

Large salp bloom export from the upper ocean and benthic community response in the abyssal northeast Pacific: Day to week resolution

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Abstract

A large bloom of *Salpa* spp. in the northeastern Pacific during the spring of 2012 resulted in a major deposition of tunics and fecal pellets on the seafloor at ~ 4000 m depth (Sta. M) over a period of 6 months. Continuous monitoring of this food pulse was recorded using autonomous instruments: sequencing sediment traps, a time-lapse camera on the seafloor, and a bottom-transiting vehicle measuring sediment community oxygen consumption (SCOC). These deep-sea measurements were complemented by sampling of salps in the epipelagic zone by California Cooperative Ocean Fisheries Investigations. The particulate organic carbon (POC) flux increased sharply beginning in early March, reaching a peak of 38 mg C m⁻² d⁻¹ in mid-April at 3400 m depth. Salp detritus started appearing in images of the seafloor taken in March and covered a daily maximum of 98% of the seafloor from late June to early July. Concurrently, the SCOC rose with increased salp deposition, reaching a high of 31 mg C m⁻² d⁻¹ in late June. A dominant megafauna species, *Peniagone* sp. A, increased 7-fold in density beginning 7 weeks after the peak in salp deposition. Estimated food supply from salp detritus was 97–327% of the SCOC demand integrated over the 6-month period starting in March 2012. Such large episodic pulses of food sustain abyssal communities over extended periods of time.

Episodic pulses of food reaching the deep sea are extremely important in sustaining abyssal communities over long time periods. Long time-series measurements of particulate organic carbon (POC) flux into the deep sea have revealed benthic community food shortages spanning two decades (Smith and Kaufmann 1999; Smith et al. 2009). However, short episodic pulses can quickly import enough food to sustain the benthic communities over long periods of deficit, as revealed in a 24-yr time-series study in the northeastern Pacific (Smith et al. 2013).

The principal source of food for deep-sea communities is derived from primary production of organic matter in surface waters. Packaging of this organic matter, either as phytoplankton or from higher trophic level derivatives, is critical to the transfer of food to the abyssal seafloor. One group of upper-ocean gelatinous zooplankton, salps, are adept at effectively filtering large volumes of water, extracting phytoplankton and other particles as small as picoplankton, and having high defecation rates (Andersen 1998) of compact fecal pellets that sink rapidly. Salps can occur in large swarms or “blooms,” which are induced by high filtration (feeding) rates, rapid growth, and alternation of sexual and asexual reproduction (Madin et al. 2006). Such salp swarms have been recorded over extensive areas, as great as 9065 km², in many regions of the world ocean, including the northeastern Pacific (Berner 1967; Lavaniegos and Ohman 2003), the southwestern Pacific (Henschke et al. 2013), the northwestern Atlantic (Wiebe et al. 1979; Madin et al. 2006), and the northeastern Atlantic (Bathmann 1988). These blooms have been observed to last

from weeks to several months (Berner 1967; Andersen 1998).

Rapid sinking of salp fecal pellets and tunics effectively transports enriched organic matter into the deep ocean (Matsueda et al. 1986; Morris et al. 1988; Lebrato et al. 2013). Although salps have prolific feeding rates, much of the material in their fecal pellets can be undigested phytoplankton with intact chloroplasts (Madin 1974; Silver and Bruland 1981; Harbison et al. 1986). Once on the seafloor, these salp products can serve as a food source for deep-sea benthic organisms (Wiebe et al. 1979; Pfannkuche and Lochte 1993; Henschke et al. 2013). To date, studies of salp bloom effects on deep-sea ecosystems have shown an efficient downward transport mechanism of organic carbon toward the seafloor. However, to our knowledge, previous studies have not monitored the magnitude of the salp flux reaching benthic communities or the longer-term effects of such food pulses on deep-sea processes. Here we present a multifaceted monitoring of a spring salp bloom as a food supply to the deep ocean and its resulting effect on the benthic community within the temporal context of a 24-yr time-series study of abyssal processes. We use these data to show how salps can provide an episodic but substantial mechanism of carbon transport from surface waters to abyssal depths and that this food source can quickly elicit carbon mineralization by benthic communities.

Methods

This study was conducted at a long time-series station (Sta. M; 34°50'N, 123°00'W) in the northeastern Pacific Ocean, where measurements of deep-sea processes combined

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with atmospheric and surface ocean conditions have been monitored over the past 24 yr. Waters overlying this abyssal site (~ 4000 m depth) show strong seasonal primary production corresponding to upwelling events within the California Current. Seasonal records of phytoplankton and zooplankton in the upper 210 m of this general area have been collected over the past 65 yr (California Cooperative Ocean Fisheries Investigations [CalCOFI] program; Ohman and Smith 1995). The continuous monitoring efforts at Sta. M were begun in 1989 with sediment traps moored at 3400 and 3950 m depth to collect sinking particulate matter as an estimate of food supply reaching the seafloor (Smith et al. 1994; Smith and Druffel 1998). Concurrently, a time-lapse camera at the bottom of the mooring monitored hourly changes in sedimentation events and megafaunal movements over approximately 20 m² of the seafloor (Sherman and Smith 2009; Smith et al. 1993). Seasonal measurements of sediment community oxygen consumption (SCOC), as an estimate of organic carbon consumed, were made using a free vehicle grab respirometer (FVGR; Smith 1987) until 2011, after which continuous measurements of SCOC were recorded using an autonomous bottom-transiting vehicle (*Benthic Rover*; McGill et al. 2009; Sherman and Smith 2009). This dual-tracked vehicle transited the seafloor, stopping every 10 m to make 2 d measurements of SCOC. The *Benthic Rover* also took high-resolution images of the seafloor while transiting between measurement sites, providing monitoring of megafauna density and quantitative assessment of sedimentation events (155 transits, 1423 frames examined). A camera mounted obliquely, 112 cm above the seafloor, on the *Benthic Rover* frame provided clear images of salp tunics and phytodetrital aggregates. The *Benthic Rover* was also equipped with a blue-light source and a camera utilizing a 675 nm low-pass filter (Henthorn et al. 2010) to document sediment–surface fluorescence that might result from chlorophyll excitation (McGill et al. 2009; Sherman and Smith 2009). When annotating *Rover* transit images to count megafauna, reference objects on the seafloor were used to determine a unique field of view for each frame and prevent duplicate counts of the same individual in successive frames. Detailed descriptions of the methods used in this study are given below.

Satellite estimates of chlorophyll and net primary production—We used regionally optimized algorithms (Kahru et al. 2012) based on satellite measurements from four ocean color sensors (OCTS, SeaWiFS, MODIS-Aqua, and MERIS) to estimate near-surface chlorophyll *a* (Chl *a*) concentration. A version of the Behrenfeld and Falkowski (1997) VGPM algorithm was applied to the satellite-derived Chl *a* data from the California Current region (Kahru et al. 2009) to estimate net primary production (NPP). Monthly mean values of all satellite-derived variables were averaged in a circle with a 100 km radius circle around Sta. M (Smith et al. 2006, 2008; Kahru et al. 2012).

