Marine Biology (2006)
DOI 10.1007/s00227-005-0226-8

RESEARCH ARTICLE

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The tunicate *Salpa thompsoni* ecology in the Southern Ocean II. Proximate and elemental composition

Received: 28 July 2004 / Accepted: 16 October 2005

Abstract Detailed determination of *Salpa thompsoni* elemental composition has been carried out on specimens collected in the Eastern Bellingshausen Sea and at the northern edge of the Weddell Gyre during austral autumn (April and May) of 1996 and 2001. More than 170 Antarctic tunicates *S. thompsoni* were analysed to determine wet weight (WW), dry weight (DW), ash-free dry weight (AFDW) and elemental composition (C, N content, proteins, carbohydrates and lipids) of different sizes and stages. Dry weight comprised 6.4% (aggregate form) to 7.7% (solitary form) of the WW. AFDW amounted to ~44% of the DW. Carbon and nitrogen contents (Carbon: 17–22%, Nitrogen: 3–5% of the DW) of both aggregate and solitary forms were found to be high relative to data reported in the literature. Although some unidentified organic compounds are not included in our carbon budget, the findings of this study show higher than previously reported nutritional values of *S. thompsoni*. In spite of this, a shift from a krill-dominated towards a salp-dominated ecosystem would have dramatic consequences for organisms at higher trophic levels.

Communicated by O. Kinne, Oldendorf/Luhe

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Introduction

Salpa thompsoni is the most numerous salp species of the Southern Ocean (Foxton 1966). It is also recognized as an important filter feeder in the Southern Ocean (Voronina 1998). Due to their capacity for rapid asexual reproduction (budding), salps are able to form dense swarms, which have been reported to dominate macrozooplankton in different Antarctic regions (Park and Wormuth 1993; Hosie 1994; Nishikawa et al. 1995; Dubischar and Bathmann 1997; Chiba et al. 1998). Salps are microphagous species and their grazing impact may account for 10–100% of the daily primary production in several regions of the Southern Ocean (Huntley 1989; Dubischar and Bathmann 1997; Perissinotto and Pakhomov 1998a). A fine-mesh feeding net enables salps to feed efficiently on a wide range of food particles. Most of this material, however, is removed from the surface layers through fast sinking faecal pellets (Bruland and Silver 1981), thus channelling biogenic carbon out of the surface waters into long-living "pools" in the deep sea (Le Fèvre et al. 1998).

Distribution patterns of *S. thompsoni* were first investigated by Foxton (1966), using samples from expeditions conducted between 1925 and 1951 on the R.V. Discovery. These investigations showed that *S. thompsoni* has a very patchy distribution. Foxton (1966) considered *S. thompsoni* to be an Antarctic, cold-temperate species, showing a northern limit of distribution coinciding with the Subtropical Convergence (~45°S) and a southern limit near the ice edge (~60°S). During the last 20 years, salps have been reported with increasing frequency in more southerly regions (Kawamura 1986, 1987). Pakhomov et al. (2002) recently updated the map of *S. thompsoni* distribution, compiling the data available from 1980 to 1998. Striking evidence of a southward shift of salp distribution has been found (Pakhomov et al. 2002; Atkinson et al. 2004), but the factors that caused this shift are still under discussion. Have the southern populations reproduced successfully or have they been passively transported within warmer water masses? There is some evidence to show that, when salps were found in southern areas, they were restricted to warm water intrusions or layers (e.g. Pakhomov and Fronemann 2004). Chiba et al. (1999) for example found no solitary forms but only small-sized aggregates in high latitudes (off Adélie Land), suggesting that *S. thompsoni* aggregates were transported into the area and not produced therein. It has been suggested that *S. thompsoni* may be close to its physiological limits at high latitudes (Casareto and Nemoto 1986; Chiba et al. 1999).

