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Salp contributions to vertical carbon flux in the Sargasso Sea

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Abstract

We developed a one-dimensional model to estimate salp contributions to vertical carbon flux at the Bermuda Atlantic Time-series Study (BATS) site in the North Atlantic subtropical gyre for a 17-yr period (April 1994 to December 2011). We based the model parameters on published rates of salp physiology and experimentally determined sinking and decomposition rates of salp carcasses. Salp grazing was low during non-bloom conditions, but routinely exceeded 100% of chlorophyll standing stock and primary production during blooms. Fecal pellet production was the largest source of salp carbon flux (78% of total), followed by respiration below 200m (19%), sinking of carcasses (3%), and DOC excretion below 200m (<0.1%). Thalia democratica, Salpa fusiformis, Salpa aspera, Wheelia cylindrica, and Iasis zonaria were the five highest contributors, accounting for 95% of total salp-mediated carbon flux. Seasonally, salp flux was higher during spring-summer than fall-winter, due to seasonal changes in species composition and abundance. Salp carbon export to 200m was on average 2.3 mg C m$^{-2}$ d$^{-1}$ across the entire time series. This is equivalent to 11% of the mean 200m POC flux measured by sediment traps in the region. Salp blooms were particularly productive, accounting for 79% of the total modeled salp POC flux at 200m across the time series. Salp carbon flux attenuated slowly, and at 3200m the average modeled carbon from salps was 109% of the POC flux measured in sediment traps at that depth. Migratory and carcass carbon export pathways should also be considered (alongside fecal pellet flux) as facilitating carbon export to sequestration depths in future studies.

Keywords: Salps, Thaliacea, Carbon export, Sargasso Sea, Biological Pump, fecal pellet
Introduction

The Sargasso Sea is an oligotrophic region in the North Atlantic subtropical gyre, with patterns in biogeochemistry influenced by physical forcing, moderated by strength of winter mixing, and tied to decadal-scale climate oscillations (Saba et al. 2010, Álvarez-García et al. 2011, Wu et al. 2011). In years with increased frequency of winter mixing, increased surface nutrients fuel new production, ultimately leading to higher particulate organic carbon fluxes to 150 m (Lomas et al. 2010). As this mass flux continues to sink, organic carbon content decreases from 11.4% of the total at 500m to only 4.6% at 3200m, indicating high remineralization by bacteria and deep-sea zooplankton (Conte et al. 2001), although physical fragmentation of larger particles into smaller, non-sinking particles may also occur. In the Sargasso Sea, flux to the meso- and bathypelagic zones consists of phytodetritus, amorphous aggregates, zooplankton fecal pellets, and foraminifera shells (Shatova et al. 2012, Conte & Weber 2014), with variation in mass flux closely coupled to seasonal changes in epipelagic particle flux (Conte et al. 2001, Lomas et al. 2010). Flux is also influenced by climate oscillations, with higher nitrogen flux to 3200m in years with a negative North Atlantic Oscillation (NAO) anomaly (Conte & Weber 2014).

Interannual variations in mesozooplankton biomass in this region also affect vertical export (Steinberg et al. 2012); we examine here how fluctuations in salp populations (Stone and Steinberg 2014) contribute to vertical carbon flux through a variety of mechanisms.

Salps are gelatinous, tubular zooplankton which alternate life stages between solitary, sexually-produced individuals and aggregated, asexually-produced colonies—ranging in size from a few mm’s to tens of m’s in length. Salps are highly efficient filter feeders, with clearance rates up to several liters salp^{-1} hour^{-1} (Madin and Cetta 1984, Andersen 1985, Vargas and Madin 2004), and they can consume a broad size range of phytoplankton and bacteria (Bone et al. 2003, Sutherland et al. 2010). Salps feed incessantly as they propel themselves through the water, and when numerous, can consume up to 3.5% of the chlorophyll standing stock (Hereu et al. 2006). Their continuous ingestion of a wide range of particle sizes promotes rapid rates of growth, reproduction, and defecation. Salp fecal pellets are relatively large.
(Caron et al. 1989, Sutherland et al. 2010), and sink at rates up to 1600 m day$^{-1}$ (Bruland and Silver 1981, Phillips et al. 2009). Due to fast sinking velocities, salp pellets can reach bathypelagic depths relatively intact, and are found in high numbers in sediment traps (Iseki 1981, Matsueda et al. 1986, Caron et al. 1989, Conte et al. 2001). This observation suggests remineralization or scavenging of these particles by microbes or other metazoans may be limited.

Dead carcasses of salps also contribute to vertical export of organic matter (Lebrato et al. 2013a). While the fate of many salp blooms is unknown, seasonal blooms of salps often quickly collapse (Purcell et al. 2001), and this sudden production of carcasses can represent an important source of food for deep-sea animals and bacteria (Cacchione et al. 1978, Wiebe et al. 1979, Lebrato et al. 2012). Flux from salp fecal pellets and carcasses are estimated to contribute up to 72% of the measured flux in the coastal Mediterranean (Andersen and Nival 1988), and a Salpa sp. bloom in the northeastern Pacific resulted in a major deposition of fecal pellets and carcasses to the seafloor (Smith et al. 2014). In addition to producing fecal pellets and carcasses, several abundant species of salps in the Sargasso Sea and elsewhere undergo diel vertical migration, spending time well below the pycnocline during the day and migrating to surface waters at night (Wiebe et al. 1979, Madin et al. 1996, Stone and Steinberg 2014). While at depth, vertical migrators metabolize particulate organic carbon (POC) consumed in surface waters, respiring it as CO$_2$ and excreting dissolved organic carbon (DOC), contributing to vertical transport of carbon to depth (Steinberg et al. 2001).

