

Distribution and population structure of salps off Adelie Land in the Southern Ocean during austral summer, 2003 and 2005

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Abstract: To investigate the distribution and population structure of salps which sustain the Antarctic ecosystems, stratified and quantitative samplings using a plankton net with mouth area of 8 m² (RMT 8) were conducted off Adelie Land during austral summer of 2003 and 2005. Observed were two salp species: *Salpa thompsoni* and *Ihlea racovitzai*, the former being dominant numerically. Mature aggregates and immature solitaries mainly occurred in the deep layer while immature aggregates and mature solitaries were observed in the surface layer. This result implies that *S. thompsoni* are ontogenetic vertical migrators. No mature individuals of aggregates and/or solitaries of *S. thompsoni* occurred in the south of 65°20'S. This observation suggests that the *S. thompsoni* population distributed at high latitude (south of 65°20'S) was not reproducing.

Keywords: *Salpa thompsoni*, distribution, population structure, Southern Ocean

1. Introduction

Salpa thompsoni is the most abundant salp species and major herbivorous zooplankton together with krills and copepods in the Southern Ocean (VORONINA, 1998). *S. thompsoni* is known to be distributed at middle latitude (45–55°S) of the Southern Ocean (FOXTON, 1966). Recent reports have suggested that the distribution of *S. thompsoni* has been shifting southward (PAKHOMOV *et al.*, 2002; ATKINSON *et al.*, 2004). *S. thompsoni* has high reproductive (DAPONTE *et al.*, 2001) and ingestion abilities (HUNTLEY *et al.*, 1989; DUBISCHAR and BATHMANN, 1997; PERISSINOTTO and PAKHOMOV, 1998). This species occasionally forms a dense swarm and dominates macrozooplankton communities (e. g., HOSIE, 1994; NISHIKAWA *et al.*, 1995; DUBISCHAR and BATHMANN, 1997; CHIBA *et al.*, 1998; HOSIE *et*

al., 2000). Possible negative effects of the salp swarm on reproduction and survival of larvae of *Euphausia superba* have been emphasized (HUNTLEY *et al.*, 1989; LOEB *et al.*, 1997), thus altering the Southern Ocean food web (ATKINSON *et al.*, 2004); however, *S. thompsoni* life cycle strategies in the Southern Ocean still remain unknown.

Like the other Thaliacea, salps have a unique reproductive strategy, that is, a generation change happens between sexually reproducing aggregates and asexually reproducing solitaries (GODEAUX *et al.*, 1998). Therefore, reproductive states of both aggregates and solitaries need to be studied to understand salps' generation mechanism (CHIBA *et al.*, 1999). CALDWELL (1966) and FOXTON (1966) reported *S. thompsoni* also distributed in the depths deeper than 200 m. FOXTON (1966) found solitaries occurred in the deeper layers and explained individuals occurring in the deeper layers may be of importance in the life cycle of *S. thompsoni* and in the maintenance of the shallower population. Furthermore, previous studies

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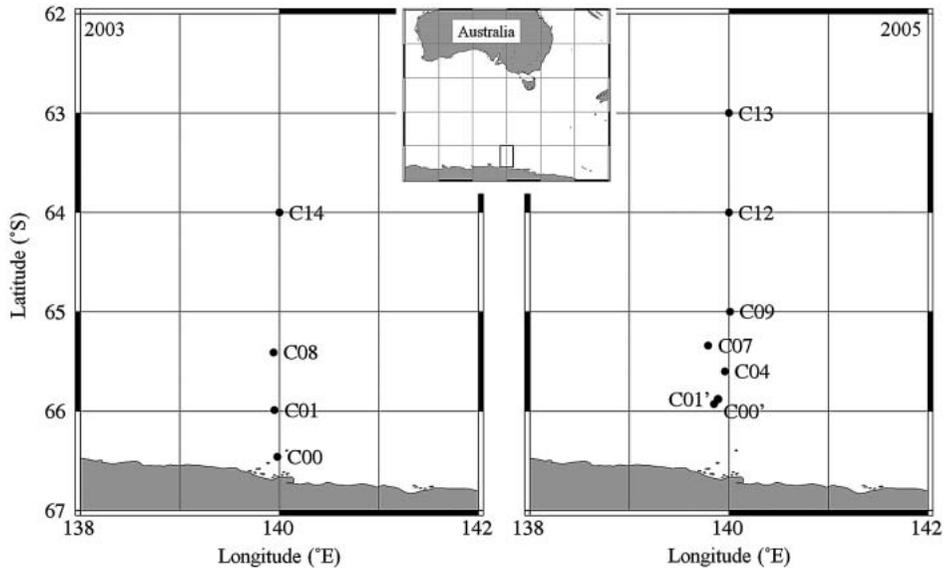


Fig. 1. Sampling and observation stations off Adelie Land in 2003 and 2005.

(FOXTON, 1966; CASARETO and NEMOTO, 1986) have reported the different vertical distribution of the maturity stage's composition of *S. thompsoni*. It is thus necessary to clarify the vertical distribution and population structure in the mesopelagic zone to understand the life cycle strategies of *S. thompsoni*; however, there is little information on the life cycle strategies below 200 m.

Therefore, we conducted stratified and quantitative samplings to understand the distribution and population structure of salps off Adelie Land in the Southern Ocean during austral summer of 2003 and 2005.

2. Materials and methods

Samplings were conducted by TR/V Umitaka-Marui (1886 ton) of Tokyo University of Marine Science and Technology from 4 to 7 February in 2003 and from 12 to 15 February in 2005 along 140°E off Adelie Land in the Southern Ocean (Fig. 1). Samples were collected using an RMT 8 (Rectangular Midwater Trawl, mouth area: 8 m², mesh opening: 4.5 mm, Ocean Scientific International Ltd., Baker *et al.*, 1973), which was obliquely towed in 3–6 different strata between the surface and 2886 m (Table 1). In 2003, maximum sampling depths at Stns. C14 and C08 were 2886 and 2300 m,

respectively. At Stns. C01 and C00, deepest depths sampled were 180 and 835 m, respectively. In 2005, samplings were basically conducted in 6 strata between the surface and 2000 m (0–50–100–200 m and 200–500–1000–2000 m). At Stns. C04, C01' and C00' where bottom depths are shallower than 1000 m, maximum sampling depths were 950, 200 and 194 m, respectively. The ship's speed during the net tows was 1 m s⁻¹. Samples were immediately preserved onboard in buffered 5% formalin-seawater solution. The filtered volume was calculated from the mouth area of the net and flow meter counts. Samples collected from 200–500 m at Stn. C07 and 100–194 m at Stn. C00' in 2005 were excluded from the analysis because of defective preservations.

In the laboratory, subsamples were taken and divided into 1/2 to 1/8 using a MOTODA plankton splitter (MOTODA, 1959) when the initial catch was large. The zooplankton were divided into the eleven taxa (Salpida, Siphonophora, Medusae, Chaetognatha, Polychaeta, Ostracoda, Copepoda, Amphipoda, Euphausiacea, Decapoda and Pteropoda), and wet weight to the nearest 0.01 g were determined for each taxon using an electrobalance. The conversion factors from wet weight to carbon weight was from CAUFFOPÉ and HEYMANS

Table 1. List of sampling data during TR/V Umitaka-maru cruises in 2003 and 2005.

