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SHORT COMMUNICATION

Zooplankton feeding ecology: clearance and ingestion rates of the salps *Thalia democratica*, *Cyclosalpa affinis* and *Salpa cylindrica* on naturally occurring particles in the Mid-Atlantic Bight

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Aggregate stages of the salps Thalia democratica, Cyclosalpa affinis and Salpa cylindrica collected by SCUBA diving in the Mid-Atlantic Bight were fed with naturally occurring food assemblages. This is one of the few studies where salps have been fed with natural food assemblages. The estimated clearance rate for all species based on disappearance of chlorophyll varied from 82 to 444 mL individual^{-1} day^{-1}. Cell counts showed that T. democratica mostly ingested carbon from autotrophic nanoflagellates and autotrophic dinoflagellates. Ingestion by S. cylindrica was primarily on larger prey, such as dinoflagellates, while C. affinis ingested auto- and heterotrophic nanoflagellates. All main prey types ingested by salps corresponded to those that contributed most to biomass at each experimental station. Thus, salps fed on naturally occurring particles primarily in proportion to prey biomass and to their mechanical capacity to be retained and ingested. Feeding by salps on dinoflagellates and ciliates implies that they may act not only as potential competitors with microzooplankton, but also as consumers of them.

During the last three decades, a large effort has been directed at understanding the feeding ecology of salps, their grazing impacts on phytoplankton populations and their role in vertical carbon fluxes (Andersen, 1998). Salps exhibit considerably higher grazing rates than either crustacean herbivores or microzooplankton, on an individual basis (Alldredge and Madin, 1982; Madin and Purcell, 1992). Salps are generalist feeders, and can consume a wide range of food particles. Bacteria, flagellates, diatoms, radiolarians, detritus, copepod parts, and even pteropods have been observed in the faecal pellets and gut contents of salps (Silver, 1971). In experiments with artificial diets, salps were able to graze upon various size ranges of particles from 2 μm to 1 mm (Harbison and McAlister, 1979; Kremer and Madin, 1992). However, the particle sizes that can be retained by salps when feeding on naturally occurring particles have rarely been reported [e.g. (Deibel, 1985)]. Therefore, it is important to improve our knowledge about the trophic niche of these pelagic tunicates in coastal and oceanic food webs.

Previous studies suggest that salp populations develop regularly during the summer in the Mid-Atlantic Bight region (Wiebe *et al.*, 1979; Madin *et al.*, 1994). If salps are able to define or modify the fate of bacteria and small-sized phytoplankton and microprotozoan production, they could have a significant impact on the pathway of carbon export and cycling in this area. In order to provide insight on this matter, the present study aimed

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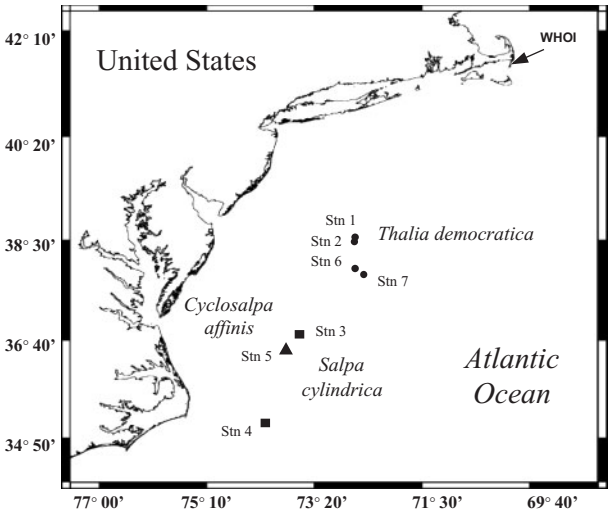

Fig. 1. Study area in the Mid-Atlantic Bight showing the position of the sampling stations. The occurrence of salps in the study area is also shown (●, *T. democratica*; ■, *S. cylindrica*; ▲, *C. affinis*).

to study the feeding of salps on the full size spectrum of food particles (phytoplankton, protozoans and bacteria) in the Mid-Atlantic Bight area. We measured the clearance and ingestion rates of the salps *Thalia democratica*, *Cyclosalpa affinis* and *Salpa cylindrica* on natural assemblages of bacteria, protozoans and phytoplankton.