Since warming of the oceanic current systems south of 45°S has been documented (Levitus et al. 2000; Gille 2002), the possibility of the establishment of salp populations further south may become real. Should *S. thompsoni* survive and propagate in southern areas, it would have a dramatic impact on ecosystem structure and biogeochemistry. The extremely efficient yet sensitive feeding tools of salps may have a strong impact on microplankton biomass and composition, while the fundamentally different elemental and structural body plan of salps may result in significant impacts on sea water chemistry and food acquisition by higher order predators, such as whales and birds. So far, little is

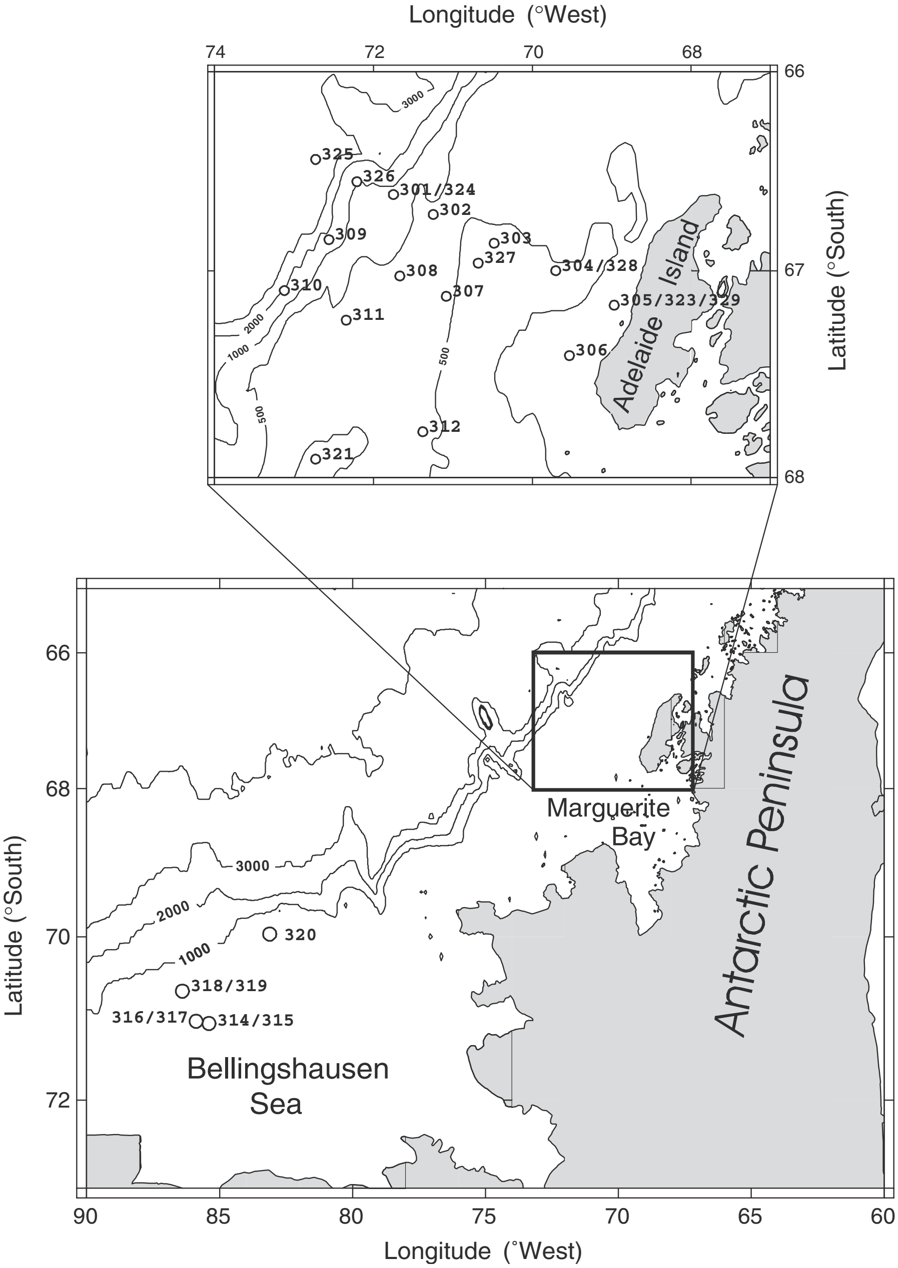

Fig. 1 Investigation area of the expedition ANT XVIII/5b

known on the value of salps as food as compared to other herbivores such as krill.

We investigated salp abundance and ecology in a high Antarctic area, the Bellingshausen Sea, during April/May 2001 and in the Atlantic sector of the Southern Ocean during April/May 1996 (Fig. 1, Table 1). The results are published in two sister papers: part I concerns biological stages, feeding ecology and faecal pellet production rates (Pakhomov et al. 2005) and part II, the present paper, mainly deals with the proximate and elemental composition and their implications for food web dynamics. Additionally, the results reported here show dry weight (DW), carbon and nitrogen content of different salp stages and sizes and, therefore, can be used to provide estimates of salp standing stocks based on net collections.