Water column sampling for zooplankton—Mesozooplankton were sampled with a 71 cm, 505 μ m mesh bongo net in the upper 210 m (Ohman and Smith 1995) or shallower depths on the CalCOFI cruises. All salp zooids

were enumerated by species from springtime CalCOFI cruises and converted to carbon biomass using the species-specific length–carbon relationships in Lavaniegos and Ohman (2007). For most cruises, individual samples were pooled prior to enumeration, according to the protocol in Lavaniegos and Ohman (2007). Spring 2012 samples were analyzed individually and thus not pooled. Zooplankton displacement volume was determined as the “large” fraction (i.e., summed displacement volume of individual organisms > 5 mL individual volume) and the “small” fraction (all remaining organisms). Displacement volume and salp carbon biomass are expressed as the total epipelagic biomass integrated under 1 m² of sea surface, from surface to 210 m depth.

POC flux—POC flux was measured from samples collected by sequencing sediment traps with a sampling resolution of 10 d (Smith et al. 1994). Traps were moored at 50 and 600 m above bottom (mab), respectively. From 1989 to 2010, sediment traps with a 13-sample-cup sequencer were used, each with a Teflon-coated fiberglass funnel (0.25 m² opening; Baldwin et al. 1998). From 2011 to 2012, we used 21-cup sediment traps (McLane Research Laboratories, model Particle Flux Mark 78H-21), each with a plastic funnel. The sediment trap opening was 0.5 m² and covered by a hexagonal-opening baffle (1.5 cm per side of each cell). Trap cups were filled with a poison prior to deployment (3.0 mmol L⁻¹ HgCl₂ from 1989 to 2009, 3% buffered formalin from 2009 to 2012). Cups were examined immediately after recovery, and zooplankton swimmers were removed. The remaining samples were frozen at -20°C. Salp fecal pellets and tunics were also counted in the sediment trap cups immediately after recovery but not removed from the sample. The organic carbon content of salp fecal pellets was estimated using 0.119 mg C pellet⁻¹ because pellet size was not measured (Wilson et al. 2013).

Samples were subsequently thawed and split, and three-quarters of each sample was analyzed for organic carbon content. This portion was freeze-dried, weighed, and analyzed in duplicate for total carbon (Perkin-Elmer or Exeter Analytical elemental analyzer, University of California [UIC] Santa Barbara Marine Science Institute Analytical Lab) and inorganic carbon (UIC coulometer). Because salt can represent a substantial portion of salp dry weight (Madin 1982), the samples were then corrected for salt content estimated from AgNO₃ titration (Strickland and Parsons 1972). Salt content averaged 59% \pm 3% standard deviation of total dry weight. Salt-corrected inorganic carbon values were subtracted from salt-corrected total carbon to determine organic carbon. In order to obtain the most complete sediment trap record possible, we filled gaps in the 600 mab trap data with values from the 50 mab trap based on the linear regression $POC_{600\text{ mab}} = 3.2 + (0.44 \times POC_{50\text{ mab}})$. Of the 5841 total POC data points, 1045 were infilled using this method.

Water column and seafloor observations of salps and phytodetrital aggregates—Two remotely operated vehicle (ROV) dives (402 and 403) were conducted at Sta. M in June 2012 with the ROV *Doc Ricketts*, from R/V *Western*

Flyer. A high-definition video camera recorded the number of salps on descent to 4000 m and the subsequent ascent back to the surface on both dives at constant speed (35 m min⁻¹).

A camera tripod at the base of the sediment trap mooring photodocumented the seafloor by taking one image every hour. A Canadian grid system (Wakefield and Genin 1987) was used to estimate percent cover of detrital aggregates in daily images. Between 1989 and 2006, the tripod was equipped with a film camera (Smith et al. 1993). A Graf Bar Mark II digitizer was used to determine the area coverage of individual aggregates in these images. Since 2007, the tripod has been equipped with a digital camera of comparable image quality, as verified by overlapping sampling (Sherman and Smith 2009). Individual detrital aggregate coverage of the seafloor in digital images was determined using the Video Annotation and Reference System (VARS), an open-source video annotation software (Schlining and Stout 2006), and a script that returns areas within digitized outlines. Because the effective detection radius (EDR) for identifying detrital aggregates varied between deployments according to water clarity, strobe illumination, and other factors, we used the program Distance (Thomas et al. 2010) to calculate the EDR for each deployment (version 2.1 for deployments in 2006 and prior and version 4.1 for deployments after 2006). EDR was then used to calculate effective area viewed. This program uses the radial distance from a point in each detrital aggregate (center pixel of the small aggregates documented from 1989 to 2006 [Smith et al. 2008] and farthest pixel in the large aggregates documented from 2007 to 2012) to the bottom center pixel of each frame to fit a probability density function to the observed distribution of aggregates. EDR as generated by Distance 4.1 was highly variable, leading to variable effective viewed areas as well (13–32 m²) and aggregate percent cover exceeding 100% calculated for some frames. We applied a correction factor of 0.6061 to aggregate percent cover values determined using Distance 4.1-generated EDR, thereby referencing all frames against those with 100% coverage visible in original frames. Biases that might be caused by this correction would cause an underestimate of aggregate organic carbon flux from 2006 to 2012.

SCOC measurements—Measurements of SCOC were obtained using an FVGR (Smith 1987) and the *Benthic Rover* (Sherman and Smith 2009). Each instrument measured oxygen depletion during ~ 2-d-long incubations. The FVGR measured SCOC in the top 15 cm of sediment and overlying water using four grabs that each covered 413 cm² of seabed. The *Benthic Rover* transited across the seafloor's soft substrate and stopped every 10 m to make SCOC measurements within two acrylic chambers, each enclosing 730 cm² of sediment surface and overlying water. Cameras imaged each *Benthic Rover* chamber insertion depth into the seabed and allowed for identification of megafauna that might have been enclosed. An optode (Aanderaa, model 3830) was used to measure dissolved oxygen depletion within each chamber, and data were recorded for 1 min every 15 min. A respiratory quotient of

0.85 was used to calculate sediment community carbon consumption rates based on rates measured by the FVGR and *Benthic Rover* (Smith 1987). These two instruments and an earlier model of *Benthic Rover* provided similar estimates (Smith et al. 1997, 2013).

Megafauna density—Holothurian megafauna were identified to the lowest possible taxon and counted in daily camera tripod images. A voucher specimen of an abundant undescribed species, *Peniagone* sp. A., was deposited in the invertebrate collections of the California Academy of Sciences (San Francisco, California). To ensure that megafauna could be detected in the entire field of view, only the well-illuminated seafloor near the camera (the bottom half of each image) was annotated. The area coverage of this restricted field of view as determined by VARS (5.75 m²) was used to calculate holothurian density. We calculated Spearman rank correlation coefficients (Siegel 1956) between weekly averages of salp percent cover and holothurian density, with the latter lagged at 1-week intervals from 0 to -27 weeks. Resulting test statistics were compared to find the peak in correlation strength (highest Spearman ρ) and the range of lags for which correlations were significant ($p < 0.05$).