All collections and experiments were carried out during a cruise from 3 to 16 July 2001 on board the RV 'Oceanus' (Woods Hole Oceanographic Institution; WHOI). Grazing experiments were conducted at seven stations (Stns) in the Mid-Atlantic Bight area (Figure 1). Since salps are fragile organisms that are easily damaged by plankton net sampling, swimming chains of salps were collected gently under water by SCUBA diving and kept completely immersed during handling. Within 1 h after collection, 1–3 salp chains, consisting of 3–9 aggregate generation salps, were used in experiments. Only on 7 July was an experiment with solitary generation salps of *T. democratica* performed. Water for incubations was collected from the surface by using 10 L buckets lowered from the deck. The animals were carefully transferred into 1 L containers with a large-bore pipette or a small spoon. Three control containers without animals and three containers with animals were placed on a rotating plankton wheel (0.2 r.p.m.) in darkness and at *in situ* temperature (26–29°C) for 5–8 h. The number of salps in experimental containers ranged from 7 to 15 individuals (ind.) L^{-1} depending on their size (Table I). An initial control sample was immediately preserved with 2% acid Lugol's and a subsample was preserved in glutaraldehyde (6.0% w/v in 0.2 μm prefiltered seawater). At the end of the incubation, subsamples from all containers were taken and preserved in glutaraldehyde for bacterial biomass (20 mL), nanoflagellate counts (30 mL) and in acid Lugol's (60 mL, as above) for cell concentration (100 mL). Subsamples (100 mL) for determination of chlorophyll (Chl) *a* were also filtered and dark extracted in 95% acetone before measurement on a TD 700 Turner fluorometer (Strickland and Parsons, 1972).

Samples were counted with the aid of a Zeiss epifluorescence microscope. Bacteria and nanoflagellates were quantified by the acridine orange technique (Hobbie *et al.*, 1977; Davis and Sieburth, 1982). Bacteria were separated into two groups: small (rods < 1 μm) and large bacteria (bacillus > 1 μm). Bacterial volume was calculated from length and width measurements of at least 50 cells per sample. The biovolumes were converted to carbon using the equation C (fg) = 90.06 × $V^{0.59}$, where V is bacterial

Table I: Feeding experiments conducted with different salp species in the Mid-Atlantic Bight area during summer July 2001

Experiment	Date	Location	Species	Stage	Size (mm ± SD)	Density (no L^{-1} ± SD)	*n*	Duration (h)	Temperature (°C)	Clearance rate (mL ind.$^{-1}$ day^{-1} ± SD)
1	5 July	38°29′N–73°W	*Thalia democratica*	Aggr	8.6 ± 0.1	14.2 ± 3.4	3	8	26	123.9 ± 22.2
2	7 July	38°25′N–73°W	*Thalia democratica*	Sol	7.3 ± 0.3	14.2 ± 1.6	3	7	27	82.1 ± 76.1
3	9 July	36°27′N–74°02′W	*Salpa cylindrica*	Aggr	4.1 ± 0.1	15.3 ± 5.7	3	5.5	27	444.4 ± 252.9
4	10 July	35°02′N–74°29′W	*Salpa cylindrica*	Aggr	4.0 ± 0.1	11.7 ± 0	3	6.5	29	151.1 ± 54.7
5a	11 July	36°38′N–74°23′W	*Cyclosalpa affinis*	Aggr	13.7 ± 0.8	7.7 ± 1.6	3	7	26.5	185.2 ± 36.8
5b	11 July	36°38′N–74°23′W	*Cyclosalpa affinis*	Aggr	13.7 ± 1.2	8.4 ± 0	3	7	26.5	259.2 ± 163.0
6	12 July	37°59′N–72°59′W	*Thalia democratica*	Aggr	7.5 ± 0.05	11.6 ± 0	3	8	26	224.5 ± 89.5
7	13 July	37°54′N–73°01′W	*Thalia democratica*	Aggr	7.2 ± 0	14.6 ± 4	3	5.5	26	166.8 ± 52.2

Clearance rates based on changes in total Chl *a* are shown for the solitary forms and aggregate chains. Aggr, aggregates; Sol, solitary stage; *n*, number of replicate grazing bottles; SD, standard deviation.

