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Note

Feeding of the pelagic tunicate, *Salpa thompsoni*, on flagellates and size-fractionated chlorophyll particles

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The pelagic tunicate, *Salpa thompsoni* is one of the key macrozooplankton species in the Southern Ocean, exhibiting large biomass stocks at various locations, mainly in the oceanic region (e.g. Piatkowski et al. 1994; Table 3 in Nishikawa et al. 1995; Chiba et al. 1998; Perissinotto & Pakhomov 1998a). However, trophic relationships concerning this antarctic salp are poorly understood, both concerning its predators and prey. Feeding studies on salps from other oceans have clarified that: they are typical filter feeders using mucous feeding nets (Madin 1974), and are able to feed upon various size ranges of particles from 3–4 μm to 1 mm (Harbison & McAlister 1979; Kremer & Madin 1992). Reported clearance rates for mid-latitude salps are several liter animal^{-1} h^{-1}, and much higher than almost any other zooplanktonic grazer, on an individual basis (Madin and Deibel 1998). However, information on the feeding ecology of antarctic salps is still limited. For *Salpa thompsoni*, clearance rates have been studied (Reinke 1987; Huntley et al. 1989; Perissinotto & Pakhomov 1998b). However, the particle-size range that can be utilized by *S. thompsoni* has not been reported, even though this may be important in characterizing their unique trophic niche as macrozooplankters in antarctic off-shore food-webs. The goal of our study is to clarify the mechanism by which *S. thompsoni* maintain large stocks in the Southern Ocean. In this study, feeding characteristics such as clearance rates and ingestable particle-size ranges are investigated.

All collections and experiments were carried out during the Southern Ocean Expedition of the R/V *Hakuho Maru* KH-94-4. Grazing experiments were carried out at a station (64°10′S, 140°40′E) north of the Antarctic Divergence from 11 to 12 January 1995. Since salps are fragile animals that can be damaged by ordinary net sampling, swimming chains of salps were scooped up gently using 20-liter buckets lowered from the deck during the night when they moved up to the surface. Five salp chains, consisting of 3 to 65 blastozooids, with body lengths (oral–atrial distance) from 20 to 40 mm were used for the experiments (Table 1). The buckets with salps and surface seawater (temperature at 3°C with no remarkable change during experiments) were incubated without any additional manipulation on deck under natural light conditions. The surface seawater without salps was used as a control. Incubations lasted 2 or 4 h. At the beginning and the end of the experiments, seawater samples were taken from both experimental and control buckets. The concentrations of flagellates and that of chlorophyll-*a* were measured. For the total flagellate counts, 100 ml of the seawater was preserved with gultaraldehyde (final concentration was 2%) and 2 to 5 ml of the samples were

Table 1. Grazing experiments on salps. Filtering rate on size-fractionated chlorophyll-*a* and on flagellates are shown for the five blastozooid chains.

Exp. number	On chlorophyll ·		On flagellates
	(ml h^{-1} indiv.$^{-1}$)		
1 (BL 40 mm, 5 indiv.)	0.2–2 μ	257	
	2–20 μ	118	208
	>20 μ	75	
	Total	75	
2 (BL 34 mm, 13 indiv.)	0.2–2	33	
	2–20	90	43
	>20	45	
	Total	47	
3 (BL 20 mm, 65 indiv.)	0.2–2	failed	
	2–20	7	65
	>20	2	
	Total	1	
4 (BL 35 mm, 13 indiv.)	0.2–2	60	
	2–20	94	190
	>20	92	
	Total	91	
5 (BL 34 mm, 3 indiv.)	0.2–2	42	
	2–20	61	368
	>20	55	
	Total	55	

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DAPI-stained and thereafter filtered onto black-stained Nucleopore filters (2 μm opening). The stained flagellates were enumerated with an epi-fluorescence microscope (Zeiss Axioplan). To examine the size range of particles upon which salps can feed, three size categories of chlorophyll-*a* containing particles; 0.2–2.0, 2.0–20, and >20 μm were used. Size fractionation of chlorophyll particles was done using a screen (20-μm mesh) and Nucleopore filters (0.2 and 2.0 μm). The chlorophyll concentration in each fraction was determined after extraction in N,N-dimethylformamide and was measured with a fluorometer (Turner Model 111). Clearance rates were calculated according to Frost (1972).

During the experiments, no significant changes in either the chlorophyll-*a* concentration of each size fraction or the flagellate concentrations were observed in the control. In situ seawater used for the grazing experiments contained predominately microplankton (>20 μm), most of which were diatoms (Fig. 1). The clearance rate of salps on in situ flagellates varied from 43 to 368 ml indiv.$^{-1}$ h^{-1} (Table 1). Clearance rates calculated for flagellate prey were higher than those for chlorophyll particles. Nano-sized particles were most frequently grazed in 4 out of 5 cases, but a wide size range from pico- to micro- sized phytoplankton were grazed at only slightly slower rates. Fecal pellets, which were fragile and amorphous particles, were observed at the bottom of the experimental bucket at the end of the experiments.

The lower clearance rates calculated for chlorophyll particles may have been partially caused by re-suspension of fecal pellet material. Although we gently agitated and sampled the water at the end of the experiments, fragments of the fecal pellets may have contaminated the water as the pellets were relatively fragile compared with those from mid-latitude salps. Therefore, we believe that the clearance rates calculated with flagellates are more realistic values.

