



The variability in abundance and shell size of the thecosome pteropods *Limacina* spp. in the seasonal ice zone of the Southern Ocean in March

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Abstract

Thecosome pteropods form an important part of marine food webs, especially in polar ecosystems, and are the focus of research on ocean acidification. Although the larval stages of species in the genus *Limacina* often form major components of zooplankton communities, little is known of their population dynamics. We report high *Limacina* spp. abundance in March 2000 during surface zooplankton community sampling via a Continuous Plankton Recorder (CPR; 270- μ m mesh) in a large area within the seasonal ice zone of the Southern Ocean. Regions with high *Limacina* spp. abundances extended to 600 nautical miles (*ca* 1110 km). Annual variability in *Limacina* spp. abundance and shell size is evaluated using North Pacific standard net (100- μ m mesh) data from the same area and sampling periods (March) from 1997 to 2006. Although the relative total abundance of *Limacina* spp. in 2000 was the highest in the study period, its overall abundance was lower than the mean value for that period. Mean shell size for most years ranged 160–300 μ m, while a relatively large mean size (444.7 μ m) occurred in 2000. We conclude that a CPR with 270- μ m mesh could catch large *Limacina* individuals that dominated in March 2000. The timing of reproduction and growth of the new generation may influence *Limacina* abundance throughout the sampling area.

Keywords *Limacina* · Continuous plankton recorder · North Pacific standard net · Seasonal ice zone · Population dynamics

Introduction

Pteropods, ubiquitous components of Southern Ocean zooplankton communities, can be extremely abundant regionally among mesozooplankton size fractions (Hunt et al. 2008; Steinberg et al. 2015). It has recently been demonstrated that thecosome pteropods may be severely affected by ocean acidification caused by increased atmospheric CO₂ concentrations (Bednaršek et al. 2012a; Manno et al. 2016). They contribute to the carbon cycle through their fast-sinking

fecal pellets, and deposition of shells after mass die-offs (Manno et al. 2007, 2010, 2018; Bednaršek et al. 2012b, 2016; Thibodeau et al. 2019). Although the biomass-dominant genus *Limacina* is widespread throughout the Southern Ocean, aspects of its life cycle remain uncertain (Hunt et al. 2010). Two Southern Ocean species are known: *Limacina retroversa australis* (Eydoux and Souleyet, 1840) and *L. rangii* (d'Orbigny, 1835), previously referred to as *L. helicina antarctica* Woodward, 1854 (Janssen et al. 2019). Of them, *L. retroversa* is thought to be a sub-Antarctic species, and *L. rangii* to occur largely south of the Polar Front (PF) to the Antarctic coast (Hunt et al. 2008). Spawning in *L. rangii* occurs primarily from late summer to autumn (Hunt et al. 2008; Thibodeau et al. 2020), and its larval stages are sometimes major contributors to total zooplankton abundance during autumn, especially in the seasonal ice zone—an ecologically important region in the Southern Ocean (Brierley and Thomas 2002).

The Continuous Plankton Recorder (CPR; 270- μ m mesh size) provides an effective and rapid means of monitoring micro- and mesozooplankton distribution patterns within

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approximately 10 m of the surface to assess the effects of environmental change over large oceanic scales (Hosie et al. 2003; Takahashi and Hosie 2021). Since its launch in 1991, the Southern Ocean CPR (SO-CPR) survey program has produced the largest, most comprehensive and systematic spatial and temporal data set of Antarctic zooplankton. Because data have been collected using a consistent sampling methodology, the mapping of seasonal, inter-annual, long-term, and spatial variation in plankton diversity is possible, as is the identification of select planktons which can act as indicators of environmental change for monitoring the health of the Southern Ocean (Takahashi and Hosie 2021).

While SO-CPR survey data has revealed high-density patches of pteropods (Hunt et al. 2008; Pinkerton et al. 2020), shell damage during collection has hampered accurate species identification, for which reason taxa have been identified to *Limacina* spp. (Takahashi et al. 2011). Abundances of *Limacina* spp. collected south of Australia from 1997 to 2006 were typically low over the austral winter, and increased slowly from November to January, peaked in February, and remained relatively high in March, and declined until the end of May (Hunt et al. 2008). Their lifespan is estimated at one year based on the seasonal abundance data integrated using > 200- μ m mesh nets. Although the strong seasonal cycle of CPR data has complemented this scenario, these are only surface data and are considered to be an underestimate of the new generation resulting from the large mesh size used. Several polar region studies suggest a range of one or two generations of *Limacina* occur per year, longevity from 1 to 3 years, continuous or discrete reproduction to occur once or twice a year, and for peak densities to occur from spring to late summer (Gannefors et al. 2005; Hunt et al. 2008; Bednaršek et al. 2012b; Nishizawa et al. 2016; Wang et al. 2017; Thibodeau et al. 2020; Boissonnot et al. 2021). The highly complex nature of data, and differences in its interpretation, limits our ability to generalize from these studies. Therefore, to fully understand the CPR data, the complementary use of the species identification data and shell size of the genus *Limacina* via the simultaneous use of a finer net is required. In particular, it is important to accumulate data on the abundance and size structure in March just before the abundances decrease.

We focus on CPR data from the seasonal ice zone in 2000, during which time high abundances of *Limacina* spp. occurred over a large area, and for which abundance peaked in March. As a part of the zooplankton monitoring program of the Japanese Antarctic Research Expedition (JARE), regular sampling using a North Pacific (NORPAC) standard net (100- μ m mesh size) from a depth of 150 m to the surface was conducted simultaneously on the CPR transect. The comparative studies by Hunt and Hosie (2003) already demonstrated that despite sampling differences between the CPR and NORPAC nets, the evenness index indicated that

all communities had a similar distribution of abundance amongst species. The objectives of this study were, first, to discuss the spatial distribution, abundance, and species composition of zooplankton communities based on the CPR samples in March 2000, with an emphasis on their pteropod composition, and second, to evaluate the annual variability of abundance and shell size of *Limacina* spp. using NORPAC net data collected in the same area and same sampling periods (March) from 1997 to 2006 (with the exception of 1999 and 2005, during which samples were not collected).