Salp carbon flux—Decay adjustments: Salps partially decay as they sink from their living depths in surface waters through the water column to the deep sea. Because we measured carbon content of salps collected from shallow depths, we accounted for this decay using a temperature-dependent biomass decay ratio (Lebrato et al. 2011). We used a conservative depth of death of 100 m based on salp depth distributions at Sta. M in June 2012 (Fig. 1A), a sinking rate of 1009 m d⁻¹ (average for *Salpa* in Lebrato et al. 2013), a final depth of 4000 m, and average Sta. M water temperatures recorded at 100 m intervals through the water column from 2006 to 2012 (conductivity, temperature, depth records on ROV descents and ascents). We assumed that biomass decay rates were comparable to organic carbon decay rates. Based on this model, we estimated that carbon content of salps on the seafloor was 16% that of salps at a depth of 100 m (Fig. 1B).

Salp tunic carbon flux: Organic carbon content of individual salps was estimated from representative *Salpa fusiformis* collected by ROV in March 2013 and adjusted for decay (Lebrato et al. 2011) as outlined above. Fourteen salps were placed individually in a petri dish with a ruler, blotted dry, and photographed from directly above using a Nikon D200 digital camera mounted on a tripod. Image J (Rasband 1997–2012) was used to calculate the area coverage for each salp in cm². Following this step, each whole salp was freeze-dried, weighed, and analyzed for salt-corrected organic carbon content following the same methods used to estimate POC from sediment trap samples. Organic carbon content was then decay adjusted by multiplying these values, derived in the laboratory from surface-collected specimens, by 0.16. The relationship between size and decayed carbon content of individual salps was found to be:

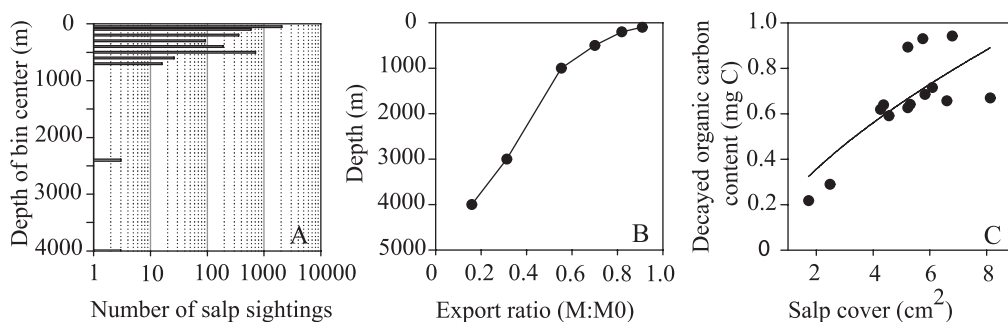


Fig. 1. Data used to estimate salp carbon content. (A) Vertical distribution and abundance of salps at Sta. M in June 2012 as determined from vertical transects through the water column at 35 m min⁻¹. Note log scale of x-axis. (B) Salp biomass export ratio (M : M₀ = biomass at depth × biomass at surface⁻¹) used to estimate decayed organic carbon content of salps on the seafloor. Equations in Lebrato et al. (2013) were applied using a sinking speed of 1009 m d⁻¹, depth of death of 100 m, and temperatures recorded at Sta. M since 2006. (C) Relationship between salp tunic area coverage and estimated decayed organic carbon content.

Decayed organic carbon content of *Salpa fusiformis*

$$= (\text{salp area in cm}^2)^{0.9} \times 0.15$$

as illustrated in Fig. 1C. Using this relationship, we calculated the decayed organic carbon content of an average sized salp (average 5.2 cm² in our samples) to be 0.66 mg C per individual salp. This value was multiplied by the salp tunic flux (individual salps m⁻² d⁻¹) measured from sediment trap collections to arrive at the salp tunic carbon flux (mg C m⁻² d⁻¹).

Salp fecal pellet carbon flux: Salp fecal pellet carbon flux was calculated by multiplying the salp fecal pellet flux (number of salp fecal pellets m⁻² d⁻¹) collected in the 600 mab sediment traps by 0.119 mg C per salp fecal pellet, an average value (Madin 1982; Wilson et al. 2013).

Salp detrital aggregate carbon flux: Salp aggregate organic carbon flux was estimated following a method previously used to determine phytodetrital aggregate organic carbon flux (Smith et al. 1994, 1998). The supply of organic carbon to sediment communities through the decay of salp aggregates on the seafloor, or salp detrital aggregate organic carbon flux, was calculated by dividing decayed organic carbon per area coverage of salps by residence times of 109 and 365 h, the duration for which two individual salps were visible on the seafloor in hourly time-lapse camera images taken at Sta. M in April and May 2012, using the following formulae:

Salp detrital aggregate organic carbon flux₁₀₉ =

$$0.15 \times (\text{salp detrital aggregate percent cover} \times 100)^{0.9} \times (24/109)$$

Salp detrital aggregate organic carbon flux₃₆₅ =

$$0.15 \times (\text{salp detrital aggregate percent cover} \times 100)^{0.9} \times (24/365)$$

Organic carbon supplies vs. demand: Organic carbon flux curves were integrated over a period from 01 March to 23 August 2012 using the trapezoidal rule (Hall 1876) to calculate the area under the curves and estimate total

organic carbon supply or total organic carbon demand (mg C m⁻²) for this period.

Analytical approach—The study of the salp bloom and its effect on abyssal processes is presented here first from a long-term perspective of the 24-yr time series at Sta. M, 1989 through 2012, and then more closely examined over a 1-yr segment between November 2011 and November 2012. The entire time-series perspective, a portion of which was published previously (Smith et al. 2013), is necessary to show the overall temporal significance of the salp deposition event. This study was further narrowed to the salp bloom and deposition event that spanned a nearly 6-month period from 01 March through 23 August 2012. We trace the evolution of this episodic carbon transport and mineralization event in time series from primary production, the abundance and composition of salps and other zooplankton in surface waters, salp distribution in the water column, the flux of salp detritus from sediment traps to the seafloor, and the sediment community mineralization rates using carbon as the common denominator. In addition, we monitored the change in abundance of a dominant megafaunal species over a 1-yr period encompassing the salp deposition event.

Results

24-yr time series—Surface Chl *a* concentration, derived from satellite color over a 100 km radius circle above Sta. M, beginning in 1996, exhibited seasonal highs in spring and summer with a tendency toward increasing duration of peaks, especially notable since 2010 (Fig. 2A). Similarly, satellite-inferred NPP was elevated each spring and summer with higher peaks over the last 7 yr (Fig. 2B). Displacement volume of large and small zooplankton in the upper 210 m of the water column, collected seasonally in the vicinity of Sta. M, showed a marked increase in displacement volume during 2011–2012 compared to the previous 20 yr (Fig. 2C). However, peaks of equivalent magnitude were recorded each decade from 1951 to 1989 (Lavaniegos and Ohman 2007; CalCOFI website, <http://www.data.calcofi.org/zooplankton/calcofi-nets-description.html>). The carbon