While salps are important contributors to vertical carbon flux while they are present, their populations are quite variable. Salps periodically bloom throughout the world’s oceans, including in the Sargasso Sea (Madin et al. 1996, 2001, Roman et al. 2002, Stone and Steinberg 2014), where they are occasionally the dominant epipelagic zooplankton (Stone and Steinberg 2014). Salps are sensitive to interannual and longer-term changes in the environment, mostly related to variations in temperature and stratification. Shifts in prevailing wind led to temperature and primary production changes that caused salp species composition in the Mediterranean to alternate between Thalia democratica and Salpa
fusiformis (Ménard et al. 1994, Licandro et al. 2006). Increases in temperature, as measured by the Northern Hemisphere Temperature anomaly, caused observed increases in the pelagic tunicate Pyrosoma atlanticum due to more stable water masses and decreases in phytoplankton community size (Lebrato et al. 2013b). Long-term regional changes in salp populations have been reported in the California Current (Lavaniegos & Ohman 2007) where shifts in temperature regimes caused changes to both their species composition and biomass. In the Southern Ocean, changes in El Niño–Southern Oscillation (ENSO) and regional warming are correlated with increases in salps (Atkinson et al. 2004, Loeb et al. 2010), and worldwide, gelatinous zooplankton fluctuations are linked to oscillations in climate indices (Condon et al. 2013). In the Sargasso Sea, biomass of the salps Thalia democratica and Cyclosalpa polae increased over the last 20 years, and was positively correlated with water column stratification (Stone and Steinberg 2014). T. democratica abundance was also higher within cyclonic eddies in the Sargasso Sea, possibly through increased eddy-induced production or through eddy-wind aggregation (Stone and Steinberg 2014). These long-term changes in salps in the Sargasso Sea could increase carbon export to the deep sea.

In this study, we hypothesize that all three mechanisms of salp-mediated carbon export – 1) sinking of fecal pellets, 2) sinking of carcasses, and 3) respiration and excretion at depth – represent significant pathways of export. To test this hypothesis, we used salp abundance and species composition data from the Bermuda Atlantic Time-series Study (BATS) to individually model each species’ contributions to vertical carbon flux. This one-dimensional model includes previously-published rates of salp fecal pellet production and sinking, newly measured rates of salp carcass decomposition and sinking, and previously published rates of salp metabolism. By modeling each species and export mechanism separately, we can estimate total salp contributions to vertical flux in an oligotrophic, open-ocean environment and how those fluxes change through the water column as salp abundance and species composition change.
Methods

Sinking and decomposition rate experiments

Salps used in sinking and decomposition rate experiments were collected in the western North Atlantic subtropical gyre at stations within ~100km of the Bermuda Atlantic Time-series Study (BATS) sampling site (31°40’N, 64°10’W). Cruises were aboard the R/V Atlantic Explorer during the ‘Trophic BATS’ project from July 19-31, 2012 and on regular monthly BATS cruises from March 4–7, April 28 – May 3, and August 19-23, 2014. Salps were collected using a net with a 0.8 x 1.2m rectangular mouth, 202 μm mesh, and a non-filtering cod end to minimize damage to the salps. Tows were conducted during both day and night to depths of 50-150m, and lasted ~50 minutes each. Immediately after each tow, captured salps were separated from other zooplankton and brought into the lab for experimentation. Any particles or other zooplankton stuck to the outside or inside of the salps were first removed. Salps were then identified to species and life stage, and individual salp length was measured as the oral-atrial distance using digital calipers. Salps that were not already dead post capture were killed by placing them in a shallow pan of seawater (~2mm deep) to collapse and suffocate them while allowing them to remain moist.

To determine sinking rates, dead salps were placed individually into a sinking chamber comprised of a clear acrylic tube 60cm long and 15cm in diameter filled with surface seawater. This experimental set up and sinking chamber is similar to those used in Lebrato et al. (2013a), which were 12.5cm and 19cm in diameter. The chamber diameter in relation to the size of some of the salps may allow flow interactions between the salp and the wall, slowing the salp sinking rate. To correct for this, we used equation 12 from Ristow et al. (1997) to apply a sidewall correction factor to each individual salp’s sinking rate based on the size of the salp. Water temperature was measured using a Cole-Parmer Traceable® 90205-22 temperature probe, and salinity was determined from the ship’s flow-through salinometer. Water temperature in the sinking chamber changed less than 1°C throughout each
experimental run, and salps were stored in water with the same temperature and salinity as the sinking chamber. After placement in the sinking chamber using forceps, salps were gently shaken to remove any bubbles on or inside the salps. If any bubbles remained, the salp was discarded. Each salp was then gently released and allowed to sink. Depth of each salp in the sinking chamber was determined by comparison to measurement markings on the outside of the chamber. Once each salp appeared to reach terminal velocity (after ~20cm), a timer was started, and the time to sink a distance between 5 and 30cm was recorded. Different sinking distances were used when an individual salp sank particularly quickly or slowly, as we attempted to time each sinking salp for 30-60 seconds. Each salp was sunk once to avoid retrieving the salp from the bottom of the chamber and introducing turbulence.

Decomposition rate experiments were conducted with *Cyclosalpa polae, Iasis zonaria, S. fusiformis, S. maxima, Thalia democratica, Wheelia cylindrica*, and *Ritteriella retracta* in March, May, and August of 2014. Dead salps were placed in small (~5x5cm) 200 μm mesh bags submerged in a large beaker in the dark with a continuous flow-through of surface seawater (19-23 °C) for the duration of the experiment, simulating the decomposition process in warm epipelagic waters with the resident microbial assemblage. Several salps were removed at each time point from their mesh bags and “sacrificed” from the experiment to be frozen for analysis onshore. This removal occurred at regular intervals (~8-12 hours) until all salps were either removed or completely decomposed. Once onshore, salp remains were placed in a drying oven at 60°C for at least one week and then weighed. Initial salp dry weight (i.e., $T_0$) was estimated from length measurements of freshly caught, whole salps using published salp live length to carbon weight regression equations for each species (see Table 5.3 in Madin & Deibel 1998, and references therein). Occasionally, the measured dry weights of the initial, undecomposed salps were consistently different from the dry weights calculated by the regression equations. When this occurred, a correction factor was applied to all salps in that experiment by adding or subtracting the difference between the mean calculated and mean measured dry weights of the time zero ($t_0$) salps. Decay rate of
salp carcasses was calculated by plotting the percent remaining of initial salp dry weight over time and
fitting a first-order exponential decay curve:

\[ P = a \cdot e^{(-k \cdot t)} \]

Where ‘P’ is percent of starting salp dry weight remaining, ‘a’ is the percent remaining at time zero \( t_0 \), ‘k’
is the decay constant, and ‘t’ (hours) is time from the start of the experiment. Similar experiments were
carried out at 8°C using water collected from 1000m, to simulate meso- and bathypelagic conditions. For
these experiments, instead of water continuously flowing through the decomposition chamber, carcasses
were placed in 4L bottles in a refrigerator, and the water in each bottle was replenished every 12 hours.

