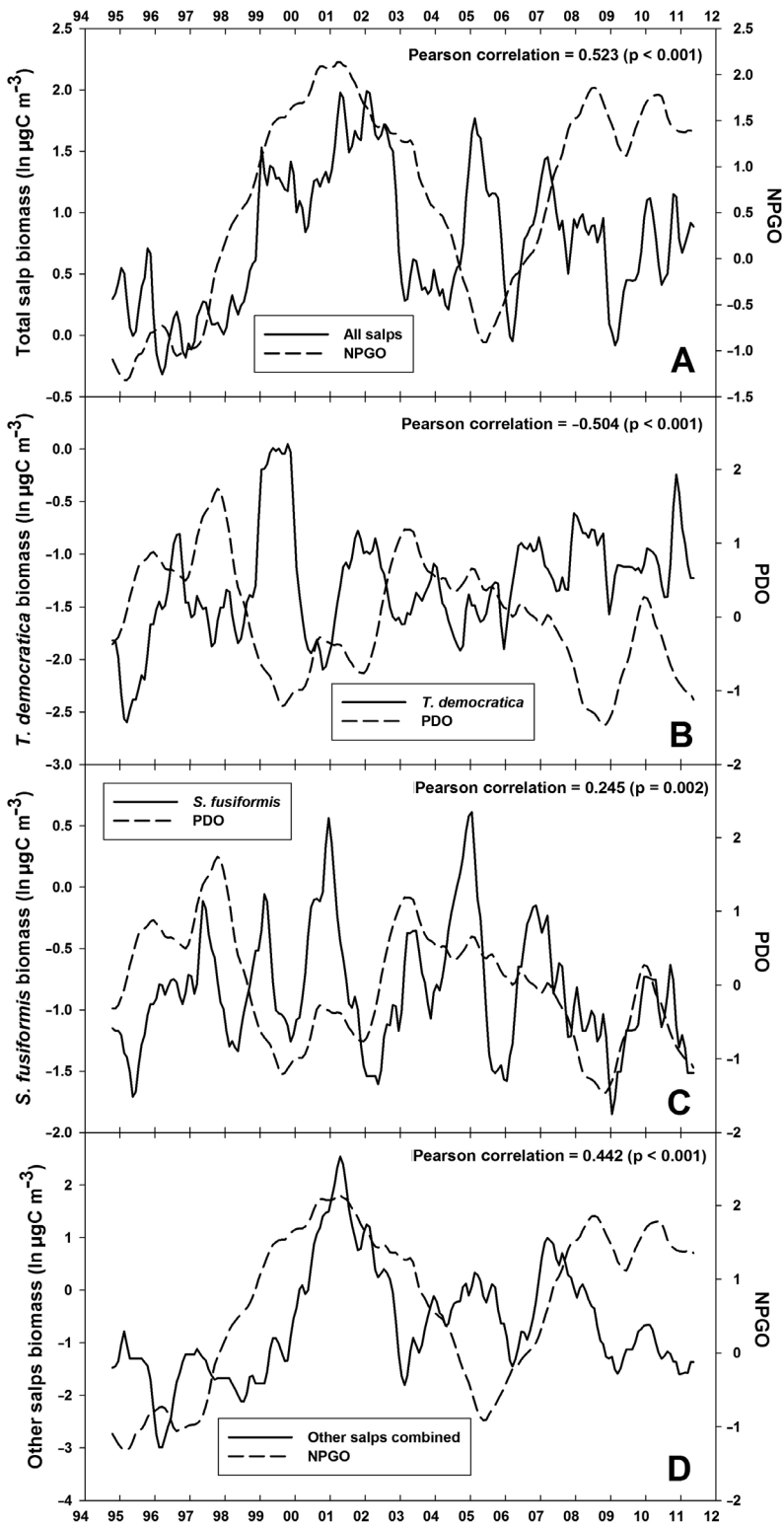
2012), presumably due to the clogging of the salp's mucous feeding net (i.e. at chl *a* concentrations  $>1 \mu\text{g l}^{-1}$ ; Harbison et al. 1986). However, phytoplankton biomass in the oligotrophic BATS region, typically ranging from 0 to  $0.8 \mu\text{g l}^{-1}$  (Steinberg et al. 2001, Lomas et al. 2013), rarely would approach the level required to negatively impact salp feeding.