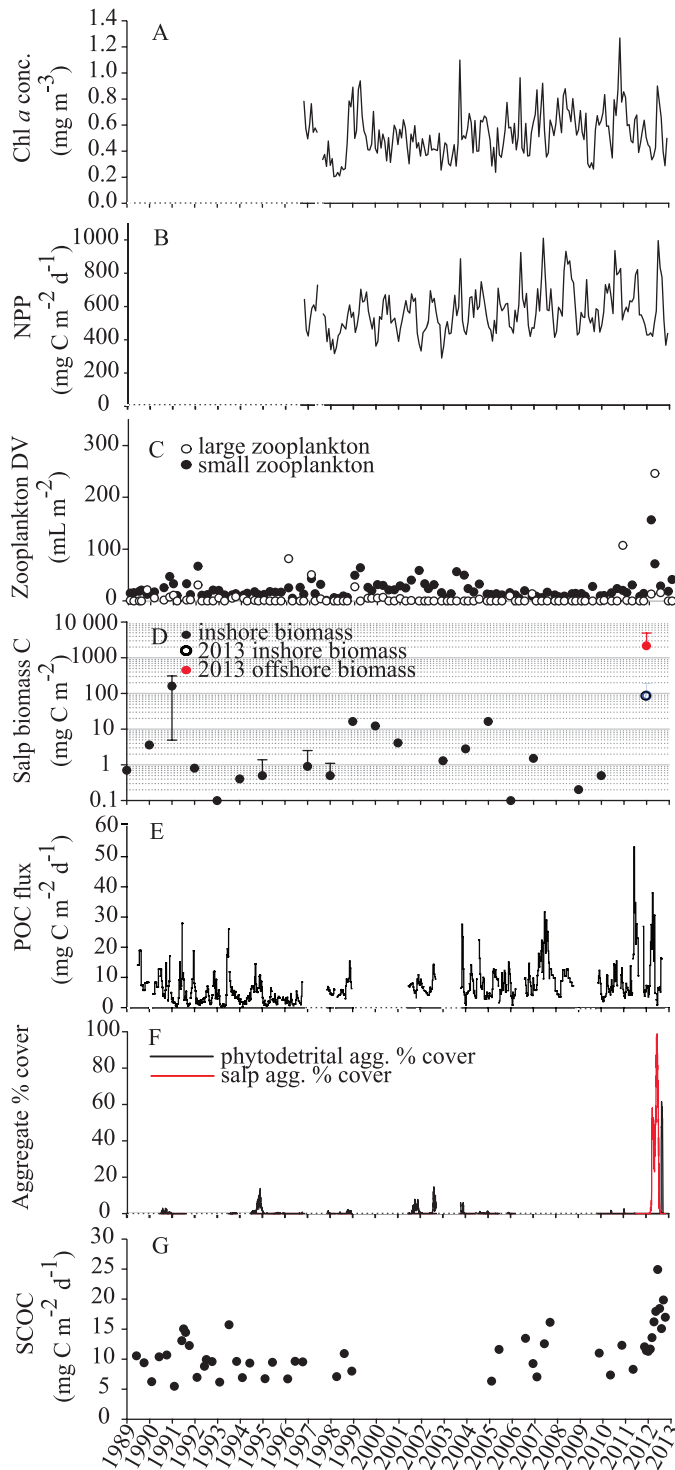


Fig. 2. Long time-series measurements of surface ocean to benthic parameters from July 1989 through November 2012 at Sta. M in the northeastern Pacific Ocean. Dashed portions of x-axes indicate data gaps of time periods exceeding 1 month. (A) Chl *a* concentration around Sta. M (100 km radius circle). (B) NPP around Sta. M. (100 km radius circle). (C) Displacement volume of large (> 5 mL, open circles) and small (< 5 mL) zooplankton. (D) Salp biomass carbon content. Carbon biomass of salps in the more inshore region and the offshore. (E) POC flux measured from sediment traps, with 10 d resolution. (F) Percent

biomass of salps from springtime samples collected inshore of CalCOFI Sta. 70 (Lavaniegos and Ohman 2007) was above the long-term mean for the period 1989–2012 (Fig. 2D, blue symbol; note log scale) and in the offshore region (Sta. 80–120, lines 80–93) was the highest value in the 24-yr time series (Fig. 2D, red symbol; note log scale). At least 13 species of salps were identified from the spring 2012 samples, but 99% of the salp carbon biomass was *Salpa aspera*. As with displacement volume, comparable salp carbon biomass values have been observed in decades preceding 1989 (Lavaniegos and Ohman 2007).

The sinking flux of POC at 3400 m depth (600 mab) exhibited two major peaks in POC flux over the last 18 months of the time series, the highest on record at Sta. M. One peak occurred in June 2011 and another between March and May 2012 corresponding to peaks in surface ocean Chl *a* and primary production (Fig. 2E; Smith et al. 2013). The major peak in POC flux in March 2012 (Fig. 2E) included a relatively high number of salps, as tunics and fecal pellets, originating from the upper 500 m of the water column (Fig. 1A). This spring 2012 peak in POC flux was followed by another major sedimentation event in September that consisted of a combination of salp fecal pellets and phytodetritus (Fig. 2E).

On the seafloor, daily phytodetrital aggregate cover (Fig. 2F, black line) was higher in 2012 than any previous year. The salp deposition event from March through late August 2012 was the largest detrital aggregate deposition event on record, with daily seafloor coverage 6.7 times higher than any pre-2012 peak (Fig. 2F, red line). This salp deposition event was followed by a peak in phytodetrital aggregate cover in late August and September that reached four times the coverage of any pre-2012 peak. The response of the sediment community, estimated by SCOC, also showed record peaks concurrent with these deposition events (Fig. 2G). It is interesting that a smaller peak in SCOC during 1991 coincided with a peak in salp carbon biomass (Fig. 2D).

November 2011–November 2012—Surface Chl *a* reached a high of 0.9 mg m⁻³ in late June and early July 2012, concurrent with a peak in the estimated NPP of 988 mg C m⁻² d⁻¹ (Fig. 3A). Compared to the average values for the entire data set (1951–2013) displacement volume of zooplankton was anomalously high during the April 2012 net-tow sampling (large zooplankton: 237 mL m⁻² anomaly; small zooplankton 40 mL m⁻² anomaly; Fig. 3B). During the following sampling in July 2012, both size fractions of zooplankton returned to the long-term mean displacement volume values.

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seafloor coverage of phytoplankton-derived and salp detrital aggregates (agg.), daily average from camera tripod images. (G) SCOC measured seasonally from 1989 until 2011 and monthly averages of daily measurements taken from 2011 through 2012. Oxygen consumption has been converted to mg carbon using a respiratory quotient of 0.85 (Smith 1987). A, B, E–G are adapted from Smith et al. (2013).