Model development

We developed a one-dimensional model to calculate salp contributions to total vertical carbon
flux (Figure 1). Fecal pellet production, grazing, production of carcasses, and respiration at depth was
calculated daily for each species’ biomass. Data forced into the model included biological,
environmental, and process rate data (e.g., salp biomass, temperature, primary production) collected
through the BATS program (http://bats.bios.edu/), previously published rates of salp metabolic and export
processes (fecal pellet production, respiration, and DOC excretion), as well as results from the above
sinking and decomposition experiments. Salp ‘blooms’ were defined as in Stone and Steinberg (2014),
i.e., when total salp biomass is in the top 10% of all observations.

Salp biomass (mgC m\(^{-2}\)) and vertical migration was calculated from monthly and bimonthly tows
at the BATS site as detailed in Stone and Steinberg (2014). Species-specific biomass was averaged from
duplicate day and night tows, with only the night tow biomass used for species that exhibited diel-vertical
migration. Salp blooms are generally short-lived, and typically do not remain at high abundance for
several months. Because the duration of each salp bloom could not be accurately estimated from monthly
sampling, the biomass data were linearly interpolated between each sampling date to give a biomass
estimate for each day from April 15, 1994 to November 14, 2011. This was done for each of the 21
species and 4 higher taxa categories (Pegea sp., Salpidae, Salpa sp., and Thalia sp.) in the dataset; the 25 biomass time series were then used to force the flux model. Based on Stone and Steinberg (2014), all species were split into those which exhibited diel vertical migration (DVM; Salpa fusiformis, Wheelia cylindrica, Iasis zonaria, S. aspera, and Ritteriella retracta) and those that did not exhibit DVM (Brooksia rostrata, Cyclosalpa affinis, C. floridana, C. pinnata, C. polae, Helicosalpa virgula, Ihlea punctata, Pegea bicaudata, P. confoederata, P. socia, Pegea sp., S. maxima, Salpa sp., Salpidae, Thalia cicar, T. democratica, T. orientalis, Thetys vagina, and Traustedtia multitentaculata). For each DVM species, an overall average migrating proportion of the biomass was calculated by dividing each sampling date’s day biomass by night biomass and subtracting from 1 to obtain a percentage of biomass that was migrating. These percentages were then averaged for each species across the entire time series. For non-DVM species, we calculated the amount of carbon reaching 200m from both fecal pellet production (FPP) and from sinking of carcasses (i.e., the ‘passive flux’). For DVM species, we additionally calculated respiration and dissolved organic carbon (DOC) excretion while at depth (i.e., the ‘active flux’).

Fecal pellet production, sinking of dead carcasses, respiration and DOC excretion at depth, and grazing were all resolved daily from April 1994 to November 2011 as described in the following sections. For fecal pellet production, species-specific FPP rates were used when available from the literature; for species without a specific rate, rates from the same genus or family were averaged (Supplementary Table 1; Deibel 1982, Madin 1982, Mullin 1983, Small et al. 1983, Cetta et al. 1986, Andersen 1985, Huntley et al. 1989, Madin and Purcell 1992, Sreekumaran Nair et al. 1995). Fecal pellet decomposition was based on rates averaged from Caron et al. (1989), who measured the loss of ash free dry weight over a 10-day experiment. Based on literature values for fecal pellet sinking rates (Bruland and Silver 1981, Caron et al. 1989, Phillips et al. 2009), salp fecal pellets would reach the Sargasso Sea floor well within 10 days. Because the experiments in Caron et al. (1989) looked at fecal pellet decomposition over a total of 10 days through a temperature gradient (1 day at 22°C followed by 9 days at 5°C) and did not measure pellet decomposition at only one temperature, we were unable to separately model the decomposition taking
place in the warm surface waters from that at colder depths. Thus, we applied the total 10-day
decomposition measured by Caron et al. (1989), and no additional decomposition parameter was applied
after the fecal pellets reached 200m. Because fecal pellets would sink below 200m much more quickly
than 10 days, our estimates are conservative. For DVM species, we assumed the following: 1) FPP was
the same in the surface waters and at depth, as salps with full guts would continue to produce fecal pellets
after migrating to depth for some time and would not immediately begin producing them again after
returning to the surface, 2) migrators spent 12 hours per day above 200m and 12 hours per day below
200m, and 3) while physical breakup or resuspension of fecal material may occur, we had no reliable
estimates of these processes, and they were not included in the model.

We modeled carcass sinking and decomposition by incorporating the experimentally-determined
rates for each species (Figure 2 and Table 1), and averaging across genus or family when species-specific
rates were not available. Daily biomass of each species and life stage was multiplied by the proportion
dying each day (the mortality rate), which gave a biomass of dead salps produced each day. All salps
were conservatively assumed to have died at the surface, and the amount of time required to sink 200m
was calculated by using the species-specific corrected rates in Figure 2. The decomposition equations in
Table 1 were then used with the time required to sink 200m to determine the sinking carcass biomass.
The monthly proportion of salp biomass in each life stage (blastozooid or oozoid) was calculated from
BATS count data, and then linearly interpolated to obtain a daily value. Life spans were estimated as 3
days for *Thalia* blastozooids, 14 days for *Thalia* oozoids, 15 days for all other salp blastozooids, and 30
days for all other salp oozoids (Henschke et al. 2011, Deibel and Lowen 2012). Daily death rates were
estimated as the proportion of the population reaching the end of its lifespan each day; for example, the
14-day lifespan of *Thalia* oozoids translates as 1/14 of *Thalia* oozoid biomass dying each day. For DVM
species, we estimated that half of the population died above 200m, and half below 200m. Since we did
not measure decomposition at colder temperatures or under increased pressure at depth, we calculated
biomass of carcasses produced below 200m (reaching depths of 300m, 500m, 1500m, and 3200m) by
applying the decomposition rates of Lebrato et al. (2011, 2013a) separately to *T. democratica* (due to slower sinking speeds of this species), and then to all other species combined. We assumed a constant temperature of 18°C from 200-500m, 8°C from 500-1000m, 5°C from 1000-1500m, and 3°C from 1500-3200m (http://batsftp.bios.edu/BATS/ctd/).