In contrast to other salp species, *W. cylindrica* abundance was positively correlated with both SST and water column stratification, while it was not significantly correlated with chl *a*, and was most abundant during the late summer (July, August, and September). This difference in seasonal abundance may be due to *W. cylindrica*'s

apparent preference for warm tropical waters. *W. cylindrica* is not reported in waters colder than  $17^\circ\text{C}$  (van Soest 1975), and Harbison & Campenot (1979) experimentally determined that *W. cylindrica* stopped swimming at temperatures colder than  $\sim 5^\circ\text{C}$ . However, Harbison & Campenot (1979) also reported that *C. polae* demonstrated a response to cold temperatures similar to that of *W. cylindrica*. This is in contrast to our results, which indicate higher *C. polae* abundance in cool, high-phytoplankton-biomass conditions, suggesting that food availability has more influence than temperature on *C. polae* abundance.

### Diel vertical migration

Five species (*S. fusiformis*, *I. zonaria*, *S. aspera*, *Ritteriella retracta*, and *W. cylindrica*) exhibited clear DVM, with significantly higher night vs. day biomass in the top 150 m. Madin et al. (1996) also found DVM off Bermuda in *S. fusiformis*, *I. zonaria*, *S. aspera*, and *R. retracta*, but additionally in *Ihlela punctata*. In the slope waters of the NE USA, *S. aspera* also exhibited DVM (Madin et al. 2006). The most abundant vertically migrating species, *S. fusiformis*, was also negatively correlated with mesopelagic zone temperature (300–600 m), suggesting that warming of waters at typical daytime residence depths for vertical migrators in the region (e.g. Steinberg et al. 2000, 2012, Bianchi et al. 2013) could have a negative impact on *S. fusiformis* populations, such as increasing their metabolism at depth. While the most abundant species, *T. democratica*, did not exhibit DVM during times of average or low abundance, there was an



indication of DVM (both 'normal' and reverse) during different large *T. democratica* blooms. However, this is likely an artifact of horizontal movement of the salps rather than vertical, as extremely high abun-

Fig. 10. Salp biomass and climate index 12 mo moving average. Monthly salp biomass trend (solid line) is shown with the most strongly correlated monthly climate index trend (dashed line). (A) Total salps with North Pacific Gyre Oscillation (NPGO), (B) *Thalia democratica* and (C) *Salpa fusiformis* with Pacific Decadal Oscillation (PDO), and (D) total salps minus *T. democratica*, *S. fusiformis*, *Weelia* (*Salpa*) *cylindrica*, and *Cyclosalpa polae* with the NPGO. Correlations between salp trends and climate indices were tested using the Pearson correlation (see Table 3 for full results of analysis) for the period of the salp time series (October 1994–May 2011)

dances could amplify the patchiness of the bloom. This is supported by both 'normal' and reverse *T. democratica* DVM on different sampling days during individual blooms in both 1996 and 2011. Other studies in the Agulhas Bank (Gibbons 1997), off SW Taiwan (Tew & Lo 2005), and in the Kuroshio Current (Tsuda & Nemoto 1992) found that *T. democratica* did not exhibit DVM and generally stayed within the upper 200 m. Thus, we conclude that the diel differences we detected in *T. democratica* were likely due to bloom patchiness and that *T. democratica* likely does not undergo significant DVM.

### Mesoscale eddies

Mesoscale eddies can enhance nutrient upwelling and PP in the BATS region (McGillicuddy et al. 2007, Mouriño-Carballido 2009) as well as the oligotrophic North Pacific gyre (Landry et al. 2008). Eddy presence can also lead to increases in biomass and changes in the community composition of mesozooplankton (Goldthwait & Steinberg 2008, Eden et al. 2009). The only salp species that significantly changed in biomass in response to mesoscale eddies was *T. democratica*, which had elevated biomass in cyclonic eddies compared to the absence of eddies or anticyclonic eddies (Fig. 5). The first eddy data set we used (Chelton et al. 2011) does not distinguish between the 2 anticyclonic eddy types: anticyclonic eddies that are downwelling, and anticyclonic mode-water eddies with isopycnal displacement and upwelling. However, when using the Mouriño-Carballido (2009) data, which do distinguish these eddy types, we found no significant difference between *T. democratica* median biomass

between anticyclonic mode-water and anticyclonic eddies, although the low number of anticyclonic eddies (4) may be an insufficient sample size with which to detect a significant difference.