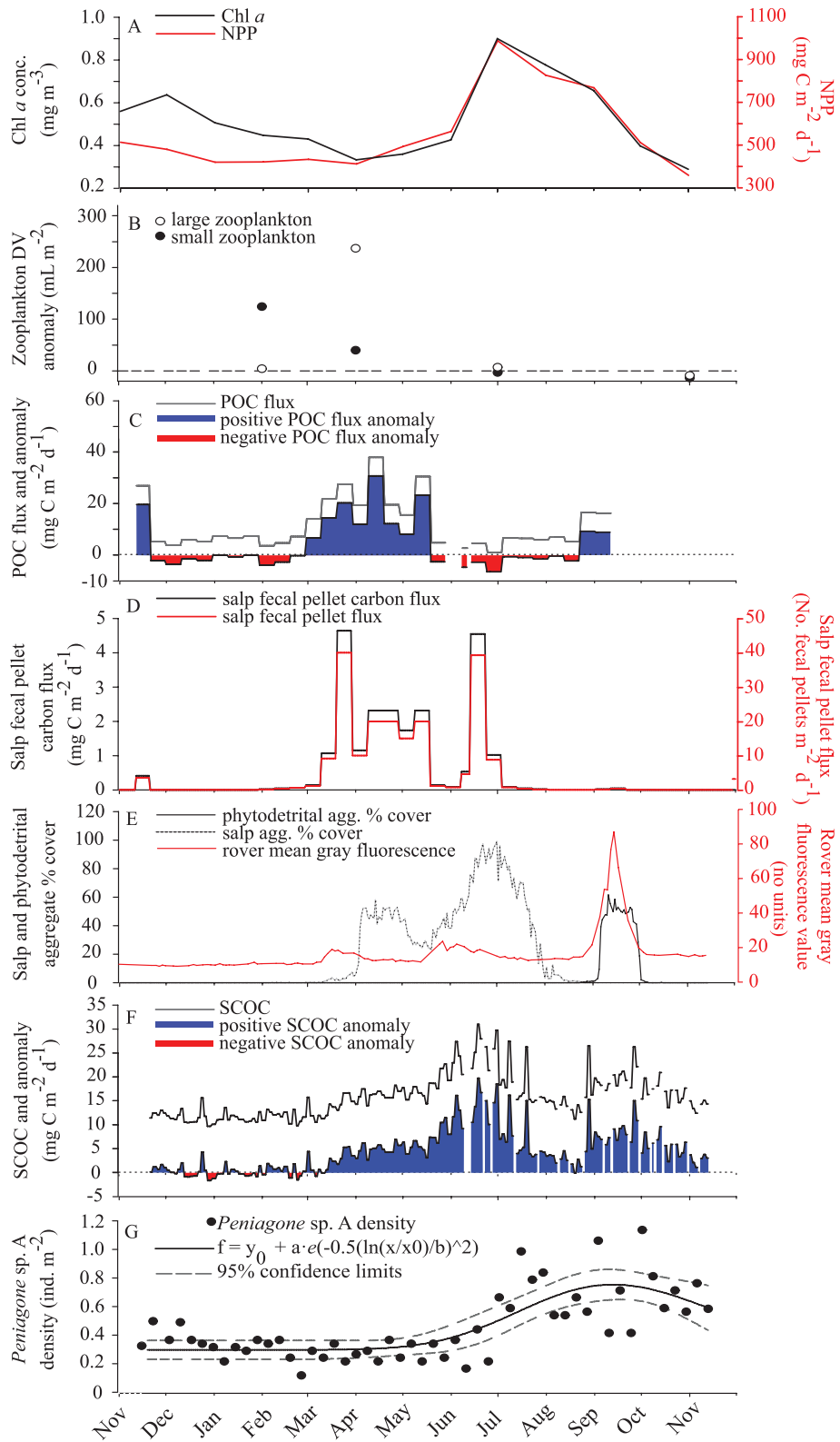


Fig. 3. Surface-water conditions, POC flux, and benthic community responses over a time series from 01 November 2011 to 30 November 2012 at Sta. M. (A) Chl *a* concentration (conc.) and NPP (right y-axis). (B) Zooplankton displacement volume anomaly from full time-series mean (1951–2013), large zooplankton (difference from overall mean of 9 mL m⁻²), small zooplankton (difference from overall mean of 32 mL m⁻²). (C) POC flux and anomaly from full time-series mean of 7.3 mg C m⁻² d⁻¹. (D) Salp fecal pellet flux (right y-axis) measured from

Living salps, tentatively identified as *Salpa* spp., were most abundant in the upper 500 m of the water column as observed during two ROV dives in June 2012 (Fig. 1A). Over 99% of midwater sightings occurred shallower than 600 m depth, as estimated from vertical transects through the water column. Salp tunics were otherwise rare in the water column. As noted above, zooplankton net tows conducted by the CalCOFI program during April 2012 in the vicinity of Sta. M were dominated by *S. aspera*. Given these data, we are referring to the salps on the seafloor at Sta. M as *Salpa* spp. because no seafloor specimens were collected during this period.

The POC flux increased sharply beginning in early March 2012 with a peak of $38 \text{ mg C m}^{-2} \text{ d}^{-1}$ in mid-April before declining precipitously over the next 2 months (Fig. 3C). The decline in this measure might be due to the clogging of the sediment traps between mid-May and early June until the mooring was recovered and then redeployed in mid-June. The POC flux rose with a secondary peak in September before the traps appeared to have clogged once again. These periods of high flux in spring and early fall were well above the mean POC flux over the entire 24-yr period ($7 \pm 6 \text{ mg C m}^{-2} \text{ d}^{-1}$), reaching positive anomalies of $30 \text{ mg C m}^{-2} \text{ d}^{-1}$ in April (Fig. 3C).

Salp fecal pellets in the sediment trap collections were distinguishable in small numbers beginning in mid-November 2011 but became more prevalent the following year from early March through the end of June, peaking between 20–30 March and 14–24 June at 40 salp fecal pellets $\text{m}^{-2} \text{ d}^{-1}$ at 600 mab (Fig. 3D). Until these spring peaks, the quantity of salp fecal pellets did not exceed 10 fecal pellets $\text{m}^{-2} \text{ d}^{-1}$ during the time series from 1993 through 2012. The estimated carbon content of the fecal pellets reached $4.7 \text{ mg C m}^{-2} \text{ d}^{-1}$ in late March and mid-June (Fig. 3D). Salp tunics were collected in sediment traps between 19 April and 18 May 2012 but in numbers ≤ 8 per 10-day sampling period, perhaps because of the difficulty of such large particles passing through the sediment trap baffle.

In April and May 2012, a peak in POC flux coincided with peaks in the percent of the seafloor covered with salp detritus (Fig. 3E). The coverage rose sharply in the beginning of April, reaching a high of 58% cover throughout most of the month then declining in May. The second increase in salp detrital coverage began in late May and reached a high of 98% from late June and early July before declining below 1% by the second week in August (Fig. 3E). This second peak corresponded with a negative anomaly in POC flux. The surface sediment fluorescence increased slightly at the beginning of each

salp detrital peak but then declined while the salps covered a substantial portion of the seafloor (Fig. 3E). The highest fluorescence in the seafloor surface sediments occurred in September, coinciding with a large phytodetrital deposition event.

The sediment community responded to these pulses of detritus with sustained, anomalously high SCOC, starting with the initial stages of the first salp deposition and extending over a month past the phytodetrital deposition event. SCOC reached a peak of $31 \text{ mg C m}^{-2} \text{ d}^{-1}$, corresponding to maximum salp coverage on the seafloor (Fig. 3F). The peaks in SCOC during June represent the highest recorded rates measured at Sta. M over the 24-yr time series. There was no perceptible lag between the arrival of salp detritus and phytodetritus on the seafloor and the increased SCOC. The high fluorescence in the seafloor surface sediment during the early stages of the salp deposition peaks suggests that material with a high content of chlorophyll reached the seafloor in a relatively non-degraded state (Fig. 3E).

