

Grazing of *Salpa thompsoni* on phytoplankton in summer in the Prydz Bay region, Antarctica

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Abstract During the CHINARE-Ⅷ(九) cruise in austral summer of 1998/1999, the abundance and feeding activity of *Salpa thompsoni* were investigated in the Prydz Bay region. Salps samples were collected by vertical tows from the depth of 200 m to the surface with a conical net of 330 μm mesh size. At Ⅷiv-3 station, the grazing rates were studied by the gut fluorescence method and culture experiments. *S. Thompsoni* was mainly distributed in the northern part of the survey area, and its maximum densities reached to $2795 \text{ ind.} \cdot 1000 \text{ m}^{-3}$. A dramatic decrease in salp stock was observed at the Marginal Ice Zone. The results of the feeding experiments at the Ⅷiv-3 show that the gut pigment contents of *S. thompsoni* ranged from $(0.14 - 1.27) \mu\text{g ind.}^{-1}$ (average $0.98 \mu\text{g ind.}^{-1}$). The individual ingestion rate is $7.9 \mu\text{g ind.}^{-1} \cdot \text{day}^{-1}$, and the filtration rate is $28 \text{ L ind.}^{-1} \cdot \text{day}^{-1}$. Through the daily grazing rate of *S. thompsoni*, which takes account of less than 1% of the phytoplankton standing stock, it shows a relatively higher grazing impress on the primary production (72.2%).

Key words *Salpa thompsoni*, gut pigment, grazing, Prydz Bay.

1 Introduction

Since the whaling was going on in the Southern Ocean, scientists have paid more attention to the marine production and trophic structure in this area. Recently, many reports pointed that the marine food web was not so simple as we previously believed: from diatom to krill, to whale. Copepods and salps also play an important role on the energy transport in this marine ecosystem, especially when the krill was scarce (Witek *et al.* 1985; Kawamura *et al.* 1994; Schnack-Schiel and Mujica 1994; Perissinotto and Pakhomov 1998). *Salpa thompsoni*, belonging to tunicata, is one of the most abundant and widespread zooplankton in the southern Ocean. Owing to the fast growth rates and high reproductive capacity of their asexual individuals, *S. thompsoni* reproduces abundantly in a very short period of time under the suitable condition and dominates over the planktonic biomass (Siegel *et al.* 1992; Perissinotto and Pakhomov 1998). The Prydz Bay region was chosen as one of the SO-GLOBEC studying areas. *S. thompsoni* was one of the major planktonic species in this area (Hosie *et al.* 1997). Thereby the distribution and feeding activity of *S. thompsoni* were investigated during the CHINARE-Ⅷ(九) cruise in austral summer of 1998/1999 in the Prydz Bay region to advance our understanding of the trophic dynamics and the role of zooplankton on primary production in this region.

2 Materials and methods

Sampling was carried out at 26 stations from December 1998 to January 1999 (Fig. 1). Zooplankton samples were collected by a single closing net with mouth area of 0.5 m^2 and mesh size of $330 \text{ }\mu\text{m}$ from the depth of 200 m to the surface. A flowmeter was mounted in the center of the net mouth to measure the volume of water filtered. Samples were preserved in seawater solution with 5% formalin for quantitative analyses of species composition. At each experiment station, CTD, nutrients (N, P, Si), chlorophyll *a* (fluorescence) and primary production (^{14}C) were measured simultaneously.

