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Periodic swarms of the salp *Salpa aspera* in the Slope Water off the NE United States: Biovolume, vertical migration, grazing, and vertical flux

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Abstract

Sampling during four summers over a twenty-seven year period has documented dense populations of *Salpa aspera* in the Slope Water south of New England, northeastern United States. The salps demonstrated a strong pattern of diel vertical migration, moving to depth (mostly 600–800 m) during the day and aggregating in the epipelagic (<100 m) at night. Filtration rates determined from both gut pigment analysis and direct feeding experiments indicated that both the aggregate and solitary stages filtered water at rates ranging from 0.5 to 61 h^{-1} ml^{-1} biovolume. Maximum displacement volumes of salps measured were 5.71 m^{-2} in 1986 and 1.61 m^{-2} in 1993. Depending on the year, the sampled salp populations were calculated to clear between 8 and 74% of the upper 50 m during each 8 h night. Total fecal output for the same populations was estimated to be between 5 and 91 mg C m^{-2} $night^{-1}$. These results, and other observations, suggest this region is a salp "hot spot", with swarms of *S. aspera* developing seasonally on a frequent basis.

Keywords: Salps; Zooplankton; Atlantic Slope Water; Vertical migration; Grazing; Vertical flux

1. Introduction

Several salp species are known to occur periodically in dense "blooms" that can cover large areas. A number of locations have been identified that seasonally support salps in high densities on a recurrent basis. For example, the widely distributed *Thalia democratica* is known to occur in dense populations off Australia, New Zealand, Japan, South Africa, and the southeastern United States (Gibbons, 1996; Heron and Benham, 1984; Paffenhöfer et al., 1994; Tsuda and Nemoto, 1992; Zeldis et al., 1995). Large populations of both *T. democratica* and *Salpa fusiformis* have been routinely observed in the Western Mediterranean

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Sea (Menard et al., 1994), and the California Current (Lavaniegos and Ohman, 2003), and swarms of *S. fusiformis* are also well known from the eastern North Atlantic (Fraser, 1962; Brattstrom, 1972) and in the Gulf of Guinea (Le Borgne, 1983). Blooms have also been reported for *Iasis zonaria* (Mianzan et al., 2000; Nagabushanam, 1960) and *Cyclosalpa bakeri* (Madin et al., 1997), and in the Southern Ocean, *S. thompsoni* periodically occurs in high densities in several locations (e.g. Foxton, 1966; Loeb et al., 1997; Pakhomov et al., 2002).

Development of such large populations is presumably made possible by the high rate and efficiency of filter feeding by salps (Madin and Kremer, 1995; Madin and Deibel, 1998), their rapid growth (Heron, 1972; Heron and Benham, 1985; Andersen and Nival, 1986; Madin and Deibel, 1998) and their alternation of sexual and asexual reproduction (Alldredge and Madin, 1982). These characteristics permit a rapid population response by salps to favorable food availability, such as may result from seasonally high phytoplankton productivity in oceanic regions of water mass intrusions and mixing along fronts (Le Borgne, 1983; Fortier et al., 1994; Menard et al., 1994). In some locations, high population densities of salps can be produced in as little as a few weeks (Alldredge and Madin, 1982; Andersen and Nival, 1986). Such densities of salps appear to reduce the abundance of copepods and other crustaceans (Paffenhöfer et al., 1994; Dubischar and Bathmann, 1997) and can interfere with fishing (Brattstrom, 1972).

Salps can also transform small particulate material into large compact feces that sink rapidly (Bruland and Silver, 1981; Madin, 1982; Caron et al., 1989). When salps occur in high densities, this vertical flux can constitute a major mechanism for transport of particulate matter from the euphotic zone to deeper layers (Iseki, 1981; Matsueda et al., 1986; Morris et al., 1988; Bathmann, 1988). Some of the *Salpa* species may also accelerate the vertical flux by their diel vertical migration (Wiebe et al., 1979).

Although the particular physical and biological conditions that produce and sustain high salp densities are not yet well known, there seem to be several geographic "hot spots" where large salp swarms recur on a regular or irregular basis with strong interannual variability. The Slope Water region south of New England in the western North Atlantic is one of these locations (Fig. 1). Sampling

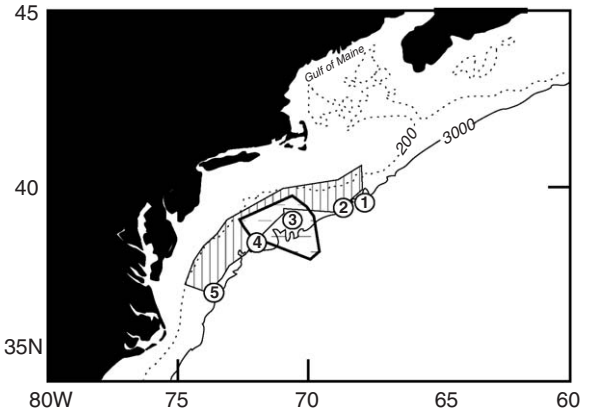

Fig. 1. Map of the region in the northwest Atlantic where *Salpa aspera* is documented to be intermittently seasonally abundant. Estimated area of salp swarm August 1975 (horizontal stippling) from Wiebe et al. (1979); sampling Stations 1–3 (May 28–31, 1986); sampling Stations 4–5 (July 23–25,1993); measured area of 2002 swarm (vertical stippling). Location of January 2004 collection indicated by A; October 2004 sightings indicated by B. All areas with high densities of *S. aspera* were located between the continental shelf break (approx. 100 m depth) and the Gulf Stream.

in this region during August 1975 documented both high abundance and strong diel vertical migration of *S. aspera* (Wiebe et al., 1979). In this paper we extend the findings of that earlier study adding data from cruises in May 1986, July 1993, and 2002 in these same waters, with additional evidence from January and October 2004. Details of results from June and September 2002 will be reported elsewhere (Madin et al., unpublished). Measurements of both feeding and defecation rates for *S. aspera* are also included here to make more refined estimates of grazing impact and vertical flux by swarms of *S. aspera* than were possible earlier from data from other species (Wiebe et al., 1979).

2. Methods

2.1. Sampling

The principal data reported here are from cruises conducted in 1986, 1993, and 2002, at locations indicated in Fig. 1. Depth stratified sampling was carried out with two versions of a multiple opening/closing net system (MOCNESS). The smaller MOC-1 design, used in 1986, is capable of sampling sixteen discrete depths. Its frame holds two sets of 10 nets, each net having a mouth area of 1.4 m^2 and 335 μm mesh (Wiebe et al., 1985). The larger MOC-10

design, used in 1993, samples four discrete depths with a mouth area for each net of 10 m^2 and mesh size of 3 mm. One additional collection of *S. aspera* was made with a MOC-1 net in January 2004 during the course of another program. Video images of *S. aspera*, but not specimens, were obtained in October 2004 in the Slope Water during the testing of a video-imaging device. We are not aware of any other collections of *S. aspera* in this region between 1975 and 2005.