Materials and methods

CPR towing

CPR sampling was conducted between 9 and 16 March 2000 aboard the icebreaker *Shirase* during the 41st JARE cruise (JARE-41), from the Japanese Showa Station, Antarctica, toward Sydney, Australia, along two transects: West to East (WE1), latitude 63° 00' S, from 133° 00' E to 149° 22' S, and South to North (SN1–4), longitude 150° 00' E, from 62° 59' S to 47° 40' S (Fig. 1, Table 1). The CPR (Type II, Mark

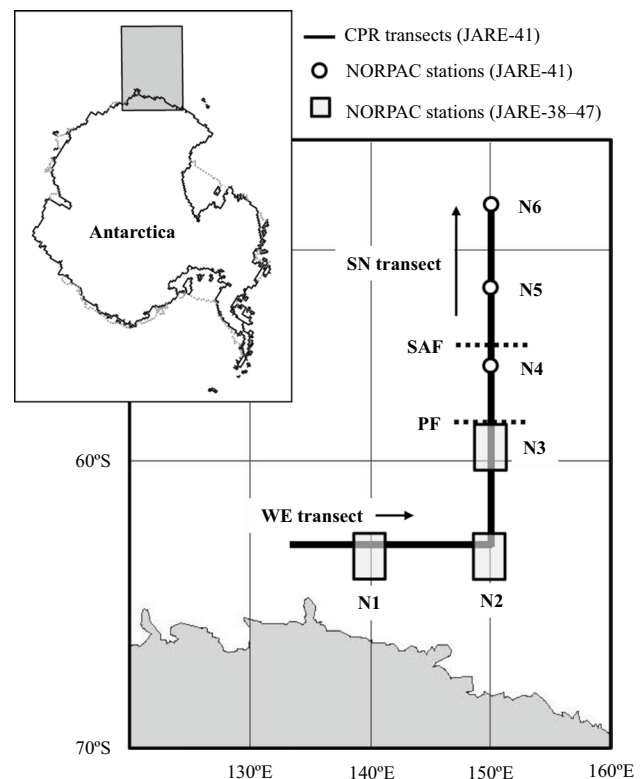


Fig. 1 Survey area, indicating the position of the Continuous Plankton Recorder (CPR) transect of the Japanese Antarctic Research Expedition (JARE) 41 and North Pacific (NORPAC) standard net sampling stations. SN South–North, WE West–East, PF Polar Front, SAF Sub-Antarctic Front

Table 1 Zooplankton data collected by the Continuous Plankton Recorder (CPR) along the 63°S latitude (WE1) and 150°E longitude tows (SN1–4) during the Japanese Antarctic Research Expedition (JARE) 41 in March 2000

CPR	Start		End		No. of ^a	Distance
	Date & Time	Position	Date & Time	Position		
Run #	GMT		GMT		Segments	towed (km)
WE1	Mar 9, 2000; 07:54	62° 59.9' S 133° 00.4' E	Mar 11, 2000; 07:15	62° 59.5' S 149° 22.0' E	89	827
SN1	Mar 12, 2000; 04:24	62° 59.1' S 150° 02.4' E	Mar 13, 2000; 02:48	59° 39.0' S 149° 57.0' E	40	372
SN2	Mar 13, 2000; 04:22	59° 39.9' S 150° 03.4' E	Mar 14, 2000; 02:50	56° 35.0' S 149° 59.4' E	37	343
SN3	Mar 14, 2000; 04:39	56° 36.4' S 150° 02.5' E	Mar 15, 2000; 02:50	52° 17.7' S 149° 58.9' E	52	481
SN4	Mar 15, 2000; 04:47	52° 17.8' S 150° 07.1' E	Mar 16, 2000; 04:28	47° 40.1' S 150° 05.1' E	57	525

WE West–East, SN South–North

^aEach segment of cut silk corresponds to 5 nautical miles of towing distance

V) was towed horizontally from the stern at a ship speed of approximately 14 knots, using a cable paid out to 100 m, with the CPR sampling at approximately 10 m depth. The CPR has a square mouth with a 1.27×1.27 cm area, expanding into a tunnel 10×5 cm, with water passing through a 270- μ m silk mesh filter within the CPR. During sampling, zooplankton captured on the silk were preserved in a formaldehyde bath within the CPR. After sampling, zooplankton samples retained between silk meshes were preserved in a 10% v/v neutral buffered formalin solution. In the laboratory, 275 separate silk segments were cut from five tows, each representing 5 nautical miles of filtration. The length of each segment was calculated based on the stop and start positions of each transect and estimated from 1-min interval GPS positions recorded between start and stop times.

The zooplankton on each segment were identified to the lowest taxonomic level possible and counted using a

to be 100% of the volume calculated from the length of each segment and the mouth opening of the CPR.

Simultaneous measurements of surface temperature, salinity, and in vivo fluorescence intensity were made with an on-board surface monitoring system (Fukuchi and Hattori 1987), pumping seawater from a depth of approximately 8 m. Chlorophyll *a* concentration was determined by filtering water samples onto glass fiber filters; filters were then soaked immediately in *N,N*-dimethylformamide (Suzuki and Ishimaru 1990), the pigment extracted, and pigment concentrations determined fluorometrically with a Turner Designs model 10R fluorometer (Parsons et al. 1984). For chlorophyll *a* calibration, pumped surface water was sampled two or three times daily. In vivo fluorescence data were calibrated as follows:

$$\text{Chlorophyll } a = 0.0604 \times \text{FLU} + 0.432 (r^2 = 0.5736; n = 107)$$

FLU = in vivo fluorescence intensity data measured by the surface monitoring system.

stereomicroscope (SMZ1500, Nikon, Japan). Pteropod shells were usually damaged by the silks; therefore, no attempt was made to differentiate between species of *Limacina*. Ostracods and most small hyperiid amphipods were not identified to species. *Rhincalanus gigas* (Copepoda: Calanoida) nauplii were distinguished from other calanoid nauplii by their large size and morphology. Copepodite stages of smaller calanoid copepod adults such as *Clausocalanus* spp. and *Microcalanus pygmaeus* are difficult to identify and were grouped as “copepodite indet.” Calyptopis and furcilia stages of euphausiid species were distinguished from adults (post-furcilia). Zooplankton abundance was converted to individuals m^{-3} , with the volume of water filtered assumed

Nighttime samples were defined as those where photosynthetically active radiation (PAR) was $< 100 \mu\text{mol s}^{-1} \text{m}^{-2}$. Species richness (*r*), i.e., number of species, was calculated for each sample.

NORPAC net sampling

NORPAC-net sampling in the seasonal ice zone (defined as south of 59°E in the present study) was regularly carried out in three areas (N1: 140° E, 63–65° S; N2: 150° E, 63–65° S; and N3: 150° E, 59–61° S) on board the icebreaker *Shirase* during JARE–38 (1997) to JARE–47 (2006) (except JARE–40 (1999) and 46 (2005)) in the Indian sector of the Southern Ocean en route from Syowa Station in March

Table 2 Location of North Pacific (NORPAC) standard net sampling (0–150 m) stations and time of each sampling event, and corresponding environmental information for temperature (T) and salinity (S) during the Japanese Antarctic Research Expeditions (JARE) 38 (1997) to 47 (2006) in March