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volume (μm^3) (Simon and Azam, 1989). Nanoflagellates were counted and separated into two groups: <5 and 5–20 μm. Autotrophic cells were distinguished by their autofluorescence. Large cells were identified, counted and measured under an inverted microscope. Plasma volumes were calculated (Edler, 1979) and averaged from a minimum of 40 cells per species. Biovolumes of ciliates were calculated assuming conical shapes with length to diameter ratios of 1.25 for ciliates <50 μm and of 2 for ciliates >50 μm (Tiselius, 1989). Carbon to plasma volume ratios of 0.11 pg C μm^{-3} for diatoms (Edler, 1979), 0.3 and 0.19 pg C μm^{-3} for heavily thecate and athecate dinoflagellates forms, respectively [E. J. Lessard, unpublished data, *fide* (Gifford and Caron, 2000)], and 0.148 pg C μm^{-3} for ciliates (Ohman and Snyder, 1991) were applied. Clearance and ingestion rates were calculated on changes in Chl *a* concentration (for all stations) and prey biomass (for Stns 1, 3 and 5) according to Frost (Frost, 1972) for the following groups: small and large bacteria, auto- and heterotrophic nanoflagellates (<5 and 5–20 μm), auto- and heterotrophic dinoflagellates, ciliates, pennate and centric diatoms, and chain-forming diatoms. Clearance was calculated only when the difference in prey biomass between control and experimental bottles proved to be significant (*t*-test: $P < 0.05$).

One of the biases in using this incubation method is that the prey suspension contains several trophic levels, and cells may be consumed by other components besides the salps. In order to correct for this bias, a three-component equation template that considers interactions among three grazers in differently structured food chains (Tang *et al.*, 2001) was applied. Values for potential protozoan ingestion used in this equation template were estimated using an equation proposed by Peters, which includes temperature, cell volumes, and concentrations of both prey and predator as explanatory variables (Peters, 1994). Corrections were made for the interactions bacteria–flagellates–salp, flagellates–ciliates–salp and diatoms–heterotrophic dinoflagellates–salp.

The natural phytoplankton and protozoan provided as food varied in abundance among the experiments. As is typical in the open ocean, particle abundance in the study area was dominated by small cells, mostly bacteria (10^7–10^8 cells L^{-1}), followed by small auto- and heterotrophic flagellates (10^5–10^6 cells L^{-1}), and then a low number of ciliates, dinoflagellates and diatoms (10–10^3 cells L^{-1}), particularly at Stn 5 (Figure 2). In terms of carbon biomass available to be ingested, seawater contained predominantly carbon from small nanoflagellates between 5 and 20 μm, most of which were autotrophic cells (Figure 2). The exception occurred at Stn 3, where auto- and heterotrophic dinoflagellates constituted the most important fraction of the biomass.