Both day and night tows were made with the MOCNESS systems to document diel vertical migration by *S. aspera*. Most tows sampled to depths of 800 or 1000 m, but two night tows with the MOC-10 system were made to a depth of only 200 m in order to resolve the night depth distribution more precisely. In each trawl, the deepest stratum was sampled first, followed by shallower strata as the net was hauled toward the surface. The time open for each net varied with the anticipated abundance of salps. If too many salps were sampled with the MOC-10 system for complete enumeration, the total catch volume was measured and an aliquot was preserved in 5% buffered formalin.

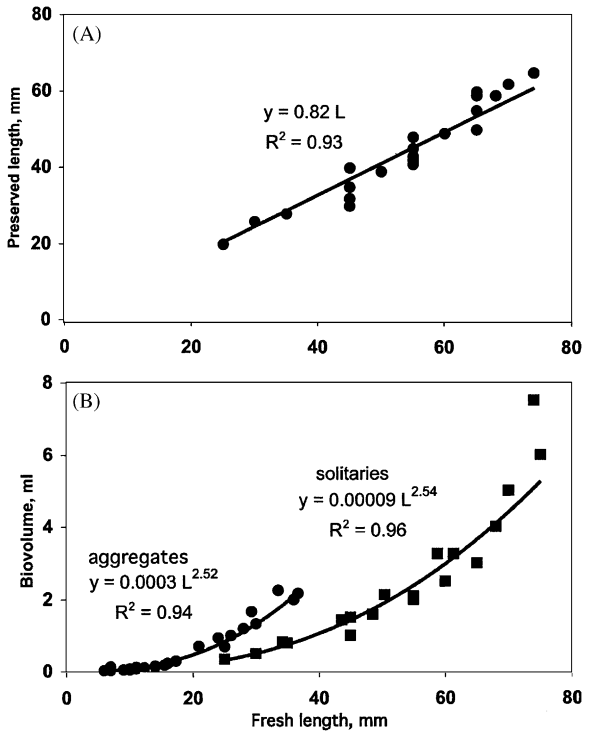

Fig. 2. (A) Relationship between lengths of freshly collected and preserved *Salpa aspera*, both aggregate and solitary forms combined. (B) Relationship between length and biovolume for freshly collected aggregates and solitaries of *S. aspera*.

Measurements of the preserved samples were made within a few weeks of collection. Results take into account a 20% shrinkage in length due to preservation (Fig. 2A). Length of *S. aspera* was measured as the distance between the oral and aboral openings, omitting the pointed tips of the aggregate form. A conversion between length and fresh biovolume was made with freshly collected salps (Fig. 2B). Graduated cylinders of different sizes were used to make accurate biovolume measurements of groups of salps of similar size.

At night, *S. aspera* was available within range for SCUBA diving. During four consecutive nights in 1993, divers used hand-held jars to collect undamaged salps, including intact chains of aggregates, for a range of measurements and experiments.

2.2. Analysis of particulate material

Five CTD casts were made in 1993 at Stations 4 and 5, where high densities of *S. aspera* were sampled. Water was collected from five depths, including the chlorophyll maximum. Two-liter water samples from each sampled depth were filtered through 24-mm glass-fiber (GFF) filters. A second set of 2-l samples was filtered through glass fiber prefilters (nominal pore size 2 μm). Both sets of filters were extracted in 6 ml of 90% acetone for 24 h at 5 °C, decanted and read on a Turner Designs fluorometer that had been calibrated with pure chlorophyll *a*. Samples were acidified to determine the proportion of phaeopigments present in the samples (Parsons et al., 1984).

Additional sets of 2-l samples were filtered through pre-ashed GFF and 2-μm glass fiber prefilters. These filters were folded, stored in glassine envelopes in a drying oven at 60 °C on shipboard, and then frozen prior to elemental analysis for carbon and nitrogen at the Horn Point Laboratory.

Pigment content and elemental carbon and nitrogen were also measured for samples of salp feces. Feces were collected by pipet from diver-collected salps that were maintained in large aquaria in ambient surface seawater. These samples were divided, with half stored on pre-combusted GFC filters for analysis of carbon and nitrogen (as described above), and the other half analysed for pigment, following the method for gut pigment described below.

2.3. Gut pigment

To determine rates of filtration using the gut pigment approach, it is necessary to have measurements of gut pigment for freshly collected salps, and also estimates of background fluorescence signal for salps with cleared guts, gut passage times, and in situ pigment concentrations for all particles large enough to be retained by salps (Madin and Cetta, 1984; Madin and Kremer, 1995). Filtration rate can then be calculated as

$$f = \frac{(g - b)}{t \cdot p}$$

where f is the filtration rate, $1\,h^{-1}$, g the pigment in guts, μg, b the 'background' pigment in guts cleared of food, μg, t the gut passage time, h from ingestion to defecation, p the ambient pigment of particles large enough to be retained by salps, $\mu g\,l^{-1}$.

Some of the diver-collected *S. aspera* were used for determination of gut pigment. In addition, on each of four consecutive nights a single long chain of aggregates was gently divided underwater, and subsections of the chain were used in experiments to determine particle clearance and defecation rates as well as analyses for gut pigment. Gut pigment was also measured for a subset of the salps collected by trawl near the time of the dive each night.

Gut pigment was determined by excising the gut, grinding with a Teflon pestle in 3 ml 90% acetone, rinsing with another 3 ml acetone, extracting in screw-top fluorometer tubes at 5 °C in the dark for 24 h, and centrifuging, prior to reading fluorescence (Madin and Cetta, 1984). Samples were diluted if necessary to prevent quenching, and after an initial reading were acidified to determine the proportion of phaeopigments. Any fecal material defecated prior to excising the gut was collected and analysed according to the same protocol. The pigment values for feces were added to the salp's gut pigment to calculate the total amount of pigment in the gut at the time of collection.

To determine the background fluorescence signal of salp guts that were cleared of food, diver-collected *S. aspera* of a range of sizes were held in cylindrical tanks (20 l) of filtered seawater (Millipore cartridge nominal size $<1\,\mu m$) that had been spiked with a dilute suspension of cornstarch. After the white cornstarch appeared in the feces, indicating that all pre-existing gut contents had been defecated, guts were excised and measured for fluorescence as above. The cornstarch does not fluoresce.

2.4. Gut passage time

The elapsed time from ingestion to defecation was measured with a suspension of a particulate marker (carmine particles or cornstarch) that was introduced into the oral opening of salps underwater prior to collection by divers (Madin and Cetta, 1984). The ingested particles make a distinct red or white band in the gut. On shipboard, marked salps were held in cylindrical tanks (20 l) of unfiltered seawater until the marker was seen in the feces. Gut passage time was calculated as the time from marking the salps' feeding nets underwater until the first observation of marked feces in the tanks.

2.5. Particle ingestion experiments

Salp chains collected by divers were gently transferred in the dark to cylindrical tanks (volume 15 l) and held in the dark at 21–24 °C. Both experimental and control tanks (without salps) were spiked with an aliquot of *Isocrysis galbana* (diameter 5 μm) from a culture maintained on shipboard. The initial algal concentration was about $10^4\,cells\,ml^{-1}$. Observations throughout the experiments confirmed that the salps were swimming actively and the chains stayed intact. Aliquots of water (200–500 ml) from both experimental and control tanks were collected periodically over the duration of the experiment (total 2–3 h). The pigment content of these aliquots was measured by the same protocol as for water samples from the CTD casts. Water was filtered through GFF filters, extracted in 6 ml of 90% acetone for 24 h at 5 °C, decanted, and read on the fluorometer both before and after acidification.