The clearance rates obtained in this study as "Fo" values (Harbison & Gilmer 1976) were similar to those reported in Huntley et al. (1989), although we did not find a clear correlation with animal size (Fig. 2). These values are much lower than those reported for the temperate and subtropical salps (see Table 6 in Huntley et al. 1989). Several explanations are possible for the lower clearance rates of this antarctic salp. Feeding of antarctic salps may be restricted by reduced metabolic activity due to the extremely low ambient temperatures. If we assume a Q_{10} value of 2.03, as was reported for the pulse rate of *Salpa fusiformis* aggregates (Harbison & Campenot 1979), a clearance rate of 43–368 ml h^{-1} indiv.$^{-1}$ for *S. thompsoni* of 20–40 mm in length living at 0°C is equivalent to 140–1195 ml h^{-1} indiv.$^{-1}$ for salps at 16°C. These values are of a similar order but are about 2.2–2.5 times lower than the values of 302–3012 ml h^{-1} indiv.$^{-1}$ reported for *S. fusiformis* of the same size range at the same temperature (16°C) (Andersen 1985). Another possible explanation could be that the higher water viscosity at lower temperatures may interfere with active "pumping" by the animal or with effective filtration by the mucous net. Feeding net clogging due to high particle concentrations may also explain low clearance rate (Perissinotto & Pakhomov 1998b). However, in situ concentrations of chlorophyll particles used in our experiments were below the "threshold" level they suggested. Further study is necessary to explain the low clearance rates of this antarctic salp.

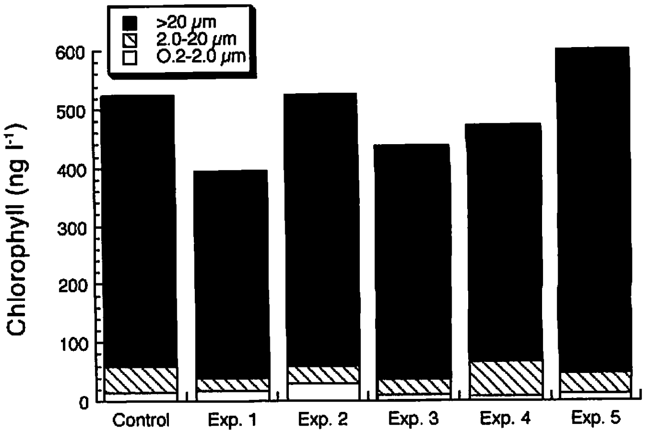

Fig. 1. Size fractionated chlorophyll-*a* concentrations in the surface water used for salp feeding experiments.

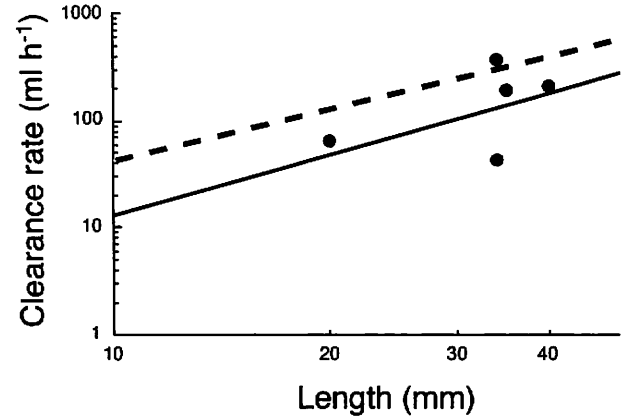

Fig. 2. Clearance rates of *Salpa thompsoni* blastozooids as a function of body length. Values from Table 1, which were calculated on flagellates, are shown as dots. The continuous and the dotted line indicates the "Fo" (overall) and "Fh" (maximum) values reported in Huntley et al. (1989), respectively. Calculations were based on Table 2 and Table 3 in Huntley et al. (1989).

There have been few studies on the minimum size of ingestable particles by antarctic salps. Previous studies investigating the particle retention efficiency of mid-latitude species have clarified that warm-water salps can retain particles of >3 μm with high efficiency (Harbison & McAlister 1979; Caron et al. 1989; Kremer & Madin 1992). Our results for *Salpa thompsoni* indicate that it can feed on >0.2 μm particles. This suggests that this salp may be able to retein finer particles than mid-latitude salps. In order to clarify the particle retention efficiency of antarctic salp, more information is needed, such as feeding net mesh size and clearance rates of a gradation of particle sizes in intervals of 0.1 or 1.0 μm.

Generally, pico- and nano-sized phytoplankton dominate the Southern Ocean (Jochem et al. 1995; Hewes et al. 1985; Kosaki et al. 1985), and these primary producers are continuously kept in check through microzooplanktonic grazing (Burkill et al. 1987, 1995; Tsuda & Kawaguchi 1997). The dominant non-salp antarctic zooplankters, such as euphausiids and large copepods are basically suspension feeders that feed mainly on particles $>5\,\mu$m (Ishii 1986; Atkinson 1995). Therefore, the dominant phytoplankton fraction would not be effectively grazed by these suspension feeders. In other words, resource partitioning between microzooplankton and these larger suspension feeders occurs, or suspension feeders act as predators of microzooplankton. This was the scenario proposed during the investigation on the "high nutrient/low chlorophyll" conditions in the subarctic Pacific (Frost 1991; Miller et al. 1991). The salps, however, can graze particles in any of the size ranges we measured, including the pico- and micro- plankton. This suggests that *Salpa thompsoni* is unique among the suspension-feeding macrozooplankton as it acts not only as a consumer of microzooplankton but also as a potential competitor with them. The unique feeding characteristics of *Salpa thompsoni*, which enables it to utilize particles of a pico- and nano-sized particles, together with the unique patterns of vertical migration, which may increase feeding opportunities (Nishikawa & Tsuda 2001), may contribute to its predominance in the oceanic region of the Southern Ocean.

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