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# MARKED INVERSE DISTRIBUTION OF SALPS TO OTHER MACROZOOPLANKTON IN WATERS ADJACENT TO THE SOUTH SHETLAND ISLANDS

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Abstract: Spatial distributions of salps and other zooplankton in the waters around the South Shetland Islands were examined. Two salp species, Salpa thompsoni and Ihlea racovitzai, were identified, and occurred with the latter more dominant than the former. At stations where salps dominated in terms of numerical abundance, other zooplankton were extremely scarce. Numerically, salps showed marked inverse distribution to copepods, amphipods, chaetognaths and polychaetes. This inverse distribution pattern covered the wide surface ranges of approximately  $110 \times 10^3$  km<sup>2</sup>. Its cause cannot be explained by either behavioral functions of organisms such as swarm formations or ecological regime such as interspecific exclusion. Predation by salps on zooplankton is also unlikely because only diatoms were found in the digestive tracts of salps. Salps inhabited waters with higher chl-a concentration than other zooplankton, and the contours of 0.3 mg·m<sup>-3</sup> chl-a concentration corresponded roughly with the limit of salp distribution. This zonation by chl-a may be related to the distribution of Antarctic Winter Water (AWW), the subsurface temperature minimum. Higher chl-a together with low temperatures in the water column corresponded to the Antarctic Peninsula shelf water. Marked inverse distribution of salps and other zooplankton might be induced by an unknown function of the AWW.

#### 1. Introduction

Many studies on macro- and mesozooplankton distributions in the Southern Ocean have been reported elsewhere, especially during and after the BIOMASS Program. From the community component point of view, however, the bulk of the past studies treated mainly copepods, euphausiids and other crustaceans due to their relative dominance and ecological importance in the zooplankton community. Except for some zoogeographical and taxonomical studies (APSTEIN, 1906; FOXTON, 1961, 1971; CASARETO and NEMOTO, 1986, 1987), salps in the Southern Ocean have been one of the less studied organisms. Recently, WIEBE *et al.* (1979) reported the important role of salps in the North Atlantic marine ecosystem.

In the Southern Ocean, occurrence of salps is usually occasional. Of eightytwo N70V net stations throughout the DISCOVERY investigations, 'Salpa fusifor-

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mins' (= S. thompsoni + S. gerlachei, see FOXTON, 1966) was recorded only at thirty stations, the highest number was 163 individuals per haul (Table I in HARDY and GUNTHER, 1935). HOPKINS (1971) did not find notable occurrence of salps in his ELTANIN collections in the Pacific sector of the Antarctic. Although 'S. fusiformis' shows circumpolar distribution, its frequencies of occurrence in the plankton catches greatly differ locally (BAKER, 1954), suggesting that the salp distribution is spatially heterogenous. Salps are often missed in usual plankton catches due to their somewhat sparse and patchy distributions, and they are often treated as a rather minor component in the Southern Ocean zooplankton community (BODEN and PARKER, 1986; VORONINA and NAUMOV, 1968), or even mentioned little (MACKINTOSH, 1937; HOPKINS, 1971; VINOGRADOV and NAUMOV, 1964; BRODSKII, 1964; VORONINA, 1967).

Recently, however, WORMUTH (1984) reported salps to be the dominant organisms in the waters around Elephant Island and the Bransfield Strait region, where salps showed less pronounced depth ranges in the diel vertical migrations. The studied region approximately coincides with the geographical range of high frequency of occurrence in the DISCOVERY investigations (BAKER, 1954). WORMUTH (1984) also pointed out that abundance of copepods was low relative to salps. Predominance of salps was also reported in the Bransfield Strait region (WITEK *et al.*, 1985). In some cases salps play an important role in transporting organic matter to great depth through their vertical migrations (*e.g.* WIEBE *et al.*, 1979). In the light of increasing information on distribution ecology of salps, we aim to report two cases of occurrence of salps with marked inverse relation to copepods and other macrozooplankton in and around the South Shetland Islands.

## 2. Materials and Methods

During the 6th KAIYO MARU expedition of the Fisheries Agency to the Antarctic from November 1990 to March 1991, macrozooplankton samplings were carried out during two phases of the investigation, from December 22, 1990 to January 7, 1991 (Leg I), and from January 18 to February 4, 1991 (Leg II). The investigated area covers waters in and around the South Shetland Islands including Elephant Island (Fig. 1). A total of 106 hydrographic stations were occupied throughout the present investigation; plankton sampling was conducted at 26 stations for Leg I and 56 stations for Leg II. A UNESCO WP-2 net (56.0 cm mouth opening, 0.35 mm netting) fitted with a flow-meter was employed for 100-0 m vertical net tows. When the net was lowered, the wire cable was at an angle due to the ship's drift, so additional wire cable was paid out to reach the target depth. Samplings were conducted at different times of day. About half of the samples was obtained during morning/daytime hours, and the rest during evening/nighttime hours throughout Leg I and Leg II. Collected samples were split into two subsamples, one of which was preserved in 10% buffered formalin for the present study.