Increases in *T. democratica* biomass in response to cyclonic mesoscale eddies may be the result of several processes. Everett et al. (2011) reported *T. democratica* blooming within a 30 km cold-core, cyclonic eddy off southeast Australia, with an estimated abundance of over 5000 ind. m<sup>-3</sup>. This high abundance of salps in the cyclonic eddy was linked to an uplift of the nutricline and elevated fluorescence (Everett et al. 2011). While an increase in salps and other zooplankton in cyclonic eddies compared with the absence of eddy perturbation might be predicted, it is less clear why *T. democratica* was the only salp species to significantly increase in biomass in eddies. It is possible that only this most abundant species occurs in numbers large enough to detect differences between eddy types and that other salps may be responding to eddy perturbation as well. Alternatively, differences in phytoplankton community structure between eddy types may play a role. Previous studies showed that in anticyclonic mode-water eddies in the BATS region there was an increase in the percentage of larger phytoplankton such as diatoms and dinoflagellates (2–200 µm), while in cyclonic eddies there was an increased percentage of cyanobacteria such as *Synechococcus* and *Prochlorococcus* (0.5–1.5 µm) (Sweeney et al. 2003, Mouriño-Carballido 2009). If *T. democratica* can outcompete other salp species in cyanobacteria-dominated phytoplankton assemblages, this shift in phytoplankton may explain why only *T. democratica* increased in the presence of cyclonic eddies. Although early studies showed that smaller salps could feed more efficiently on smaller particles (Harbison & McAlister 1979, Kremer & Madin 1992) and that *T. democratica* can feed on bacteria (Mullin 1983), a recent study shows that at least one large salp (*Pegea confoederata*) can also feed on sub-micrometer particles (Sutherland et al. 2010b).

### Long-term trends

The only significant long-term trends in salp abundance or biomass at BATS were slight increases in *T. democratica* and *C. polae* biomass. While the trend in *T. democratica* was consistent over the time series, the trend in *C. polae* was mostly driven by the extremely low concentrations during the first 2 yr of the study. For *T. democratica*, the increase was

equivalent to an integrated (0–150 m) biomass increase of 1.43 µg C m<sup>-2</sup> yr<sup>-1</sup> or ~10.0 µg dry weight m<sup>-2</sup> yr<sup>-1</sup> (assuming C = 12.8% dry weight; Madin et al. 1981), and represents an increase of ~0.17 mg dry weight m<sup>-2</sup> (85%) over the 17 yr time series. While this increase is small compared to an increase of 10.7 mg dry weight m<sup>-2</sup> in total mesozooplankton biomass at BATS over the same time period (Steinberg et al. 2012), any shift in the baseline of salp biomass will have larger impacts seasonally at bloom concentrations. Significant long-term changes in salp abundance have been documented in other regions, including a long-term decrease in the California Current (Lavaniegos & Ohman 2007) and a range expansion in the Southern Ocean (Atkinson et al. 2004). In other regions, salp abundance was positively associated with changes in primary production (Baird et al. 2011, Li et al. 2011).

There has been a 2% increase per year in net PP from 1989 to 2007 at BATS (Saba et al. 2010). This may be driving the long-term increase in *T. democratica*, as suggested by the significant positive correlation with long-term trends in primary production and their close grouping in the PCA of long-term trends. Chl *a* was not as good a predictor of salp biomass; while PP and chl *a* are significantly positively correlated at BATS over the long term ( $p < 0.001$ ), salps at bloom abundances may quickly deplete chl *a* concentrations. Interestingly, long-term trends in both *T. democratica* and *C. polae* are positively correlated with the WCSI, which has also been increasing over the time series. While an increase in the WCSI would reduce the amount of mixing and nutrient influx into surface waters, this overall increase may not be affecting winter-time advective mixing, which is most important for driving the BATS spring phytoplankton bloom (Lomas et al. 2010, Lomas et al. 2013).