Salp active transport–respiration and DOC excretion at depth– was calculated for the five DVM species while they were below 200m. One rate for each parameter was applied to all species. An average respiration rate (2.2% body C h\(^{-1}\)) was calculated from data compiled in Madin and Purcell (1992) and Cetta et al. (1986). There is no published DOC excretion rate of salps, thus DOC excretion rate for this model was averaged from those of other gelatinous zooplankton (ctenophores and cnidarians) in Condon et al. (2011) (0.182 mgC h\(^{-1}\) g dry body weight\(^{-1}\)).

Daily salp grazing (mgC m\(^{-3}\) d\(^{-1}\)) was calculated by multiplying the volume of water cleared by the average carbon biomass of phytoplankton 0-140m, as phytoplankton biomass is not significant below 140m. Both daily chlorophyll *a* and primary production were linearly interpolated from the monthly BATS sampling (http://batsftp.bios.edu/BATS/bottle/bats_pigments.txt and http://batsftp.bios.edu/BATS/production/bats_production.dat). Phytoplankton carbon biomass was calculated by multiplying the daily chlorophyll *a* concentration by a seasonal carbon to chlorophyll ratio (C:Chl). These C:Chl ratios (g/g) were calculated from seasonal averages of BATS chlorophyll *a* concentration and average seasonal values of phytoplankton carbon from Wallhead et al. (2014), and were as follows (months in parentheses): 52 – winter (JFM), 60 – spring (AMJ), 52 – summer (JAS), and 47 – fall (OND). Species-specific clearance rates were used when available; otherwise, average rates for genus or family were used (Supplementary Table 1; Harbison and Gilmer 1976, Harbison and McAlister 1979, Deibel 1982, Mullin 1983, Madin and Cetta 1984, Andersen 1985, Deibel 1985, Reinke 1987, Madin and Purcell 1992, Sreekumaran Nair et al. 1995, Vargas and Madin 2004, Hereu et al. 2010). Because salps are considered non-discriminant filter feeders (Madin 1974) and only cease feeding when their internal filters become clogged at very high phytoplankton concentrations (i.e., above ~1 ug chl *a* L\(^{-1}\), Andersen
1985 and Harbison et al. 1986; concentrations rarely reached at BATS), we assumed clearance rates to be constant regardless of phytoplankton concentration. While some DVM species may migrate at different times of the day (Madin et al. 1996), further research is needed to quantify these differences, and all DVM species were assumed to graze 12 hours each 24-hr period in surface waters. All salp grazing rates were based on phytoplankton standing stocks, and FPP rates for this model were independent of calculated grazing (see above). If grazing rates were to be used in an energetic model or to calculate FPP, consumption of microzooplankton (such as dinoflagellates and ciliates shown in Vargas and Madin 2004) would also need to be taken into consideration.

Results

Sinking and Decomposition rates

Mean salp carcass sinking rate was measured for 8 species ranging in average size from 8mm *T. democratica* to 30mm *S. maxima*. Sinking rates ranged from 414-871 m d⁻¹ and 467-1002 m d⁻¹, before and after correcting for wall-interaction effects, respectively (Fig. 2), with a mean (corrected) sinking rate across all species of 727 m d⁻¹ (n=293). The corrected rates were used throughout the model calculations. There were weak linear correlations between salp length vs. sinking rate (p<0.001; r² = 0.21) and water density vs. sinking rate (p>0.05; r² < 0.01). We posit that sinking rate was not dependent on water density due to the high water content of salp carcasses, and thus there was an equally proportional change in their body density as in the surrounding seawater after adjusting to the new temperature. However, there were

Sediment trap flux

Sediment trap POC flux data (mgC m⁻² day⁻¹) for sediment traps at 150m, 200m, and 300m from April 1994 to November 2011 were downloaded from the BATS database (bats.bios.edu). Mean POC flux for traps at 500m (1984-1986, 1989-1982, and 1997-1998), 1500m (1984-1992, and 1997-1998), and 3200m (1978-1998) was calculated from Table 1 in Conte et al. 2001.
significant differences in sinking rate between individual species, with *Wheelia cylindrica* (1002 m d\(^{-1}\))
and *Salpa maxima* (927 m d\(^{-1}\)) sinking faster than the two slowest sinking species, *Cyclosalpa polae* (526 m d\(^{-1}\)) and *Thalia democratica* (467 m d\(^{-1}\)) (Kruskal-Wallis ANOVA on ranks; Figure 2). Thus, the
average rates of similar taxa were used in model calculations, and sinking was not based on salp size or
variance in water density.

Species-specific decomposition rates were calculated for species with sufficient replication to
obtain a significant exponential decay curve (*I. zonaria*, *S. fusiformis*, and *T. democratica*), while an
average of all of the warm-water experiments was used to fit a decay curve for the rest of the species
(Table 1; Figure 3). No measurable decomposition occurred over 3 days during the cold-water
experiments. As described in the methods, actual measured salp weights at \( t_0 \) were used to adjust the
calculated starting weights. This method was successful, as measured/modelled weight ratio at \( t_0 \) was
distributed normally (Shapiro-Wilk \( p=0.132 \)) and the mean was 1.07 (±0.27 SD). Modeled salp
decomposition was rapid within the first several hours, with 50% of the starting dry weight lost after only
8 hours. Decomposition of the subsequent 49% took much longer, ~44 additional hours, with some salp
biomass still present 56 hours into the experiment.

