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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 200 m (19%), sinking of carcasses (3%), and DOC excretion below 200 m ($<0.1\%$). *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 200 m was on average 2.3 mg C m^{-2} d^{-1} across the entire time series. This is equivalent to 11% of the mean 200 m POC flux measured by sediment traps in the region. During years with significant salp blooms, however, annually-averaged salp carbon export was the equivalent of up to 60% of trap POC flux at 200 m. Salp carbon flux attenuated slowly, and at 3200 m 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.

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1. 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 (POC) fluxes to 150 m (Lomas et al., 2010). This POC flux is significantly attenuated in the meso- and bathypelagic zones of the Sargasso Sea (Conte et al., 2001), where flux to these depths consists of phytodetritus, amorphous aggregates, zooplankton fecal pellets, and foraminifera shells (Shatova et al., 2012; Conte and 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 3200 m in years with a negative North Atlantic Oscillation (NAO) anomaly (Conte and 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 (Godeaux et al. 1998). Salps are highly efficient filter feeders, with clearance rates up to several liters salp^{-1} h^{-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 more than 100% of the primary production (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; Yoon et al., 2001; 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

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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; Henschke et al., 2013). 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., 2000).

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 where shifts in temperature regimes caused changes to both their species composition and biomass (Lavaniegos and Ohman, 2007). 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, 2013). *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.

2. Methods

2.1. 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 ~100 km 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 × 1.2 m 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 50–150 m, and lasted ~50 min 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 (~2 mm 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 60 cm long and 15 cm 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 12.5 cm and 19 cm 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 (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 ~20 cm), a timer was started, and the time to sink a distance between 5 and 30 cm 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 s. 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, Salpa fusiformis, S. maxima, Thalia democratica, Wheelia cylindrica,* and *Ritteriella retracta* in March, May, and August of 2014. Dead salps were placed in small (~5 × 5 cm) 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.