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Contribution of salps to carbon flux of marginal ice zone of the Lazarev Sea, southern ocean

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Abstract In order to estimate the in situ grazing rates of *Salpa thompsoni* and their implications for the development of phytoplankton blooms and for the sequestration of biogenic carbon in the high Antarctic, a repeat-grid survey and drogue study were carried out in the Lazarev Sea during austral summer of 1994/1995 (December/January). Exceptionally high grazing rates were measured for *S. thompsoni* at the onset of a phytoplankton bloom (0.2 to 0.8 μg chlorophyll *a* l^{-1}) in December 1994, with up to ≃160 μg of plant pigments consumed by an individual salp of 7 to 10 cm length per day. Dense salp swarms extended throughout the marginal ice zone, consuming up to 108% of daily phytoplankton production and 21% of the total chlorophyll *a* stock. Due to the much faster sinking rates and higher carbon content of salp faecal pellets, the efficiency of downward carbon flux through salps is much higher than through the other major grazers, krill and copepods. *S. thompsoni* can thus export large amounts of biogenic carbon from the euphotic zone to the deep ocean. With the observed ingestion rates during December 1994, this flux could have attained levels of up to 88 mg C m^{-2} d^{-1}, accounting for the bulk of the vertical transport of carbon in the Lazarev Sea. However, in January 1995, when phytoplankton concentrations exceeded a threshold level of 1.0 to 1.5 μg chlorophyll *a* l^{-1}, salps experienced a drastic reduction in their feeding efficiency, possibly as a result of clogging of their filtering apparatus. This triggered a dramatic reversal in the relationship, during which a dense phytoplankton bloom developed in conjunction with the collapse of the salp population. Increases in the biomass and geographic range of the tunicate *S. thompsoni* have occurred in several areas of the southern ocean, often in parallel with a rise in sea-surface temperature during sub-decadal periods of warming anomalies.

Introduction

Salps exhibit high, although constant, filtration rates, and are capable of retaining particles in a wide size range (4 to 1000 μm) with 100% efficiency (Fortier et al. 1994; Madin 1974; Madin and Cetta 1984). Also, due to the exceptional reproductive capacity of the stolon released by the oozooid (solitary, asexual form), dense swarms of chain-forming blastozooids (aggregate, sexual form) may be produced in a very short period of time. Individual growth rates of between ≃5 and 30% length h^{-1} have been observed in natural salp populations, with the lower rates generally associated with larger individual size (Deibel 1982; Heron and Benham 1984; Tsuda and Nemoto 1992). It has been shown that salp swarms effectively control phytoplankton production in several open oceanic areas (Fraser 1961; Bathmann 1988; Fortier et al. 1994) and even in coastal and shelf waters (Zeldis et al. 1995). The coupling between salps and phytoplankton proliferation may in fact be so close that the tunicates would swarm promptly in response to a sudden increase in phytoplankton growth rate. However, failure to control a phytoplankton bloom early in its development would result in plant cell concentrations high enough to disrupt the feeding activity of the salp population (Harbison et al. 1986; Fortier et al. 1994).

In the southern ocean, *Salpa thompsoni* is the most abundant and widely distributed salp species, and recent surveys have shown that occasionally it can form dense swarms and contribute substantially to the local zooplankton stock (Smith and Schnack-Schiel 1990; Park and Wormuth 1993). Salp years, during which swarms of *S. thompsoni* dominate planktonic biomass, often to

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the exclusion of other zooplankton, have been reported with increased frequency in high Antarctic waters. Swarms of this salp could potentially remove a major part of the daily primary production from some areas of the southern ocean, thus depriving other grazers of their food and contributing, through their faecal pellet production, to the vertical flux of particulate carbon (Foxton 1966; Huntley et al. 1989; Schnack-Schiel and Mujica 1994). However, available estimates of the grazing impact of *S. thompsoni*, based on in vitro measurements of its clearance rate, are able to account for the removal of only small proportions of the daily phytoplankton production, from $<1\%$ to $\simeq 10\%$ of the total (Reinke 1987; Huntley et al. 1989; Nishikawa et al. 1995). More recent in situ estimates have indicated that the grazing pressure of this salp species may indeed at times account for >100% of the amount of carbon fixed by the phytoplankton (Dubischar and Bathmann 1997).

During the austral summer of 1994/1995, we measured the feeding activity of *Salpa thompsoni* in the Lazarev Sea using the in situ method recommended by the JGOFS protocol (JGOFS 1990). The main aims of this study were (a) to estimate the potential of salp feeding for the sequestration of biogenic carbon in the high Antarctic, and (b) to estimate the relationships between salp feeding-dynamics and the development of phytoplankton blooms.

Materials and methods

The grazing activity of *Salpa thompsoni* and its relations to phytoplankton stock and production were investigated during the period 14 December 1994 to 15 January 1995 (S A "Agulhas", SAAMES IV cruise) in the western Lazarev Sea, in a region adjacent to the Weddell Gyre (Fig. 1). During this period, samples and measurements were taken at regular intervals within repeated grid surveys and a drogue study. The first grid survey comprised 36 stations and was completed on 25 December. During this period, *S. thompsoni* was collected using only 500 μm bongo nets. A 2 wk drogue study was started at the end of the first grid and lasted until 9 January. During this study, a body of water was tracked by following a drifting drogue positioned at 40 m depth, i.e. the average depth of the upper mixed layer in the region at the beginning of the study. Both bongo and RMT-8 (4.5 mm mesh) net tows were made at intervals varying from 2 to 24 h along the westward drogue track. This was followed by a second grid survey from 9 to 15 January. This survey consisted of alternating bongo and RMT-8 net tows at 24 stations. Net tows were generally limited to the 0 to 300 m layer, but fractionated tows were made on four occasions to a maximum depth of 1000 m to investigate the vertical distribution and the diel migration pattern of *S. thompsoni*. After each tow, one zooplankton sample was preserved in 5% hexamine-buffered formalin for identification, counting and length/weight measurements in the laboratory. These were carried out approximately one month after collection. A second sample was generally used for the measurement of the gut-pigment contents in selected individuals. Salps for feeding experiments were collected using a drifting bongo net fitted with a closed 2 litre cod-end. Salps caught in this way were generally in excellent condition and able to maintain aggregate chains for several days without deterioration (Huntley et al. 1989). In the experiments, three size-classes of salps were generally separated: 1.0 to 2.5 cm, 2.5 to 5.0 cm and >5 cm total length. Feeding parameters were measured in all three groups and the overall population impact was calculated taking into account the relative abundance of each size-class in situ. On one occasion, a comparison between solitary and aggregate stages of the same length was made, but failed to show significant differences in their feeding rates ($p \geq 0.05$).