Filtration rates can be calculated from the change in chlorophyll in the experimental tanks and the equation

$$f = \frac{v \ln(C_o/C_t)}{n \cdot t}$$

where f is the filtration rate, $1\,h^{-1}\,salp^{-1}$, v the volume of experimental tank, l, n the number of salps in chain, t the duration of experiment, h, C_o the initial chlorophyll concentration, $\mu g\,l^{-1}$, C_t the chlorophyll concentration t hours later, $\mu g\,l^{-1}$.

2.6. Defecation rates

Diver-collected *S. aspera* were held in cylindrical tanks (volume 15 l) in unfiltered surface water.

Periodically, all feces were removed from the tanks with a wide-bore pipette and excess water decanted from the sample. Pigment analyses were made of these feces by the same protocol of grinding and extraction described above for the excised guts. Pigment quantities were divided by the time elapsed between collection of the salps and removal of the feces to estimate hourly production rates.

3. Results

3.1. Abundance and vertical distribution

The occurrence pattern and abundances of *S. aspera* in 1986, 1993, and 2002 (Fig. 1 and Table 1) were consistent with the earlier findings of Wiebe et al. (1979). Our daytime tows to 1000 m also confirmed that few salps were found below 800 m at any time (Fig. 3). During the day, the bulk of the population was found at a depth of 600–800 m, while during the night it was concentrated in the top 50 m (Figs. 3 and 4). The nighttime distribution was most clearly delineated when the concentrations were the highest (Fig. 4).

At the same geographic location, there was large variability among collections in the measured salp biomass. Biovolumes based on either volume (per m^3) or integrated water column (per m^2) varied by over an order of magnitude from one day to another and one location to another (Table 1), even within a single week during a swarm event.

The single collection made on January 11, 2004 was at 39.02°N, 71.82°W and taken between about 2200 and 0000 h. This location is in the Slope Water, just beyond the edge of the continental shelf. *S. aspera* were found only in the top 100 m, with the greatest abundance (350 ml m^{-3} biovolume) in the top 25 m.

Video images of *S. aspera* chains were obtained over the shelf break at 40°N, 70°W on October 29, 2004, with the Large Area Plankton Imaging System, a new video-imaging instrument under development. The device was deployed in the top 50 m between 0100 and 0500 h. Identifiable images of *S. aspera* chains containing up to 12 aggregate salps were recorded, but no physical samples were obtained.

Table 1
Depth integrated biovolume for *Salpa aspera* collected in tows on May 28–31, 1986 (Stations 1–3) and July 22–26, 1993 (Stations 4–5). Four collections close together are combined as Station 4

Station	Position	Day/night	Max depth (m)	Biovolume (ml m^{-2})
1	39°25.7′, 68°26.7′	Day	1000	262
2	39°17.9′, 68°39.1′	Night	1000	325
3	39°15.8′, 70°20.4′	Night	1000	5713
4	38°26.6′, 72°06.0′	Day	800	67
4	38°29.9′, 72°02.1′	Night	800	1243
4	38°29.3′, 72°00.8′	Day	1000	398
4	38°26.7′, 71°58.1′	Night	200	327
5	36°46.8′, 73°26.0′	Night	200	1587

3.2. Size frequency

The size distribution of the aggregates was determined from preserved sub-samples of six depth-stratified tows, after correction for shrinkage (Fig. 2A). All these results (Fig. 5) show the aggregates were dominated by salps between 12 and 28 mm fresh length, with nearly no aggregates smaller than 10 mm. Although the smallest sizes of aggregates were likely to have been under-sampled because of the large mesh size of the nets (3 mm), other tows with the same nets have sampled even smaller salps (e.g. *T. democratica*), indicating that if smaller aggregates of *S. aspera* had been common they too would have been retained. Newly released chains of *S. aspera* aggregates are made of individuals 3 mm in length. When the fertilized female aggregates are about 30 mm they release one free-swimming solitary that rapidly takes up water and expands to about 30 mm. As these mature aggregates ($\geqslant$30 mm) made up 12% of the counted aliquots (Fig. 5), it is probable that newly released solitaries would be similarly abundant. The absence of newly released aggregates ($\leqslant$8 mm) implied that large solitaries carrying developing stolons of young aggregates were rare in these waters. Indeed, the collected solitaries were generally small (40 ± 13 mm, $n = 213$), with only three individuals large enough ($\geqslant$64 mm) to produce aggregate chains. Overall, the aggregate stage was seven times more abundant than the solitary form. Our collections in 1993 revealed a salp population with active sexual reproduction, but not in a phase of rapidly increasing numbers via asexual reproduction by large solitaries.

3.3. Gut pigment

Gut pigment as a function of salp length was comparable for aggregate *S. aspera* collected by