Station No	Position		Ship's time (LMT)		T _{mean} (°C)	S _{mean} (psu)
	Latitude (S)	Longitude (E)	Date	Time		
N1	65° 00' S	140° 06' S	Mar 11, 1997	13:03	−0.76	34.2
	63° 31' S	140° 05' S	Mar 12, 1998	13:25	1.02	34.3
	64° 01' S	140° 04' S	Mar 11, 2001	14:01	1.08	34.2
	63° 59' S	140° 01' S	Mar 8, 2004	12:50	0.74	N.D
	64° 00' S	138° 09' S	Mar 11, 2005	13:03	−0.30	34.2
	63° 56' S	140° 10' S	Mar 12, 2006	14:08	0.06	34.2
N2	64° 58' S	146° 58' S	Mar 12, 1997	13:03	−0.65	34.1
	63° 00' S	149° 57' S	Mar 12, 2000	14:03	0.25	34.1
	63° 58' S	150° 05' S	Mar 13, 2001	14:05	1.14	34.2
	64° 01' S	150° 01' S	Mar 13, 2002	13:55	1.16	34.2
	63° 12' S	150° 06' S	Mar 11, 2004	18:45	N.D	N.D
	63° 58' S	146° 45' S	Mar 13, 2006	14:14	1.25	34.2
N3	60° 35' S	147° 09' S	Mar 14, 1997	13:04	1.40	33.9
	60° 57' S	149° 59' S	Mar 14, 1998	13:13	1.42	34.1
	59° 39' S	149° 58' S	Mar 13, 2000	14:06	0.68	34.2
	60° 08' S	150° 04' S	Mar 14, 2001	14:42	1.56	34.2
	59° 12' S	150° 03' S	Mar 14, 2002	13:42	1.17	N.D
	59° 04' S	150° 03' S	Mar 15, 2003	08:30	N.D	N.D
	60° 02' S	149° 49' S	Mar 12, 2004	18:05	1.31	34.2
	60° 16' S	150° 04' S	Mar 14, 2006	14:14	1.43	34.0
N4	56° 36' S	150° 01' S	Mar 14, 2000	14:24	2.74	33.9
N5	52° 18' S	150° 01' S	Mar 15, 2000	14:28	6.71	33.9
N6	47° 39' S	150° 02' S	Mar 16, 2000	14:17	8.91	34.2

N.D. no data

(Fig. 1, Table 2). Additionally, on the SN transect of the CPR towing in JARE-41, regular sampling with a NORPAC net was conducted along 150° 00' E from 63° 00' to 47° 30' S (Fig. 1, Table 2). Sampling stations were located at intervals of 3–4 degrees of latitude (N2–N6).

The NORPAC standard net, made of nylon bolting cloth XX13 (100- μ m mesh openings), was used at all sampling stations. The net was hauled vertically at a speed *ca* 1 m s^{−1}, from an approximate depth of 150 m. The maximum depth reached was estimated from the wire angle and length of wire paid out. All samples obtained were immediately preserved onboard in a 5–10% neutral-buffered formalin-seawater solution. Volumes of water filtered through each net were estimated using a flowmeter that was mounted at the center of the mouth ring of each net. While abundances of *Limacina* may be underestimates because individuals can migrate deeper than 150 m (Bednaršek et al. 2012a; Manno et al. 2016), sampling always occurred during the daytime. Accordingly, the effects of diel vertical migration in analysis of annual variation in abundance using NORPAC sampling data are likely to be minimal.

The type of sampling device and its mesh size affect plankton catchability. A comparative study using both the

CPR and a commonly used plankton net fitted with 200- μ m mesh revealed differences in catchability, with the underestimate of abundance (Clark et al. 2001; John et al. 2001). Because Hunt and Hosie (2003) reported similar plankton abundance and species composition in 270- μ m mesh CPR and NORPAC-net collected samples from along the same sampling track, the CPR design and its sampling method appear to produce less error in estimates of plankton abundance than different-sized meshes do. Our NORPAC samples were collected from vertical hauls (0–150 m) using a net with 100- μ m mesh, which has been demonstrated to be suitable for the capture, and estimation of the quantitative abundance and community structure of micro- and mesozooplankton (Makabe et al. 2012).

Analysis of zooplankton and *Limacina* spp. of NORPAC samples

Zooplankton were identified to the lowest practical taxonomic level, generally to species or genus, using a stereomicroscope (SMZ1500, Nikon, Japan). Total zooplankton and *Limacina* abundances were converted to individuals m^{−3}.

From each sample, 50 *Limacina* individuals were randomly selected, and their shell diameter and greatest height were measured (Thibodeau et al. 2020). Our measurements of shell diameter ranged 0.14–0.68 μm . Because veligers of the Arctic *L. helicina* have diameters $<0.3 \mu\text{m}$, and juveniles $\geq 0.3 \mu\text{m}$ (Lalli and Wells 1978), our *Limacina* likely comprised both veliger and juvenile stages.

Two *Limacina* species, *L. retroversa australis* and *L. rangii*, are major components of Southern Ocean zooplankton communities: the former dominant in sub-Antarctic regions, the latter primarily south of the PF (Hunt et al. 2008). These two species differ in their shell height/diameter ratio, with that of *L. retroversa australis* being approximately 1.5 and that of *L. rangii* approximately 0.75 (World Register of Marine Species (WoRMS) database; <http://www.marinespecies.org/index.php>). Because the shell height/diameter ratio of *Limacina* collected from the seasonal ice zone south of 59°E was 0.69 ± 0.07 (mean \pm SD), these specimens are most likely to be *L. rangii*. The relationship between shell diameter and shell height is significantly correlated (Fig. 2).

Statistical analysis

Zooplankton abundance from the CPR was further analyzed by cluster analysis, using Bray–Curtis dissimilarity and unweighted pair group average linkage, to compare species/taxon composition between sampling areas, following the procedures described by Field et al. (1982). To compare community structures, data were transformed using the $\log_{10}(x + 1)$ function to reduce biases caused by highly abundant taxa. One-way analysis of variance and Tukey's tests were used to test the null hypothesis that the abundance levels of a species/taxon did not differ between sample groups. Newman–Keuls multiple-range tests were

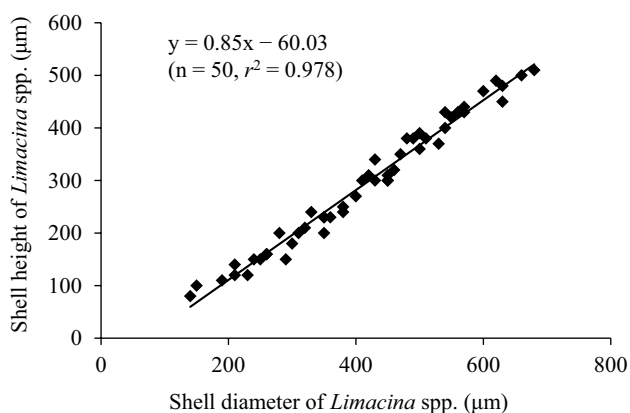


Fig. 2 Relationship between shell diameter and shell height of *Limacina* spp. in the seasonal ice zone of the Southern Ocean

performed to identify inter-cluster differences in species/taxa abundance levels. Statistical analyses were carried out in Primer Version 6 (Clarke and Gorley 2006) and IBM SPSS Statistics for Windows Version 23 (Arbuckle 2014).