In addition to a long-term increase, there were unusually large spring blooms of *T. democratica* every third year starting in 1996, as well as elevated biomass of this species throughout the remainder of those years. No other salp species showed a similar cycle of blooms or abundance. Globally, salps have been shown to follow approximately a 4 yr cycle of high and low relative abundance (Condon et al. 2013, their supplementary Fig. S2c). Condon et al. (2013) posit that this may be related to the 4.4 yr quasi-cycle of high tidal levels based on the lunar perigee (the closest distance the moon is to Earth; Haigh et al. 2011), during which an increase in internal tidal wave energy causes an increase in turbulence and mixing over the deep ocean (Garrett 2003). However, we have no mechanistic evidence of a link

between this 4.4 yr cycle of increased mixing and the slightly offset 3 yr cycle of *T. democratica* we detected, and no other explanation for the pattern.

### Climate oscillations

Decadal climate oscillations play an important role in regulating long-term trends in physical forcing and biological response in the North Atlantic (Greene et al. 2003) and specifically in the BATS region (Krause et al. 2009, Lomas et al. 2010, Saba et al. 2010, Steinberg et al. 2012). The phase of the NAO influences the ecology of the North Atlantic through changes in temperature, circulation patterns, and wind intensity (Ottersen et al. 2001). In the BATS region, a negative phase in the NAO results in increased storm activity (Dickson et al. 1996), which causes an increase in the frequency of mixing in the region (Lomas et al. 2010). This increased mixing leads to an increase in primary production (Saba et al. 2010), higher chl *a* (Lomas et al. 2010), and increased mesozooplankton biomass (Steinberg et al. 2012). In our analysis, a negative NAO correlated with an increase in chl *a* and biomass and abundance of *C. polae*, but not with an increase in biomass of the 3 most abundant species of salps.

Due to climate teleconnections between the North Atlantic and other ocean basins (Kucharski et al. 2006, Müller et al. 2008), PP and mesozooplankton biomass are also positively correlated with the NPGO (Saba et al. 2010, Steinberg et al. 2012). The NPGO was positively correlated with long-term trends in total salp biomass and abundance. The other Pacific climate indices, MEI and PDO, both decreased while total salp biomass, abundance, and the NPGO increased. This suggests that salp biomass is influenced through a similar mechanism by the 3 Pacific indices while the NAO has little or no effect on long-term trends in salp biomass. *Thalia democratica* was also significantly correlated with the Pacific oscillation indices but not with the NAO, again suggesting that variability in these climate indices affects physical forcing, ultimately leading to salp blooms in the BATS region in different ways. The PDO was negligibly correlated with long-term trends in *S. fusiformis*, and no climate index was correlated with *W. cylindrica* biomass. It is likely that the processes affecting their long-term trends are unrelated to the mechanism linking the Pacific indices and *T. democratica*. El Niño Southern Oscillation (ENSO) forcing affects Southern Ocean salp populations (*S. thompsoni*), but the nature of the environmental conditions driven by

this forcing, which leads to years with large summer blooms of *S. thompsoni*, is still unknown (Loeb & Santora 2012). Similarly, the mechanism by which forcing associated with these Pacific climate oscillations affect changes in BATS region ecology remains to be determined.

### CONCLUSIONS

The high diversity and seasonal increase in abundance of salps in the BATS region has important implications for trophic interactions in the planktonic food web, as during blooms salps periodically make up more than 90% of the mesozooplankton biomass. Grazing by salp blooms and competition with other mesozooplankton could alter the phytoplankton and zooplankton community structure in ways that persist after the salp blooms have died off by changing the relative ratios of different phytoplankton groups. These high abundances, coupled with the high filtration rates of salps, could also efficiently transfer carbon to the deep pelagic ocean and benthos, through rapid sinking of their large fecal pellets, sinking of salp carcasses, and active transport by DVM. In conjunction with a long-term increase in PP at BATS, there has been a corresponding long-term increase in *T. democratica* and *C. polae* biomass, and long-term trends in other species may emerge as the data set continues. Salp populations are clearly sensitive to both seasonal and multi-year changes in environmental conditions, and each species responds uniquely to environmental changes. While the links between climate oscillations and changes in salp populations need to be further explored, increased warming of the oceans and resultant changes in decadal climate oscillations could lead to future changes in salp abundance.

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