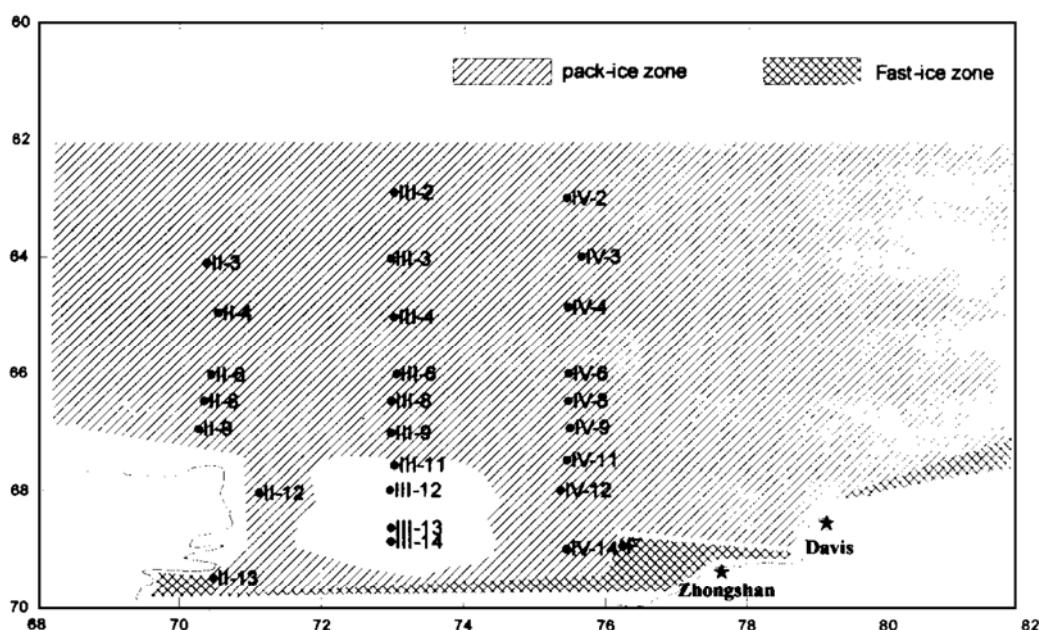


Fig. 1. Location of study site.

The experiment on the ingestion rate of *S. thompsoni* was made at station iv-13. Samples for gut pigment analysis, gut evacuation experiments and using the same net as described above, but with a sealed cod-end captured culture experiments. Determination of ingestion rate of *Salps* was carried out using two different approaches. First, gut fluorescence method was employed to determine the ingestion rate. Sample treatments and fluorescence measurements were the same as described by Mackas and Bohrer (1976) except that pigments were extracted in 100% acetone to compensate for the high water content of the salps (Dubischar and Bathmann 1997) and the gut evacuation rate was estimated in 6-h experiment. Absolute values for chlorophyll *a* and phaeopigment were calculated according to Wang and Conover (1986). The sum was used as the index of gut pigment content (GGC). An empirical equation of Hewes *et al.* (1990), $C = 80 \text{ chl}^{0.6}$, was used to convert chlorophyll *a* into phytoplankton carbon. Secondly, feeding experiments were carried out on board according to Dubischar and Bathmann (1997). Intact, swimming, single individuals were cultured in 5-L containers. The containers were filled with in situ surface seawater filtered through a sieve with a mesh size of $200 \text{ }\mu\text{m}$. Grazing was calculated as differences of chlorophyll *a* concentrations with time following Frost

(1972). Chlorophyll *a* was determined in time intervals up to 26 h as described above.

3 Results

Throughout the survey period, the study area was characterized as a typical marginal ice zone, which varied from pack ice in the south to open water in the north. The northern extent of pack ice was encountered at approximately $69^{\circ}05' \text{ S}$. Most study area was covered with 1% - 100% melting frazil ice. Station iv-3 is located at the northern of frazil ice zone and ice-covered less than 10% (Fig. 1). The spatial distribution of the average value of chlorophyll *a* from the depth of 200 m to surface is shown in Fig. 2. During the survey period, concentrations varied widely, ranged between 0.01 mg m^{-3} and 5.55 mg m^{-3} . From the point of view of horizontal distribution, the biomass of phytoplankton increased from northwest to southeast. The maximum was found in the reoccurring polynya near the pack ice. For the vertical distribution, the peak values mostly occurred at 25 m depth. *S. thompsoni* mainly is distributed in the northern part of the study area (Fig. 3). The highest value of *S. thompsoni* biomass occurred at station iv-3 ($2795 \text{ ind.} \cdot 1000 \text{ m}^{-3}$). *Salps* were almost entirely absent in the middle and southern part of study area.

The gut pigment contents of *S. thompsoni* ranged between $0.14 \text{ } \mu\text{g pigment} \cdot \text{ind.}^{-1}$ and $1.27 \text{ } \mu\text{g pigment} \cdot \text{ind.}^{-1}$, with average of $(0.98 \pm 0.47) \text{ } \mu\text{g pigment} \cdot \text{ind.}^{-1}$. The result of the gut evacuation experiment showed an exponential decline in gut pigment content over time ($y = 1155.6e^{-0.0056x}$, $r^2 = 0.8985$). Gut evacuation rate was 0.0056 min^{-1} , and the corresponding gut passage time was 3.0 h. The ingestion rate accounted for $7.9 \text{ } \mu\text{g pigment} \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$ (or $395 \text{ } \mu\text{g C} \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$). The salp population consumed $0.47 \text{ mg pigment} \cdot \text{day}^{-1}$ (or $23.7 \text{ mg C} \cdot \text{day}^{-1}$). With respect to the situ phytoplankton biomass and primary production, the daily grazing pressure of the salp assemblage accounted for 0.8% of the total chlorophyll *a* and 72.2% of the primary produc-