Results

West–East transect CPR samples

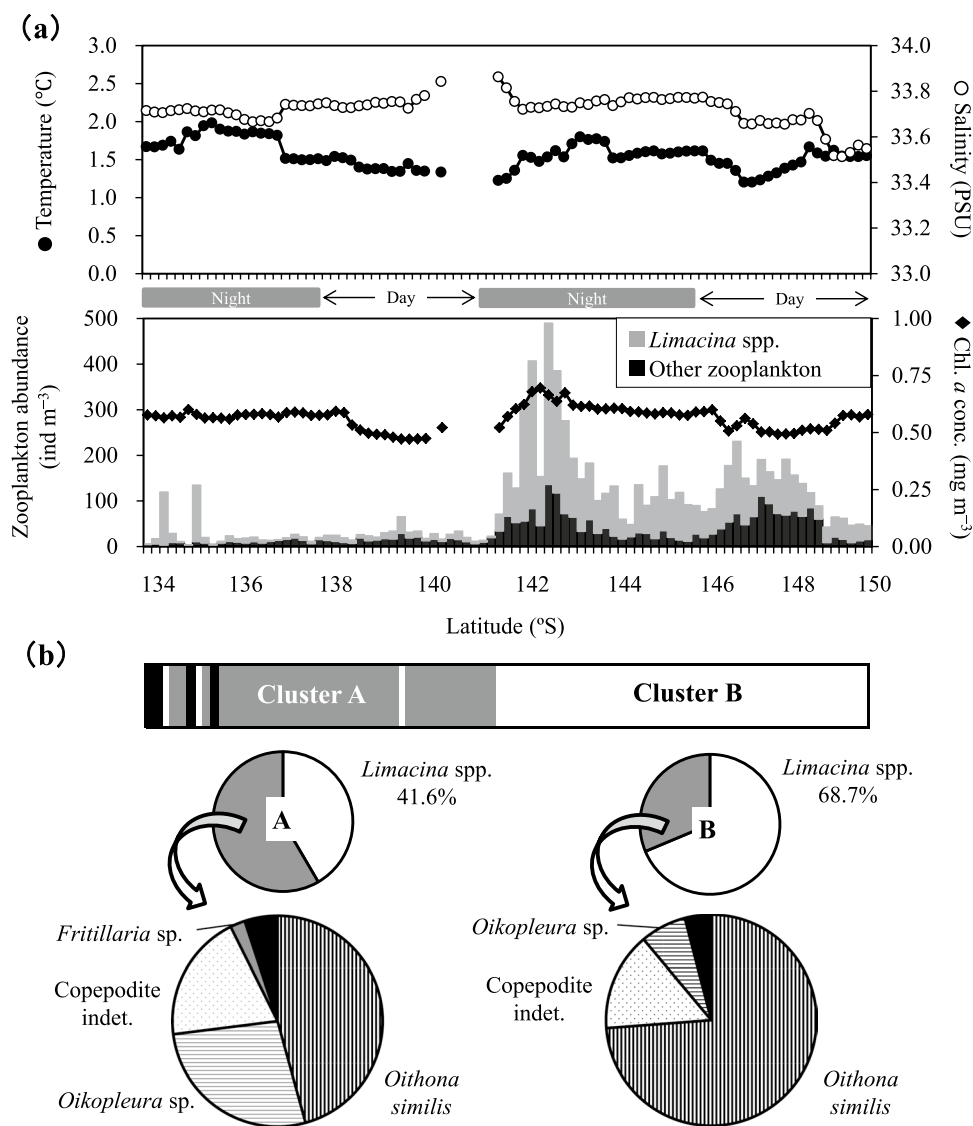
Sea surface temperature, salinity, and chlorophyll *a* concentration were relatively constant through the transect. There were some surface monitoring system errors around 139° 36' E, and between 139° 58' E and 140° 52' E (Fig. 3a). Temperature fluctuated slightly around 1.5 °C (mean \pm SD; 1.56 ± 0.18), and salinity was stable around 33.7 PSU (33.7 ± 0.066). Chlorophyll *a* concentration was also low and stable, ranging 0.47–0.70 mg m^{-3} . Twenty-four species/taxa were identified throughout the transect, and zooplankton abundance (mean \pm SD; $88.6 \pm 92.9 \text{ ind. m}^{-3}$) was high in the eastern area, especially for *Limacina* spp. (mean \pm SD; $58.5 \pm 69.9 \text{ ind. m}^{-3}$). Maximum zooplankton ($489.9 \text{ ind. m}^{-3}$) and *Limacina* spp. ($353.8 \text{ ind. m}^{-3}$) abundances occurred at 142° 26' E (Fig. 3a). Along the transect, *Limacina* spp. was the predominant taxon, contributing 66% to total zooplankton abundance.

Cluster analysis revealed two major widely distributed groups separated at 141° E, with a 37.6% dissimilarity level (Fig. 3b, Table 3). Cluster A comprised 36 segments located in the western area, whereas Cluster B had 77 segments located in the eastern area. In both clusters, sea surface temperature, salinity, and chlorophyll *a* concentration were at very similar levels (Table 3). Although species composition was also similar, abundance was significantly high in Cluster B. *Limacina* spp. was the dominant species/taxon in both clusters, comprising 41.6% of total zooplankton abundance in Cluster A, with a mean abundance of $8.9 \pm 4.6 \text{ ind. m}^{-3}$; in Cluster B, *Limacina* spp. comprised 68.7% of total zooplankton abundance, with a mean of $99.3 \pm 71.8 \text{ ind. m}^{-3}$. In both clusters, *Limacina* spp. was followed by cyclopoid copepod *Oithona similis*, and copepodite indet. as the most abundant species/taxa. In Cluster B, these three species/taxa had significantly more abundant than in Cluster A (Table 3).

South–North transect CPR samples

Sea surface temperature increased from 1.3 to 10.9 °C toward the north, and salinity also increased gradually from 33.51 to 34.25 PSU (Fig. 4a). We identified the circumpolar frontal position using both sea surface temperature and salinity data. Although the actual circumpolar

Fig. 3 a Sea surface temperature, salinity, chlorophyll *a* concentration, *Limacina* spp. abundance, and other zooplankton abundance recorded from the West–East Continuous Plankton Recorder (CPR) transect of the Japanese Antarctic Research Expedition (JARE) 41. **b** Result of cluster analysis and species composition of the two major clusters



frontal position can be reliably identified only through deep-oceanographic observations (Orsi et al. 1995), both sea surface temperature and salinity correspond well between regions of steep physical change and mean frontal position (Sokolov and Rintoul 2002). The PF and Sub-Antarctic Front (SAF), determined by sea surface temperature profile, occurred between 58° 50' S and 58° 00' S, and 55° 17' S and 54° 12' S, respectively, and were associated with an abrupt change in sea surface temperature. South of the SAF, chlorophyll *a* concentrations were relatively stable between 0.5 and 0.75 mg m⁻³, rising to 0.92 mg m⁻³ in the low latitudes. Thirty-three species/taxa were identified through this transect. Zooplankton abundance (mean ± SD; 30.9 ± 43.8 ind. m⁻³), especially for *Limacina* spp., changed dramatically on the border of the PF, with high abundances occurring on the southern

side. Maximum zooplankton (282.7 ind. m⁻³) and *Limacina* spp. (267.4 ind. m⁻³) abundances occurred at 59° 25' S (Fig. 4a). Along the transect, *Limacina* spp. was the dominant taxon, comprising 41.9% of the total zooplankton abundance.