Materials and methods

Samples were mainly taken during the Southern Ocean GLOBEC-cruise ANT XVIII/5b on board RV *Polarstern* to the Bellingshausen Sea in April/May 2001 (for further information see Pakhomov et al. 2005; Bathmann 2002). The main investigation area was located near Adelaide Island (Fig. 1). Salps were mostly collected at stations 301, 305, 328 and 329 (Pakhomov et al. 2005). In addition, six samples were taken during the expedition ANT XIII/4 on board RV *Polarstern* to the Atlantic sector of the Southern Ocean in April/May 1996 (Fahrbach 1997). Four stations were sampled along the 0° meridian, one sample in the middle of the Weddell-Gyre (st. 86) and a sixth (st. 99) close to the Antarctic Peninsula (Table 1).

During expedition ANT XVIII/5b in April/May 2001, salps were caught using an RMT 8 + 1 (mesh-size 5 mm) and a Bongo net (300 μm). For further information concerning the net catches and sample handling see Pakhomov et al. (2005). During the expedition ANT XIII/4 in April/May 1996 salps were collected using a Multinet (mesh size 100 μm). Salps for analyses of elemental composition were deep-frozen (−80°C) on board.

In the laboratory, salps were thawed overnight in the refrigerator. The size [total length (TL) and oral-atrial length (OAL)] and biological stage of 173 salps were determined and placed individually into the pre-combusted and pre-weighted aluminium foil box. After determination of the wet weight (WW) with a Sartorius R200D electro-balance, salps were freeze-dried for 24 h and DW was determined. About 30 specimens were combusted at 550°C for 24 h to determine the ash-free dry weight (AFDW). Remaining salps were used for biochemical analyses.

Table 1 Stations during the *Polarstern*-expedition ANT XIII/4 where salps were caught with the Multinet (mesh-size 100 μm)

Station	Position	Date
44	60°00.2′S/0°00.5′W	15.04.1996
48	61°59.9′S/0°00.0′E	16.04.1996
50	63°00.2′S/0°00.1′E	17.04.1996
52	64°00.1′S/0°00.2′W	18.04.1996
86	66°07.9′S/31°51.4′W	01.05.1996
99	63°44.1′S/50°50.6′W	07.05.1996

Small salps (TL < 1 cm) were used entire for further analyses. Larger specimens were ground in a small mortar (agate) with a glass pestle to give a homogeneous powder. This enabled us to take sub-samples of these specimens to perform various chemical analyses for the same animal. After freeze-drying and weighing, the animals and the powder were kept in a desiccator.

Biochemical analyses

Carbon and nitrogen (C, N), protein, lipid and carbohydrate contents of about 50 organisms of different sizes and stages were measured. Two to four milligram of the homogenised powder (for small salps entire body) have been used. Carbon and nitrogen contents were determined with a Carlo Erba CHN-analyser using acetanilide as a standard. Total lipid content was determined using a Merckotest (use of Vanillin and phosphoric acid). Carbohydrate measurements were carried out after Holland and Gabbott (1971) using a glucose standard and preceded by protein precipitation with 15% cold TCA. Protein measurements were made following a modified version of the Lowry Assay (Lowry et al. 1951, http://www.hood.edu/academic/biology/protein.htm), using bovine serum albuminum as a standard.

Statistics

Analyses of variance were performed to detect significant differences between the means of the aggregate and the solitary forms. Using the program Sigma-Stat, a one-way ANOVA was calculated and the Holm-Sidak Test was applied for multiple comparisons.

Results

Total length/oral atrial length

Since some authors use TL while others use OAL, we plotted TL as a function of OAL to enable conversions from one value to the other (Fig. 2). For the solitary forms, TL (corresponding to length A in Foxton 1966) was only slightly higher than the OAL (corresponding to length B in Foxton 1966). For the aggregate forms, differences were larger due to the appendices at both sides of their body (Fig. 2).

Wet weight/dry weight/C/N-content

Wet weight of the measured salps varied between 13.5 and 1752.2 mg/Ind (aggregate forms) and between 112.9 and 5456.4 mg/Ind (solitary forms) (Fig. 3).