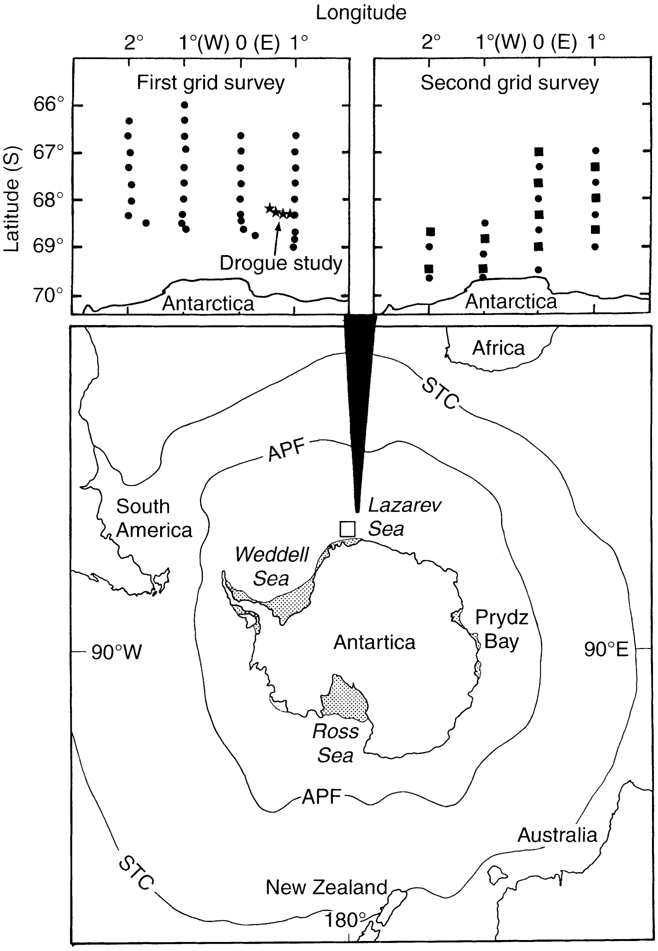


Fig. 1 Southern ocean indicating average position of Subtropical Convergence (*STC*) and Antarctic Polar Front (*APF*); bottom graph shows research area occupied during period 14 December 1994 to 15 January 1995 (●, ■ station positions where only bongo or RMT-8 nets, respectively, were used to collect *Salpa thompsoni*; ★ stations where both types of sampling gear were used)

The gut-fluorescence technique was used to estimate gut-pigment contents (*G*), gut-evacuation (*k*) and gut-pigment destruction rates (*b′*) (Mackas and Bohrer 1976; Madin and Cetta 1984; Head 1992). A recent study by Madin and Kremer (1995) has shown that the gut-pigment method, despite its many sources of potential inaccuracy, provides results which are closer to in situ feeding rates than those obtained by all other available methods. Gut pigments (*G*) were extracted from individuals in good condition with 100% methanol for 6 to 12 h, and measured with a Turner 111 fluorometer (Conover et al. 1986; Perissinotto 1992). Among the various solvents used to extract chlorophyll *a* from organic materials, methanol is one of the most efficient (Holm-Hansen and Riemann 1978). Its use is particularly recommended when extracting pigments from large zooplankton, as this allows shorter extraction time and does not require homogenisation of the sample (Simard et al. 1985).

Measured gut pigments were corrected for fluorescence due to pigmented tissues of the salps' body. Background pigment levels of salps were measured by starving them for 24 to 48 h, until a minimum level of gut fluorescence was obtained. This was generally

$\leq$20 ng individual^{-1} for small salps of $\simeq$1 cm length and $\leq$200 ng individual^{-1} for larger individuals. To estimate the gut-evacuation rate-constant, experimental salps were placed into 20 litre containers filled with 0.2 μm-filtered seawater to which charcoal particles ($<$100 μm) were added in amounts equivalent to the naturally occurring wet weight of total seston in the water (Perissinotto and Pakhomov 1996). These non-fluorescing particles were used to maintain the salps under continuous feeding conditions, thus avoiding the problem of the unnaturally slow rates obtained in the absence of normal ingestion (Madin and Kremer 1995). Gut-pigment contents of *Salpa thompsoni* were then monitored over time, and ingestion rates were calculated as described by Perissinotto (1992). During these incubations, gut-pigment content showed a consistent exponential decay over time and evacuation rates ranged between 0.24 and 0.25 h^{-1}, equivalent to a gut passage time of $\simeq$4 h.