Grazing Model

Total daily salp grazing was, on average, 0.05 mg chl a m\(^{-3}\) d\(^{-1}\) (± 0.003 standard error, SE), or
26% of the chlorophyll biomass over the 17+ year model run (6,423 days). However, median daily salp
grazing was only 0.004 mg chl a m\(^{-3}\) d\(^{-1}\), or 2% of the chlorophyll biomass; this difference being driven
by periodically high salp abundances. Likewise, while salp grazing impact was typically low (an average
of 3.9% of the chlorophyll biomass during non-bloom salp abundances), during salp blooms, calculated
grazing was an average of 220% of the phytoplankton standing stock present in epipelagic waters (Figure
4A). Grazing was also seasonally variable, with elevated mean grazing in spring and early summer
(March-June; 6.5 mg C m\(^{-2}\) d\(^{-1}\)) compared to the rest of the year (July-February; 0.7 mg C m\(^{-2}\) d\(^{-1}\)).
Annual grazing across the time series was a median of 17% of the annual primary production (Figure 4B), with annual grazing exceeding 100% of the primary production in 1999, 2002, and 2008. Additionally, the proportion of primary production exported by salps was low (<0.5%) for much (86%) of the time series, but increased to as much as 35% during large blooms (Figure 5B). On average, 0.5% of all primary production at BATS, from April 1994 to November 2011, was exported to below 200m by salps.

Flux Model Results

The daily salp-mediated carbon flux to 200m for each of 25 salp taxa from April 15, 1994 to November 15, 2011 was computed in the model. This included fecal pellet production (FPP) and export, sinking of salp carcasses, and respiration and DOC excretion by DVM at depth. The total carbon flux was generally low, with salp-mediated carbon export less than 1.0 mgC m\(^{-2}\) day\(^{-1}\) in 76% of the time series. However, due to the population dynamics of salps, this low baseline was punctuated with large salp blooms causing spikes in the flux of several orders of magnitude (Figure 5). These salp blooms cumulatively accounted for 79% of the total modeled salp POC flux across the time series, over half of which was produced by the blooms in 1999, 2008, and 2011. Total salp-mediated export to 200m was highly correlated with total salp grazing (Pearson’s correlation coefficient = 0.93, p < 0.001), and averaged across the entire time series salp carbon flux was 1.6% of the total carbon grazed by salps. The average daily salp-mediated carbon export across the time series was 2.3 mgC m\(^{-2}\) day\(^{-1}\) and the median flux was 0.4 mgC m\(^{-2}\) day\(^{-1}\). The largest proportion of salp-mediated carbon export came from fecal pellets, with an annual average of 78% (586 mgC m\(^{-2}\) year\(^{-1}\)) (Table 2). The second largest contribution to export was from respiration at depth (19%; 139 mgC m\(^{-2}\) year\(^{-1}\)), followed by sinking of carcasses (3%; 23 mgC m\(^{-2}\) year\(^{-1}\)), and DOC excretion at depth (< 0.1%; 0.1 mgC m\(^{-2}\) year\(^{-1}\)) (Table 2).

Seasonal trends in salp carbon flux varied according to the source of the flux, and trends were slightly different dependent upon whether mean or median values of export were considered (Fig. 6). As salp export is several orders of magnitude higher during periodic salp blooms, mean values were much
higher than median values for much of the model output. Mean export due to salp fecal pellets was elevated in spring and early summer (March-June), while respiration and carcass carbon flux were more elevated in late summer (July-September) (Figure 6A). Median fecal pellet and carcass fluxes were elevated through all of the spring and summer (February-September), while median respiration peaked in late winter (February and March) and summer (July-September) (Figure 6B). DOC excretion was negligible in all seasons. Both mean and median total salp carbon flux were higher in spring and summer than in fall and winter.

Five species accounted for 96% of the total salp-mediated carbon flux at BATS, with *Thalia democratica* contributing the most, followed by *Salpa aspera, S. fusiformis, Iasis zonaria*, and *Wheelia cylindrica* (Figure 7A). The other 20 species and taxa combined contributed the remaining 4%. This was calculated by summing the total flux contributed by each species for the entire time series. However, when each species' annual total contribution was averaged for each year of 1995-2010, *S. fusiformis* was the largest contributor to flux, followed by *T. democratica, S. aspera, W. cylindrica*, and *I. zonaria* (Figure 7B).

Overall, total annual salp carbon flux ranged widely, from 97 to 4580 mgC m$^{-2}$ y$^{-1}$ in 1997 and 1999, respectively (Figure 8A), with a mean and standard deviation of 748 ± 1133 mgC m$^{-2}$ y$^{-1}$ for the time series. Annual BATS 200m sediment trap flux ranged from 5260 to 9710 mgC m$^{-2}$ y$^{-1}$ in 2005 and 2002, respectively (Figure 8B) with a mean and standard deviation of 7530 ± 1050 mgC m$^{-2}$ y$^{-1}$. Annual salp-mediated export flux was equivalent to a mean of 10% ± 15 (range 1-60%) of the 200m sediment trap POC flux over the time series (Figure 8C).

While there was no consistent long-term change in total salp C export over the time series ($r^2 < 0.01$), there was a periodicity to export. We performed spectral analysis on monthly totals of salp C export to 200m, and the highest spectral densities were found at 9, 12, and 36 months (approximate p-value $< 0.001$, Bartlett's Kolmogorov–Smirnov statistic, Fuller 1996), indicating total salp carbon export
cycles on seasonal (9 months between the late summer and spring blooms), annual, and interannual time scales, respectively.

Relatively little of the total salp-exported carbon was lost as it sank through the water column (Figure 9), due to fast sinking and slow decomposition of fecal pellets and carcasses. Average daily salp carbon flux at 200m across the time series was 2.3 mgC m$^{-2}$ day$^{-1}$ and only attenuated to 1.9 mgC m$^{-2}$ day$^{-1}$ at 3200m. This was a decrease of only 19%, whereas average daily POC flux captured in sediment traps decreased by 92% between 200m and 3200m (from 20.6 to 1.7 mgC m$^{-2}$ day$^{-1}$). At 3200m, calculated salp carbon (mostly from fecal pellets) was equivalent to 109% of the POC collected in the sediment traps (Figure 9).