Cluster analysis of the SN transect identified six clusters and six outliers, with a 51.6% dissimilarity level (Table 4). Cluster A comprised 45 segments from nighttime samples around SAF and south of PF (Fig. 4b). Zooplankton abundance was relatively low at 14.05 ind. m⁻³, and the small copepods *O. similis* and copepodite indet. were dominant. Cluster B comprised 68 segments located mainly north of the SAF. Surface water in this region was warm (7.94 °C), and chlorophyll *a* concentration was highest at 0.79 mg m⁻³. Species richness was relatively high at 6.53 (Table 4). This cluster was also characterized

Table 3 Results of cluster analysis using West–East (WE) transect data

	Cluster A	Cluster B	Outlier	<i>F</i>	<i>p</i> -value	
Number of segments	36	77	4			
Sea surface temperature (°C)	1.59	1.52	1.80	No test		
Salinity (PSU)	33.73	33.71	33.72	No test		
Chlorophyll <i>a</i> (mg m ⁻³)	0.55	0.57	0.58	2.57	0.083	n.s
Species richness (<i>r</i>)	5.06	5.59	3.50	5.03	0.009	
Total abundance (ind m ⁻³)	21.42	144.52	8.29	35.10	<0.001	
Species/taxa						
<i>Calanoides acutus</i>	0.06	0.04		0.17	0.847	n.s
<i>Calanus simillimus</i>	0.02	0.42		8.46	<0.001	
Copepoda indet	0.02	0.01		0.07	0.931	n.s
Copepodite indet	2.46	6.83	0.35	16.33	<0.001	
Copepoda nauplius		0.04		1.26	0.289	n.s
<i>Ctenocalanus citer</i>	0.10	0.04		0.75	0.476	n.s
<i>Eukrohnia hamata</i>	0.10	0.08	0.17	0.14	0.866	n.s
<i>Euphausia frigida</i>	0.04	0.10		0.87	0.421	n.s
<i>Euphausia frigida</i> calyptopis	0.06	0.07		0.06	0.941	n.s
<i>Euphausia triacantha</i> calyptopis	0.02			0.73	0.484	n.s
Euphausiidae indet	0.04	0.01		0.27	0.765	n.s
Foraminifera		0.10		0.97	0.385	n.s
<i>Fritillaria</i> spp.	0.29	0.10		2.91	0.060	n.s
Hyperiididae spp.	0.04			1.51	0.228	n.s
<i>Limacina</i> spp.	8.91	99.26	4.49	31.44	<0.001	
<i>Oikopleura</i> spp.	3.42	3.20	0.35	1.42	0.247	n.s
<i>Oithona similis</i>	5.72	33.40	2.59	23.40	<0.001	
<i>Oncaea</i> spp.	0.02			0.73	0.484	n.s
Ostracoda	0.02	0.01		0.07	0.931	n.s
<i>Paraeuchaeta</i> spp.		0.01		0.40	0.670	n.s
<i>Rhincalanus gigas</i> nauplius	0.04	0.23	0.35	4.48	0.014	
<i>Salpa thompsoni</i>		0.07		1.16	0.318	n.s
<i>Themisto gaudichaudii</i>	0.02	0.04		0.36	0.699	n.s
<i>Thysanoessa macrura</i> furcilia	0.06	0.44		5.46	0.006	
Total species/taxa	20	21	6			

Mean sea surface temperature, salinity, species richness, and abundance values within two clusters, including outliers. Differences between clusters were investigated by one-way ANOVA and Newman-Keuls multiple range tests. Significant differences are in bold. The total numbers of species/taxa recorded per cluster are indicated

n.s. not significant

by the occurrence of the euphausiids *Euphausia frigida* and *E. triacantha*, amphipods *Hyperietta antarctica* and *Primno macropa*, and ostracoda, none of which occurred in any other cluster. Cluster C comprised the three samples located in the PF (Fig. 4b). Foraminifera abundance levels were significantly higher in Cluster C than in any other cluster (Table 4).

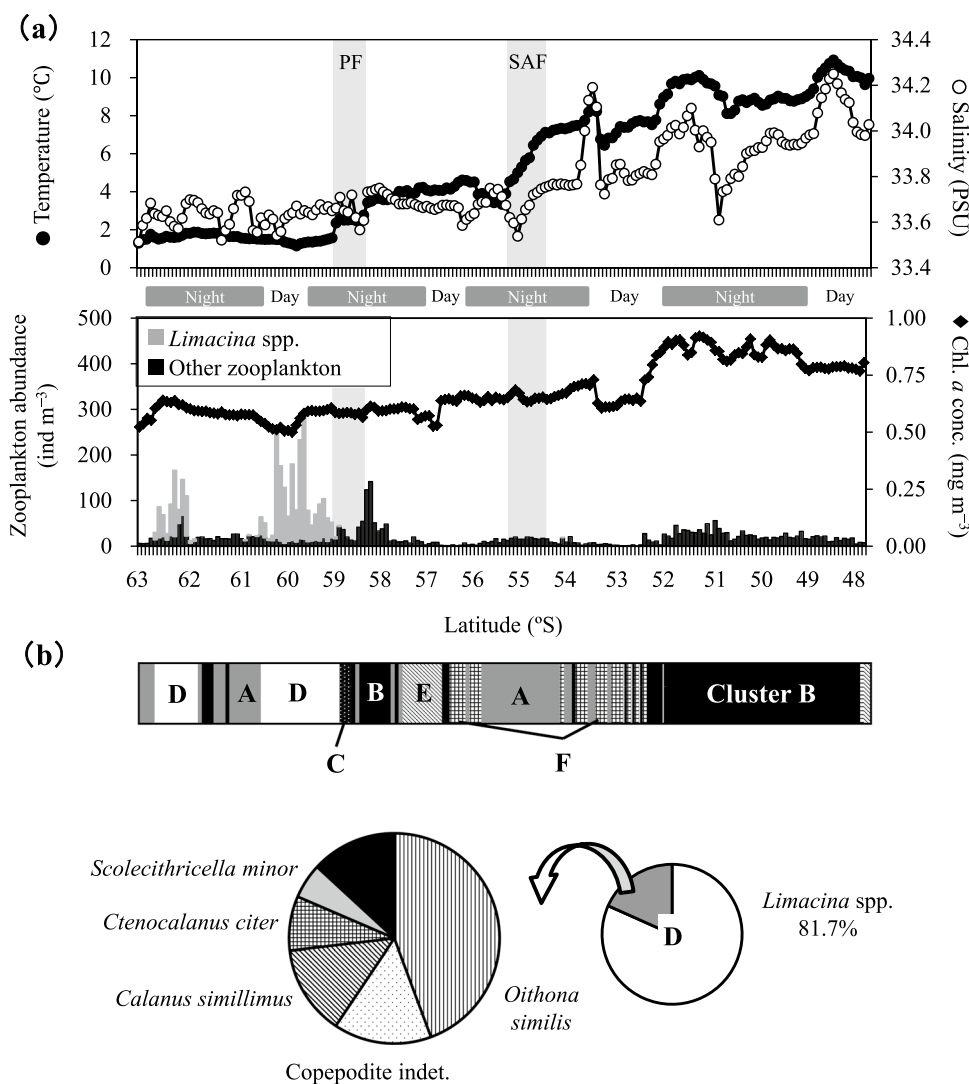
Cluster D comprised 31 segments located south of the PF (Fig. 4b). This cluster had the lowest sea surface temperature (1.52 °C) and highest zooplankton abundance of any of the clusters (Table 4). Total zooplankton abundance had a mean of 94.6 ind. m⁻³, and included the highest abundance levels of *Limacina* spp. with 77.3 ind. m⁻³.