Station	Location		Date	Local time	Sampling layer (m)
	(S)	(E)			
C00	66° 25.6′	139° 47.0′	2003/2/4	05:02–06:42	0–200–500–835
C01	65° 55.8′	139° 55.7′	2003/2/4	14:55–15:28	0–50–100–180
C08	65° 25.3′	140° 02.2′	2003/2/5	13:41–15:34	0–500–1000–2300
C14	63° 54.6′	139° 52.0′	2003/2/7	13:19–15:13	500–1000–2000–2886
	63° 48.0′	139° 50.4′	2003/2/7	16:49–17:32	0–77–193–474
C00′	65° 54.3′	139° 57.1′	2005/2/12	05:37–07:37	0–50–100–194
C01′	65° 51.5′	139° 59.0′	2005/2/12	00:36–02:11	0–50–100–200
C04	65° 35.2′	139° 55.6′	2005/2/12	19:55–22:13	200–500–800–950
	65° 31.9′	139° 46.8′	2005/2/12	22:42–00:20	0–50–100–200
C07	65° 20.2′	139° 45.7′	2005/2/13	09:25–12:24	200–500–1000–2000
	65° 24.7′	139° 35.1′	2005/2/13	12:47–14:27	0–50–100–200
C09	65° 03.1′	139° 58.5′	2005/2/13	23:21–02:26	200–500–1000–2000
	65° 05.0′	139° 53.9′	2005/2/14	02:52–03:30	0–50–100–200
C12	64° 03.4′	139° 58.6′	2005/2/14	16:56–20:03	200–500–1000–2000
	64° 06.0′	139° 57.8′	2005/2/14	20:16–22:12	0–50–100–200
C13	62° 56.7′	140° 03.9′	2005/2/15	05:05–08:19	200–500–1000–2000
	62° 54.5′	140° 07.8′	2005/2/15	08:35–10:16	0–50–100–200

Table 2. Description of each maturity stage of *Salpa thompsoni* aggregate.

Maturity stages	Embryonic state	Placenta	Muscle bands	Eleoblast	Remark
0	unfertilized	×	×	×	
1	fertilized	×	×	×	
2	developing	○	×	×	
3	developing	○	○	○	Small eleoblast
4	fully developed	○	○	○	Eleoblast as large as placenta and clear muscle bands
spent	released	–	–	–	Only placental scar
X	empty or no embryo	–	–	–	

Table 3. Description of each maturity stage of *Salpa thompsoni* solitary.

Maturity stages	Stolon state	Remark
1	unsegmented	With short stolon
2	developing	With segmented stolon and longer than stage 1
3	developing	The first stolon block not differentiated
4a		The first stolon block differentiated
4b	mature	Presence of well-developed the second block
5a		The first block released and presence of the test scar

(2005) for Siphonophora and DAVIS and WIEBE (1985) for other taxa except for Salpida. Species and generations of salps were identified and counted. For species identification, CASARETO and NEMOTO (1987) considered *Salpa thompsoni* and *S. gerlachei* were synonyms to each other. In the present study, we thus treated these two species as *S. thompsoni*. Abundance of salps was calculated from the

number of individuals and filtered volume. Carbon weights of salps were estimated using wet and carbon weight relationship after HUNTLEY *et al.* (1989) for *S. thompsoni* and NISHIKAWA *et al.* (1995) for *Ihlea racovitzai*. For body length (BL: oral-atrial distance) and maturity stages of aggregates and solitaries of *S. thompsoni*, all individuals in the initial or subsamples were examined. The BL was measured to the nearest

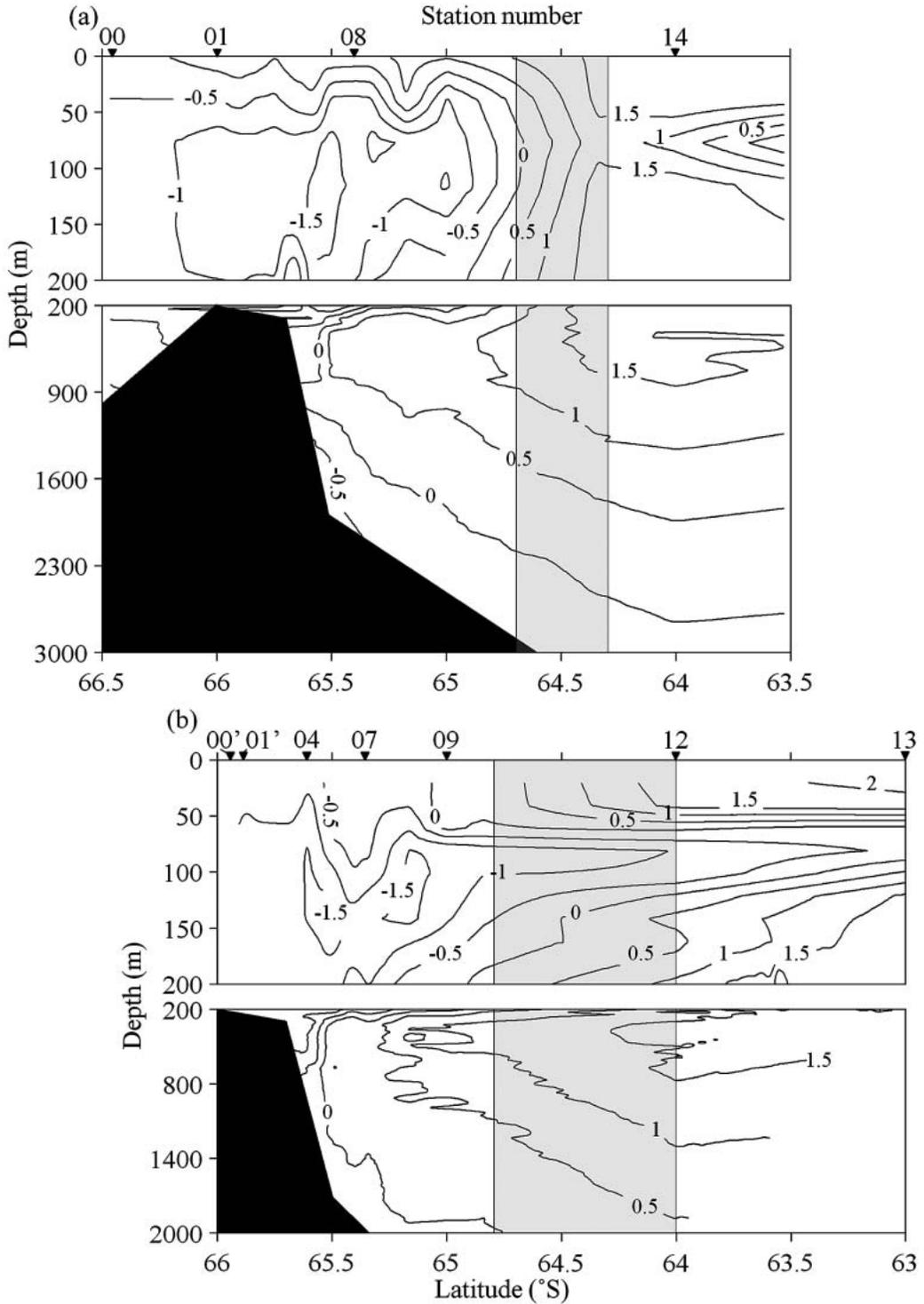


Fig. 2. Vertical sections of potential temperature ($^{\circ}\text{C}$) along 140°E off Adelie Land in 2003 (a) and 2005 (b). Shaded areas indicate the Southern Boundary of the Antarctic Circumpolar Current.