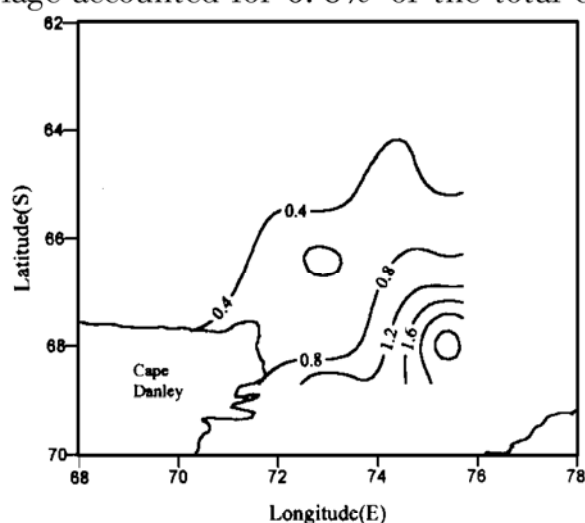


Fig. 2. Horizontal distribution of the average concentration of chlorophyll *a* (mg m^{-3}) from the depth of 200 m to surface in the Prydz Bay during Dec. 1998 - Jan. 1999.

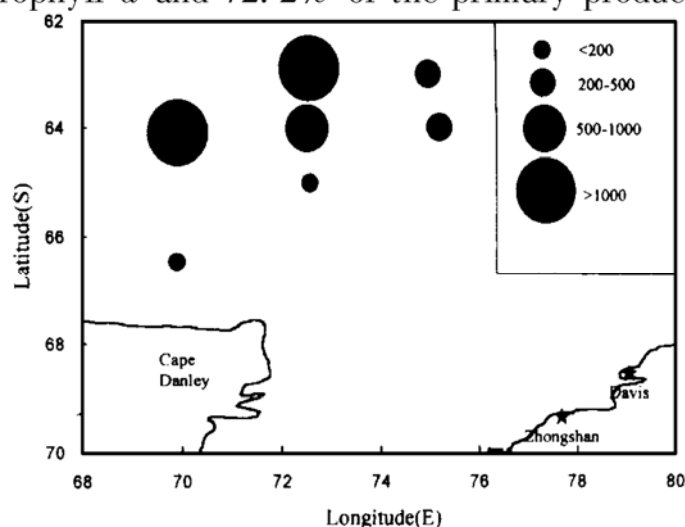


Fig. 3. Numerical distribution of *S. thompsoni* ($\text{ind.} \cdot 1000 \text{ m}^{-3}$) in the Prydz Bay region during Dec. 1998 - Jan. 1999.

tion. The Filtration rate calculated from the ingestion rate accounted for $28 \text{ L} \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$). The results of the shipboard culture experiments are presented in Fig. 4. The filtration rates and ingestion rates of salps estimated from these experiments were $(15.3 \pm 4.6) \text{ L} \cdot \text{ind.}^{-1}$ and $215 \mu\text{g C} \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$, respectively. These results were lower than that of gut fluorescence method.

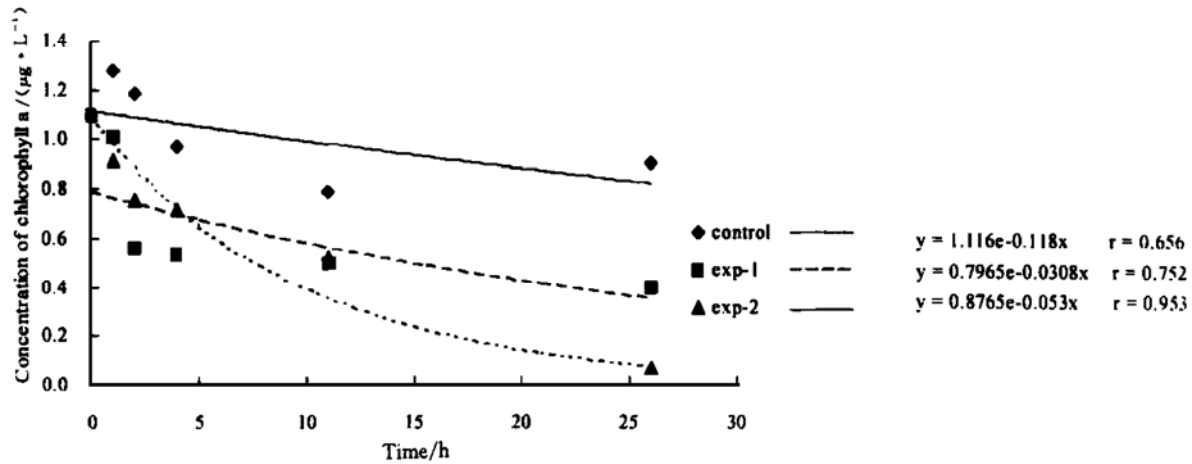


Fig. 4. Variation of chlorophyll *a* concentrations during the Shipboard culture experiments of *S. thompsoni*. The exponential regression equations of each experiment are given.