To estimate the gut-pigment degradation efficiency, a two-compartment pigment budget approach was employed, comparing the decrease in pigment content in the grazing bottles with the increase in gut-pigment levels of individuals incubated in these bottles (Lopez et al. 1988; Mayzaud and Razouls 1992). Significant levels of gut-pigment destruction ($p < 0.05$) occurred in only two out of the six experiments completed with *Salpa thompsoni*. These ranged between 6.4 and 40.9% of the total pigment ingested, with an average value over all experiments of 9.5%. The only other data available for salps show higher losses, of ~30 to 50% (Madin and Purcell 1992; Madin and Kremer 1995). All grazing parameters were combined with salp density and measurements of phytoplankton biomass and production to calculate in situ ingestion rates at 53 stations throughout the cruise track. Salp individual ingestion rates (I) were calculated using the relation: $I = kG/(1 - b')$ (Wang and Conover 1986; Perissinotto 1992). For each station, individual rates were then multiplied by salp density and compared with the euphotic zone-integrated chlorophyll *a* concentration and primary production in order to estimate the percentage levels of phytoplankton consumed.

Chlorophyll *a* and phaeopigment concentrations were measured fluorometrically from samples collected at discrete depths in the upper 300 m layer. Aliquots of 250 ml were filtered onto GF/F glass-fibre filters, and pigments were extracted for 24 h in 90% acetone (Parsons et al. 1984; JGOFS 1990). Pigment concentrations were then estimated from measurements of fluorescence taken before and after acidification using a Turner Designs, Model 10-AU fluorometer (Parsons et al. 1984). Primary production rates were measured with dawn-to-dawn, simulated in situ incubations (JGOFS 1990). Water was obtained from the 100, 50, 25, 10, 5 and 1% subsurface light-depths and pre-filtered through a 200 μm mesh to remove grazers. For each light level, three replicate polycarbonate bottles were inoculated with 25 to 50 μCi of $NaH^{14}CO_3$ (Amersham), and incubated on deck for 24 h in running surface seawater to maintain ambient temperature. The specific activity was obtained by removing and filtering 50 ml aliquots from each productivity bottle. Filters were then placed in liquid scintillation vials with 10 ml fluor, and their radioactivity was measured on board using a Beckman scintillation counter.

A 13 yr time-series of krill biomass and salp-abundance data was obtained from measurements and samples collected in the Prydz Bay region of Antarctica (Fig. 1) during each austral summer (December to February) from 1978 to 1990. Annual cruises to the research area along the 75°E meridian and to the south of 60°S were undertaken regularly using the following research or fishery vessels: "Fiolent" (1978, 1984, 1987, 1988); "Chatyr-Dag" (1979, 1982, 1984); "Skif" (1980 to 1983); "Zvezda Chernomorja" (1985); "Zvezda Azova" (1986); "Professor Mesyatsev" (1989, 1990). Krill stock was estimated from acoustic integration (38 and 120 kHz), while salp abundances were derived from 200 m-depth, oblique tows made with Isaac-Kidd midwater trawls (4.5 mm mesh) and bongo nets (500 μm mesh). Krill biomass data were obtained from several published sources (Bibik and Yakovlev 1991; Samyshev 1991).

Results and discussion

Maximum abundances of *Salpa thompsoni*, with $>$4 individuals m^{-3} were recorded in the marginal ice zone (MIZ) during the first grid survey in early summer (December). At this stage, chlorophyll *a* concentrations were generally well below 1 mg m^{-3} (Fig. 2, Table 1) and maximum primary production rates $<$300 mg C m^{-2} d^{-1}. A dramatic decrease in salp stock was observed during the drogue study, at the beginning of January. During this period, *S. thompsoni* virtually disappeared from the most productive area of the MIZ, where chlorophyll *a* concentration and phytoplankton production had by then reached bloom levels of 2 to 3 mg m^{-3} and 270 to 450 mg C m^{-2} d^{-1}, respectively.

This collapse in the salp population appeared to be related to the inability of salps to regulate their filtration rate and avoid clogging of their filtering apparatus when particle concentrations exceeded a threshold of $\simeq$1 mg chlorophyll *a* m^{-3}. A reduction in the feeding rate of *Salpa thompsoni* in response to increasing concentrations of chlorophyll *a* could not be conclusively demonstrated during the study. Average grazing rates were substantially higher during the first grid survey, when chlorophyll *a* levels were low compared to the rates measured during the bloom (Table 1). However, the negative correlation between salp feeding-rate and chlorophyll concentration was not significant ($r = -0.23, p > 0.05$; $n = 53$, $\log_{10}$-transformed data). This is a problem that is most probably related to the shortcomings of the gut-fluorescence method employed. During the bloom, salps exhibited levels of gut pigment higher than previously. This was presumably the result of the high concentrations of phytoplankton cells collected in the food strands at that stage. However, due to clogging, this food was

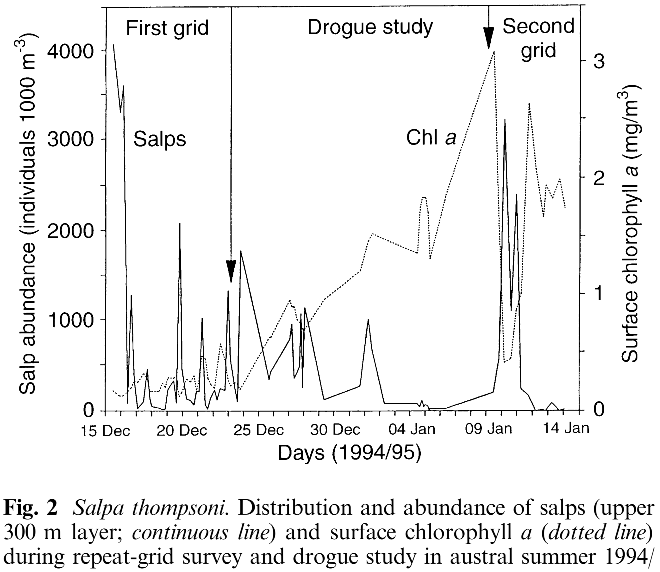


Fig. 2 *Salpa thompsoni.* Distribution and abundance of salps (upper 300 m layer; *continuous line*) and surface chlorophyll *a* (*dotted line*) during repeat-grid survey and drogue study in austral summer 1994/1995 (*First arrow on left* indicates end of first grid survey and beginning of the drogue study; *second arrow* indicates end of drogue study and beginning of second grid survey)