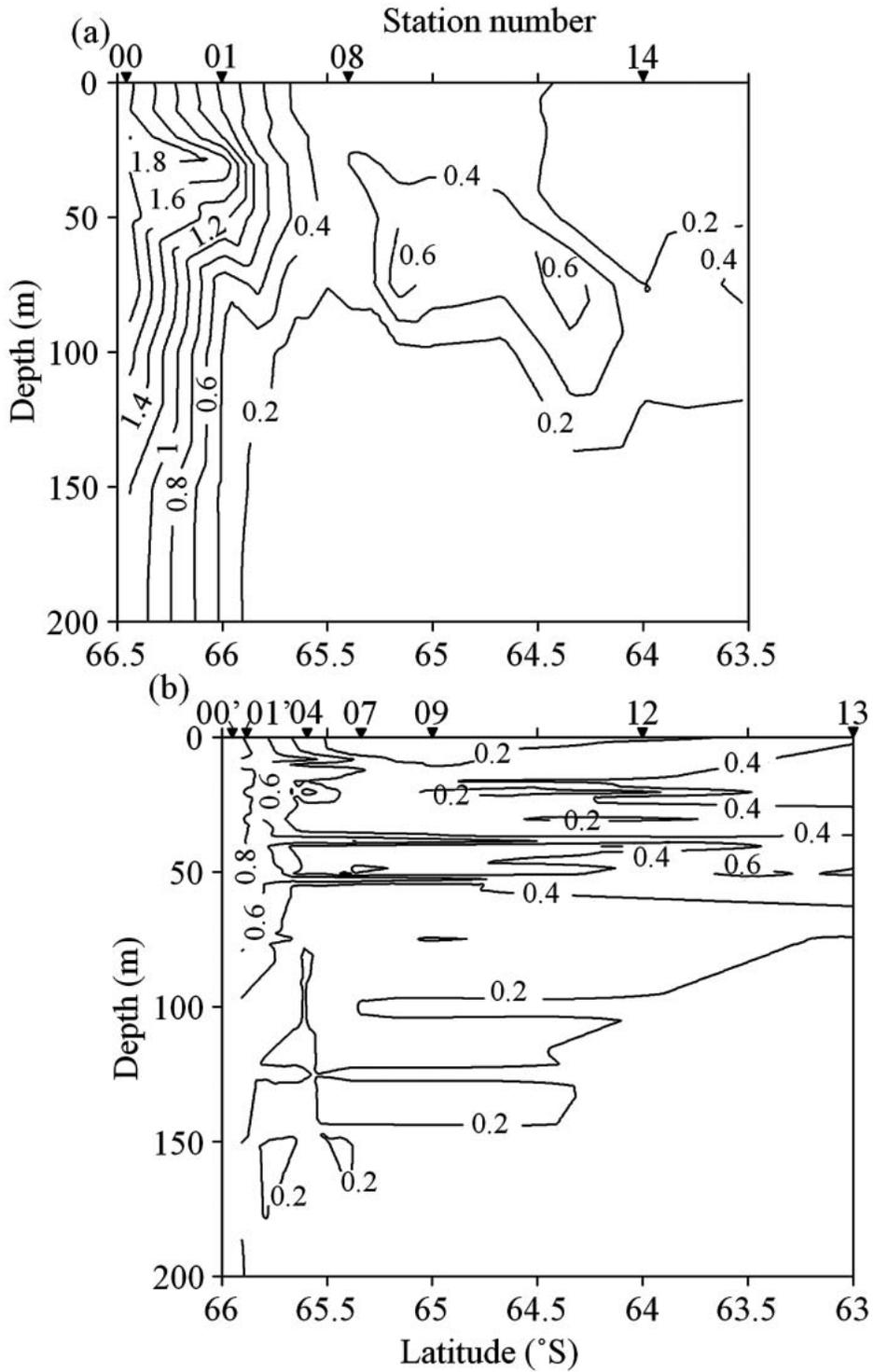


Fig. 3. Vertical sections of chlorophyll *a* concentration ($\mu\text{g L}^{-1}$) along 140°E off Adelie Land in 2003 (a) and 2005 (b).

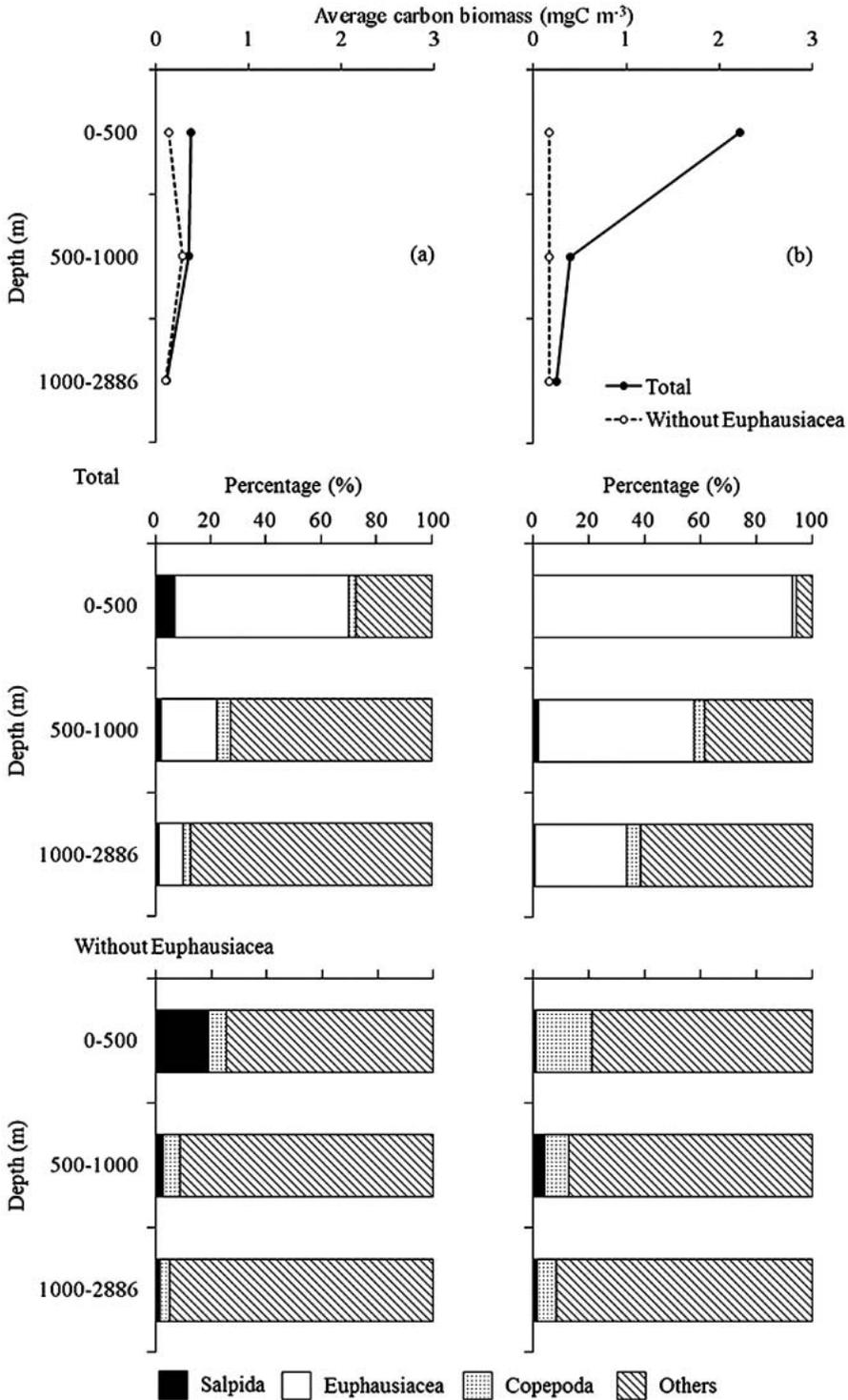


Fig. 4. Vertical distributions of average carbon biomass (top) and relative biomass of major macrozooplankton taxa (middle: all taxa, bottom: without Euphausiacea) off Adelie Land in 2003 (a) and 2005 (b).