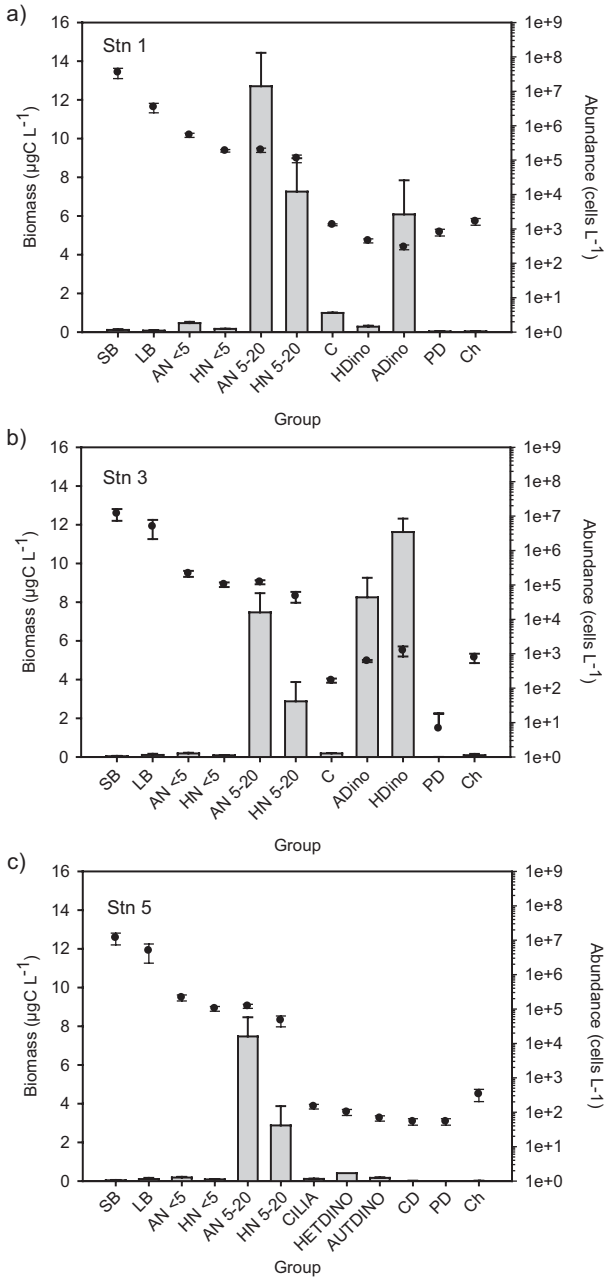

Fig. 2. Contribution of major taxonomic groups to the surface (2 m depth) biomass (bars in μg C L^{-1}) and abundance (● in cells L^{-1}) of the autotrophic and heterotrophic community at the sampling stations during the feeding experiments. Error bars are standard deviations from replicate samples ($n = 3$).

Bacteria and diatoms were less important in terms of biomass throughout the study area. The salp *T. democratica* occurred mostly in the northern part of the Mid-Atlantic Bight at Stns 1, 2, 6 and 7, while blastozooids of *C. affinis* occurred at Stn 5 (Figure 1). Some blastozooids of *S. cylindrica* were found in the southern part of the

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study area at Stns 3 and 4. The clearance rate of all these species, based on changes in Chl *a* varied from 82 to 444 mL ind.$^{-1}$ day^{-1} (Table I). Some differences in clearance between individuals and experiments were observed. For instance, the smallest salp studied here, *S. cylindrica*, exhibited higher clearance at Stn 3 than Stn 4. Even though non-significant differences among species were observed in clearance based on Chl *a* depletion, *S. cylindrica* showed the maximum clearance and *T. democratica* the lowest.

Large faecal pellets, which were fragile and amorphous particles, were usually observed at the bottom of the experimental container at the end of each experiment. These faecal fragments may have contaminated the water sample for Chl measurements, causing clearance rate calculated from Chl *a* depletion to underestimate the actual removal of particles. In fact, the ratio of Chl *a*:phaeopigment in experimental bottles ranged from 0.05 to 0.09, which suggests a possible effect of faecal resuspension on Chl measurements. Even though we did not include phaeopigment in clearance estimations, this artifact could help explain differences observed between clearance rates from Chl *a* depletion and from cell counts. We believe that the clearance rates calculated from cell counts are more reliable values than those based on changes in total Chl *a*.