Table 1 *Salpa thompsoni*. Range and mean values of abundance and grazing activity of salps during grid surveys and drogue study of December 1994 to January 1995 on SAAMES IV cruise of S. A. "Agulhas" (*ind* individuals)

Survey/experiment	Salp density (ind 1000 m^{-3})	Chlorophyll *a* conc (100 m) (mg m^{-2})	Primary production (mg C m^{-2} d^{-1})	Grazing rate		Grazing impact	
				(mg pigment m^{-2} d^{-1})	(mg C m^{-2} d^{-1})	(% chlorophyll *a*)	(% production)
First grid survey (12–24 Dec.94)							
Max.	4065	67.02	274	5.22	215.6	21.42	108.5
Min.	8	12.13	102	0.004	2.9	0.02	1.4
Average (SD)	632 (1025)	28.0 (10.8)	196 (32)	0.42 (0.87)	37.8 (37.9)	1.7 (3.6)	19.6 (19.1)
Drogue experiment (26 Dec.94–8 Jan.95)							
Max.	1005	100.3	442	0.5	52.7	0.84	17.4
Min.	61	59.7	269	0.024	8.5	0.03	1.9
Average (SD)	529 (298)	74.5 (14.8)	313 (59)	0.26 (0.16)	33.7 (15.3)	0.4 (0.3)	11.6 (5.6)
Second grid survey (10–15 Jan.95)							
Max.	3209	216.3	646	2.1	124.2	3.54	47.8
Min.	0	58.8	223	0	0	0	0
Average (SD)	363 (799)	125.7 (43.7)	358 (107)	0.29 (0.54)	27.1 (33.7)	0.4 (0.9)	9.4 (12.9)

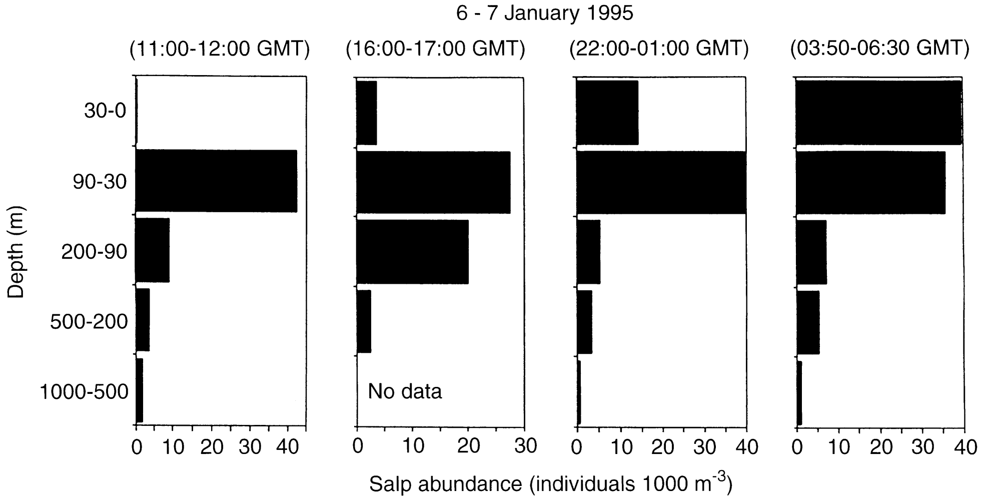
not being digested. So, while the gut-fluorescence technique would allow for these gut contents to be included in the calculation of salp grazing-rates, most of them were actually not utilized by the salps. The net result was apparently normal feeding activity even when salps were experiencing severe clogging. Further, there is also a possibility that gut-evacuation rates may have varied widely in response to changes in food concentrations, with clogged salps possibly exhibiting much slower rates than individuals in normal conditions. Unfortunately, because of experimental constraints and the high mortality of clogged salps it was not possible to measure gut-evacuation rates under bloom conditions. Thus, the average value for gut-evacuation rate used in the estimation of salp grazing-rates may have resulted in biased values being calculated for salps sampled during the bloom period.

It has been documented, at least in the large oceanic species *Pegea confoederata*, that high food concentrations can disrupt the feeding activity of salps to the extent that they starve to death (Harbison et al. 1986; Zeldis et al. 1995). Although direct observations of clogging were made during the investigation, it was not clear whether salps were able to eject clogged nets and resume feeding in situ. When incubated in filtered seawater, however, salps were able to dislodge the bolus and resume swimming and feeding activities after a relatively short period of time (Perissinotto and Pakhomov 1997).

The alternative hypothesis, that high chlorophyll levels may be due to a lack of salps in the area, can be dismissed in the case of summer 1994/1995, since the sudden decrease in the salp population and the increase in phytoplankton biomass co-occurred in the middle of the drogue study. This study was carried out following the same water body for 13 consecutive days, during which salp concentrations remained consistently high until the onset of the bloom (Fig. 2), thus exerting an uninterrupted grazing pressure on the phytoplankton. The algal bloom must have been triggered by environmental factors such as water stratification and temperature, rather than lack of grazing.

During this collapse in the population of *Salpa thompsoni*, the branchial cavity of a large proportion of its blastozooids was also invaded by the copepod *Rhincalanus gigas*, with up to three copepods invading an individual salp of 2 to 5 cm (Perissinotto and Pakhomov 1997). *R. gigas* exhibited significantly (Student's *t*-test, $p < 0.05$) higher ingestion rates inside salps than outside, and invaded blastozooids were able to survive prolonged exposure (up to 48 h) to copepod invasion. The possibility thus exists that this association is a novel type of symbiosis, whereby *S. thompsoni* could potentially benefit from *R. gigas* cleaning its filtering apparatus when clogging occurs. However, no conclusive evidence supporting this hypothesis could be obtained during the investigation, and it is quite likely that the association is just a form of opportunistic parasitism on the part of *R. gigas*.