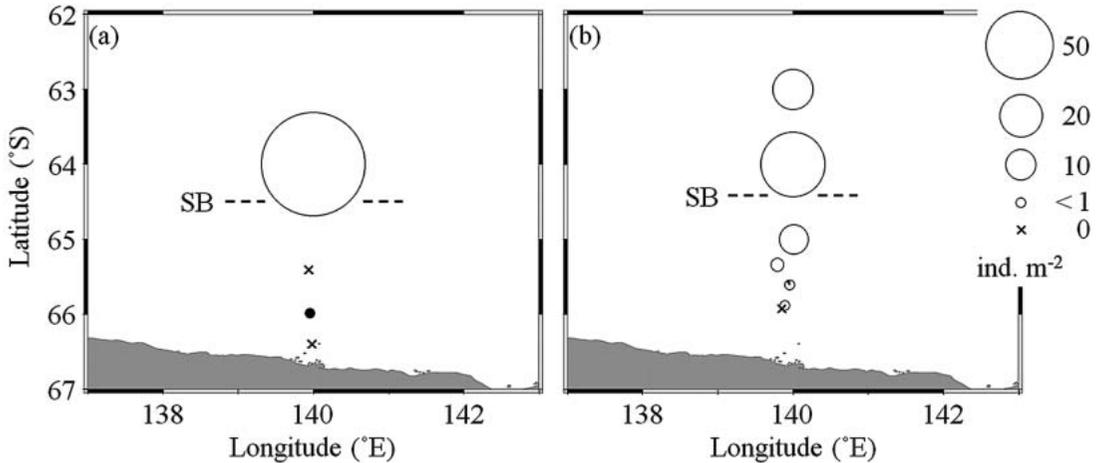


Fig. 5. Horizontal distributions of salps off Adelie Land in 2003 (a) and 2005 (b). SB: the location of the Southern Boundary of the Antarctic Circumpolar Current. Open and solid circles are for *Salpa thompsoni* and *Ihleia racovitzai*, respectively.

1 mm using a caliper. It is known that formalin shrinks the BL of salps (NISHIKAWA and TERAZAKI, 1996). REINKE (1987) reported that the BL of *S. thompsoni* aggregates shrank up to 14.9% of their live length for 15 months after preservation, but NISHIKAWA and TERAZAKI (1996) found, for other salp species (*Thalia democratica*), that the BL became almost constant in about five months of preservation. Because our BL measurements were done after eight months of preservation, considering the BL had been already constant, the BLs in 2003 and 2005 were comparable. In the present study, we thus did not correct the BL shrinkage to compare with previous studies which have not corrected the BL. Maturity stages of *S. thompsoni* aggregates (Table 2) were determined according to the morphological characteristics of the embryo inside an aggregate body following FOXTON (1966). In the present study, we observed individuals with empty and no embryos, and classified them into stage X following CHIBA *et al.* (1999). Although maturity stages of the solitaries (Table 3) were determined according to the morphology of the stolon following FOXTON (1966) who classified new born solitaries into stage 0, in the present study, we combined stages 0 and 1, and defined them as stage 1 because the classification between stages 0 and 1 was difficult due to damage. Stages 4 and spent of the

aggregates and over stage 4a of the solitaries were defined as mature stages following CASARETO and NEMOTO (1986), respectively.

Vertical profile as to water temperature at each station was obtained by a CTD (SBE911, Sea-Bird Electronics), except for Stn. C01' in 2005 where CTD observation was not conducted. Alternatively, CTD data from another profiler (ICTD, Falmouth Scientific Inc.) was used for analysis of Stn. C01' in 2005. The CTD observation at Stn. C13 in 2005 was conducted in only upper 200 m due to CTD trouble. The location of the Southern Boundary of the Antarctic Circumpolar Current (SB-ACC) was estimated from potential temperature (θ) following SOKOLOV and RINTOUL (2002). Seawater for chlorophyll *a* concentration (Chl *a*) analysis was sampled by Niskin bottles at each station from 7 to 24 layers between the surface to 200 m; 200 mL of the water sample was filtered through a Whatman GF/F filter; the filter was then soaked in 6 mL N, N-Dimethylformamide to extract chlorophyll *a* pigment (SUZUKI and ISHIMARU, 1990). Chl *a* was then determined by fluorometric method (STRICKLAND and PARSONS, 1972) using a fluorometer (Turner Design 10R).

3. Results

3-1. Environmental conditions

While vertical profile of water temperature

Table 4. Abundance and solitary to aggregate ratio (S/A) of *Salpa thompsoni* in 2003 and 2005.

Station	Abundance (ind. m ⁻²)			Solitary/total (%)	S/A
	Aggregate	Solitary	Total		
2003					
C14	95.47	22.64	118.11	19.17	0.24
C08	0.00	0.00	0.00	—	—
C01	0.00	0.00	0.00	—	—
C00	0.00	0.00	0.00	—	—
Average	23.87	5.66	29.53	19.17	0.24
2005					
C13	8.08	9.39	17.47	53.73	1.16
C12	34.33	11.26	45.59	24.70	0.33
C09	6.29	3.06	9.35	32.75	0.49
C07	1.04	0.77	1.81	42.42	0.74
C04	0.74	0.11	0.85	12.50	0.14
C01'	0.01	0.00	0.01	0.00	0.00
C00'	0.00	0.00	0.00	—	—
Average	7.21	3.51	10.73	32.74	0.49

Table 5. Abundance of *Salpa thompsoni* (ind. m⁻²) in the Southern Ocean.