Monitoring the removal of particles from the water over time is a common technique for measuring clearance of zooplankton [e.g. (Deibel, 1985)]. However, most particle depletion experiments have used artificial or uni-algal diets. Cell counts showed that salps removed different particle types in proportion to their abundance in field stations where experiments were carried out (Figures 2 and 3). For instance, *T. democratica* mostly ingested carbon from autotrophic nanoflagellates (5–20 μm) and autotrophic dinoflagellates (Figure 3), the most abundant items in terms of biomass at Stn 1 (Figure 2a). Only large bacteria (bacillus > 1 μm) were cleared efficiently by this species. Conversely, most of the carbon ingestion by *S. cylindrica* was based on large prey, such as auto- and heterotrophic dinoflagellates, because they contributed most to the biomass at Stn 3 where the experiments were carried out. Therefore, this could explain why this small species retained larger particles than the other species included in this study. Most carbon ingestion by *C. affinis* was based on auto- and heterotrophic nanoflagellates between 5 and 20 μm. This species was also able to feed on small and large bacteria at high rates (~500 mL ind.$^{-1}$ day^{-1}). However, dinoflagellates and diatoms were removed at very low rates for this species. Even though the small *T. democratica* and *S. cylindrica* did not exhibit such high clearance values as exhibited by *C. affinis* on nanoflagellates, particle removal was relatively homogeneous on whole naturally occurring cells (200–600 ml ind.$^{-1}$ day^{-1}). Therefore, the total carbon ingestion by these small species would not be significantly different to that exerted by *C. affinis* on nanoflagellate carbon (Figure 3). This could explain why *S. cylindrica* showed a high

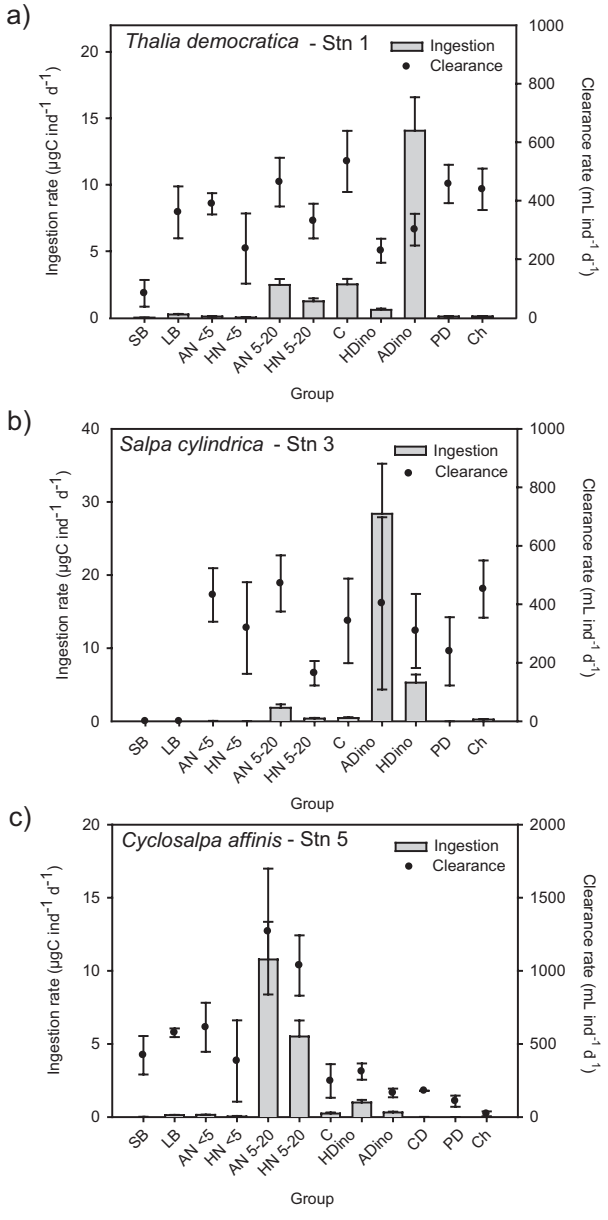

Fig. 3. Clearance (●) (mL ind.$^{-1}$ day^{-1}) and ingestion rate (bars) (μg C ind.$^{-1}$ day^{-1}) of major autotroph and heterotroph groups by the salps (**a**) *T. democratica*, (**b**) *C. affinis* and (**c**) *S. cylindrica*. SB, small bacteria; LB, large bacteria; HN, heterotrophic nanoflagellates; AN, autotrophic nanoflagellates; C, ciliates; HDino, heterotrophic dinoflagellates; ADino, autotrophic dinoflagellates; CD, solitary centric diatoms; PD, pennate diatoms; Ch, chain-forming diatoms. Error bars are standard deviations from replicates (n = 3).