Fig. 3 *Salpa thompsoni*. Vertical distribution of salps during 24 h sampling cycle at beginning of January 1995 during drogue study (*GMT* Greenwich Mean Time)



During the second grid survey, salp abundance was again much depressed throughout the area of high chlorophyll *a* concentration (Fig. 2). A patch of high salp density was observed however at the northern edge of the grid, in conjunction with low chlorophyll *a* levels of 0.5 to 1 mg m^{-3}. This is consistent with the threshold levels observed during the previous grid, and may support the hypothesis that *Salpa thompsoni* is unable to feed on phytoplankton stocks above these concentrations.

Depth layer-fractionated sampling carried out during the drogue study showed that *Salpa thompsoni* was virtually restricted to the upper 200 m. There was a clear movement of salps from below the upper 30 m layer to the surface during the late night and early morning hours (03:00 to 06:00 hrs Greenwich Mean Time, Fig. 3). Gut-pigment contents and ingestion rates increased dramatically with increasing salp length. Rates of small individuals (1 to 2.5 cm) ranged between 0.007 and 7.9 μg pigment individual^{-1} d^{-1}, with an average of 1.7 ∓ 1.2 SD. Medium-sized individuals (2.5 to 5 cm) exhibited a range of 0.53 to 16.6 μg pigment individual^{-1} d^{-1} ($\bar{x} = 3.3 \mp 1.8$ SD) and larger salps (>5 cm) had levels of 3.0 to 160 μg ($\bar{x} = 65 \mp 41$ SD). Clearance rates ranged between 430 ml h^{-1}, in small and medium salps, and 5400 ml h^{-1} in the largest individuals.

In situ grazing measurements showed that *Salpa thompsoni* exhibited the highest ingestion rates per individual of any of the most abundant grazers in the pelagic community, with maxima of ≃160 μg chlorophyll equiv individual^{-1} d^{-1}. This is even an order of magnitude higher than the values obtained by Dubischar and Bathmann (1997) for the same species in the Antarctic Circumpolar Current (i.e. 13 to 16 μg chlorophyll equiv individual^{-1} d^{-1}). Using the empirical equation of Hewes et al. (1990, $C = 80\ \text{chlorophyll}^{0.6}$) to convert chlorophyll concentrations into autotrophic carbon, the daily carbon consumption of the population of *S. thompsoni* would range between 2 and 216 mg C m^{-2} d^{-1} ($\bar{x} = 36.8 \pm 35.8$ SD). These rates are equivalent to 0.01 to 21.4% ($\bar{x} = 1.3 \pm 3.1$) chlorophyll *a* and 0.30 to 108% ($\bar{x} = 17.3 \pm 17.5$) primary production consumed per day (Table 1), and are among the highest yet recorded for a grazer in the southern ocean (Conover and Huntley 1991; Schnack-Schiel and Mujica 1994). Similar levels of grazing impact were obtained by Dubischar and Bathmann (1997) for *S. thompsoni* in the Antarctic Circumpolar Current, and by Pakhomov et al. (1997) for *Euphausia superba* in the South Georgia region.

Salps produce faecal pellets which are very compact, exhibit extraordinarily high sinking rates of up to 2.7 km d^{-1} (Bruland and Silver 1981; Fortier et al. 1994), and maintain their chemical composition virtually intact throughout the course of downward transportation (Matsueda et al. 1986; Bathmann 1988; Caron et al. 1989). Also, due to preferential nitrogen assimilation, salp faecal pellets are unusually rich in carbon, which forms up to 37% of their total dry weight (Bruland and Silver 1981; Iseki 1981). No direct measurements of the faecal pellet production of *Salpa thompsoni* were made during this study. However, an estimate can be obtained by multiplying their carbon ingestion rates by the value of 40.7% egestion of ingested carbon, derived by Huntley et al. (1989). Faecal production by salps during the cruise period would have amounted to 0.8 to 88 mg C m^{-2} d^{-1} ($\bar{x} = 15.0 \pm 14.6$ SD). This constitutes a vertical transport of biogenic carbon higher than the average particulate organic carbon (POC) flux measured in most oceanic areas (Fisher et al. 1988). It is also equivalent to 6–90% of the POC flux in the most productive areas of the southern ocean and is ≃ 1.5 times higher than the maximum particle flux in the Weddell Gyre, adjacent to the Lazarev Sea (Von Bodungen et al. 1986; Fisher et al. 1988) (Fig. 1). Thus, *S. thompsoni* is an important, occasional contributor to the export of particulate biogenic carbon from the euphotic zone to the deep ocean in the Lazarev Sea, and possibly in other regions of the southern ocean.

If proved, the inability of salps to graze at particle concentrations >1 mg chlorophyll m^{-3} may have important implications for the recent proposal of fertilizing the southern ocean with iron to increase phytoplankton production and sequester more CO_2 in the deep ocean (Martin et al. 1990; ASLO 1991; Peng and Broecker 1991; De Baar et al. 1995). Our results suggest that such fertilization could result in the elimination of *Salpa thompsoni* from large areas of the ocean because of its inability to cope with phytoplankton blooms. This would depend, however, on the time scale of the salp–phytoplankton interaction. According to the hypothesis of Fortier et al. (1994), salps may only be able to produce swarms in response to a sudden increase in their phytoplankton food. In order to prevent blooms, it is vital that the salp population proliferate synchronously with the phytoplankton. Failure to control an algal bloom early in its development would result in cell concentrations high enough to disrupt salp feeding (Fortier et al. 1994; Zeldis et al. 1995).