Location	Date	Sampling depth (m)	Sampling gear	Range	Source
Adelie Land	Feb. 2003	0–2886	RMT	0–118.1	present study
	Feb. 2005	0–2000		0–45.6	
	Jan.–Feb. 1996	0–200	ORI	Max. 5974.6	Chiba <i>et al.</i> (1998)
	Dec. 1994	0–500	ORI-VMPS	156.4–2297.4	Nishikawa and Tsuda (2001)
	Jan. 2002	0–1000	RMT	Max. 219.6*	Tanimura <i>et al.</i> (2008)
	Feb. 2002	0–200		Max. 71.6	
Mar. 2003		Max. 3.2			
EBS	Apr.–May 2001	0–400	RMT	0–4.8	Pakhomov <i>et al.</i> (2006)
SSI	Dec. 1990–Jan. 1991	0–100	KYMT	0–132.0	Nishikawa <i>et al.</i> (1995)
	Jan.–Feb. 1991			0–30.0	
Scotia Sea Elephant Island	Jan.–Feb. 2000	0–200	RMT	Max. 361.2	Kawaguchi <i>et al.</i> (2004)
	Nov.–Dec. 1994			Max. 8.6	
	Dec. 1996			Max. 208.3	

EBS: Eastern Bellingshausen Sea

SSI: South Shetland Islands

*Calculated as the abundance in the upper 200m

in 2003 showed a relatively warm water mass (≥ 1.0 °C) in the north of 65°S (Fig. 2a), such warm water by contrast was extending to the south of 65°S in 2005 (Fig. 2b). The SB-ACC defined by the southern limit of θ_{\max} warmer than 1.5 °C (SOKOLOV and RINTOUL, 2002) was located between 64°20' and 64°40'S in 2003, and between 64° and 64°50'S in 2005 (Figs. 2a, b). In 2003, Chl *a* generally was increasing toward the south (Fig. 3a). Mean Chl *a* in the upper 200 m ranged between 0.13 and 1.75 $\mu\text{g L}^{-1}$. In 2005, mean Chl *a* in the upper 200 m was lower (0.14–0.67 $\mu\text{g L}^{-1}$; Fig. 3b) than in 2003.

3-2. Carbon biomass of macrozooplankton

The macrozooplankton biomasses in 2003 were higher in 0–500 m and 500–1000 m (0.38 ± 0.07 and 0.36 ± 0.05 mgC m⁻³, respectively; Fig. 4a) than in 1000–2886 m. Excluding Euphausiacea, the biomass was reduced in 0–500 m. Salps occupied 1.5–7.0% of the biomass, and especially abundant in 0–500 m (Fig. 4a).

In 2005, total zooplankton biomass peak was seen in 0–500 m (2.22 ± 0.61 mgC m⁻³; Fig. 4b), where Euphausiacea dominated. The contribution of salps increased in 500–1000 m (1.9%; Fig. 4b).

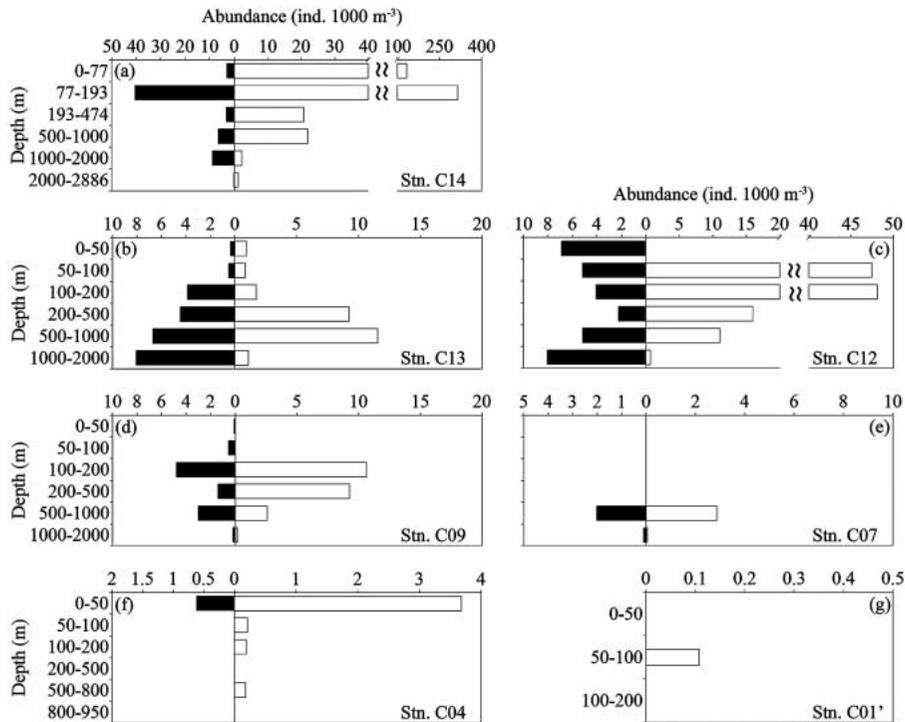


Fig. 6. Vertical distributions of *Salpa thompsoni* off Adelie Land in 2003 (a) and 2005 (b–g). Open bars: aggregate, solid bars: solitary.

3-3. Horizontal and vertical distribution of salps

Two species of salps, *Salpa thompsoni* and *Ihlea racovitzai*, were observed and the former numerically dominated in 2003 and 2005 (Fig. 5). In 2003, *S. thompsoni* occurred only at Stn. C14 located in the north of the SB-ACC (118.1 ind. m⁻²; Fig. 5a). Solitaries comprised 19.2% of *S. thompsoni*; solitary to aggregate ratio being 0.24 (Table 4). Conversely, *I. racovitzai* occurred only at Stn. C01 located in the south of the SB-ACC (0.2 ind. m⁻²; Fig. 5a). In 2005, *S. thompsoni* abundance was lower than that of 2003 (Table 4). *S. thompsoni* occurred at all stations except for Stn. C00' (Fig. 5b). Many *S. thompsoni* were observed in the north of 65°S, with the highest abundance at Stn. C12 near the SB-ACC (45.6 ind. m⁻²). Solitaries were distributed at five stations (Stns. C13, C12, C09, C07 and C04); solitary to aggregate ratio ranging from 0.14 (Stn. C04) to 1.16 (Stn. C13) (Table 4). *I. racovitzai* occurred only at Stn. C04 located in the south of SB-ACC (0.1 ind. m⁻²;

Fig. 5b) along with the distribution pattern of 2003. *S. thompsoni* abundance in the present study was lower than that in the same season reported by CHIBA *et al.* (1998), KAWAGUCHI *et al.* (2004) and TANIMURA *et al.* (2008) but higher than that in autumn (PAKHOMOV *et al.*, 2006; TANIMURA *et al.*, 2008) (Table 5).

In 2003, *S. thompsoni* was observed between the surface and 2886 m (Fig. 6a). The aggregates and solitaries densely occurred in the 77–193 m (315.0 and 40.5 ind. 1000 m⁻³, respectively). In 2005, *S. thompsoni* was distributed at almost every sampling layer at Stns. C13, C12 and C09 (Figs. 6b–d). At Stn. C07, both aggregates and solitaries were observed in layers lower than 500 m depth (Fig. 6e). At Stn. C04, the aggregates occurred between the surface and 800 m. On the other hand, solitaries were observed only in 0–50 m (Fig. 6f). Only aggregates occurred in 50–100 m at Stn. C01' (Fig. 6g). *I. racovitzai* was observed in the upper 200 m both in 2003 and 2005 (figure not shown).