Discussion

Carcass Sinking Rates

Salp carcass sinking rates varied between 467 and 1002 m d$^{-1}$, similar to the few previously published measurements. Moseley (1880) recorded a sinking rate of ~860 m d$^{-1}$ for an unknown species of salp, and Wiebe et al. (1979) reported Salpa aspera carcasses sank 240-480 m d$^{-1}$. Lebrato et al. (2013a) found Salpa thompsoni carcasses sink 800-1700 m d$^{-1}$, and other gelatinous zooplankton, including Cyanea sp., Pelagia noctiluca, Mnemiopsis leidyi, and Pyrosoma atlanticum, had average sinking rates of 400-1500 m d$^{-1}$. While Lebrato et al. (2013a) found a positive relationship between salp biovolume and sinking rate, we found no significant relationship overall between salp length and sinking rate but that there were some significant differences between species. In our study the smallest species of salp (Thalia democratica) did have the slowest sinking rate. Differences between species in sinking rate other than body size could be related to different relative sizes of the dense, phytoplankton-filled gut or sinking orientation of each individual salp.
Decomposition rates

Decomposition rates of salps were fast enough that while much of the carcass carbon would be exported out of the epipelagic, very little would reach bathypelagic depths before complete decomposition. We found the exponential decay constant ‘k’ of all salp species combined to be 2.2 d\(^{-1}\) at 21 °C, which is close to the calculated k of 2.9 d\(^{-1}\) for all gelatinous zooplankton using Equation 2 in Lebrato et al. (2011). However, the decay constant for *Thalia democratica* (*k* = 14.5) was much higher than that calculated for all gelatinous zooplankton in Lebrato et al. (2011). While this may be due to a higher surface area-to-volume ratio of the small *T. democratica* compared to larger salps, decomposition of *T. democratica* was included in Equation 2 of Lebrato et al. (2011), albeit at a lower experimental temperature of 16.5°C (Sempere et al. 2000). Sempere et al. (2000) observed that salp carcasses consist of a quickly decomposing, labile fraction and a more slowly decomposing fraction, which is consistent with our experimental results showing exponential decay.

While slow-sinking salp species or small individuals, which make up the majority of salp biomass at BATS, may decompose before reaching the benthos, less common blooms of larger and faster sinking species would be able to reach the deep sea. Additionally, DVM species could die at their daytime mesopelagic residence depth, and thus be more likely to reach the benthos since much of the decomposition occurs in warmer surface waters. While we used a depth horizon of salp DVM of 200m for the purpose of our model, at least one species of salp in the North Atlantic subtropical gyre (*Salpa aspera*) migrates to depths >800m (Wiebe et al. 1979), where temperatures are ~10°C and decomposition much slower. Thus, our estimates of salp carcass carbon export to the deep sea are likely conservative.

Grazing

Salp grazing had relatively low impact on phytoplankton standing stock and primary production (PP) for much of the year, but periodically extremely high grazing during salp blooms resulted in demand often exceeding phytoplankton supply, with grazing over 100% phytoplankton standing stock and PP.
Similarly, salp grazing in the Humboldt Current averaged 16% but was up to 60% of PP (Gonzalez et al. 2000), off NW Spain averaged 7% of chlorophyll standing stock but was as much as 77% (Huskin et al. 2003), in the California current system ranged from <1 to >100% of daily PP and phytoplankton biomass (Hereu et al. 2006), and in the Eastern Tropical North Pacific ranged from 0.01 to 3.5% of chlorophyll standing stock each day (Hereu et al. 2010). The high grazing impact seen during salp blooms would only be sustained for a short time before phytoplankton standing stocks were depleted, suggesting bottom-up control and a mechanism for the rapid demise of salp blooms (Henschke et al. 2014).

Seasonal patterns of grazing by salps were similar to other mesozooplankton at BATS, with elevated grazing in spring compared to the rest of the year. Total mesozooplankton (>64 µm) grazing in the Sargasso Sea was 88 mg C m\(^{-2}\) day\(^{-1}\) in March/April 1990 (82% of PP) and 13 mg C m\(^{-2}\) day\(^{-1}\) in August 1989 (25% of PP) (Roman et al. 1993). In both seasons, salps contributed a similar proportion to the total mesozooplankton grazing, with average salp grazing in both March/April and August 6% of the total grazing reported in Roman et al. (1993).

Salp-mediated carbon flux

On average, total salp-mediated C flux is significant compared to the POC flux measured by sediment traps at 200m, consistent with previous studies of fecal pellet contributions to carbon flux in the Sargasso Sea (Steinberg et al. 2012) and the temperate North Pacific (Iseki 1981). Annual average salp fecal pellet flux in our study is equivalent to 7.8% of sinking trap POC flux and active transport by DVM is 1.9% of trap POC flux. During blooms, however, salps account for a higher portion of C flux out of the euphotic zone, and high-abundance years can produce total salp-mediated carbon fluxes up to 60% (as in 1999) of trap POC flux at 200m. These high fluxes are mostly a result of *Thalia democratica* blooms, where daily total export fluxes reached up to 144 mg C m\(^{-2}\) d\(^{-1}\), and these bloom fluxes are more comparable to those found in coastal regions. For example, Madin et al. (2006) found FPP by *Salpa*
aspera in the summer in slope waters off New England was 5-91 mgC m$^{-2}$ night$^{-1}$, and Phillips et al. (2009) found *S. thompsoni* produced up to 20 mg C m$^{-2}$ day$^{-1}$ in fecal pellets off the Antarctic Peninsula.

Dissolved organic carbon flux was low compared to other sources of salp carbon export, likely because the most abundant species, *Thalia democratica*, did not vertically migrate, and any DOC excretion by non-DVM species would remain in the surface waters. However, uncertainties in our applied weight-specific salp DOC excretion rate could lead to underestimates of DOC export. There are limited measurements of DOC excretion by zooplankton, and none for salps. We used DOC excretion rates based on those measured for gelatinous zooplankton by Condon et al. (2011). Kremer (1977) found that DOC excretion by the ctenophore *Mnemiopsis leidyi* is equal to 61% of respiration, and Steinberg et al. (2000) found that average DOC excretion was 31% of respiration for several migrating crustacean zooplankton taxa and a gelatinous polychaete. Using an intermediate DOC excretion rate of 40% of respiration, our estimates of salp DOC export at BATS would increase to 56 mgC m$^{-2}$ y$^{-1}$, or 7% of the yearly total salp-mediated carbon flux. Experimental measurements of salp DOC excretion rates are needed to resolve this issue.