Salps were sorted out from the subsample series. Both salps and other zooplankton were subjected to wet weight measurements, and then counted



Fig. 1. Hydrographic stations on Leg I and Leg II during the 6th KAIYO MARU expedition in the austral summer of 1990/91. Hydrographic observations were carried out at all stations, and plankton samplings were done at the solid circled stations.

under the microscope. Wet weight data, however, were not used in this study because there were great size differences between, for instance, large salps and copepods. Salp and other zooplankton concentrations were expressed in individuals m<sup>-3</sup>. Salps were identified by consulting Foxton (1966, 1971), and CASARETO and NEMOTO (1986, 1987). Zooplankton other than salps were counted by higher taxonomical groups such as copepods, amphipods, chaetognaths, euphausiids and polychaetes. Major copepods were also identified by species and counted using 1/4 to 1/8 aliquots of subsamples.

#### 3. Results and Discussion

## 3.1. Species of salps

The number of samples (=stations) containing salps was 20 out of 26 sampling stations for Leg I, and 18 out of 56 for Leg II respectively. Two species of salps were identified: Salpa thompsoni and Ihlea racovitzai. Some specimens showed intermediate characteristics of Salpa gerlachei, but they were combined with S. thompsoni because S. gerlachei has been supposed to be a local form of S. thompsoni (CASARETO and NEMOTO, 1987). The S. gerlachei-like individuals lacked clear enough morphological features to be separated from S. thompsoni.

## 3.2. Abundance of salps

Salps, especially genus Salpa, have been known to perform a pronounced diel vertical migration (WIEBE et al., 1979; HARBISON and CAMPENOT, 1979), and thus the possible influence of sampling time on the amount of 0-100 m catch was

Total No.						
	of samples	Ira	Irs	Sta	Sts	C.V.*
Leg I						
Morning	6	2.24 (6)	0.16 (2)	absent	0.08 (1)	1.14
Day	3	7.48 (3)	0.09 (1)	3.84(1)	absent	0.99
Evening	4	4.83 (3)	0.15 (2)	0.60 (1)	0.07 (1)	0.62
Night	7	3.97 (5)	0.06(2)	0.64 (4)	abusent	0.41
Leg II						
Morning	4	1.44 (4)	0.56 (2)	0.08 (1)	0.04(1)	1.03
Day	4	1.51 (3)	0.28 (2)	1.61 (2)	absent	0.64
Evening	2	0.42(1)	0.08 (1)	0.41 (1)	0.20(1)	_**
Night	8	0.91 (5)	0.23 (5)	0.35 (3)	absent	1.53
Ira: <i>11</i>	hlea rad	covitzai – aggr	egates	Morning	: 0300 - 0900	
Irs: Ihlea racovitzai - solitaries				Day:	0900 - 1500	
Sta: Salpa thompsoni - aggregates				Evening: 1500 - 1900		
Sts: Salpa thompsoni - solitaries				Night: 1900 - 0300		

Table 1. Average number of salps (Number  $m^{-3}$ ) by different time zone of sampling. Number of samples are indicated in parentheses.

examined (Table 1).

Since no paired samples for day and night at the same sampling stations were obtained in this study, it was impossible to compare the plankton abundance by the difference in local time of catches. Table 1, however, indicates that there was no apparent difference in the catches between evening to nighttime and morning to daytime collections throughout Leg I and Leg II. Abundance of salps varied from station to station. The high coefficient of variations (C.V.) may reflect local changes in abundance of salps. CASARETO and NEMOTO (1986) found no clear day-night changes in abundance of *I. racovitzai* in the Pacific sector of the Southern Ocean. They also found less pronounced day-night changes in both aggregates and solitaries. The difference in abundance of salps seems to reflect their geographical distribution patterns rather than a difference in collection time.