A numerically dominant species of mobile megafauna, the undescribed holothuroid *Peniagone* sp. A (California Academy of Sciences Invertebrate Zoology voucher 193700), ranged from a weekly average of 0.3 individuals m^{-2} from November 2011 until early July 2012, when the density sharply increased and attained a peak of 1.1 individuals m^{-2} in late September and early October (Fig. 3G). This increased density of *Peniagone* sp. A continued through the summer and early fall, reaching the highest peak of 1.2 individuals m^{-2} in weekly averages, at the end of September before declining (Fig. 3G). Density of *Peniagone* sp. A was significantly correlated with salp detrital aggregate percent cover ($p < 0.05$) when lagged by 7–25 weeks. The strength of this correlation peaked with a lag of 14 weeks (Spearman $\rho = 0.7866$, $p < 0.0001$). *Peniagone* densities estimated from *Benthic Rover* transit images over the same time period ranged from 0.5 to 1.3 individuals m^{-2} . These animals were often observed over patches of salp detritus and phytodetritus in a suggested feeding posture with oral tentacles engaged with the detrital material.

March through 23 August 2012—The POC flux over this 6-month period was highest in mid-April with declining fluxes from late May through June (Fig. 4A). This decline was probably the result of sediment trap clogging events, especially given the large number of salp tunics reaching the seafloor over that time period. The peaks in salp fecal pellet carbon flux reached $5 \text{ mg C m}^{-2} \text{ d}^{-1}$ at 600 mab and accounted for 10% of the total carbon deposited over this period (220 mg C m^{-2} as salp fecal pellet carbon of 2279 mg

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sediment traps and estimated salp fecal pellet carbon flux estimated using an average of $0.119 \text{ mg C pellet}^{-1}$. (E) Percent cover over the seafloor of phytodetrital aggregates and salp detrital aggregates. Mean fluorescence value measured by the *Benthic Rover* showing relative seafloor excitation at 675 nm (right y-axis). (F) SCOC and anomaly from overall time-series mean of $11.26 \text{ mg C m}^{-2} \text{ d}^{-1}$. (G) Weekly averages of daily images of *Peniagone* sp. A density taken by the time-lapse camera tripod, the equation $f = y_0 + a \times e^{(-0.5(\ln(x/x_0)/b)^2)}$ with R^2 value 0.58 with 95% confidence limits.

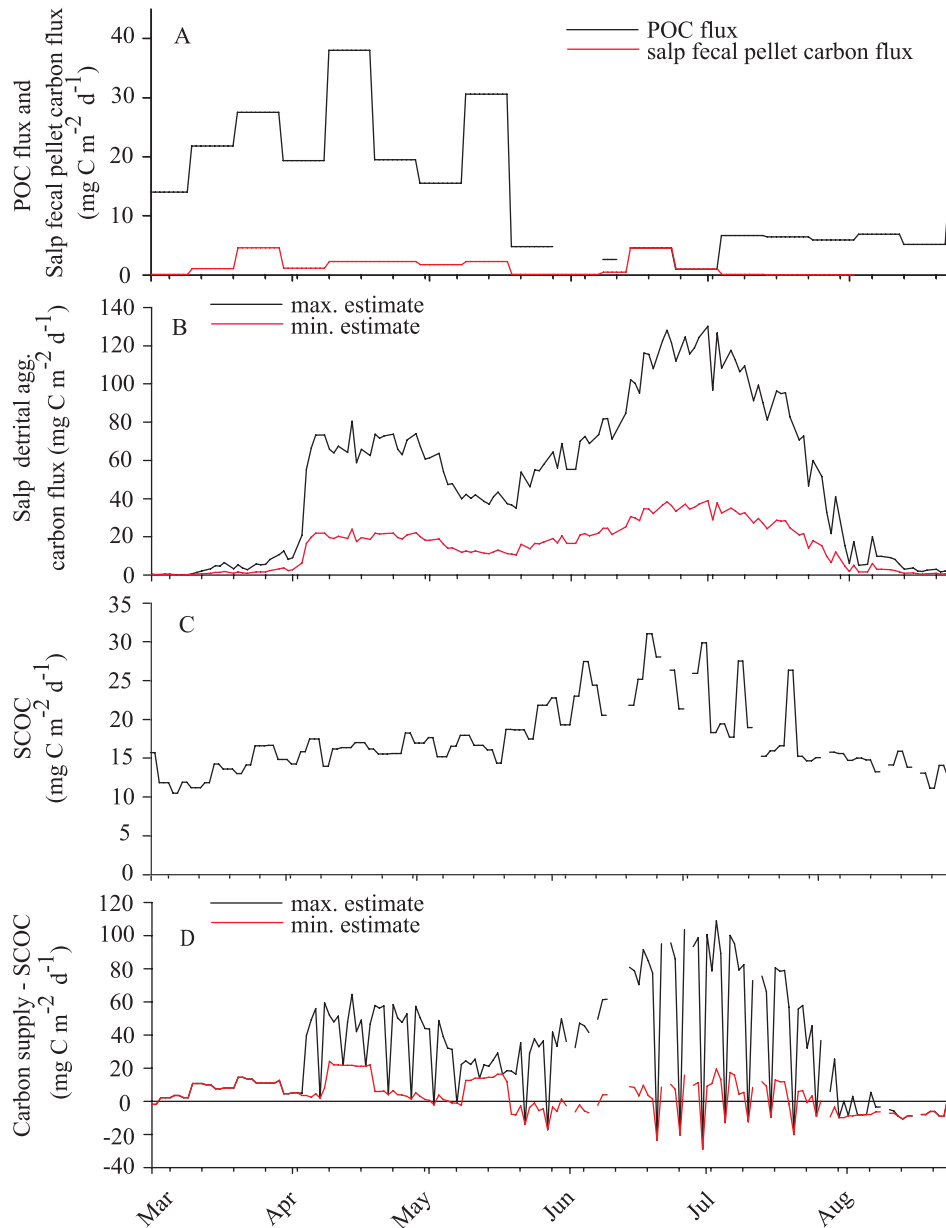


Fig. 4. Carbon supply and demand during salp pulse from 01 March to 23 August 2012. (A) POC flux (integrated curve = 2279 mg C m^{-2}) and salp fecal pellet organic carbon flux (integrated curve = 220 mg C m^{-2}). (B) Salp detrital aggregate organic carbon flux maximum (max.) estimates based on a residence time of 109 h (integrated curve = 9086 mg C m^{-2}) and minimum (min.) estimates based on a residence time of 365 h (integrated curve = 2713 mg C m^{-2}). (C) SCOC, integrated curve = 2781 mg C m^{-2}). (D) Estimated organic carbon supply (the higher of POC flux or salp organic carbon flux) – SCOC, based on residence times of 109 h (integrated curve = 4900 mg C m^{-2}) and 365 h (integrated curve = 522 mg C m^{-2}). Drastic dips in values represent dates for which only POC flux was available, which was consistently lower than salp detrital aggregate organic carbon flux.

C m^{-2} total POC collected in sediment traps; Fig. 4A). Salp tunic organic carbon flux at 600 mab did not exceed $0.5 \text{ mg C m}^{-2} \text{ d}^{-1}$.