Seasonality in average carbon export by salps can be explained by seasonality in salp blooms, with the peaks driven by periodic large blooms. The general pattern of higher flux in late winter and spring, and lower flux in late summer and fall, is consistent with the general pattern of primary production at BATS (Steinberg et al. 2001, Lomas et al. 2013). Higher respiratory DVM flux in the early spring and late summer is due to seasonal increases in large, vertically migrating species like *S. fusiformis* in the spring and *W. cylindrica* in the late summer (Stone and Steinberg 2014). Because biomass of salps increases by several orders of magnitude during blooms, average salp fluxes are often driven by a few large blooms over the time series. Thus when summing across an entire year, the difference between mean and median may not be great; however, when summing across smaller time periods, such as a single season, the difference may be large.
Differences between salp species’ effect on carbon export are primarily dependent on the size of the salp, due to increases in FPP and respiration rates with body size, and whether they vertically migrate. Vertically migrating species (Salpa aspera, S. fusiformis, Wheelia cylindrica, Iasis zonaria, and Ritteriella retracta) produce fecal pellets and carcasses and respire at depths already below the pycnocline, not only decreasing the distance they have to sink, but also spending less time in warmer surface waters where bacterial decomposition is faster. Carcasses from small species, such as Thalia sp., not only sink more slowly, but also decompose more rapidly. Thus, a small species such as T. democratica would overall export less carbon than an equivalent biomass of a larger, vertically migrating species such as S. aspera. However, in the Sargasso Sea this difference is often masked by the considerably higher biomass of T. democratica blooms compared to all other species.

There were no significant long-term trends in total annual salp C export, which is dependent on the frequency and size of blooms, and peaks in export every three years is consistent with a three-year cycle of Thalia democratica peak biomass (Stone and Steinberg 2014). However, there is a recorded long-term increase in total sinking POC flux to 150m as measured by sediment traps during the high production winter-spring transition period at BATS (Lomas et al. 2010; although there was no significant increase when averaged over the entire year). Steinberg et al. (2012) also calculated an increase in both fecal pellet POC export and active C transport by diel migrating zooplankton over time due to a long-term increase in BATS mesozooplankton biomass (including an increase in DVM zooplankton biomass). This contrast between increases in winter-spring period trap flux and no change in calculated salp flux may indicate that other, non-salp-mediated pathways of export are as efficient as salp-mediated ones during this period. Comparisons between measured trap flux and calculated flux are further complicated by sediment traps not reliably capturing exported particles from spatially and temporally variable salp blooms.

Salps contribute an increasingly higher proportion of C export with increasing depth compared to sinking POC flux measured with sediment traps. At 200m, salp flux only accounts for 11% of the daily
POC flux on average. Comparatively, average daily POC flux at 3200m of 1.7 mg C m\(^{-2}\) day\(^{-1}\) at BATS
(Conte et al. 2001) is less than our calculated salp flux of 1.9 mg C m\(^{-2}\) day\(^{-1}\) at that same depth. This
high amount of salp carbon reaching the deep sea has been directly observed on one occasion in the
northeastern Pacific, where a *Salpa* sp. bloom deposited large amounts of fecal pellets and carcasses to
the seafloor (~4000m) (Smith et al. 2014). However, Shatova et al. (2012) quantified zooplankton fecal
pellets in traps at 500, 1500, and 3200m at BATS in 2007, and found that FP carbon only contributed
4.6% of the total carbon flux at 3200m, much lower than our calculated values. Additionally, they found
that fecal pellets are subject to high rates of recycling and repackaging in the deep water column. Our
higher estimates of deep salp export may be explained by: including carcasses—which baffles on sediment
traps are likely to exclude, including DVM—which is not measured by sediment traps, and not including
scavenging and consumption of salp fecal pellets and carcasses.

Summary and Conclusion

Salp populations in the oligotrophic Sargasso Sea play an important role in transporting carbon
from the epipelagic zone to the deep sea. The primary source of salp-mediated carbon flux is the sinking
of fecal pellets, but contributions from respiration at depth by diel vertically migrating species and sinking
of salp carcasses are also important. Salp carbon flux is relatively low for much of the year, punctuated
by several orders of magnitude higher fluxes during periodic population blooms, especially in spring.
Salp grazing follows a similar pattern, with relatively low levels of grazing interspersed with removal of
100% of phytoplankton standing stock and PP during blooms. *Thalia democratica* is the highest
contributor to salp flux, but due to its small size and absence of vertical migration, most of this species’
contribution is from sinking fecal pellets. Larger species that vertically migrate (such as *Salpa fusiformis*,
*S. aspera, Iasis zonaria, and Wheelia cylindrica*) respire carbon consumed in the epipelagic in the
mesopelagic zone, and produce carcasses at depth that can reach the benthos (Cacchione et al. 1978,
While low and high periods of salp flux average out to be a small percentage of total flux captured annually in sediment traps at 200 m, salp flux contributes a much higher percentage of the total flux in the bathypelagic zone, mostly due to slow decomposition and fast sinking of fecal pellets and carcasses.

Future changes in the diversity and abundance of salp populations could affect the efficiency of the biological pump in the Sargasso Sea. As shown in Stone and Steinberg (2014), *Thalia democratica* and *Cyclosalpa polae* populations have increased, and *T. democratica* biomass was three-fold higher within cyclonic eddies than outside eddies. If these population increases continue, carbon flux would significantly increase, especially to the bathypelagic and benthos–carbon sequestration depths.

Acknowledgements

We are grateful to the many Bermuda Atlantic Time-series Study (BATS) technicians involved in the sampling and maintenance of the zooplankton time series over the last 2 decades. We appreciate the support of the officers and crew of the R/V ‘Weatherbird II’ and the R/V ‘Atlantic Explorer’ for help with sample collection. Special thanks go to Mark Brush for assistance with model development. The BATS zooplankton time series was initially funded by National Science Foundation (NSF) grant OCE-9202336 to L. P. Madin, and continued by the BATS program through the NSF Chemical and Biological Oceanography programs (OCE-9301950, OCE-9617795, and OCE-0326885), and through OCE-0752366 and OCE-1258622 to D.K.S., which funded this current effort. Data collected onboard the ‘Trophic BATS’ cruise was supported by OCE-1090149 to R. Condon. This paper is Contribution No. xxxx of the Virginia Institute of Marine Science, College of William & Mary.
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Madin LP, Purcell JE (1992) Feeding, metabolism, and growth of Cyclosalpa bakeri in the subarctic Pacific. Limnol and Oceanogr 37: 1236-1251


Figure and table captions

Table 1: Warm-water decomposition rates for three species of salps and for all measured species combined. The equation solves for the percent (P) of the starting salp dry weight remaining after H hours. Decomposition follows an exponential decay curve, with a faster decay rate followed by slower decomposition.