Cluster E comprised 12 segments located between the PF and SAF. Zooplankton abundance was relatively low with 9.27 ind. m⁻³, and the abundance of appendicularians of the genus *Oikopleura* spp. was the highest of any cluster (Table 4). Cluster F comprised 21 segments located in the vicinity of SAF. This cluster had the lowest zooplankton abundance of any of the clusters.

South-North transect NORPAC samples

Species in NORPAC-net samples from five stations, collected simultaneously with CPR, were very similar, with *Limacina* spp., *O. similis*, and copepodite indet. being

Fig. 4 a Sea surface temperature, salinity, chlorophyll *a* concentration, *Limacina* spp. abundance, and other zooplankton abundance recorded from the South-North Continuous Plankton Recorder (CPR) transect of the Japanese Antarctic Research Expedition (JARE) 41. **b** Result of cluster analysis and species composition of Cluster D, which had a high abundance of *Limacina* spp. PF Polar Front, SAF Sub-Antarctic Front



dominant (Fig. 5a). At northern stations N5 and N6, the abundance of foraminiferans was relatively high (66.5% and 28.0%, respectively). *Limacina* spp. occurred in all samples, and peaked at 357.8 ind. m⁻³ (20.2% of total zooplankton abundance) at the southernmost station N2 (Fig. 5b). The shell diameter of *Limacina* spp. was the largest at station N3 (mean \pm SD; 447.2 \pm 123.0 μ m), followed by N4 (484.4 \pm 181.4 μ m), and N2 (357.8 \pm 118.6 μ m). At the northern stations, *Limacina* spp. abundance decreased by half at N5 (189.6 \pm 89.0 μ m) and N6 (178.4 \pm 42.4 μ m).

Seasonal ice zone NORPAC samples

The relative abundance of *L. rangii* in six samples in the N1 area was stable and low, and contributed 6.4–23.5% to total zooplankton abundance (Fig. 6). The highest zooplankton and *L. rangii* abundances, *L. rangii* shell diameter, and chlorophyll *a* concentration occurred in 2006, and the lowest in

2004. Although the mean shell diameter exceeded 300 μ m in 2006, in other years it was below 270 μ m (Table 5).

The contribution of *L. rangii* to total zooplankton abundance in six samples from the N2 area fluctuated from 2.1% in 2006 to 38.7% in 2001 (Fig. 6). The highest total zooplankton and *Limacina* spp. abundances were found in 2001, 4,771.6 and 1,847.3 ind. m⁻³, respectively. The largest *L. rangii* occurred in 2001 (mean 362.6 μ m) and 2000 (mean 357.8 μ m). The mean shell diameter was <270 μ m for 4 years (1997, 2002, 2004, and 2006) (Table 5).

In eight samples from the N3 area, *L. rangii* dominated, accounting for 61.5% of the total zooplankton abundance in 2000, and 44.8% in 2001 (Fig. 6). Conversely, total zooplankton abundance was lowest in 2000 at 229.4 ind. m⁻³. The highest *L. rangii* abundance was found in 2001, at 2083.3 ind. m⁻³. Furthermore, large *L. rangii* occurred in 2002 (mean 540.2 μ m) and 2000 (mean 444.7 μ m). The mean shell diameter was <270 μ m for 4 years (1997, 1998, 2001, and 2004) (Table 5).

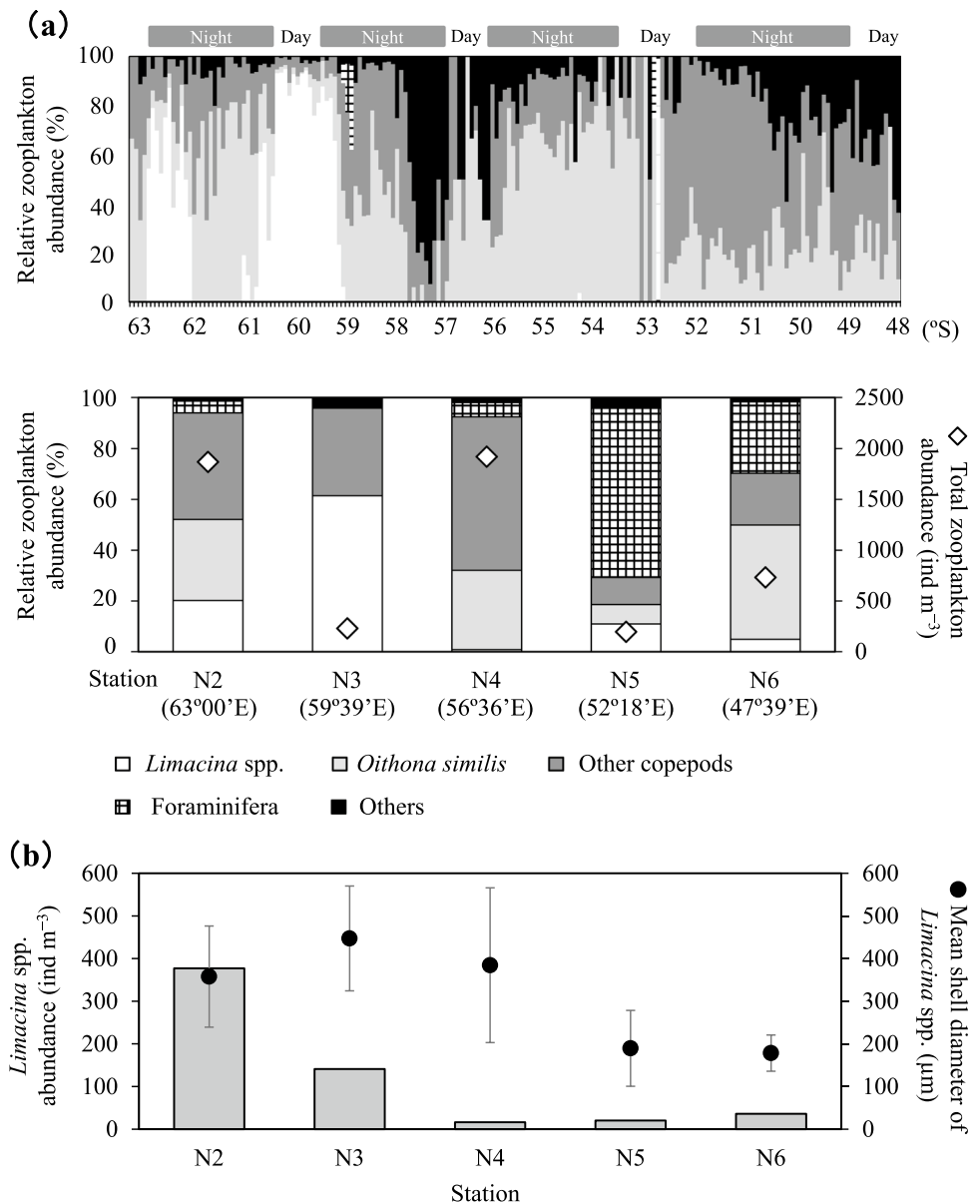
Table 4 Results of cluster analysis using South-North (SN) transect data