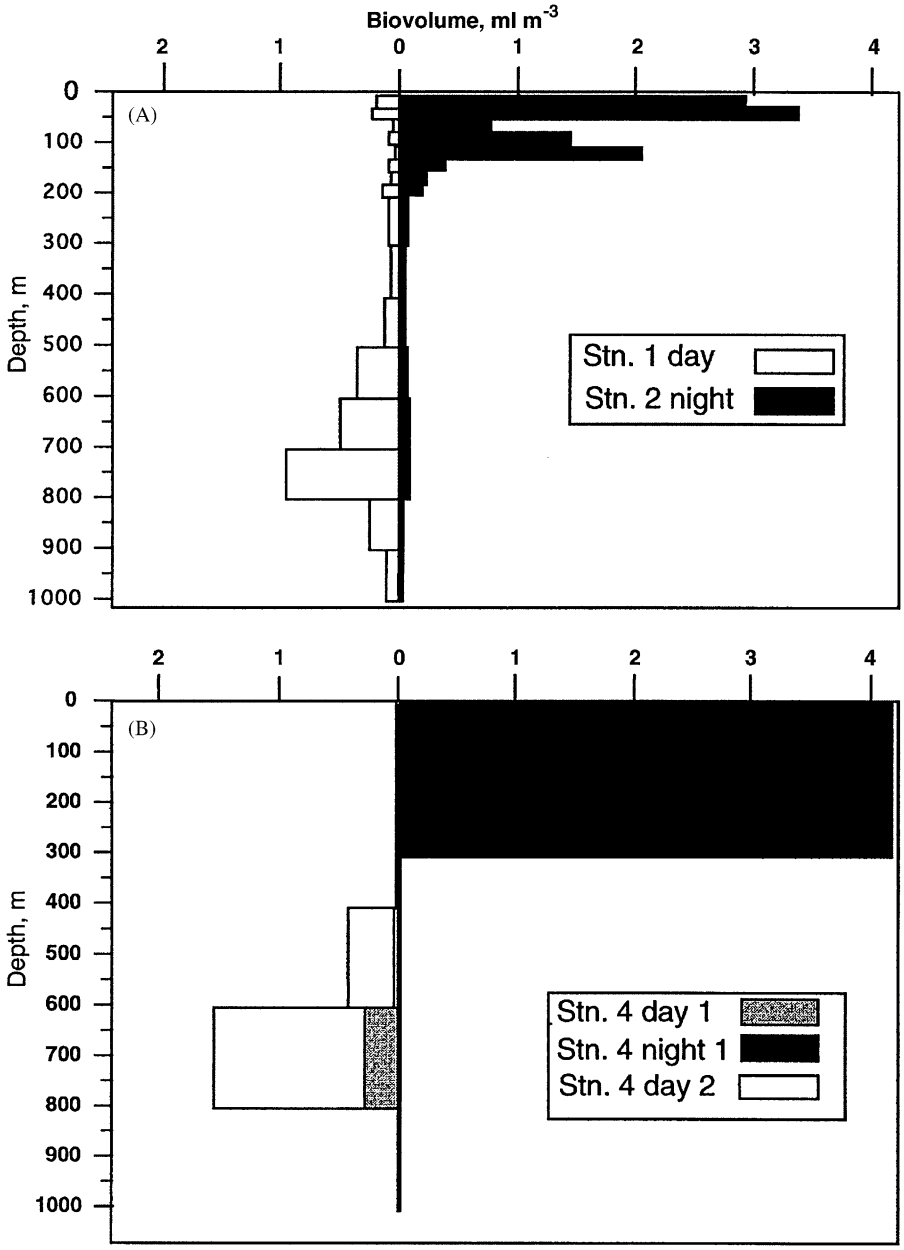

Fig. 3. (A) Biovolume, ml m^{-3}, of *Salpa aspera* collected in one day-night pair of tows from Station 1 (day) and Station 2 (night) in May 1986. Width of each bar corresponds to the depth interval for each net sample (25–100 m) to 1000 m. (B) Biovolume, ml m^{-3}, of *S. aspera* from two daytime tows and one night tow to 800 m at Station 4 in July 1993.

SCUBA on four consecutive nights (Fig. 6A). These results indicate that the salps of similar size were ingesting generally similar quantities of pigmented particles prior to collection. Measurements of particulate pigments from daily CTD casts confirmed that pigment values at Station 4 were similar over that time period, while near surface pigment values at Station 5 were slightly higher (Table 2).

Values for gut pigment were similar for both diver-collected and net-collected samples taken in the same location a few hours apart (Fig. 6B). Two large net-collected aggregates appear as low outliers. As it is impossible to distinguish the in situ condition of salps that are collected by net, these aggregates may have been moribund and not in chains prior to collection. Daytime SCUBA

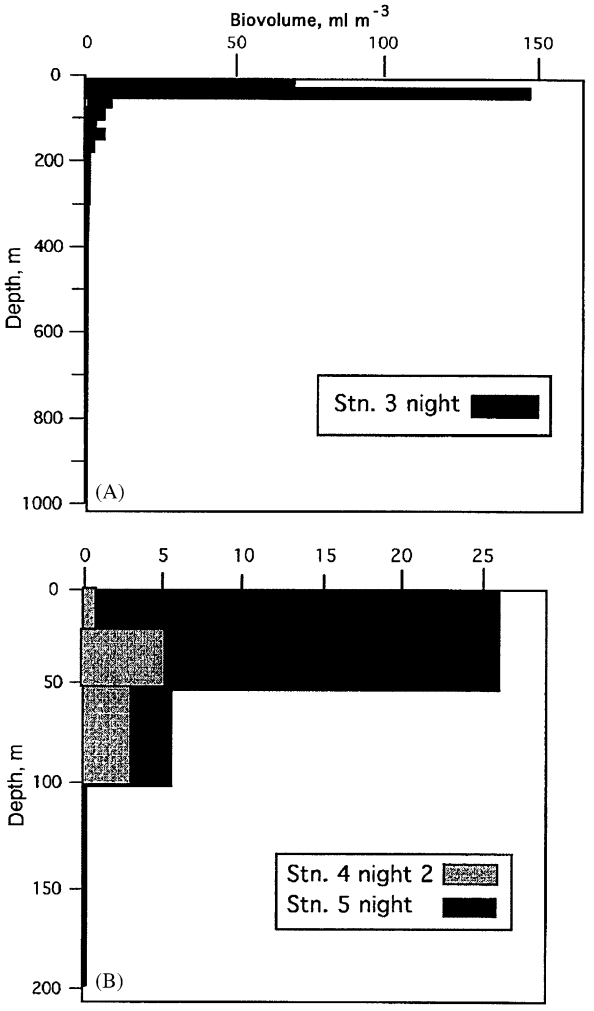

Fig. 4. Biovolume, $ml\,m^{-3}$, of *Salpa aspera* collected in night tows only. Width of each bar corresponds to depth interval for each net. (A) Station 3 with 95% of the biomass in the top 50 m (tows to 1000 m). (B) Tows to 200 m depth from two consecutive nights at Stations 4 and 5.

collections often included a small percentage of larger aggregate *S. aspera* in poor condition and unable to vertically migrate. The similarity of the results from diver and net collected samples indicates no large systematic loss of pigment in the majority of the net collected specimens. Therefore, where necessary, we supplemented results with gut pigment measurements from salps collected by net in calculating rates of ingestion and filtration.

3.4. Filtration rates from gut pigment content

Background fluorescence and gut passage times were determined for a range of sizes of *S. aspera*, both aggregate and solitary forms (Fig. 7). The relationship between background fluorescence and body length was clearly different for the two generations (Fig. 7A), but gut passage time for both the aggregate and solitary forms fit a single relationship with size (Fig. 7B). Some variability in the measurement of gut passage time is to be expected; the salps must be confined to make this measurement, and this is likely to cause intermittent feeding.

Filtration rates were calculated from gut pigment for both aggregates and solitary *S. aspera*. For aggregates, pigment values were used only from diver-collected salps (Fig. 8A). When multiple measurements were made on salps from the same chain, they were averaged and presented as a single point. Gut-pigment values for diver-collected solitaries ($n = 6$) were supplemented with 17 net collected salps from the top 50 m on the same night to increase both the sample number and size range (Fig. 8B). Filtration rates were calculated from size-specific values for gut-pigment background (Fig. 7A) and gut passage time (Fig. 7B), combined with estimates of ambient pigment concentration for particles $>2\,\mu m$ (Table 2), based on earlier studies of size retention efficiency for salps (Harbison and McAlister, 1979; Kremer and Madin, 1992). These calculations assume no pigment degradation, and therefore are conservative estimates of actual in-situ clearance rates.

Calculated filtration rates were variable, but showed a clear increase with salp length for both aggregates and solitaries (Fig. 8C and D). Aggregates were estimated to filter $0.2-21\,h^{-1}\,salp^{-1}$, and solitaries $0.4-71\,h^{-1}\,salp^{-1}$. Specific filtration rates (Fig. 8E and F) were calculated based on the biovolume of the salps, with most rates ranging from 0.5 to $21\,h^{-1}$ per ml biovolume for both aggregates and solitaries. Smaller salps generally had higher volume-specific rates than did larger ones (Fig. 8E and F).