The salp detrital aggregate organic carbon flux on the seafloor ranged from 0 to $130 \text{ mg C m}^{-2} \text{ d}^{-1}$ over this 6-month period (Fig. 4B). The estimated supply of organic carbon from salp detritus over this time period, based on

integration of the flux curve, was 2713 mg C m^{-2} for salps decaying over a conservative 365 h residence time. This salp supply represents a 19% increase over the POC supply estimated from trap samples over the same period of time. Using a residence time of 109 h for salp detritus, the organic carbon supply was estimated to be 9086 mg C m^{-2} (Fig. 4B). Based on these estimates, food supply from salp

Table 1. Organic carbon supply and demand based on integration of salp pulse curves (Fig. 4) estimated for the period from 01 March to 23 August 2012. Negative values identify organic carbon uses, while positive values indicate organic carbon supplies.

	Carbon supply or demand totals integrated for the period 01 Mar–23 Aug 2012	Organic carbon (mg C m ⁻²)	Organic carbon (mmol C m ⁻²)
Supplies	Salp fecal pellets	200	17
	POC	2279	190
	Salp detrital aggregates, 365 h residence time	2713	226
	Salp detrital aggregates, 109 h residence time	9086	756
Demand	SCOC	-2781	-232
	Supply vs. demand: (higher of POC flux or detrital aggregate flux) – SCOC	365 h residence time 109 h residence time	522 408

detritus provided from 97% (365 h residence time) to 327% (109 h residence time) of the demand estimated from SCOC over the 6-month period. This salp deposition event clearly provided a major influx of organic carbon to the seafloor.

SCOC began to increase slowly beginning in early March, reaching a series of peaks extending from early June through the later part of July before slowly declining (Fig. 4C). The highest SCOC was 31 mg C m⁻² d⁻¹ in mid-June. Increased SCOC corresponded with the peaks in salp detritus percent cover and estimated POC flux on the seafloor (Fig. 4B). There was an immediate response in SCOC to the salp fluxes as detected with daily resolution. No temporal lag existed in cross correlations between salp detrital aggregate C flux and *Benthic Rover* SCOC (time lag = 0, $r_s = 0.69$, $p < 0.001$). After the highs in SCOC during June and July, the rates declined, only to increase again in late August. The summed demand for organic carbon, SCOC, over the period from 01 March to 23 August was 2781 mg C m⁻² (Fig. 4C).

The balance of food supply to and demand by the sediment community over the 6-month period was estimated by calculating the difference between total food supply (the greater of POC flux or salp detritus flux on the seafloor for any given period) and food demand (SCOC for that same period) and integrating the plot of this value over time. This estimate of supply conservatively accounts for any overlap in salp organic carbon flux and POC flux sources. Although some portion of the POC flux was invariably included in the salp pulse, most of the POC flux consisted of smaller particulate matter that excluded a large fraction, including the majority of salp tunics, because of the small size of the sediment trap baffle openings (hexagonal grid, 1.5 cm per side of each cell). Because both carbon supply estimates overlap and are not mutually exclusive, we chose to use the salp detritus estimates for the range of food reaching the seafloor. The organic carbon supply exceeded the SCOC demand consistently from March until late June using the 365 h residence time estimates for salp tunics (Fig. 4D). A deficit in food supply followed through August for both estimates (Table 1).

Discussion

The salp bloom in spring 2012 at Sta. M provided an exceptionally high supply of organic carbon to the benthic community, which rapidly utilized this rich planktonic food source over a period of at least several months. Although not observed frequently at Sta. M, such blooms provide an excellent conduit for the rapid transfer of primary producers to the abyssal seafloor.

Pelagic tunicates, specifically salps, provide an efficient mechanism to consume primary production in surface waters and export it to the deep ocean. Salps are adept at filtering small particulate matter $\geq 0.7 \mu\text{m}$ from the water column (Harbison et al. 1986), ultimately forming compact fecal pellets that sink rapidly to the deep ocean (Andersen 1998). Salp blooms occur primarily in the upper 100 m of the water column, with densities up to 1000 individuals m⁻³ (Andersen 1998). However, swarms of *S. aspera* can undergo diel vertical migrations to depths of 600–800 m, as observed in the western North Atlantic (Wiebe et al. 1979; Madin et al. 2006). The continuous feeding behavior of salps (Madin 1974) can result in a substantial reduction in surface phytoplankton in 1 day during such blooms (Bathmann 1988; Perissinotto and Pakhomov 1998). The coincidence of the high concentration of salps and low chlorophyll in April 2012 at Sta. M (Fig. 2A,B) might be attributable to extensive grazing pressure on phytoplankton by salps.

Most species of salps, including *Salpa* spp., have high defecation rates (Madin 1982) and form large compact fecal pellets that sink rapidly at velocities up to 2700 m d⁻¹ (Bruland and Silver 1981). Salp fecal pellets vertically transport organic matter to the deep ocean with C:N ratios of 5.4–6.2, which are similar to those of living plankton (Bruland and Silver 1981). Cyanobacteria incorporated in salp fecal material represent a small size fraction of the particulate matter originating in surface waters and traced to the abyssal seafloor in the eastern North Atlantic (Pfannkuche and Lochte 1993). During the vertical flux of *Salpa* spp. fecal pellets through the water column, a 36%

Table 2. Comparison of salp fecal pellet and tunic carbon fluxes estimated in nine other studies conducted in seven different regions of the world ocean.

Region	Sample depth (m)/water depth if available	Collection method	Direct measures	Salp carbon flux (mg C m ⁻² d ⁻¹)		Taxon	Citation
				Total POC flux	Fecal pellets		
Western North Atlantic	/~ 2000	Trawls	Salp biomass, defecation rates in aquaria	8.5–137	3.6	<i>Salpa aspera</i>	Wiebe et al. (1979)
Western North Atlantic	25/ 50/	SCUBA and trawl SCUBA and trawl	Salp biomass, filtration rates in aquaria, fecal pellet carbon content, fecal pellet decay in aquaria	0.01–0.04 0.01–0.07		<i>S. cylindrica</i> <i>S. cylindrica</i> , <i>S. maxima</i> , <i>Pegea confederata</i>	Caron et al. (1989)
Central North Atlantic	25/3300	SCUBA	Defecation rates in aquaria, fecal pellet organic carbon content	142±72		<i>Cyclosalpa pimatta</i>	Madin (1982)
Southern Ocean	100/ to 500/	SCUBA and trawl	Defecation rates in aquaria, salp biomass and size frequencies, fecal pellet total carbon content	0.04–0.3 0.8–23.4		<i>S. thompsoni</i>	Phillips et al. (2009)
Southern Ocean	0–1000/	Trawl	Salp ingestion rates, biomass	88		<i>S. thompsoni</i>	Perissinotto and Pakhomov (1988)
Arabian Sea	140/ 300/	Sediment traps, plankton net	Defecation rates in aquaria, salp and fecal pellet concentrations, total POC flux	8.8 2.6		Salps	Ramaswamy et al. (2005)
Southwestern Pacific	237–1831/	Trawl	Total biomass, gut-free salp tunic organic carbon content		3.1–26.1*	<i>Thetys vagina</i>	Henschke et al. (2013)
Central North Pacific	200/ 900/	Sediment traps	Total POC flux	10.5 6.7		Salps	Iseki (1981)
Northeastern Pacific	740/ 940/ 1440/ 3440/ 4240/	Sediment traps	Sinking particle flux, sinking particle organic carbon content	23 18 6.7 6.7 8.7		Salps	Matsueda et al. (1986)
Northeastern Pacific	3400/4000	Sediment traps, ROV collection	Fecal pellet flux, salp whole tunic flux, total POC flux, salp organic carbon content	≤4.8	≤0.5	<i>S. fusiformis</i>	This article

* Only salp standing stock presented (mg C m⁻²).

loss in carbon content was found between 200 and 900 m depth in the central North Pacific (Iseki 1981). Similar losses were found in organic carbon, nitrogen, and lipid content of salp fecal material between 740 and 4240 m in the eastern North Pacific (Matsueda et al. 1986). At Sta. M, salp fecal pellets were estimated to have contributed 10% of the total POC flux (220 of 2279 mg C m^{-2}) over the duration of the salp pulse (Fig. 4A).