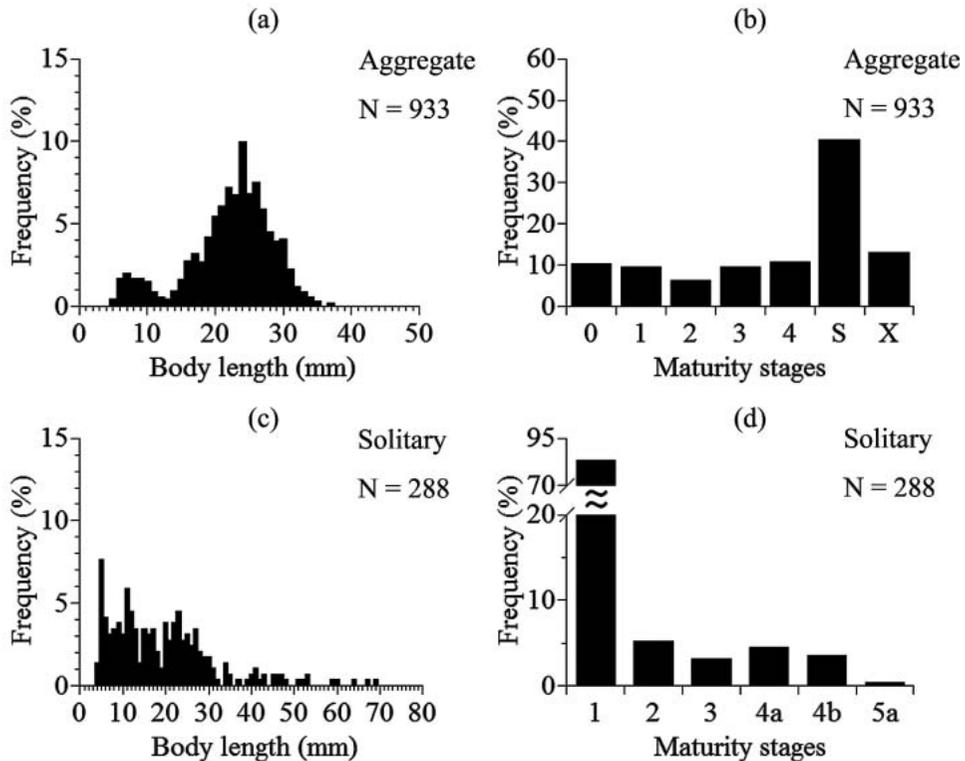


Fig. 7. Body length frequency and maturity stages of *Salpa thompsoni* aggregate (a, b) and solitary (c, d) off Adelie Land in 2003. N: number of measured individuals, S: stage spent, X: stage X.

3-4. Population structure of *Salpa thompsoni*

In 2003, BL of *S. thompsoni* aggregates ranged between 5 and 37 mm with two peaks at 7 mm and 24 mm (Fig. 7a). Mature stages (stage 4 and spent) predominated, accounting for 51.2%, and stage X occupied 13.0% of all aggregates (Fig. 7b). As to the solitaries, the BL ranged from 4 to 69 mm; of all solitaries, small individuals (<30 mm BL) comprised 85.8% (Fig. 7c). While the number of mature solitaries (over stage 4a) were small (8.3%), immature individuals (stage 1–3) predominated, accounting for 91.7% of all solitaries (Fig. 7d). In 2005, the size of the aggregates ranged from 4 to 38 mm (Fig. 8a). Early maturity stages (0–2) predominated comprising 68.8%, and stage X occupied 4.8% of all aggregates (Fig. 8b). The solitaries ranged from 5 to 63 mm BL (Fig. 8c). The youngest stage (stage 1) dominated (comprising 62.4%) while mature solitaries contributed 16.2% of all solitaries (Fig. 8d). As to the density weighted length frequency distribution

of *S. thompsoni* population included in both aggregates and solitaries in 2003 and 2005, the modal lengths were 24 mm (Fig. 9a) and 8 mm (Fig. 9b), respectively.

Mature aggregates of *S. thompsoni* mainly occurred in 500–1000 m at Stns. C13 and C12 in 2005 (8.9 and 7.7 ind. 1000 m⁻³, respectively; Figs. 10a, c). Immature aggregates were abundant in the upper 500 m at Stns. C13, C12 and C09 (max. 7.0, 46.5 and 9.1 ind. 1000 m⁻³, respectively; Figs. 10a, c, e). As to solitaries, mature individuals mainly distributed in the upper 500 m. In contrast, immature solitaries densely occurred in deeper layers (500–2000 m) at Stns. C13, C12 and C09 (Figs. 10b, d, f).

The average body length of *S. thompsoni* solitaries decreased with increasing depth at Stns. C13, C12 and C09 in 2005 (Figs. 11a–c). Although a change of the average length of *S. thompsoni* aggregates on the sampling layers was not observed at Stn. C13 (Fig. 11a), large-size aggregates constituted the deeper layer

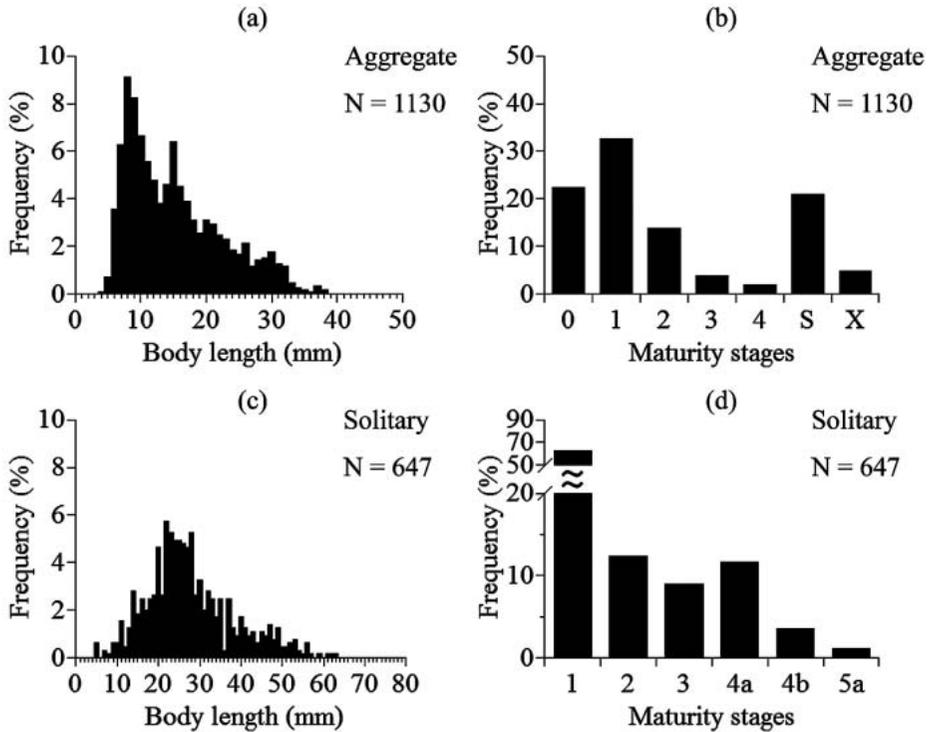


Fig. 8. Body length frequency and maturity stages of *Salpa thompsoni* aggregate (a, b) and solitary (c, d) off Adelie Land in 2005. N: number of measured individuals, S: stage spent, X: stage X.

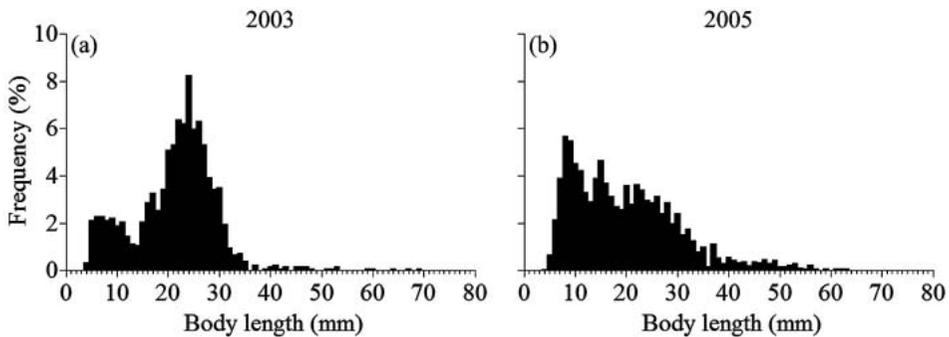


Fig. 9. Density weighted length frequency distributions of *Salpa thompsoni* population (aggregate + solitary) in 2003 (a) and 2005 (b).

population at Stns. C12 and C09 (Figs. 11b, c).