3.5. Filtration rates from particle ingestion experiments

Filtration rates were also determined experimentally for comparison with the gut-pigment data. One experiment was conducted on each of four consecutive nights with aggregate salps that had been collected by divers. The decrease in the measured chlorophyll concentration in the experimental tank was used as a proxy for particle depletion. Time

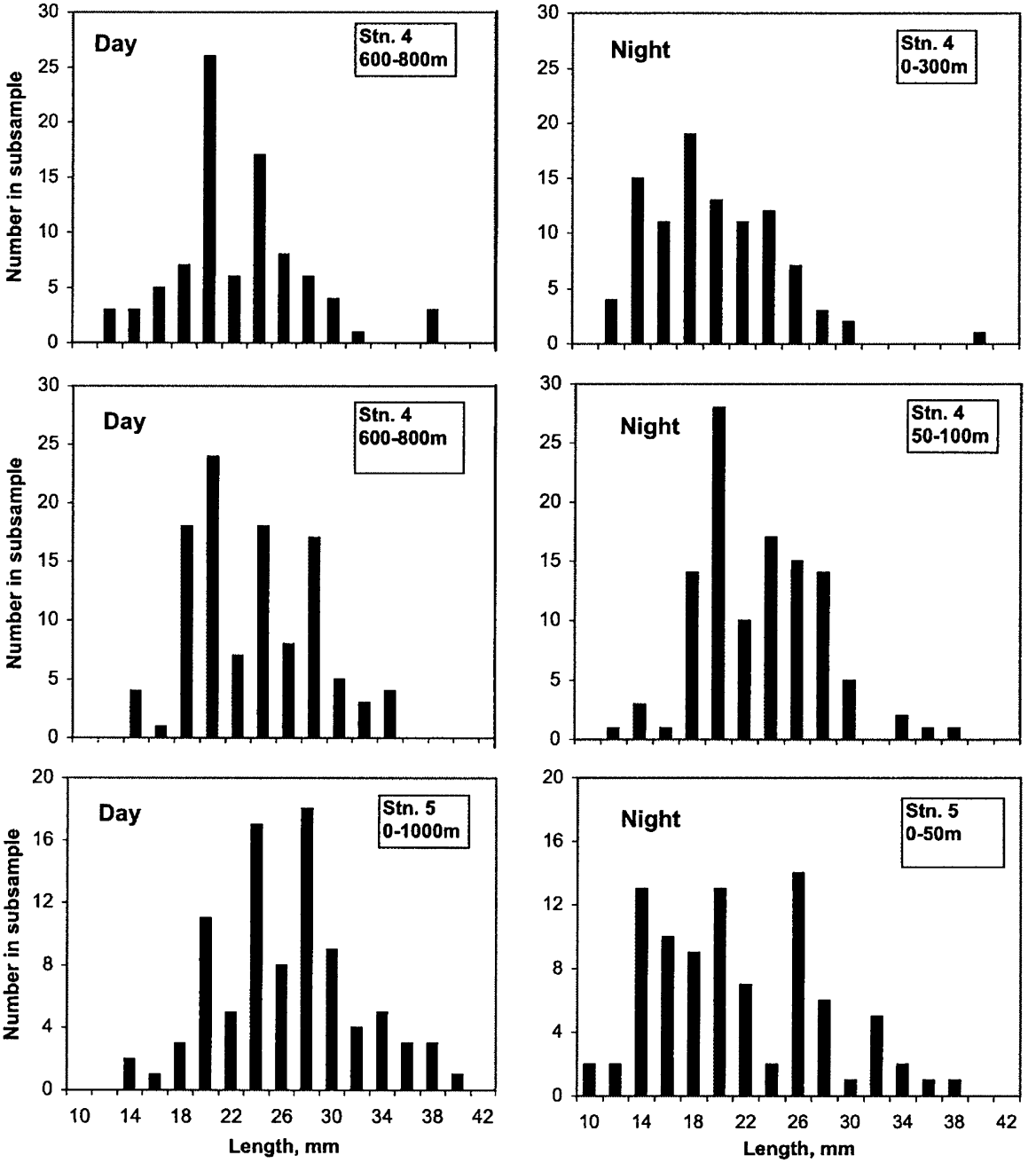

Fig. 5. Size-frequency plots for aggregate *Salpa aspera* collected during six MOCNESS tows. Collections made both during day and night. Each plot is for a subsample taken from the net that sampled the highest biomass for the tow.

series measurements of chlorophyll demonstrated a pattern of exponential decrease in experimental tanks but negligible changes in the control without salps (Fig. 9). It is likely that laboratory-derived filtration rates are conservative estimates of feeding rates due to artifacts associated with confinement of these fast-swimming salps in relative small (15 l) containers. Nevertheless, observations during the feeding experiments confirmed that the salp chains were intact and swimming continuously during the incubation. Results of the four feeding experiments compared favorably with filtration rates calculated from gut pigment from the same chain of aggregates (Table 3) and from other chains with aggregates of

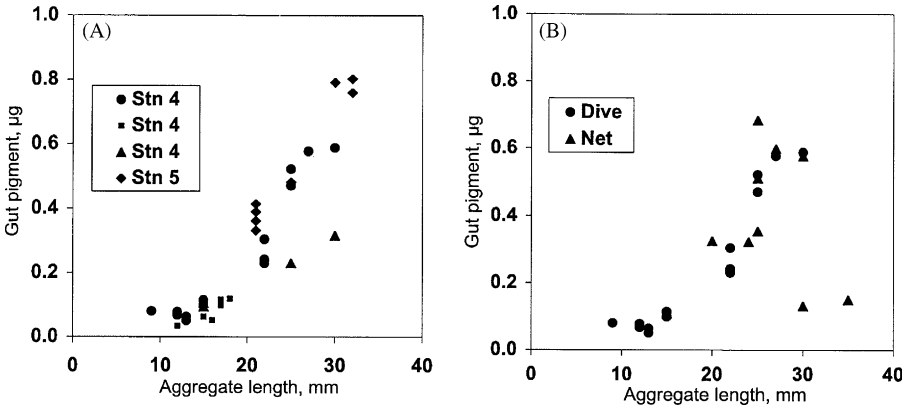

Fig. 6. Gut pigment (µg of Chl *a* equivalents) with length for aggregate *Salpa aspera*. (A) SCUBA collections on four consecutive nights at Stations 4 and 5. (B) Comparison of two collection methods, SCUBA and MOC-10 net in the top 20 m at Station 4.

Table 2
Composite results from 5 CTD casts at two stations for chlorophyll plus phaeopigment, carbon and nitrogen for two size fractions of particulates

Station	Casts	Depth	Total pigment	Pigment >2 µm	Carbon	Carbon >2 µm	Nitrogen	Nitrogen >2 µm	Total weight ratios	
	no.	(m)	(µg l^{-1})	(µg l^{-1})	(µg l^{-1})	(µg l^{-1})	(µg l^{-1})	(µg l^{-1})	C:pigment	C:N
4	3	20	0.15	0.04	95	43	8	4	633	12
		70	0.94	0.08	101	60	12	6	107	8
		300	0.03	0.02	46	44	3	3	1533	15
5	2	20	0.23	0.08	98	59	13	7	426	8
		35	0.84	0.11	121	89	17	11	144	7
		70	1.06	0.11	109	106	16	8	103	7
		300	0.04	0.02	62	48	4	3	1550	16

similar length (Fig. 8C and E). Estimates for clearance rates ranged nearly fourfold, 300–1100 ml h^{-1} salp^{-1}, with rates for the smaller aggregates (16 mm) lower than the rates for the chains of larger salps (20–22 mm).