The extremely low particle flux generally recorded in the Weddell Sea (Fisher et al. 1988) may be partly the result of the absence of *Salpa thompsoni* from its peculiarly cold waters (Foxton 1966; Pakhomov 1993). *S. thompsoni* is a circumpolar southern ocean species, the northern limit of its occurrence coinciding with the mean position of the Subtropical Convergence (Foxton 1966; Casareto and Nemoto 1986). To the south, the range of its distribution is less well defined, and in the high Antarctic, where salp biomass declines sharply as ice cover increases (Siegel et al. 1992), it seems restricted to the warmer water masses and layers derived from upwelling/advection of Antarctic deep water or from summer capping (Priddle et al. 1988; Pakhomov 1993). This indicates that at higher latitudes the species exists close to its thermo-physiological limits.

Krill and copepods have traditionally been regarded as the dominant components of the Antarctic zooplankton, together generally accounting for >90% of total biomass and grazing impact on the pelagic subsystem (Foxton 1956; Conover and Huntley 1991). However, during the last decade, the tunicate *Salpa thompsoni* has shown occasional and dramatic increases in biomass in some regions of the southern ocean, becoming at times the main contributor to the pelagic stock (Pakhomov 1993; Park and Wormuth 1993; Nishikawa et al. 1995). "Salp years", during which swarms of *S. thompsoni* dominate planktonic biomass, often to the exclusion of other zooplankton, have been reported with increased frequency in high-latitude waters (Huntley et al. 1989; Schnack-Schiel and Mujica 1994). Our long-term data set from the Prydz Bay region (Fig. 1) shows on average a four-fold increase in the summer abundance of *S. thompsoni* over a 10 yr period, particularly during the years 1984 to 1988 (Fig. 4). This has occurred in parallel with a three-fold decrease in krill biomass starting from 1984 (present Fig. 4; and Savich 1993). In general, high krill abundances occurred in the early years (1978, 1979 and 1984), in conjunction with lower salp stocks. *S. thompsoni* dominated during the following four seasons, but towards the end of the series a reversal in the pattern again occurred, with the re-establishment of a krill-dominated system in 1989 to 1990 (Fig. 4).

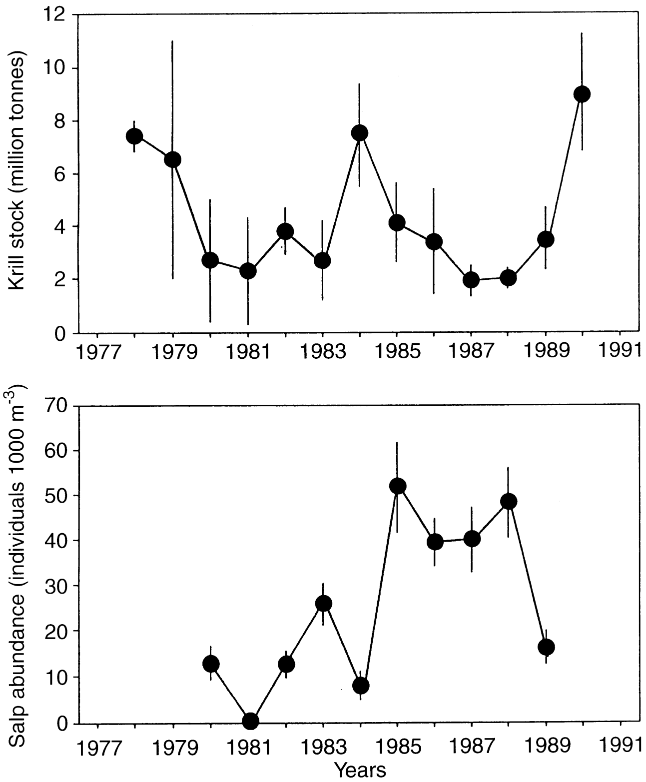


Fig. 4 *Salpa thompsoni.* Time-series of salp abundance and krill biomass for period 1978 to 1990 in Prydz Bay region of Antarctica

Recent estimates of climatic warming in the Antarctic Peninsula region have shown that temperatures have been rising at 0.05 to 0.1 C° per year over the past 40 yr (Gloersen and Campbell 1991; Zwally 1991; Rott et al. 1996). This has already been associated with an increase in the average percentage of open water, in the form of leads and polynyas, and with the disintegration of entire ice-shelves (Doake and Vaughan 1991; Gammie 1995; Vaughan and Doake 1996). The extent and thickness of sea-ice cover have been proposed as potential indicators of global warming in the polar regions (Mercer 1978). Although such a signal has been identified in the Arctic (Johannessen et al. 1995) and in the Antarctic Peninsula (Vaughan and Doake 1996), there is no evidence as yet suggesting large-scale circum-Antarctic warming. There is, however, a strong interannual variability in ice cover around the Antarctic continent which is linked to subdecadal events such as the El Niño/Southern Oscillation (Gloersen 1995). A recent analysis of a long-term record of fast-ice duration at the South Orkney Islands has also shown a pronounced cyclicity in sea-ice configuration, with an approximate 7 to 9 yr cycle of precession around the Antarctic continent (Murphy et al. 1995). The perceived response of *Salpa thompsoni* to changes in temperature in the upper mixed layer needs to be urgently investigated. If warming events in the southern ocean can indeed promote periodical increases in the biomass and distribution of salps, these would have important implications for the regional carbon flux.