Dry weight ranged from 0.91 to 103.1 mg/Ind (aggregate forms) and from 6.8 to 361.7 mg/Ind (solitary

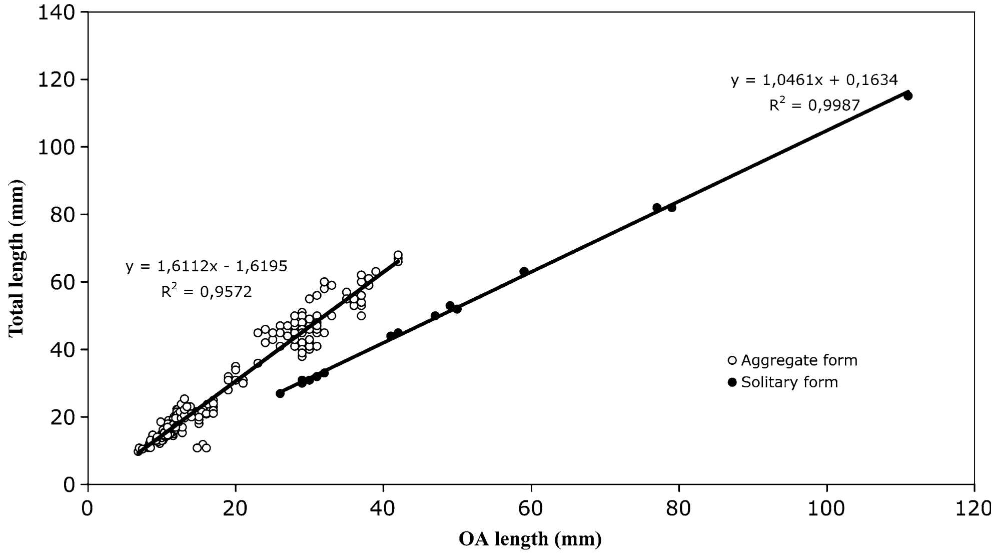

Fig. 2 Total length of aggregate and solitary forms of *S. thompsoni* compared to their oral-atrial length (*OAL*)

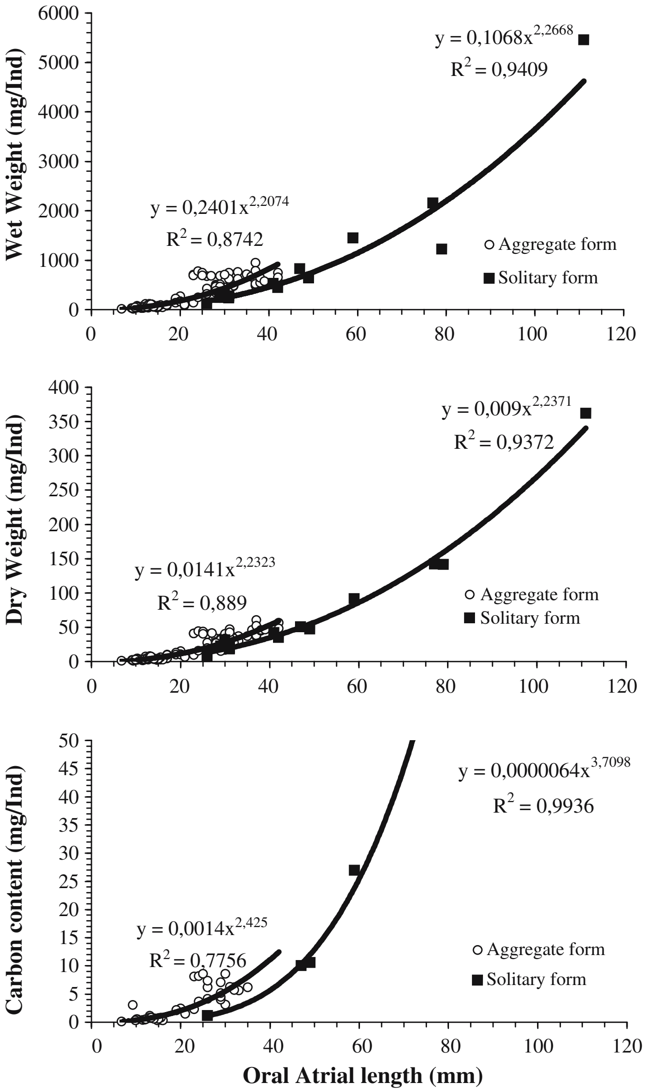

Fig. 3 Wet weight (*WW*), dry weight (*DW*), and carbon content of of *S. thompsoni* as a function of oral atrial length (*OAL*)

forms, Fig. 3). On average, DW accounted for 6.4 ± 0.9% (aggregate forms) to 7.7 ± 1.4% (solitary forms) of the WW (Table 2). Differences in DW between both stages are statistically significant (Table 2).