3.6. Defecation rate

Cumulative defecation was linear over time (Fig. 10) for four chains measured as part of this study. The rates of pigment release were calculated from linear regressions on these data, and converted to rates of carbon and nitrogen defecation (Table 3) from results of independent samples ($n = 4$) that were divided in half and analysed for both pigment and elemental carbon plus nitrogen. These analyses gave a ratio of µg carbon: µg Chl *a* equivalent of 111 ± 20 (s.d.) by weight with a C:N ratio by weight of 12.7 ± 2.6 (s.d.).

4. Discussion

4.1. Periodic swarms of S. aspera

The results presented here show clearly that *S. aspera* intermittently forms "blooms" in the Slope Water south of New England. Over a period of 27 years, our sampling documented salp biomass in excess of 100 ml m^{-2} in four years, or 15% of the time. As these waters are appreciably offshore and not routinely sampled for zooplankton or micronekton, it is impossible to estimate the regularity and areal extent of these blooms, but if similar conditions of circulation, temperature, nutrients and phytoplankton distributions occur commonly in this region during summer, then it seems likely that *S. aspera* grow to swarm densities in this region more frequently. This hypothesis is supported by the supplementary observations reported here of *S. aspera* present in the slope water in January and

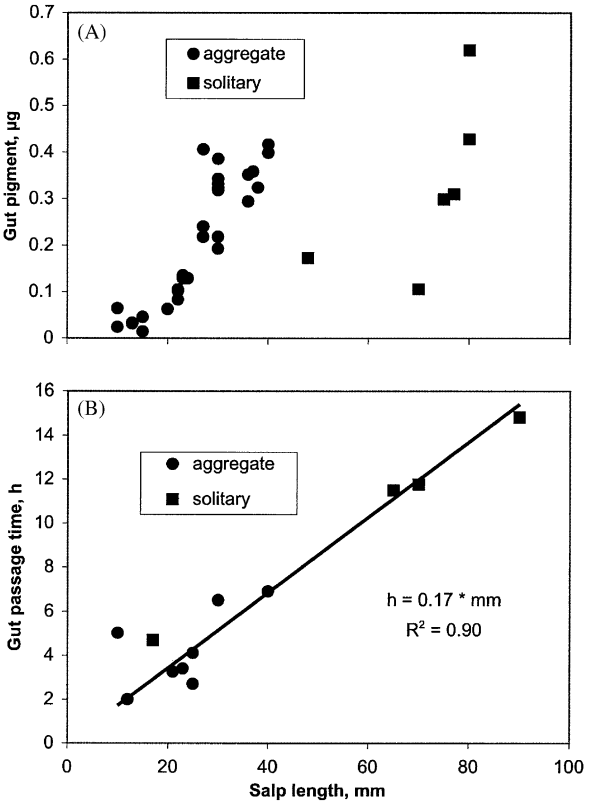

Fig. 7. (A) Gut background pigment with length for *Salpa aspera*. (B) Gut passage time (h) as a function of body length for *S. aspera*.

October 2004. There is additional indirect evidence for occurrences in other years. Both *S. aspera* and *S. fusiformis* were found along the southern flank of George Bank in May and June of 1995 and 1999 in association with warm water intrusions from the Slope Water south of the Bank (Brown et al., 2005). They were absent from any part of Georges Bank in 1996, 1997 and 1998, which might be due to their absence in the Slope Water, or the absence of water intrusions carrying them into the sampling area.

Unfortunately, prior to 2002, there was no systematic sampling to determine the areal extent of the high densities of *S. aspera*, but based on the results from 2002 (Fig. 1), we estimate the area of high salp density to be on the order of $100,000\,km^2$, comparable to the extent extrapolated by Wiebe et al. (1979) from a more limited set of samples. Using the biomass for two different years reported here, the estimated biomass of *S. aspera* during bloom conditions would exceed 100 ml biovolume m^{-2}, extrapolating to at least 10^7 metric tons wet weight of salps for the entire region.

4.2. Population grazing impact

The values for *S. aspera* gut pigment measured in this study were comparable to values measured for three other species of oceanic salps collected in the Atlantic Ocean (Madin and Cetta, 1984) but were generally lower than gut pigment for *S. thompsoni* in the Southern Ocean (Pakhomov et al., 2002). Differences in the gut pigment of *S. cylindrica* collected at different depths were shown previously to reflect pigment stock as measured by in vivo fluorescence (Madin and Kremer, 1995). The clearance rates measured in this study were comparable to rates determined for several other species of salps by several methods (Madin and Kremer, 1995) and also similar to clearance rates determined for *S. thompsoni* in the Southern Ocean, which lives at temperatures around 0 °C (Perissinotto and Pakhomov, 1998).

Using our estimates of clearance rates for *S. aspera*, we were able to calculate the grazing pressure, as percent of water cleared of particulates $\geqslant 2\,\mu m$, due to the entire salp population sampled at night at Stations 2–5 (Table 4). These calculations assume the salps are uniformly distributed in the top 50 m for 8 h per night, with an average clearance rate of $1.51\,h^{-1}\,ml^{-1}$ biovolume for the entire population (Fig. 8E and F). Assuming the particulate concentration decays exponentially in response to salp grazing, the calculated rate of removal of epipelagic particulates ranged from 8 to 74% d^{-1}, varying with the salp biomass (Table 4).

These calculations are conservative due to artifacts in the gut pigment and experimental feeding approaches, which lead to underestimates in both cases. Pigment degradation in the gut can be a significant loss in copepods (Conover et al., 1986; Dam and Peterson, 1988; Head, 1992), and in another salp species pigment appeared to be degraded by 50% (Madin and Purcell, 1992). This suggests that actual in-situ clearance rates could be as much as double the measured rates. Nevertheless, even with these conservative clearance rates, this study shows that when abundant *S. aspera* is a major pelagic grazer.

Furthermore, it should be noted that salps graze on a wide range of particulate matter, from quite small ($<2\,\mu m$) to relatively large (about 1 mm) particles, including all organisms unable to swim away (Madin, 1974; Kremer and Madin, 1992). *S. aspera* is capable of consuming picoplankton through microzooplankton. Depending on the salp