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References

ASLO (1991) What controls phytoplankton production in nutrient-rich areas of the open sea? In: Weiler S (ed), Report, American Society of Limnology and Oceanography Symposium, San Marcos, California, February 22–24, 1991. American Society of Limnology and Oceanography, Washington, pp 1–17

Bathmann UV (1988) Mass occurrence of *Salpa fusiformis* in the spring of 1984 off Ireland: implications for sedimentation processes. Mar Biol 97: 127–135

Bibik VA, Yakovlev VN (1991) The status of krill (*Euphausia superba* Dana) resources in CCAMLR statistical divisions 58.4.2 and 58.4.3 from 1988 to 1990; results of acoustic surveys. In: Sabourenkov E (ed) Selected Scientific Papers (SC-CAMLR-SSP/7). Commission for the Conservation of Antarctic Marine Living Resources, Hobart, Australia, pp 163–173

Bruland KW, Silver MW (1981) Sinking rates of fecal pellets from gelatinous zooplankton (salps, pteropods, doliolids). Mar Biol 63: 295–300

Caron DA, Madin LP, Cole JJ (1989) Composition and degradation of salp fecal pellets: implications for vertical flux in oceanic environments. J mar Res 47: 829–850

Casareto BE, Nemoto T (1986) Salps of the Southern Ocean (Australian sector) during the 1983–84 summer, with special reference to the species *Salpa thompsoni*, Foxton 1961. Mem natn Inst polar Res, Tokyo 40: 221–239

Conover RJ, Durvasula R, Roy S, Wang R (1986) Probable loss of chlorophyll-derived pigments during passage through the gut of zooplankton and some of the consequences. Limnol Oceanogr 31: 878–887

Conover RJ, Huntley M (1991) Copepods in ice-covered seas – distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. J mar Syst 2: 1–41

De Baar HJW, de Jong JTM, Bakker DCE, Loscher BM, Veth C, Bathmann U, Smetacek V (1995) Importance of iron for plankton blooms and carbon dioxide drawdown in the Southern Ocean. Nature, Lond 373: 412–415

Deibel D (1982) Laboratory-measured grazing and ingestion rates of the salp, *Thalia democratica* Forskal, and the doliolid, *Dolioletta gegenbauri* Uljanin (Tunicata, Thaliacea). J Plankton Res 4: 189–201

Doake CSM, Vaughan DG (1991) Rapid disintegration of the Wordie Ice Shelf in response to atmospheric warming. Nature, Lond 350: 328–330

Dubischar CD, Bathmann UV (1997) Grazing impact of copepods and salps on phytoplankton in the Atlantic sector of the Southern Ocean. Deep-Sea Res. 44: 415–433

Fisher G, Fütterer DR, Gersonde R, Honjo S, Ostermann D, Wefer G (1988) Seasonal variability of particle flux in the Weddell Sea and its relation to ice cover. Nature, Lond 335: 426–428

Fortier L, Le Fèvre J, Legendre L (1994) Export of biogenic carbon to fish and to the deep ocean: the role of large planktonic microphages. J Plankton Res 16: 809–839

Foxton P (1956) The distribution of the standing crop of zooplankton in the Southern Ocean. 'Discovery' Rep 28: 191–236

Foxton P (1966) The distribution and life-history of *Salpa thompsoni* Foxton with observations on a related species, *Salpa gerlachei* Foxton. 'Discovery' Rep 34: 1–116

Fraser JH (1961) The role of ctenophores and salps in zooplankton production and standing crop. Rapp. P-v Cons perm int Explor Mer 153: 121–123

Gammie F (1995) Breakaway iceberg due to warming. Nature, Lond 374: p. 108

Gloersen P (1995) Modulation of hemispheric sea-ice cover by ENSO events. Nature, Lond 373: 503–506

Gloersen P, Campbell WJ (1991) Recent variations in Arctic and Antarctic sea-ice covers. Nature, Lond 352: 33–36

Harbison GR, McAlister VL, Gilmer RW (1986) The response of the salp, *Pegea confederata*, to high levels of particulate material: starvation in the midst of plenty. Limnol Oceanogr 31: 371–382

Head EJH (1992) Gut pigment accumulation and destruction by arctic copepods *in vitro* and *in situ*. Mar Biol 112: 583–592

Heron AC, Bhenam EE (1984) Individual growth rates of salps in three populations. J Plankton Res 6: 811–828

Hewes CD, Sakshaug E, Reid FMH, Holm-Hansen O (1990) Microbial autotrophic and heterotrophic eucaryotes in Antarctic waters: relationships between biomass and chlorophyll, adenosine triphosphate and particulate organic carbon. Mar Ecol Prog Ser 63: 27–35

Holm-Hansen O, Riemann B (1978) Chlorophyll-a determination: improvements in methodology. Oikos 30: 438–447

Huntley ME, Sykes PF, Marin V (1989) Biometry and trophodynamics of *Salpa thompsoni* Foxton (Tunicata; Thaliacea) near the Antarctic Peninsula in austral summer, 1983–1984. Polar Biol 10: 59–70

Iseki K (1981) Particulate organic matter transport to the deep sea by salp fecal pellets. Mar Ecol Prog Ser 5: 55–60

JGOFS (Joint Global Ocean Flux Study) (1990) Core measurements protocols. In: Tidmarsh E (ed). Report No. 6. Reports of the core measurements working group. Scientific Committee on Oceanic Research, Halifax, Canada, pp 1–40

Johannessen OM, Miles M, Bjorgo E (1995) The Arctic's shrinking sea ice. Nature, Lond 376: 126–127

Lopez MDG, Huntley ME, Sykes PF (1988) Pigment destruction by *Calanus pacificus*: impact on the estimation of water column fluxes. J Plankton Res 10: 715–734

Mackas D, Bohrer R (1976) Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. J exp mar Biol Ecol 25: 77–85

Madin LP (1974) Field observations on the feeding behavior of salps (Tunicata: Thaliacea). Mar Biol 25: 143–147

Madin LP, Cetta CM (1984) The use of gut fluorescence to estimate grazing by oceanic salps. J Plankton Res 6: 475–492