Of studies published to our knowledge, estimates of organic carbon flux associated with salp fecal pellets from surface waters to depths up to 4240 m spanned four orders of magnitude (Table 2). The lowest flux, 0.01 $\text{mg C m}^{-2}\text{d}^{-1}$, was recorded for *Salpa cylindrica* in the northwestern Atlantic (Caron et al. 1989), and the highest flux, 142 $\text{mg C m}^{-2} \text{d}^{-1}$, was measured for *Cyclosalpa pinnata* in the central North Atlantic (Madin 1982). The salp fecal pellet carbon flux measured at Sta. M falls within this large range and closely agrees with similar measurements from sediment trap collections at similar depths in the northeastern Pacific (Matsueda et al. 1986; Table 2).

On the seafloor, salp tunics have been observed previously to depths of 3000 m in the western North Atlantic. Wiebe et al. (1979) estimated from trawl results that 0.4% of a migrating swarm of *S. aspera* died per day and that their sinking flux contributed 3.6 $\text{mg C m}^{-2} \text{d}^{-1}$ to the benthic food supply (Table 2). They estimated that the combined daily contribution of fecal pellets and tunics would supply 180% of the daily metabolic demand of the sediment community at slope depths (Wiebe et al. 1979). Using our conservative estimate of a 365 h residence time, salp detrital aggregates alone would have contributed 2713 mg C m^{-2} during the period of the salp pulse (Fig. 4B), almost enough to fuel the demand of the sediment community (2781 mg C m^{-2} ; Fig. 4C). Again using this conservative estimate, overall organic carbon flux was positive almost continuously from the beginning of the pulse in early March through mid-June, when SCOC exceeded instantaneous supply.

Salp fecal pellets also make up a useful food source to benthic communities at abyssal depths. They have been collected in sediment cores from 4500 to 4800 m in the eastern North Atlantic (Pfannkuche and Lochte 1993), and this salp fecal material containing cyanobacteria was identified in the guts of two species of benthic holothuroids and their fecal casts (Pfannkuche and Lochte 1993). In the southwestern Pacific, benthic crustaceans were observed feeding on tunics of the salp, *Thetys vagina*, at depths between 200 and 2500 m (Henschke et al. 2013).

We observed an increase in abundance of *Peniagone* sp. A by a factor of seven approximately 14 weeks after the salp deposition began on the seafloor at Sta. M (Fig. 3G). These animals were often observed in a feeding posture over salp tunics. The surface-water salp bloom in spring 2012 was widespread, covering extensive areas along the central and southern California coast, including waters over Sta. M and out to at least 650 km offshore (M. Ohman and L. Sala pers. comm.). The large increase in the population of *Peniagone* sp. A lagged 14 weeks behind the salp deposition, suggesting a major immigration response rather than reproduction alone. Although we do

not know the growth rate of *Peniagone* sp. A, to our knowledge the maximum growth rate estimated for a congener is 6 mm month^{-1} (Ruhl 2007). This growth rate would be insufficient to allow new recruits to reach the minimum size of individuals observed during the *Peniagone* sp. A population peak (minimum length 4.1 cm; L. Clary pers. comm.). The question arises as to where these immigrant animals came from given the widespread coverage of the salp bloom in overlying waters and assuming similar deposition conditions over a large area of the seafloor. Members of the genus *Peniagone* are capable of swimming (Miller and Pawson 1990; Rogacheva et al. 2012). We have frequently observed *Peniagone* sp. A swimming in video images by flexing their entire body in longitudinal muscle expansions and contractions in the water above the sediment. This mobility greatly increases this animal's ability to cover larger areas of the seafloor compared to most other members of the megafauna at Sta. M that are restricted to the seafloor. These observations are very intriguing but must await further examination of the size distribution of *Peniagone* at Sta. M and the estimated spatial and temporal extent of the salp bloom in surface waters.

Other gelatinous zooplankton form blooms in surface waters and export large amounts of organic carbon to the deep seafloor. In the Arabian Sea, there was a large deposition of jellyfish, *Crambionella orsini*, recorded on the seafloor between 300 and 3300 m depth (Billett et al. 2006). The contribution of this deposition event was estimated to be as high as 78 g C m^{-2} , which would exceed the annual POC flux estimated from sediment trap collections in this region. A similar deposition event of carcasses of the pyrosome *Pyrosoma atlanticum* occurred in the eastern equatorial Atlantic, with estimated organic contributions up to 22 g C m^{-2} at depths to 1275 m (Lebrato and Jones 2009).

More generally, zooplankton appear to have an important but ill-defined role in facilitating carbon transport and sequestration in the ocean. Both passive and active transport by mesozooplankton are significant processes in the southern California Current System (Stukel et al. 2013). Global-scale biogeochemical models are driven mainly by the supply of nutrients, which in some cases can then drive fast- and slow-sinking flux of POC (Yool et al. 2013). However, such models do not include mechanisms to represent the episodic carbon fluxes observed here (Lampitt et al. 2009). Such episodic fluxes are also likely to have substantially different POC attenuation curves with depth compared to the "steady-state" conditions represented in static attenuation curves (Martin et al. 1987; Buesseler et al. 2007). It remains unclear as to how global-scale models might reproduce these major episodic events while still having a reasonable number of state and rate variables and parameters (i.e., reasonable complexity).

Large episodic pulses of POC reach the abyssal seafloor and serve as a vital food supply to sustain the benthic community at Sta. M. The increased frequency of these food pulses over the last several years, especially the 2012 salp deposition event, was unprecedented over the 24 yr of monitoring this station.

Acknowledgments

This research was supported by the National Science Foundation and the David and Lucile Packard Foundation. We thank our many colleagues over the many years of this time-series study, including R. Baldwin, A. Uhlman, R. Wilson, J. Ellena, and the crews of R/V *New Horizon*, R/V *Atlantis*, and R/V *Western Flyer*. The ROV *Doc Ricketts* pilots provided great support for our project. L. Kuhnz and L. Clary identified many of the benthic fauna and spent many hours digitizing time-lapse images. Holothurian voucher specimens were identified by A. Gebruk and A. Rogacheva and deposited at the California Academy of Sciences thanks to Christina Piotrowski and Kelly Markello. L. Sala and B. Lavaniegos identified the CalCOFI salps. This is a contribution from the National Science Foundation-supported California Current Ecosystem Long-Term Ecological Research site. We thank two anonymous reviewers and the associate editor for their comments that improved this article.

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Associate editor: Markus H. Huettel

Received: 22 October 2013

Accepted: 27 January 2014

Amended: 28 January 2014