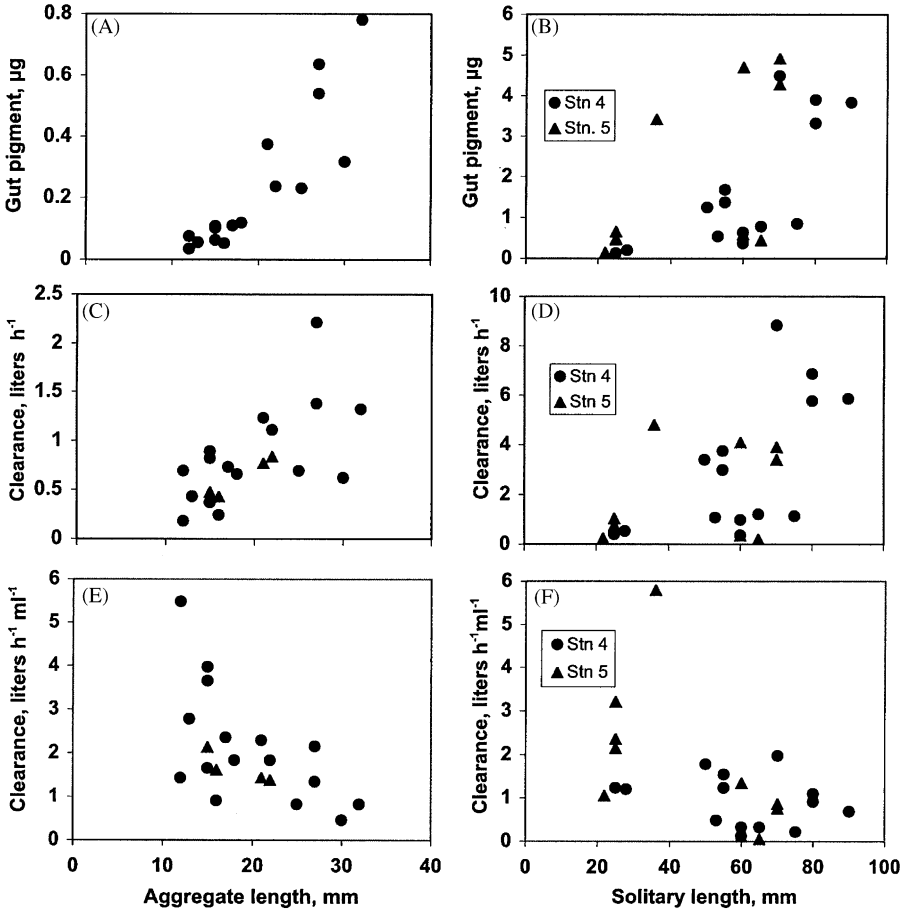

Fig. 8. Gut pigment per salp, filtration rate per salp, and volume-specific filtration rate ($l\,h^{-1}\,ml^{-1}$ biovolume) for aggregates (A, C, E) and solitaries (B, D, F) with length. All aggregates were collected by divers at Station 4. Data for solitaries are from both dive and net collections at both Stations 4 and 5. Results for feeding experiments using aggregates included in panels C and E (triangles).

biomass and the relative growth rates of the prey organisms, salps may substantially alter the trophic structure as well as transform a large fraction of the plankton productivity into large, rapidly sinking fecal pellets (Bruland and Silver, 1981; Madin, 1982). For example, a biovolume of 1000 ml *S. aspera* m^{-2}, typical of the biomass sampled in this study, would be expected to remove about 25% of the stock of small epi-pelagic particulates each night. If phytoplankton typically grow at rates of $0.6-0.7\,d^{-1}$ (Calbet and Landry, 2004), this stock of salps could remove about 35–40% of the primary production. In addition, the salps would be ingesting microzooplankton, the dominant grazers of the small phytoplankton (Calbet and Landry, 2004), potentially reconfiguring the epipelagic food web.

4.3. Contribution to vertical flux

Defecation rates measured in this study for chains of larger *S. aspera* aggregates (20 and 22 mm) were comparable to rates measured in earlier work for similarly sized salps of other species (Madin, 1982). Likewise the C:N ratio for feces of *S. aspera* (13:1 by weight) were similar to other species of salps from other collection areas (Madin, 1982; Caron et al., 1989), but 60% higher than the C:N ratio of 8 measured by Bathmann (1988) for *S. fusiformis* in swarm concentrations in the slope water west of Ireland, and about double the ratio measured for the same species in the California Current (Bruland and Silver, 1981). It should be noted that Bathmann's study also measured the C:pigment ratio by weight as 17:1, compared with >100: 1 in this study,

an indication that living phytoplankton composed more of the particulate matter in his study. Both higher nitrogen and pigment content relative to carbon would be expected in feces from salps grazing in more productive regions, compared to the relatively oligotrophic waters of this study.

The estimated vertical flux of carbon from the salps sampled at night in this study (Stations 2–5) ranged from 5 to 91 mg C m^{-2} $night^{-1}$ (Table 4) and was comparable to a previous estimate for a swarm of *S. aspera* in the same region (Wiebe et al., 1979). If an assimilation efficiency of 60% is applied to the ingestion estimates of *S. thompsoni* from the Southern Ocean (Perissinotto and Pakhomov, 1998), calculated egestion rates for that species would range between 0.8 and 88 mg C m^{-2} d^{-1}. The upper end of that range is nearly identical to the maximum estimates from this study of *S. aspera*.

The feces produced by *S. aspera* vary with salp size, but are large relative to fecal pellets of other zooplankton that graze the same size range of particulates. It is logical to assume the large, fast sinking salp feces (rates up to 2700 m d^{-1}; Bruland and Silver, 1981) are subject to less ingestion and recycling than material released from other, smaller, zooplankton and protists. Thus, a larger fraction of the particulate organic matter released by the salps would be expected to leave the upper water column and reach the ocean floor. This conjecture is supported by collections of recognizable salp feces in sediment traps (Iseki, 1981; Matsueda et al., 1986; Bathmann, 1988; Morris et al., 1988) that gave

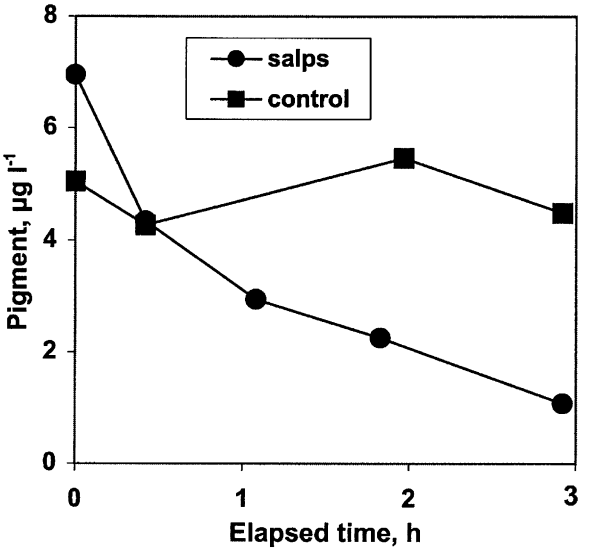

Fig. 9. Pigment (Chl *a*) concentration over time for water of experimental tank (with *Salpa aspera*) and control (without salps).

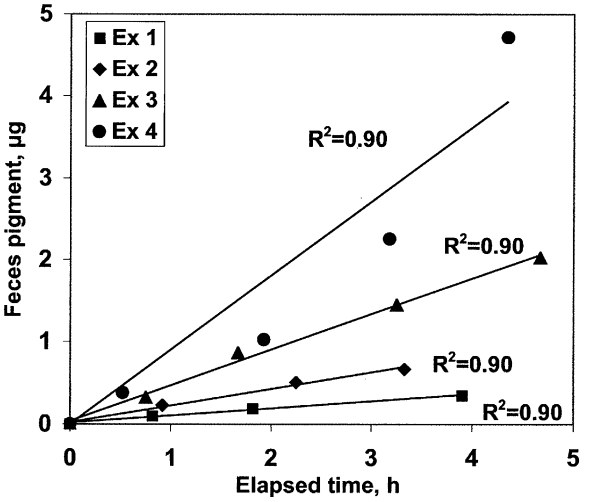

Fig. 10. Feces production by *Salpa aspera* with time, as measured by pigment. Feces quantitatively collected from chains of aggregates on four consecutive nights. Defecation rates per salp in terms of pigment, carbon and nitrogen given in Table 3.