Madin LP, Kremer P (1995) Determination of the filter-feeding rates of salps (Tunicata, Thaliacea). ICES J mar Sci 52: 583–595

Madin LP, Purcell JE (1992) Feeding, metabolism and growth of *Cyclosalpa bakeri* in the subarctic Pacific. Limnol Oceanogr 37: 1236–1251

Martin JH, Gordon RM, Fitzwater SE (1990) Iron in Antarctic waters. Nature, Lond 345: 156–158

Matsueda H, Handa N, Inoue I, Takano H (1986) Ecological significance of salp fecal pellets collected by sediment traps in the eastern North Pacific. Mar Biol 91: 421–431

Mayzaud P, Razouls S (1992) Degradation of gut pigment during feeding by a subantarctic copepod: importance of feeding history and digestive acclimation. Limnol Oceanogr 37: 393–404

Mercer JH (1978) West Antarctic ice sheet and CO_2 greenhouse effect: a threat of disaster. Nature, Lond 271: 321–325

Murphy EJ, Clarke A, Symon C, Priddle J (1995) Temporal variation in Antarctic sea-ice: analysis of a long term fast-ice record from the South Orkney Islands. Deep-Sea Res 42: 1045–1062

Nishikawa J, Naganobu M, Ichii T, Ishii H, Terazaki M, Kawaguchi K (1995) Distribution of salps near the South Shetland Islands during austral summer 1990–1991, with special reference to krill distribution. Polar Biol 15: 31–39

Pakhomov EA (1993) Macrozooplankton communities in the Cooperation Sea, Antarctica. [*In* Russ] Antarktika 32: 94–110

Pakhomov EA, Perissinotto R, Froneman PW, Miller DGM (1997) Energetics and feeding dynamics of *Euphausia superba* in the South Georgia region during the summer of 1994. J Plankton Res 19: 399–423

Park C, Wormuth JH (1993) Distribution of Antarctic zooplankton around Elephant Island during the austral summers of 1988, 1989, and 1990. Polar Biol 13: 215–225

Parsons TR, Mayta Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford

Peng TH, Broecker WS (1991) Dynamical limitations on the Antarctic iron fertilization strategy. Nature, Lond 349: 227–229

Perissinotto R (1992) Mesozooplankton size-selectivity and grazing impact on the phytoplankton community of the Prince Edward Archipelago (Southern Ocean). Mar Ecol Prog Ser 79: 243–258

Perissinotto R, Pakhomov EA (1996) Gut evacuation rates and pigment destruction in the Antarctic krill *Euphausia superba*. Mar Biol 125: 47–54

Perissinotto R, Pakhomov EA (1997) Feeding association of the copepod *Rhincalanus gigas* with the tunicate *Salpa thompsoni* in the southern ocean. Mar Biol 127: 479–483

Priddle J, Croxall JP, Everson I, Heywood RB, Murphy EJ, Prince PA, Sear CB (1988) Large-scale fluctuations in distribution and abundance of krill – a discussion of possible causes. In: Sahrhage D (ed), Antarctic Ocean and resources variability. Springer-Verlag, Berlin Heidelberg, pp 169–182

Reinke M (1987) On the feeding and locomotory physiology of *Salpa thompsoni* and *Salpa fusiformis*. Ber Polarforsch (Bremerhaven) 36: 1–89

Rott H, Skvarca P, Nagler T (1996) Rapid collapse of northern Larsen Ice Shelf, Antarctica. Science, NY 271: 788–792

Samyshev EZ (1991) Antarctic krill and plankton community structure in its distribution range. [*In* Russ] Nauka Press, Moscow

Savich MS (1993) Multi-year dynamics of phytoplankton biomass in the Cooperation Sea during the summer vegetation period of 1977–1988. In: Voronina NM (ed) Pelagic ecosystems of the Southern Ocean. [*In* Russ] Nauka Press, Moscow, pp 111–115

Schnack-Schiel SB, Mujica A (1994) The zooplankton of the Antarctic Peninsula region. In: El-Sayed SZ (ed) Southern Ocean ecology: the BIOMASS perspective. Cambridge University Press, Cambridge, pp 79–92

Siegel V, Skibowski A, Harm U (1992) Community structure of the epipelagic zooplankton community under the sea-ice of the northern Weddell Sea. Polar Biol 12: 15–24

Simard Y, Lacroix G, Legendre L (1985) *In situ* twilight grazing rhythm during diel vertical migrations of a scattering layer of *Calanus finmarchicus*. Limnol Oceanogr 30: 598–606

Smith SL, Schnack-Schiel SB (1990) Polar zooplankton. In: Smith WO Jr (ed) Polar oceanography. Part B: Chemistry, biology, and geology. Academic Press, San Diego, pp 527–598

Tsuda A, Nemoto T (1992) Distribution and growth of salps in a Kuroshio warm-core ring during summer 1987. Deep-Sea Res 39: S219–S229

Vaughan DG, Doake CSM (1996) Recent atmospheric warming and retreat of ice shelves on the Antarctic Peninsula. Nature, Lond 379: 328–331

Von Bodungen B, Smetacek VS, Tilzer MM, Zeitzschel B (1986) Primary production and sedimentation during spring in the Antarctic Peninsula region. Deep-sea Res 33: 177–194

Wang R, Conover RJ (1986) Dynamics of gut pigment in the copeopd *Temora longicornis* and the determination of in situ grazing rates. Limnol Oceanogr 31: 867–877

Zeldis JR, Davies CS, James MR, Ballara SL, Booth WE, Chang FH (1995) Salp grazing: effects on phytoplankton abundance, vertical distribution and taxonomic composition in a coastal habitat. Mar Ecol Prog Ser 126: 267–283

Zwally HJ (1991) Breakup of Antarctic ice. Nature, Lond 350: p. 274