The compositions of *S. thompsoni* maturity stages were different at each station in 2005 (Fig. 12). Both mature aggregates and solitaries were observed at Stns. C13, C12 and C09. At Stn. C07, mature solitaries were absent while mature aggregates occurred. Both aggregates and solitaries were composed of immature individuals at Stn. C04, only immature aggregates

were observed at Stn. C01'.

4. Discussions

4-1. Distribution of *Salpa thompsoni* in relation to oceanographic conditions

Our result agrees with the previous report by CASARETO and NEMOTO (1986) showing *Ithlea racovitzai* was distributed at higher latitude than *Salpa thompsoni*.

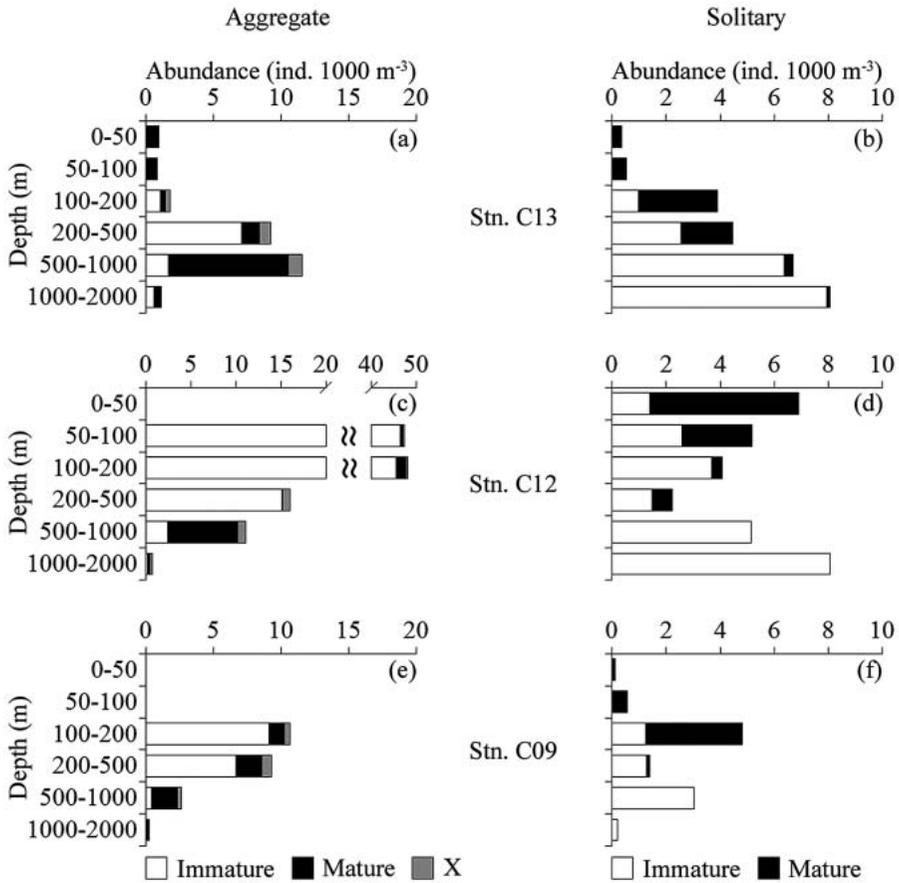


Fig. 10. Vertical distributions of immature and mature *Salpa thompsoni* at Stns. C13 (a, b), C12 (c, d) and C09 (e, f) off Adelie Land in 2005.

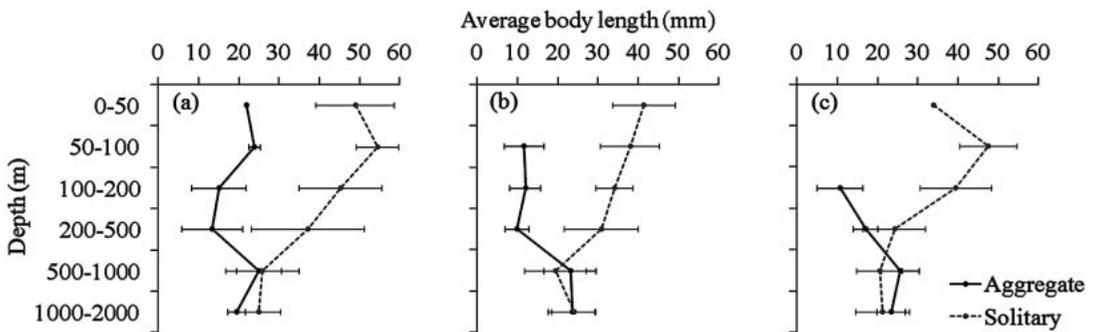


Fig. 11. Average body length (mm) of *Salpa thompsoni* aggregate and solitary at Stns. C13 (a), C12 (b) and C09 (c) off Adelie Land in 2005. Horizontal bars range standard deviations.

We observed that *S. thompsoni* in 2005 was distributed at higher latitude than in 2003 (Fig. 5). Previous reports have shown that *S. thompsoni* occurred at high latitudes off Adelie

Land in the Southern Ocean (CASARETO and NEMOTO 1986; CHIBA *et al.*, 1998, 1999; NICOL *et al.*, 2000; TANIMURA *et al.*, 2008). PERISSINOTTO and PAKHOMOV (1998) reported that *S.*