Carbon content was found to be 17.4% (± 4.1) of the DW for aggregate and 22.5% (± 5.5) for solitary forms. These differences in carbon content between both forms were also statistically confirmed (Table 2).

Biochemical compounds/elemental composition (proteins, total lipids, carbohydrates)

The largest portions of biochemical compounds were proteins and lipids, ranging from 4 to 8% of the DW (Table 3). Solitary forms contained slightly higher percentages of proteins and lipids compared to the aggregate forms, whereas the percentage of carbohydrates was very similar. Protein content weight was 0.07–3.73 mg/Ind and 1.53–18.5 mg in aggregate and solitary forms, respectively (Fig. 4). Total lipid weight ranged from 0.1 to 2.82 mg/Ind in aggregate forms and from

Table 2 Wet weight (WW), dry weight (DW), ash-free dry weight (AFDW), carbon (C) and nitrogen (N) content of different stages of *Salpa thompsoni*, expressed as percentage of the different values

	n	Aggregate form	*n*	Solitary form	*P*
% DW/WW	158	6.4 ± 0.9	15	7.7 ± 1.4	<0.001
% AFDW/DW	28	44.0 ± 8.5	0	–	–
% C/DW	50	17.4 ± 4.1	4	22.3 ± 5.3	<0.05
% N/DW	50	3.53 ± 1.1	4	4.93 ± 1.2	<0.05
C/N	50	5.07 ± 0.8	4	4.53 ± 0.1	NS
% C/AFDW	1	42.4	0	–	–
% N/AFDW	1	9.22	0	–	–

n Number of salps measured

Table 3 Protein, carbohydrate and lipid content of *Salpa thompsoni*, expressed as percentage of the dry weight (DW)

	n	Aggregate form	*n*	Solitary form	*P*
Protein content (% DW)	37	4.4 ± 1.6	11	7.7 ± 1.8	< 0.001
Carbohydrates (% DW)	21	0.9 ± 0.8	8	0.8 ± 0.3	NS
Lipids (% DW)	33	5.7 ± 4.4	11	6.8 ± 2.3	NS

n Number of salps measured, *NS* Not significant

1.11 to 30.76 mg/Ind in solitaries (Fig. 4). Carbohydrates amounted to 0.01–0.41 mg/Ind and 0.14–2.32 mg/Ind in aggregates and solitaries, respectively (Fig. 4).