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clearance based on total Chl depletion, but medium–low clearance on different particles of the cell size spectrum (Table I). Although field abundance of bacteria and flagellates was relatively high (Figure 2), and a high clearance on these particles was observed, their contribution to carbon ingested by salps was low (Figure 3). Considering the mean cell carbon concentration in the study area, salps could ingest in the field a range between ~6 and 8 μg C ind.$^{-1}$ day^{-1}.

Retention efficiency (%), as a function of the equivalent spherical diameter (ESD) of cells (Figure 4), showed that maximum retention efficiency by *T. democratica* and *S. cylindrica* occurred on cells between 20 and 50 μm. *Cyclosalpa affinis* showed the highest capacity for retention on bacteria and flagellates, which corresponds to the dominant items at Stn 5. *Salpa cylindrica* was not able to feed on any kind of bacteria. Similar to findings by Kremer and Madin (Kremer and Madin, 1992) for *Pegea confoederata*, *Salpa aspera*, *Cyclosalpa polae* and *Brooksia rostrata*, cells <2 μm (bacteria in our study) are inefficiently caught by *S. cylindrica*, while particles >10 μm were retained with almost 100% efficiency (Figure 4b). However, retention efficiency around 40–50% on bacteria of size 1–2 μm by *T. democratica* and *C. affinis* suggests that this species may be able to retain small particles as effectively as can high-latitude salps [e.g. *S. thompsoni* (Nishikawa and Tsuda, 2001)]. Large prey such as large diatoms and ciliates were not efficiently retained by *C. affinis* and *S. cylindrica*. An explanation for this result could be clogging of the oesophagus when salps encounter high particle concentrations or too large prey, because the feeding mechanism in salps is not modulated in response to food size and density (Harbison *et al.*, 1986).

Although these results suggest a role of small bacteria as a food source for salps, it is possible that salps may feed not only on solitary small cells, but also on small bacteria attached to detrital aggregates or on transparent exopolymeric particles (TEPs). Salps are non-selective, omnivorous filter feeders (Madin and Kremer, 1995), but it has usually been reported that they cannot graze particles smaller than ~2 μm. Previous studies on particle retention efficiency have shown that warm-water salps can retain efficiently particles >3 μm (Harbison and MacAlister, 1979; Caron *et al.*, 1989; Kremer and Madin, 1992). However, our results for *T. democratica* and *C. affinis* indicate that these species can indeed feed on particles <1 μm, such as small bacteria. Since the species-specific retention capabilities of salps should define the kind of particle to be ingested, there is no selection of particles on a qualitative basis (i.e. autotrophic versus heterotrophic cells). Unfortunately, there are few direct measurements of the structural characteristics in the pharyngeal filter of salps. Our results showed that all these salp species were feeding on naturally occurring particles primarily in proportion to their abundance at field stations and to their mechanical capacity to be retained and ingested (Figures 2 and 3) [selectivity index (Jacobs, 1974) = <−0.2].