## 3.3. Spatial distributions

Figures 2 and 3 demonstrate spatial distributions of salps together with total numbers of copepods in Leg I and Leg II respectively. Both *S. thompsoni* and *I. racovitzai* were largely composed of aggregates (see also Table 1), and were combined into one column in the histograms. In Leg I *I. racovitzai* was predominant over most stations located in the southern half of the investigated area including Bransfield Strait. On the other hand, *S. thompsoni* was concomitant



Fig. 2. Distributions of Salpa thompsoni (black), Ihlea racovitzai (open) and total copepods (shaded) in Leg I. The southern boundary of the Antarctic Winter Water (AWW)(solid line) and chl-a concentration of 0.3 mg·m<sup>-3</sup> (average, 0–100 m) are shown by broken lines. Chlorophyll concentration increases toward the south. Scales in the figure denote copepods (a) and salps (b) in individuals·m<sup>-3</sup>. Triangles indicate the occurrence of copepods in concentration less than 10·m<sup>-3</sup>. Stations without triangles indicate no occurrence of copepods.



Fig. 3. Same as in Fig. 2, but for Leg II. The AWW exists between two solid lines. Legends as in Fig. 2.

with *I. racovitzai* and distributed rather sporadically (Fig. 2). The highest number for *I. racovitzai* was 18.5 salps·m<sup>-3</sup> at Stn. 49, which was a massive number compared to 6.5 salps·m<sup>-3</sup> found in the case of *Salpa aspera* (WIEBE *et al.*, 1979). Large abundance of copepods was found only at the northern four stations (Stns. 41-43, 45). Numbers of copepod were very small (<10 inds·m<sup>-3</sup>) at many stations, especially in the area adjacent to the South Shetland Islands. There was no station where salps were accompanied by a large number of copepods. On the whole it was very clear that salps and copepods were in marked inverse distribution over all stations on Leg I.

An inverse distribution pattern between salps and copepods was again observed on Leg II, although salps were concomitant with cope-pods at some stations (Stns. 88, 95, 107, 108, 116), especially in the northern half of the sampling grid where S. thompsoni prevailed (Fig. 3). A large number of S. thompsoni was recorded only at one station (Stn. 88) on Leg II. Copepods were more abundant on Leg II than Leg I with southerly decreasing gradient in abundance. However, a large abundance of copepods in Leg II as well as Leg I



Fig. 4. Distributions of amphipods (dotted), polychaetes (solid) and chaetognaths (open) in Leg I in number  $\cdot m^{-3}$ . Triangles indicate the station where salps occurred. No triangles indicate no salp occurrence.

was found at the stations located in the northern part of the investigated grids. Of copepods on Leg II Oithona similis, Metridia gerlachei, Rhincalanus gigas, Calanoides acutus, and Clausocalanus laticeps were relatively abundant, whereas the latter two species were predominant on Leg I. Although copepods at the southern stations of Leg II were less abundant, copepod distribution was perhaps at the stage of southward expansion with the progress of season. On the whole S. thompsoni was less abundant and sparse than I. racovitzai, the true Antarctic species (FOXTON, 1971). CASARETO and NEMOTO (1986), on the other hand, found a greater predominance of S. thompsoni than I. racovitzai in the Australian sector of the Antarctic. The large amount of cold Antarctic Winter Water may be related to the predominance of I. racovitzai, a species which thrives at low temperature.

A similar inverse distribution can be observed in any couple of salps with euphausiids, amphipods, polychaetes, and chaetognaths. It was more clear especially in the latter three groups (Figs. 4 and 5). Polychaetes dominated among them on Leg I whereas chaetognaths dominated on Leg II. In the latter case, however, amphipods or chaetognaths or both showed concomitant occurrence within the abundance ranges less than 1 individual  $m^{-3}$ .

Some animal groups having patchy distributions sometimes prevail in plankton net tows, especially when they are fished well within the local swarms (KAWAMURA and HIRANO, 1985, KAWAMURA, 1990). In a study of the Gulf Stream, BIGELOW (1909) stated that, 'as is usually the case when any one large organism is swarming throughout a considerable period, the yields of the surface



Fig. 5. Same as in Fig. 3, but for Leg II.

hauls were qualitatively corresponding poor'. Inverse distribution patterns in zooplankton occur only occasionally, but are a widely recognized feature in distribution ecology. It may related to many aspects of organisms and environments, but causation for this would hardly be explained by the present samples obtained under poor process-oriented sampling scheme.

In this study, the inverse distribution in the upper 100 m water column covered a wide geographical range. In this context, it seems to be unlikely that the inverse distribution was caused either by the patchiness of salps or by their predation on copepods and others. Of the latter, we found only diatoms in the digestive tracts of salps. The phenomenon may be related to the whole water mass structure in the investigated area.