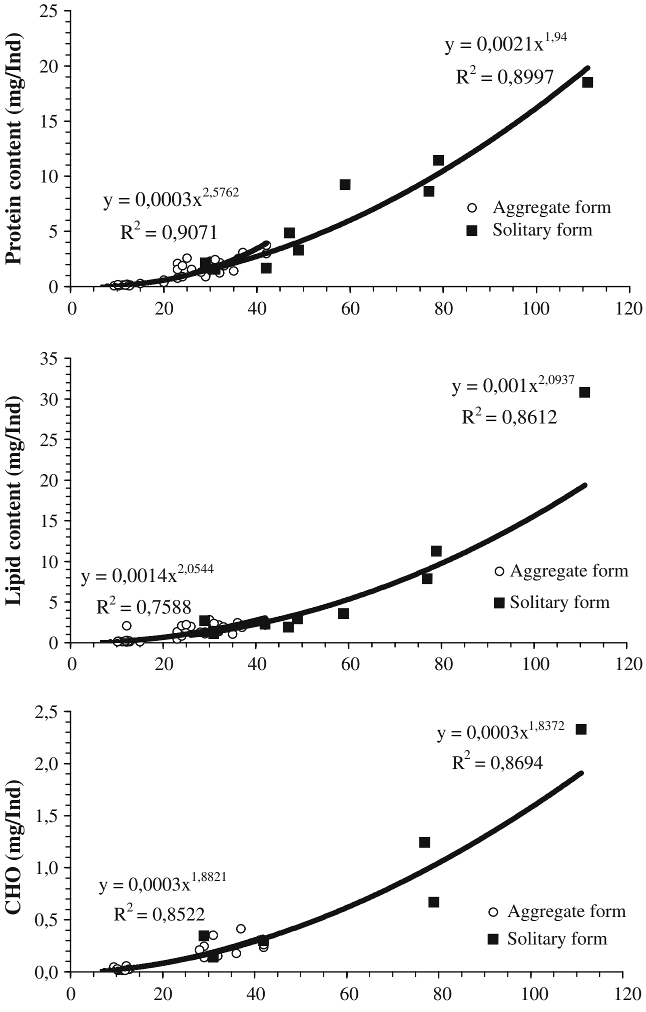

Fig. 4 Elemental composition (proteins, lipids and carbohydrates) of *S. thompsoni* as a function of oral atrial length (*OAL*)

Large embryos

At station 328, we sampled surprisingly large salp embryos (ca. 3–3.5 cm), detached from their mother salp but still connected to their placenta and eleoplast (see photo in Pakhomov et al. 2005). Their values for DW, carbon etc. showed no differences compared to the other stages of same size ($P > 0.05$).

Discussion

To our knowledge, few data on elemental composition of *S. thompsoni* has been published (Ikeda and Mitchell 1982; Ikeda and Bruce 1986; Huntley et al. 1989; Donnelly et al. 1994; Iguchi and Ikeda 2004). We, therefore, also compared our data with measurements carried out on other species from different regions of the world oceans (Madin et al. 1981; Heron et al. 1988; Clarke et al. 1992).

In gelatinous zooplankton, an important source of variability in biochemical composition has been ascribed to the gut contents (Clarke et al. 1992). In the present study, although we measured a large number of salps (> 150), variability in parameters measured was negligible and as a consequence the standard deviations of parameters appeared to be small. This indicates that sources of variability such as differences in gut fullness were negligible.

It is noteworthy, that no significant differences were found in elemental composition between salps collected during the expeditions in April/May 1996 and 2001, despite these being collected in different regions of the Southern Ocean. The data obtained for specimens from both cruises were, therefore, pooled.

Wet weight/dry weight/AFDW

Determination of DW of gelatinous zooplankton is known to be difficult. Gelatinous tissue tends to retain a significant amount of water after drying by traditional techniques. This "water of hydration"-phenomenon probably occurs because of the high content of gel-forming components, e.g. polymeric polysaccharides and proteins in salp bodies, which retains water very strongly (see discussion in Madin et al. 1981; Clarke et al. 1992). This leads to an overestimation of the salp DW.

Generally, the DW of salps ranges between 4 and 8% of the WW (Table 4). While most of the authors dealing with the composition of salps used traditional oven drying techniques, we used the freeze-drying technique to determine the DW. Clarke et al. (1992) investigated a variety of gelatinous species and determined DW by drying at 60°, for up to 155 h. According to their findings, DW of the Southern Ocean species *Salpa fusiformis* accounted for 4.7% of the WW (Table 4). Huntley et al. (1989) also used the 60°C oven drying

Table 4 Comparison of our study with recent studies on salp composition

Species	DW as % WW	AFDW % DW	C % DW	References
Salpa thompsoni	7	44.0	17–22	This study
	3.9–4.0	–	4.2–4.7	Ikeda and Bruce (1986)
	∼4	27	3.4	Huntley et al. (1989)
	∼4	29.1	∼10	Reinke (1987)
Salpa fusiformis	4.7	33.5	11.9 ± 2.0	Clarke et al. (1992)
Thalia democratica	8.04	46.5	18	Heron et al. (1988)
Salpa thompsoni	3.8	–	4.7	Ikeda and Mitchell (1982)
	3.1–3.5	28.4–29.7	5.1–6.0	Iguchi and Ikeda (2004)
Pegea confoederata, Salpa cylindrical, Salpa maxima	–	26.6	7.8	Madin et al. (1981)

See legend of Table 2 for abbreviations

technique and arrived at similar (4%) values for *S. thompsoni*. Heron et al. (1988) used higher temperatures (105°C) for up to 72 h and found the DW of *Thalia democratica* to be 8% of the WW (Table 4).