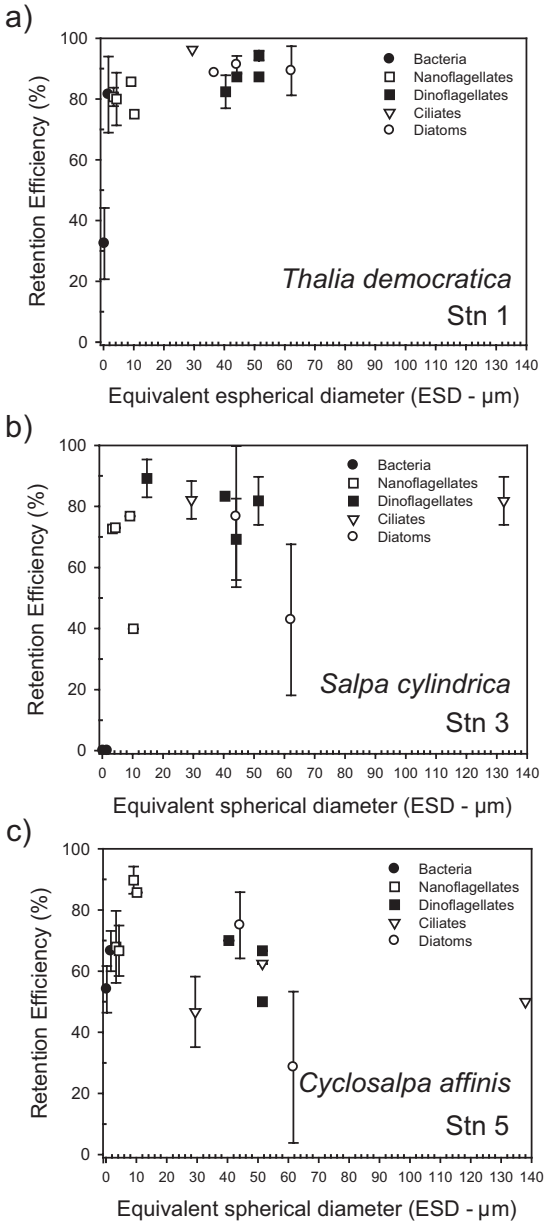

Fig. 4. Particle retention efficiency (%) for three species of salps, (**a**) *T. democratica*, (**b**) *S. cylindrica* and (**c**) *C. affinis*, on different taxon-specific cell sizes (ESD; μm) of bacteria, nanoflagellates, dinoflagellates, ciliates, pennate and centric diatoms. Errors bars indicate ±SE of the mean.

Another potential bias in our study could be the 'food chain effects' during incubations. We corrected our estimates using the three-component equation template proposed by Tang *et al.* (Tang *et al.*, 2001), which indeed

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resulted in grazing values on phytoplankton ~10% higher than uncorrected values. We believe that trophic artifacts may have been partially corrected in our clearance rate estimates by this method. Container effects are also sources of error in particle clearance experiments, but results from our relatively short incubations and small salp species probably should be more realistic (Madin and Kremer, 1995). In fact, most of these clearance rates are comparable to those reported elsewhere for the same species. For instance, rates given by Deibel (Deibel, 1985) for *T. democratica* ranged between 0.5 and 18 mL ind.$^{-1}$ h^{-1}, and those by Madin and Deibel (Madin and Deibel, 1998) for *C. affinis* showed clearance rate values around 100 mL ind.$^{-1}$ h^{-1} for aggregates and 30–80 mL ind.$^{-1}$ h^{-1} for *T. democratica*.

Extensive populations of salps (e.g. *S. aspera*) have been reported from the Mid-Atlantic Bight region on several occasions (Wiebe *et al.*, 1979; Madin *et al.*, 1994), occupying some part of an area bounded by Cape Hatteras and Georges Bank, the shelf break and the Gulf Stream. The Chl *a* concentration is low in this region, and generally pico- and nanophytoplankton dominate the autotrophic biomass (Ryan *et al.*, 1999). Since small copepods are basically suspension feeders that feed mainly on particles >5 μm (Paffenhöfer, 1986; Turner and Tester, 1989), the pico–nanophytoplankton fraction would be available only for the large microphagous salps and microzooplankton. Feeding on autotrophic and heterotrophic dinoflagellates and ciliates indicates that salps may act not only as potential competitors with the 'microbial loop', but also as a consumer of its constituents.

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