	Cluster A	Cluster B	Cluster C	Cluster D	Cluster E	Cluster F	Outlier	<i>F</i>	<i>p</i> -value
Number of segments	45	68	3	31	12	21	6		
Sea surface temperature (°C)	4.08	7.94	2.53	1.52	4.99	6.47	6.65	No test	
Salinity (PSU)	33.69	33.90	33.67	33.63	33.73	33.78	33.78	No test	
Chlorophyll <i>a</i> (mg m ⁻³)	0.62	0.79	0.58	0.58	0.61	0.66	0.68	35.45	<0.001
Species richness (<i>r</i>)	4.42	6.53	9.67	6.42	4.08	2.14	1.67	31.12	<0.001
Total abundance (ind m ⁻³)	14.05	27.75	34.09	94.63	9.27	3.42	1.38	26.24	<0.001
Species/taxa									
<i>Calanoides acutus</i>		0.09	1.38	0.09				13.88	<0.001
<i>Calanus simillimus</i>	0.15	4.73	5.07	2.39	0.63	0.20	0.12	26.80	<0.001
<i>Candacia maxima</i>				0.02				0.83	0.549 n.s
Copepoda indet	0.20	0.22	0.69	0.27	0.17			0.85	0.531 n.s
Copepodite indet	2.21	7.85	3.92	2.61	1.32	0.03	0.69	15.42	<0.001
Copepoda nauplius	0.32	0.14		0.09		0.07	0.12	1.20	0.307 n.s
<i>Ctenocalanus citer</i>	0.08	1.04	0.23	1.45	0.17	0.03		3.78	0.001
<i>Eukrohnia hamata</i>	0.02	1.07		0.13	0.17			8.28	<0.001
<i>Euphausia frigida</i>		0.11						0.78	0.587 n.s
<i>Euphausia frigida</i> calyptopis		0.06		0.02				1.05	0.392 n.s
<i>Euphausia frigida</i> furcilia	0.06	0.06	0.69	0.11	0.29			4.16	0.001
<i>Euphausia triacantha</i>		0.05						1.50	0.180 n.s
<i>Euphausia triacantha</i> furcilia	0.20	0.27				0.07		2.79	0.013
Euphausiidae indet	0.02							0.51	0.797 n.s
Foraminifera			5.99			0.03		305.61	<0.001
<i>Fritillaria</i> spp.	0.15	0.05		0.11		0.03		1.16	0.329 n.s
<i>Haloptilus oxycephalus</i>	0.03	0.01						0.34	0.917 n.s
<i>Hyperietta antarctica</i>		0.01						0.28	0.945 n.s
<i>Limacina</i> spp.	0.17		0.92	77.29				30.30	<0.001
<i>Metridia lucens</i>	0.11	0.01	0.69	0.22				4.99	<0.001
<i>Oikopleura</i> spp.	0.69	1.47		0.22	5.87	0.59	0.12	27.92	<0.001
<i>Oithona similis</i>	9.03	9.43	12.21	7.69	0.58	2.30	0.35	3.10	0.006
<i>Oncaea</i> spp.	0.02	0.01	0.23					3.65	0.002
Ostracoda		0.12						2.89	0.010
<i>Paraeuchaeta</i> spp.	0.08	0.05	0.23	0.07				1.12	0.415 n.s
<i>Primno macropa</i>		0.01						0.28	0.945 n.s
<i>Pseudosagitta gazellae</i>		0.03				0.03		0.73	0.623 n.s
<i>Rhincalanus gigas</i> nauplius		0.02		0.09				1.00	0.430 n.s
<i>Salpa thompsoni</i>	0.02	0.10	0.23					2.21	0.044
<i>Scolecithricella minor</i>	0.46	0.56	1.61	0.94				1.09	0.371 n.s
<i>Themisto gaudichaudii</i>		0.11		0.02	0.06			1.65	0.136 n.s
<i>Thysanoessa macrura</i> furcilia	0.05	0.05		0.47				3.06	0.007
<i>Tomopteris</i> spp.				0.33				2.52	0.023
Total species/taxa	20	28	14	21	9	10	5		

Mean sea surface temperature, salinity, species richness, and abundance values within six clusters, including outliers. Differences between clusters were investigated by one-way ANOVA and Newman-Keuls multiple range tests. Significant differences are in bold. The total numbers of species/taxa recorded per cluster are indicated

n.s. not significant

Fig. 5 a Relative zooplankton abundance along the 150°E transect collected via Continuous Plankton Recorder (CPR) (upper) and North Pacific (NORPAC) standard net (lower) in March 2000. **(b)** Abundance and shell diameter of *Limacina* spp. collected via NORPAC