4 Discussion

The gut pigment contents of *S. thompsoni* measured in present investigation and ranging between $0.14 \mu\text{g pigment} \cdot \text{ind.}^{-1}$ and $1.27 \mu\text{g pigment} \cdot \text{ind.}^{-1}$, were among the low records of previous reports. For the same sea area, the value determined by Perissinotto and Pakhomov (1998) accounted for $(0.08 - 2.5) \mu\text{g pigment} \cdot \text{ind.}^{-1}$, and the value estimated by Dubischar and Bathmann (1997) occupied of $(2.0 - 2.7) \mu\text{g pigment} \cdot \text{ind.}^{-1}$. The ingestion rate of *S. thompsoni* was calculated from the culture experiments carried out on board and brought out about $215 \mu\text{g C} \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$. The rates were higher than the values (about $100 \mu\text{g C} \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$) reported by Dubischar and Bathmann (1997) using the same approach, but were lower than the result ($395 \mu\text{g C} \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$) from the gut-fluorescence method. This may be attributed to the containment effects that the ingestion rates of salps were correlated to swimming activities (Reinke 1987) so that small incubating containment (5L) resulted in decreased ingestion rates (Dubischar and Bathmann 1997).

The ingestion rates obtained by both methods in this study all fell within the range of low records reported by previous investigators (Reinke 1987; Huntley *et al.* 1989; Dubischar and Bathmann 1997; Perissinotto and Pakhomov 1998). Perissinotto and Pakhomov (1998) suggested that the ambient food concentration is an important factor to affect the feeding efficiency of salps. *S. thompsoni* was not able to graze successfully at high particle concentrations when chlorophyll *a* concentration reached levels $> 1 \text{ mg m}^{-3}$. This is related to the inability of *S. Thompsoni* individuals to regulate their filtration rate

and avoid clogging of their filtering apparatus at high particle densities (Perissinotto and Pakhomov 1998). Harbison *et al.* (1986) also reported that salp filtration rate cannot be adjusted in response to changes in particle concentrations. Their feeding mechanism may be disrupted when the mucous net used to capture particles becomes overloaded with food. This causes the breaking away of the net and the formation of an indigestible bolus at the anterior end of the oesophagus. Station iv(7)3 is located at the northern part of the floating ice field, where phytoplankton biomass reached to a high level with the ice melting. Thereby salp showed a relative lower ingestion rate in such high food concentration condition.

S. thompsoni exhibited a relatively high grazing impact on primary production (72%) at station iv(7)3, even calculated by the lower ingestion rate that we determined (see above). It implied that salps were an important phytoplankton consumer in the northern of our investigation area, especially where swarming occurs. Such high grazing impact was also reported in the previous studies. Perissinotto and Pakhomov (1998) reported that the total daily consumption of the population of *S. thompsoni* varied from 0.3% to 108% of daily primary production in the Lazarev Sea region during austral summer. The results from the south-Atlantic indicated that the grazing impact of *S. thompsoni* assemblage on primary production was more than 100% where swarming occurred (Dubischar and Bathmann 1997).

There was a discrepancy between the results yielded from two different approaches for determination of salp ingestion rates. Two possible reasons may be due to this uncertainty. Firstly, ingestion rates of salps are strictly correlated to swimming activities (Reinke 1987) so that the effects of enclosure in a 5-L container may lead to a decrease ingestion rate. Secondly, the stress during the capture and being maintained in a small container resulted in a rapid decrease of animal gut pigment during the gut evacuation rate experiment. This might overestimate the gut evacuation rates that are used to calculate the ingestion rates.

'Salp years', during which a great number of salps dominate planktonic biomass in the sea, often causing the fewness of other zooplanktons, have been reported with increased frequency in high Antarctic waters (Wormuth 1984; Witek *et al.* 1985; Park and Wormuth 1993; Kawamura *et al.* 1994; Schnack-Schiel and Mujica 1994). In the Prydz Bay region, previous results showed that krill was almost absent during the 'Salp years' (Savich 1993). During our study, krill was scarce at the stations where salp swarming occurred in the Prydz Bay region. Considering the high grazing impact of salps on primary production, we agree with the suggestion that salps may outcompete other zooplankton organisms by depriving them of food sources. Once phytoplankton concentrations exceed the threshold level of $\sim 1 \text{ mg (Chl)} \cdot \text{m}^{-3}$, salps disappear to the advantage of other zooplankton such as krill, which is more adaptable to operate in the presence of high particle concentrations (Perissinotto and Pakhomov 1998). Even in the Prydz Bay region where salps and krill appear to be geographically segregated (Hosie 1991), the two species may experience food competition as krill larvae are actively dispersed through the northern salp zone (Hosie 1991; Hosie *et al.* 1997; Perissinotto and Pakhomov 1998).

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