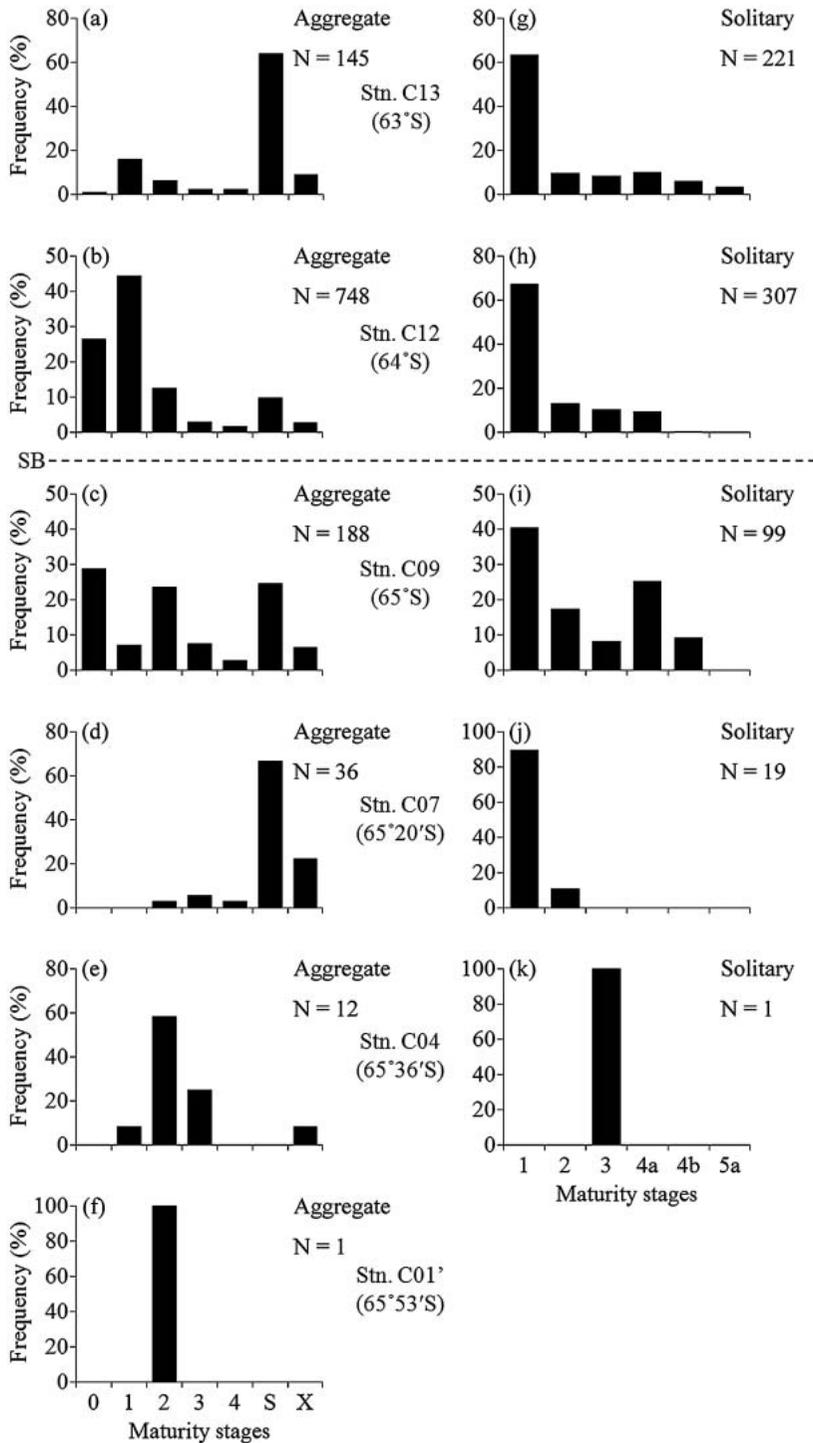


Fig. 12. Latitudinal changes of maturity stages of *Salpa thompsoni* aggregate (a-f) and solitary (g-k) off Adelie Land in 2005. N: number of measured individuals, S: stage spent, X: stage X, SB: Southern Boundary of the Antarctic Circumpolar Current.

thompsoni population collapses because of a dramatic reduction in *S. thompsoni* feeding rate when Chl *a* exceeds $1.0 \mu\text{g L}^{-1}$. In the present study, however, mean Chl *a* in the upper 200 m both in 2003 and 2005 was less than $1.0 \mu\text{g L}^{-1}$ except for Stn. C00 in 2003, suggesting that distribution of *S. thompsoni* was not limited by Chl *a*. Previous studies have clarified that *S. thompsoni* occurred mainly in the warm water and was found in the north of the SB-ACC (FOXTON, 1966; NICOL *et al.*, 2000; PAKHOMOV *et al.*, 2006; TANIMURA *et al.*, 2008). CHIBA *et al.* (1999) indicated that the southernmost *S. thompsoni* population might occur only occasionally in mid-summer due to advection when the ice edge retreats to its minimum extent. The relatively warm water ($\geq 1.0^\circ\text{C}$) extended to the south of 65°S in 2005 (Fig. 2), suggesting that *S. thompsoni* was transported from a northern area to the south of the SB-ACC.

4-2. Interannual change of *Salpa thompsoni* population structure

The abundance of *Salpa thompsoni* in 2005 was lower than that in 2003 (Table 4) and those from various areas in the summer (Table 5). The modal length of *S. thompsoni* population in 2005 (8 mm) was smaller than that in 2003 (24 mm) and coincided with that in March (8 mm) reported by TANIMURA *et al.* (2008). PAKHOMOV *et al.* (2006) reported the population in the autumn consisted of early maturity stages (0–2) of the aggregates and the young (stage 2) solitaries with 29–32 mm. The population structure of 2005 in the present study was similar to that of PAKHOMOV *et al.* (2006). Maximum solitary to aggregate ratio in 2005 was 1.16. Since the major driver of the salp bloom is the asexual budding of up to 800 buds originating from a solitary of *S. thompsoni* (DAPONTE *et al.*, 2001), high solitary to aggregate ratio indicates low reproduction (TANIMURA *et al.*, 2008). CHIBA *et al.* (1999) found the reproduction of *S. thompsoni* was reduced in autumn. The reproductive condition of *S. thompsoni* population in 2005 was similar to that in autumn, which season was considered as the end of reproduction.

4-3. Horizontal and vertical changes in population structure of *Salpa thompsoni*

We observed that the vertical distributions of immature and mature *S. thompsoni* were different at Stns. C13, C12 and C09 in 2005 (Fig. 10). The greater abundances of immature aggregates and mature solitaries occurred in the upper 500 m, suggesting that the solitary were asexually reproducing. Conversely, the abundances of mature aggregates and immature solitaries increased in the deeper layer. This reveals the young solitaries were sexually reproduced by mature aggregates in the deeper layer. FOXTON (1966) reported the young solitaries predominated in the deeper layer and kept their stocks during autumn and winter. It is thus considered that the small immature solitaries in the deeper layer overwintered.

FOXTON (1966) clarified seasonal changes in the maturity stages of *S. thompsoni* and reported the ontogenetic vertical migration of this species. CASARETO and NEMOTO (1986) observed the different vertical distribution of immature and mature individuals in the summer population of *S. thompsoni*. As with these previous reports (FOXTON, 1966; CASARETO and NEMOTO, 1986), the result of the present study suggests *S. thompsoni* are ontogenetic vertical migrators.

Generally, salps have a life cycle in which the sexual generation alternates with the asexual generation (GODEAUX *et al.*, 1998). This means life cycle of salps cannot be completed if individuals do not reproduce in both generations. CASARETO and NEMOTO (1986) reported the latitudinal variation of *S. thompsoni* population structure and linked poor reproductive performance at high latitude to the low water temperature. CHIBA *et al.* (1999) suggested that the *S. thompsoni* population at high latitude cannot complete its life cycle due to low temperature and scarcity of food. In 2005, mature individuals of both aggregates and solitaries of *S. thompsoni* were observed in the north of 65°S (Stns. C13, C12 and C09), suggesting that the life cycle there was completed. On the other hand, no mature individuals of aggregates and/or solitaries occurred, and *S. thompsoni* abundance declined in the south of $65^\circ 20'\text{S}$ (Stns. C07, C04 and C01'). The low

temperature water ($<0^{\circ}\text{C}$) was observed in the south of $65^{\circ}20'S$. Therefore, it is very likely that *S. thompsoni* in this area were not reproducing because of low temperature and so they could not complete their life cycle, which suggested a collapse of the *S. thompsoni* population. However, temperature effects on reproductive success/failure of *S. thompsoni* have never been reported, which issue being remained to be investigated by future studies.

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