Schindler et al. (1971) compared freeze-drying with oven drying at up to 100°C and found no significant difference in the weights obtained by two methods. In the Southern Ocean, only Ikeda and Bruce (1986) and Iguchi and Ikeda (2004) used freeze-drying to determine DW of *S. thompsoni* and found that they accounted for only ∼4% of the WW, very similar to the values i.e. obtained by Clarke et al. (1992) for *S. fusiformis* and Huntley et al. (1989) for *S. thompsoni*. Our values 7% (Tables 2, 4) were higher than most other measurements. We can only speculate that this might be a seasonal effect, since the other measurements were conducted during austral spring (Ikeda and Bruce 1986) and austral summer (Clarke et al. 1992; Iguchi and Ikeda 2004), thus earlier in the year compared to our study.

Ash-content was very high and accounted for about 56% of the DW (AFDW of 44 ± 8% DW). This high ash-content is characteristic of gelatinous zooplankton and some authors found even higher percentages (Huntley et al. 1989: 73%; Clarke et al. 1992: 66.4%; Donnelly et al. 1994: 55–70%). Other zooplankton species, such as copepods, show much lower values [e.g. *Calanoides acutus* ca. 8%, *Calanus propinquus* ca. 10% (Donnelly et al. 1994)]. The high percentage of AFDW indicates further difficulties of the ‘‘water of hydration’’ effect, which is not driven off by freeze-drying or oven drying, but removed during ashing.

Donnelly et al. (1994) found seasonal variations in the ash content of *S. thompsoni*. While it accounted for 70% of the DW in summer, it was significantly lower in winter (56% DW). This is consistent with our data (56%), taken in late autumn.

Compared to aggregates, solitary forms of *S. thompsoni* showed slightly higher values of DW as percentage of the WW and carbon and nitrogen content as percentage of the DW (Table 2). The elevated content in organic material was mainly due to a higher content of proteins and, to a lesser degree, lipids (Tables 2, 3). This fact is also reflected in a slightly lower C/N ratio of the solitary forms (Table 2). Madin et al. (1981) compared their C/N-measurements with other literature data and found a similar pattern.

Carbon/nitrogen-content

Our values were higher than in most of other recent studies on carbon content of salp organisms (Table 4), not only when expressed as percentage of the DW (17–20%), but also in terms of mg C per Ind (Fig. 3). Presently, only measurements of Heron et al. (1988) for *T. democratica* were in the same order of magnitude.

Most other zooplankton species have a much higher percentage of carbon per DW: e.g. *Euphausia superba* 42.6–47.1% (Ikeda and Bruce 1986), copepods close to 50% DW (Mizdalski 1988; Donnelly et al. 1994). It is difficult to believe that our values are elevated due to methodological faults. It is indeed noteworthy that AFDW, carbon and lipid (see below) content are all in good agreement showing consistently higher levels than in most other salp species. In the absence of detailed seasonal measurements, we cannot discount the possibility that the high values obtained in this study could be explained by seasonal variability.

Protein/lipid/carbohydrates

The AFDW should roughly correspond to the organic compounds of the salp body, i.e. the sum of proteins, lipids and carbohydrates. In our case, the sum of these compounds, expressed as ‘‘total organics’’ (TO after Madin et al. 1981), accounted for 25–35% of the AFDW, thus explaining only a small portion of the AFDW. Similarly, other authors reported comparably low values ranging from 19 to 51% (Madin et al. 1981). The missing part is considered to be at least partly ‘‘residual’’ or ‘‘bound’’ water, which is not driven off by drying but lost while ashing (Madin et al. 1981). Certainly, some chemical compounds of the salp bodies such as nucleic acids and other smaller molecules cannot be detected with the techniques mentioned above, but typically, they are minor fractions of the organics compounds. Nevertheless, a large proportion of the AFDW remains unaccounted for. For comparison, the sum of ash, proteins, lipids, carbohydrates and chitin in crustacean zooplankton typically accounts for 90–95% of the DW (Clarke et al. 1992). Madin et al. (1981) investigated North Atlantic salp species and found the proteins to be the major contributor (~82%) to the TO. This corresponded to 6.6% of the DW. This value is substantially higher than obtained in our study, e.g. 40–50% of the TO for aggregates and solitaries, respectively. This corresponded to ~4.4% of the DW (Table 3). Much higher protein contribution to the TO measured by Madin et al. (1981) likely resulted from lower lipid content in the salps when compared to our values.