Table 3
Estimates of clearance rates (l h^{-1} $salp^{-1}$) for four chains of *Salpa aspera* aggregates by both the gut pigment method and direct measurements from feeding experiments. Defecation rates for each chain are calculated from measurements of fecal pigment combined with independent estimates of ratio of carbon:nitrogen:pigment for salps from Station 4 only

Station	Aggregates in chain (*n*)	Length (mm)	Gut pigment clearance rate	Feeding experiment (l h^{-1} $salp^{-1}$)	Defecation rate (µg h^{-1} $salp^{-1}$)		
					Carbon	Nitrogen	Pigment
4	31	16	0.3	0.4	0.3	0.02	0.003
4	44	16	0.8	0.5	0.6	0.05	0.005
4	28	22	1.1	0.8	1.8	0.13	0.016
5	38	20	1.1	0.8	3.1	0.25	0.028

Table 4
Estimates for particle clearance and defecation by populations of *Salpa aspera* sampled at night

Station	Biovolume[a] ($ml\,m^{-2}$)	Clearance rate[b] ($l\,m^{-3}\,h^{-1}$)	% Particle removal[c] ($night^{-1}$)	Defecation rate[d] ($mg\,C\,m^{-2}\,night^{-1}$)
2	325	10	8	5
3	5713	171	74	91
4	1243	37	26	20
4	327	10	8	5
5	1587	48	32	68

[a]Assumes the whole salp biomass is distributed uniformly in the top 50 m.
[b]Based on an average clearance rate of $1.5\,l\,h^{-1}\,ml^{-1}$ biovolume (Fig. 8E and F).
[c]Assumes night equals 8 h, and particulate concentration decreases exponentially.
[d]Assumes $2\,\mu g\,C\,h^{-1}\,ml^{-1}$ biovolume for Stations 2–4 (Table 3) and Fig. 2B, and $5\,\mu g\,C\,h^{-1}\,ml^{-1}$ biovolume for Station 5.

estimates of carbon flux from salp swarms based on sediment trap collections that are consistent with the rates of defecation we calculated in this study for *S. aspera* (Table 4).

Despite faster sinking, salp fecal pellets may also be an important resource for scavengers and detritivores in the deeper water column. For example, small cyclopoid copepods are abundant throughout the water column (Paffenhöfer and Mazzochi, 2003) and consume zooplankton fecal pellets (González and Smetaceck, 1994).

In oceanic waters much of the primary production is by small cells, picoplankton less than 5 μm in diameter, and most of the consumption is by microzooplankton (Calbet and Landry, 2004), leaving relatively little energy to support the larger mesozooplankton such as copepods. As salps are capable of ingesting smaller particles than copepods can (Madin, 1974), they can directly consume the larger picoplankton (Caron et al., 1989) as well as larger protists, not only shunting energy away from the epipelagic "microbial loop" but also consuming its constituents. Salps can transform these small particulates into large, fast sinking feces, removing both particulate carbon and particulate nitrogen from the photic zone. By this process salps would play roles both in changing the food web of the epipelagic and in sequestering organic carbon in the deep sea.

4.4. Swarms of Salpa spp.

For most of the area of the open ocean one would expect production levels to be too low to support the in situ development of salp populations to swarm densities. Nevertheless, recurrent swarms of the genus *Salpa* have been documented in several locations (Table 5). Many of these report *S. fusiformis*. In older studies this could be a mistaken identification of *S. aspera*, which was usually considered a subspecies of *S. fusiformis* prior to Foxton (1961). Undoubtedly many more such sites exist, but have not yet been documented in published results. Dense populations like these occurring repeatedly in particular regions can be considered 'hot spots', defined as areas of recurrently enhanced biomass of zooplankton or related processes (Marine Zooplankton Colloquium 2, 2001). Swarms of salps can create some of the largest of these hot spots, as exemplified by the $100,000\,km^2$ distribution we found in 2002.

What do these locations have in common that makes them prime habitat for salp population growth to swarm densities? Ecological energetics dictates that relatively high primary production is a pre-requisite. There must be sufficient organic matter being formed to support the production of high salp biomass. Paradoxically, however, studies have documented that some species of salps will cease feeding if their feeding nets are clogged by phytoplankton blooms (Harbison et al., 1986; Perissinotto and Pakhomov, 1997). Since all salps have essentially the same mucous net feeding mechanism, it is likely that all may be subject to clogging of the nets at some high concentration of particulates (Madin and Deibel, 1998). The efficiency of the salps' filter feeding, while an excellent adaptation to relatively low food concentrations in oceanic waters, appears to limit their distribution in richer coastal environments, with a few exceptions, such as *T. democratica* in shelf waters and *S. thompsoni* in the Southern Ocean. Thus a favorable scenario for many salp species to form blooms would be one of sustained primary

Table 5
Documented locations for recurrent swarms of the genus *Salpa*. Some early reports of *S. fusiformis* may actually be *S. aspera*

Species	Location	Reference
S. aspera	Slope Water, NE United States	Wiebe et al. (1979); this paper
S. fusiformis	Shelf and Slope Water, NE United States	Grice and Hart (1962)
S. fusiformis	Eastern North Atlantic (North Atlantic Drift System)	Fraser (1949, 1962); Hunt (1968); Brattstrom (1972); Roskell (1983); Bathmann (1988)
S. fusiformis	Western Mediterranean sea	Menard et al. (1994)
S. fusiformis	Gulf of Guinea, West Africa	Le Borgne (1983)
S. fusiformis	California Current, E. Pacific	Berner (1967); Hubbard and Pearcy (1971)
S. fusiformis	So. California Bight, U.S.A.	Lavaniegos and Ohman (2003)
S. fusiformis	Hauraki Gulf, New Zealand	Zeldis et al. (1995)
S. thompsoni	Various locations in Southern Ocean around Antarctica	Foxton (1966); Park and Wormuth (1993); Siegel and Loeb (1995); Loeb et al. (1997); Voronina (1998); Pakhomov et al. (2002)

production, but without high concentrations of large cells. This might be regulated by a growth rate of the salp population that is sufficient to 'keep up' with the phytoplankton growth such that salp grazing can always keep the standing stock of particulates below a level at which clogging occurs (Fortier et al., 1994). Several physical mechanisms in the ocean, such as frontal convergences, upwellings or diapycnal mixing events could produce the necessary conditions for phytoplankton growth to support a salp swarm.

The variety of locations known for swarms of *Salpa* spp. (Table 5), as well as other species cited earlier in this paper, suggests that bloom populations of various species may be expected to occur repeatedly in some locations and less predictably in others. Because of the irregular zooplankton sampling that has been carried out in the Slope Water off the NE United States, it is not possible to conclude how often salp swarms occur in these waters. We are able to conclude that salps occurred in high abundance in at least four years (1975, 1986, 1993, 2002), and there is evidence for the presence of *S. aspera* in the Slope Water in 1995, 1999 and 2004. The results presented here are clear evidence that large populations of salps can occur over large areas, producing significant local impacts on the biological structure and biogeochemical fluxes of the water mass in which they occur.

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