## 3.4. Chlorophyll-a and temperature

Chl-a and temperature distributions in four vertical sections down to 100 m are shown in Fig. 6. Chl-a in this section is the average concentration in the upper 100 m. Generally, chl-a concentration was high in the southern half of stations throughout the four sections, especially in the section between stations



Fig. 6. Temperature (°C) and chl-a concentrations  $(mg \cdot m^{-3})$  along the vertical sections between stations 36-42 and 44-50 in Leg I, and between stations 123-129 and 137-143 in Leg II. Triangles indicate the southernmost extent of the subsurface temperature minimum (AWW).

137 and 143. Chl-*a* concentrations ranged from <0.15 to >3.0 mg·m<sup>-3</sup> through Leg I and Leg II (FISHERIES AGENCY, 1991). The isopleth for chl-*a* value of 0.3 mg·m<sup>-3</sup> is superimposed in Figs. 2 and 3. The 0.3 mg·m<sup>-3</sup> chl-*a* concentration is roughly consistent with the northernmost boundary of salp distribution on both Legs. Copepods occurred mainly in waters of lower chl-*a* concentration whereas salps were in waters of higher concentration. On Leg II, however, three stations in the northern sampling grids were in the lower chl-*a* concentration, and only *S*. *thompsoni* was found at these stations. Among the four water masses known in the area of present study (LIPSKI, 1982), the isopleth of 0.3 mg·m<sup>-3</sup> chl-*a* concentration roughly agrees with the boundary between the Antarctic surface waters of the Drake Passage and the Antarctic Peninsula shelf water.

Temperature profiles in Leg II indicate that the core of the Antarctic Winter Water (AWW) with minimum temperature  $(-1.46^{\circ}C)$  exists at the depth of about 50 m to 70 m, and its tongue like southernmost tip is roughly at the location of 0.3-0.5 mg·m<sup>-3</sup>chl-a isopleths (Fig. III-3-5 in FISHERIES AGENCY, 1991). Similarly, AWW was found on both Leg I and Leg II (KATAYAMA, 1992). Plots of the southernmost tip location of the AWW as demonstrated with solid lines in Figs. 2 and 3 may suggest an additional explanatory boundary for the inverse distributions of salps vs other zooplankton groups. This boundary together with the chl-a isopleth may indicate a possible relation to LIPSKI's boundary between the Drake Passage water and the Antarctic Peninsula shelf water. During the BIOMASS-SIBEX in the Bransfield Strait, GRELOWSKI and TOKARCZYK (1985) did not find cold waters that might indicate the AWW around the South Shetland Islands. Intermediate cold water below  $-1.0^{\circ}$ C existed at the stations between Elephant Island and South Orkney Islands, but they did not identify such cold water mass as the AWW. In the same investigations, WITEK et al. (1985) illustrated no inverse distribution patterns of salps with other macrozooplankton.

Although we have no data that directly explain the ecological effect of those boundaries or water masses on the zooplankton distribution, the above mentioned evidence may lead to speculation that the AWW or  $0.3 \text{ mg} \cdot \text{m}^{-3}$  chl-*a* concentration or both would probably be causative for the inverse distribution patterns. Within the region where the AWW prevails below the surface, the abundance of macrozooplankton was much poorer, and salps were in the modified shelf water with relatively high chl-*a* concentration (FISHERIES AGENCY, 1991). In the Weddell-Scotia confluence region during the winter (June-August) of 1988, only *S. thompsoni* was subdominant among macrozooplankton (LAN-CRAFT *et al.*, 1991). This species was again dominant in the same area in the present study during the austral summer of 1989/1990 (SIEGEL, 1990), but JAZD-ZEWSKI *et al.* (1982) did not find any salps during their BIOMASS-FIBEX expedition.

In the light of general distribution patterns of salps (e.g. FOXTON, 1971), dominance of *I. racovitzai* in the present study may infer a quite unusual phenomenon which is hardly explained. Our T-S-P diagram data suggested no clear difference between *S. thompsoni* and *I. racovitzai*, but the former was

suggested to be relatively stenohaline (33.85–34.28 PSU) whereas the latter species was stenothermal (0.6–1.9°C). From the occurrence of *I. racovitzai* at extremely low temperature and salinity, FOXTON (1971) defined *I. racovitzai* to be a surface species. If major distribution ranges for *S. thompsoni* were in deeper strata beyond 100 m, the lowermost sampling depth in the present study, then *I. racovitzai* might show apparent dominancy in shallow layer catches. Samples taken during the Discovery investigations showed that the maximum number of *S. fusiformis*, a complex of *S. thompsoni* and *S. gerlachei* (FOXTON, 1966), was most frequently found below 100m (HARDY and GUNTHER, 1935).

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