On average, the lipid content in the North Atlantic species accounted for 7.6% of the TO (Madin et al. 1981), corresponding to ~0.6% of the DW. Our findings showed much higher values, e.g. 45–52% of the TO, corresponding to 5.7–6.8% of the DW. Hagen (1988) found lower lipid contents (only 2.3–3.3% of the DW). This could be a seasonal effect since Hagen's measurements for *S. thompsoni* were obtained from specimens collected during austral summer in the southern Weddell Gyre. Certainly more investigations are needed to detect potential seasonal changes in salp elemental composition.

Carbohydrate concentrations in salps are very low and generally account for about 1% of the DW: e.g. 0.8–0.9% of the DW (our data), 0.8% (Madin et al. 1981) and 1.3% (Clarke et al. 1992). This is surprising, because the tunic of tunicates such as ascidians consists mainly of an extracellular product, composed of protein and polysaccharides (Smith and Dehnel 1971).

What are the missing components?

As mentioned above, the sum of proteins, lipids, carbohydrates and ash explain only about two thirds of the salps DW. Also, the missing components might partly be due to residual water, which is not driven off by oven drying, thus inflating the DW estimates, but lost during ashing, leading to an underestimate of the ash content. However, a substantial number of organic compounds may not have been detected by our techniques. Below we discuss possible scenarios for the "missing components".

The measured C accounted for 17.4% DW (aggregate forms). Clarke et al. (1992) calculated the average fraction of carbon in organic matter being 0.55–0.6. If we apply this factor to our carbon measurements, our measured C would correspond to an amount of total organics of 29–32% of the DW, whereas our measurements detected only TO of about 11% of the DW. This indicates that the "missing third" of the AFDW is not only "residual water" but must also consist of organic compounds. The low C/N-ratio excludes compounds without nitrogen, such as carbohydrates and lipids. Therefore, the unidentified OM likely consists of proteins or glycoproteins, which could be highly cross-linked leading to their ineffective extraction and detection. Furthermore, it is generally assumed that the N content of proteins accounts for 16–17%. If we calculate the protein content of *S. thompsoni* on the basis of our N measurements and using these conversion factors, the protein content of *S. thompsoni* would increase to 20–22% of the DW, which is fivefold higher than the value we measured (4.4%). Overall, from both C and N scenarios it appears that some groups of proteins have not been detected by our measurements.

In summary, although some organic compounds were likely not detected by our methods, our findings show higher nutritional values of *S. thompsoni* than previously reported. Furthermore, the seasonal variability in salp elemental composition clearly warrants further investigation.

Role of salps in the Antarctic ecosystem

A shift of salp distribution to more southerly regions and an expulsion of krill would have a dramatic impact on the structure of Antarctic ecosystems. Although results of this study revealed a higher nutrition value of salps than previously assumed, it still remains unclear whether salps will be able to meet energetic demands of higher trophic level predators in the absence of krill; the consumption of gelatinous species, such as salps, by fish has in fact been reported several times (Duhamel and Hureau 1985; Kashkina 1986; Pakhomov 1993; Mianzan et al. 2001). Furthermore, some birds may consume salps (see review in Pakhomov et al. 2002). However, it has been shown that because of warming of watery food up to the endothermic body temperature of about 40°C, a higher energetic demand will result (4.17 Joules per g water for 1°C) than the chemical energy stored in salps (Wilson and Culik 1991). Antarctic krill also have a relative high water content (80%). However, its high content of proteins and lipids, 65.1 and 14.2% of the DW (Grantham 1977), compared to only 5.2 and 6.0% of the DW of salps (Table 3), would result in a calorific value per unit of mass much higher than in salps. This makes krill an important and preferred food source for most of endotherms in the Antarctic. We therefore speculate that a large-scale switch of a krill-dominated system to a salp-dominated system (Atkinson et al. 2004) may not only alter regional carbon flux, but most probably will have a dramatic impact on feeding conditions of higher trophic levels and lead to a decrease in top predator populations.

Acknowledgements We wish to thank the captain, officers and crew of the RV "Polarstern" for their skilful help throughout both cruises. Special thanks are due to Eberhard Fahrbach (chief scientist during the ANT XIII/4-cruise) who greatly supported the work of a small biology group in the middle of a large group of oceanographers with lots of tasks. We also wish to thank Christian Hamm, Richard Crawford and two anonymous reviewers for carefully reading the manuscript and their very helpful comments. This work was partly funded by a grant of the Alexander von Humboldt-Stiftung for E.A.P.

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