Table 2: Average annual carbon flux from the 9 largest contributors to flux and all other species combined. Shown are fluxes of fecal pellets, sinking of dead carcasses, respiration at depth of diel-vertical migrators, and the total of those three categories. Values are in mg carbon m$^{-2}$ year$^{-1}$, and ± standard deviation. DOC excretion is less than 0.1 mgC m$^{-2}$ year$^{-1}$ for all species combined.

Figure 1: A summary of the model. Black boxes indicate forced values from BATS data (phytoplankton biomass, salp biomass, and salp diel vertical migration), red boxes indicate modeled rates (grazing, fecal pellet production (FPP), sinking carcasses, respiration, dissolved organic carbon (DOC) excretion, and decomposition) and outputs (shallow and deep salp carbon), and blue arrows indicate carbon flow.

Figure 2: Mean carcass sinking rate for eight species of salps, arranged from largest salp on the left to smallest on the right. Blue circles are the wall-interaction corrected values of the measured sinking rates (black circles). Error bars are standard error, and n for each species is in parentheses after name.

Figure 3: Percent of starting salp dry weight remaining after decomposing in surface waters. Data from 7 species and 96 individuals were used to fit the exponential decay regression. Experiments were carried out in March, May, and August of 2014 using surface water that ranged from 19-23°C.

Figure 4: A) Daily chlorophyll a concentration (blue) and calculated amount of chlorophyll a grazed by total salps each day (black). B) Annual primary production (integrated to 140m) from 1995 to 2010 (black bars) and calculated percent of that annual PP c grazed by total salps for each year (gray bars).
Figure 5: A) Total salp daily carbon flux to 200m (green) and 3200m (blue) at BATS. Total flux is from all salp species and is combined fecal pellet export, sinking of salp carcasses, and respiration and DOC excretion by DVM at depth. Blue lines without corresponding green indicate 3200m flux that is nearly equal to the 200m flux. B) Percent calculated total salp flux of daily primary production (integrated to 140m).

Figure 6: Seasonal variation in the salp flux to 200m of carcasses (red), fecal pellets (black), respiration below 200m (blue), and DOC excretion below 200m (green). Average (A) and median (B) daily salp carbon flux for each Julian day are shown from the entire time series.

Figure 7: The percent of the total salp carbon flux at 200m for each of the top 5 species at the BATS site for (A) the sum of each species’ contribution across the entire time series and (B) the average annual percent contribution for years 1995-2010.

Figure 8: (A) Annual totals from 1995-2010 for combined salp carbon flux to 200m, and the proportion different sources (fecal pellets, respiration, sinking of dead carcasses, and dissolved organic carbon excretion) contribute to those totals. These totals are compared to (B) the total annual BATS sediment trap flux at 200m by calculating (C) the percent salp flux of the total BATS trap flux at 200m.

Figure 9: Depth attenuation of modeled salp carbon flux (black bars) and measured sediment trap flux (red bars). Modeled data are averaged from January 1994 to December 2011; 200 and 300m sediment trap fluxes are from the BATS dataset and averaged from January 1989 to December 2011; and 500, 1500, and 3200m sediment trap fluxes are collected from Conte et al. (2001).
### Table 1

<table>
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<tr>
<th>Species</th>
<th>Fecal Pellets mgC m^{-2} year^{-1}</th>
<th>Carcasses mgC m^{-2} year^{-1}</th>
<th>Respiration mgC m^{-2} year^{-1}</th>
<th>Total mgC m^{-2} year^{-1}</th>
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<tr>
<td><em>Thalia democratica</em></td>
<td>417 ±1160</td>
<td>0.4 ±1.1</td>
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<td>418 ±1160</td>
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<td><em>Salpa aspera</em></td>
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<td><em>Salpa fusiformis</em></td>
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<td>6.5 ±5.8</td>
<td>46.0 ±41.2</td>
<td>100 ±90</td>
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<td><em>Iasis zonaria</em></td>
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<td>14.5 ±19.6</td>
<td>37 ±50</td>
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<td><em>Wheelia cylindrica</em></td>
<td>10.4 ±26.7</td>
<td>1.3 ±2.8</td>
<td>18.9 ±48.6</td>
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<td><em>Salpa maxima</em></td>
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<td>1.1 ±4.3</td>
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<td><em>Pegea confoederata</em></td>
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<td><em>Pegea socia</em></td>
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<td><em>Ritteriella retracta</em></td>
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<td>Other</td>
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<td>0.6 ±0.5</td>
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<td>Total</td>
<td>586 ±1140</td>
<td>23.0 ±19.5</td>
<td>139 ±126</td>
<td>749 ±1130</td>
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### Table 2

<table>
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<th>p</th>
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<td><em>Iasis zonaria</em></td>
<td>P=108<em>e^(-0.033</em>H)</td>
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<td>&lt;0.001</td>
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<td><em>Salpa fusiformis</em></td>
<td>P=101<em>e^(-0.164</em>H)</td>
<td>0.87</td>
<td>&lt;0.001</td>
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<tr>
<td><em>Thalia democratica</em></td>
<td>P=95<em>e^(-0.605</em>H)</td>
<td>0.84</td>
<td>&lt;0.001</td>
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<td>All species combined</td>
<td>P=104<em>e^(-0.090</em>H)</td>
<td>0.64</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Figure 2

The graph shows the sinking rates of different species, with corrected and measured sinking rates indicated. The species include C. affinis, S. maxima, S. fusiformis, W. cylindrica, L. zonaria, C. polae, P. confoederata, and T. democratica. The y-axis represents the sinking rate in meters per day, while the x-axis lists the species.
All salps warm water

$r^2 = 0.63, p < 0.001$

Figure 3
Figure 4
Figure 6
Figure 7
Figure 8
Figure 9

Depth (meters)

Average daily carbon flux (mgC m\(^{-2}\) day\(^{-1}\))

- Modeled salp flux
- Total trap flux

Figure 9