Discussion

High abundance of *Limacina* spp. in CPR samples

SO-CPR survey program data (> 42,000 samples) have accumulated over 25 years, with samples mostly collected between September and April. Data collected in the seasonal ice zone in March are based on approximately 9000 samples, in which *Limacina* spp. occurs in 31.3% of them. In the samples collected during the JARE-41 cruise in March 2000, a high abundance of *Limacina* spp. in a large area within the seasonal ice zone was observed. The maximum abundance of *Limacina* spp. in the present study was 353.8 ind. m⁻³, contributing to 72.2% of total zooplankton abundance, while the maximum abundance

of *Limacina* spp. from CPR samples collected south of Australia in February was 479 ind. m⁻³ (Hunt et al. 2008). *Limacina* spp. abundance in CPR samples peaked in February, and small hotspots have been reported as typical patchy zooplankton distributions (Hunt and Hosie 2005, 2006; Hosie et al. 2014). Conversely, in almost all segments of the WE transect and 31 segments of the SN transect in this study (Cluster D in Table 4), *Limacina* spp. was the most dominant in the zooplankton communities. These regions had 120 segments, i.e., they extended to 600 nautical miles (ca 1110 km). In particular, the eastern side of the WE transect (Cluster B in Table 3), and the south of PF in the WE transect (Cluster D in Table 4) were continuously observed to have high abundances, with a mean of 99.3 ind. m⁻³ and 77.3 ind. m⁻³, respectively. Although

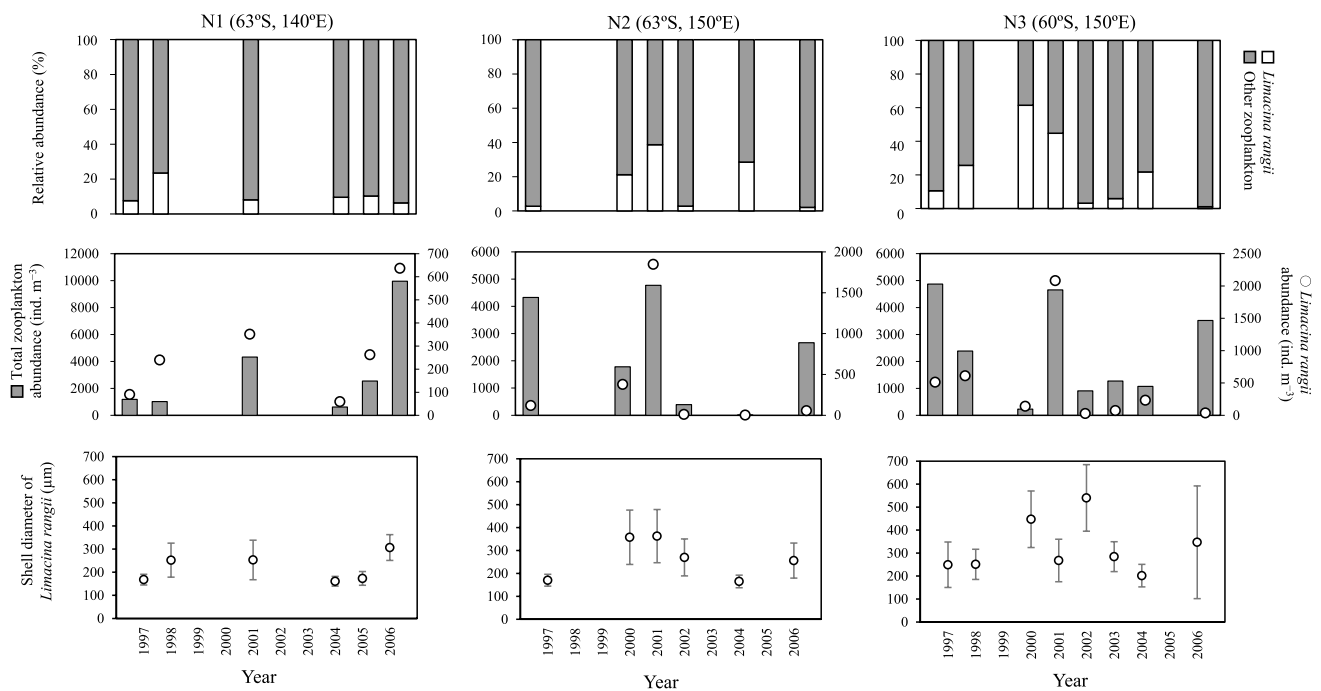


Fig. 6 Relative abundance (upper), abundance (middle), and shell diameter (lower) of *Limacina rangii* at three North Pacific (NORPAC) stand-alone net sampling areas in March from 1997 to 2006 (except 1999 and 2005)

Limacina spp. abundance in our study is similar to abundances reported in other CPR studies, they have not been previously reported over such a large area.

One factor that influences distribution on the surface of *Limacina* spp. is diel vertical migration. Because *L. rangii* and *L. retroversa* have typical diel vertical migration patterns during summer (Lalli and Gilmer 1989; Hunt et al. 2008; Conroy et al. 2020), they are observed in high abundance in the upper layer at night. The CPR is towed horizontally at a constant depth, which means that the diurnal vertical migration of some zooplankton taxa may affect abundance in the observed data on a 24-h scale (Takahashi and Hosie 2021). Along the WE line, eastern zooplankton abundances were higher, especially for *Limacina* spp. Percentages of *O. similis* also increased in the east similar to the total zooplankton abundance. The timing of the increase in the abundance synchronized with nighttime around 141° E, but not around 134° E (Fig. 3a). High abundance levels also continued during daytime around 145° E. Therefore, no clear diel change in zooplankton abundance or species composition was apparent. Zooplankton abundances along the SN transect were high on the southern side on the boundary around the PF. The most dominant species, *Limacina* spp., occurred only in very low numbers north of the PF. Cluster D, which had a high abundance of *Limacina* spp., contained both day and nighttime samples (Fig. 4b, Table 4). The areas of 60.5°S to 59.5°S, where high abundance levels were observed, included a large proportion of daytime tows. No

clear diel changes in *Limacina* spp. abundance were apparent along the SN transect.

Member species of the gymnosome pteropod genus *Clione* are monophagous predators that feed exclusively on *Limacina* (Lalli and Gilmaer 1989). Fluctuations in *L. rangii* abundance may be driven by predator–prey dynamics with *Clione limacina antarctica* (Weldrick et al. 2019). While we have no evidence of predator pressure directly reducing *Limacina* abundance, stable *L. rangii* populations may support gymnosome abundances (Thibodeau et al. 2019). Unfortunately, because gymnosome species are only rarely collected with the CPR, feeding relationships cannot be evaluated.

As with other factors, food availability is related to abundance and distribution patterns. Thecosome pteropods are predominantly omnivorous, but diatoms and dinoflagellates dominate the gut contents of *L. rangii* in the Southern Ocean (Hopkins 1987; Thibodeau et al. 2022). Regional and inter-annual variation in primary production is probably the major determinant of spatial and temporal variability in pteropod densities (Seibel and Dierssen 2003). However, chlorophyll *a* concentrations in the WE transect were stable at low levels, ranging between 0.47 and 0.70 mg m⁻³. In the south of the SAF in the SN transect, mean chlorophyll *a* concentrations were also stable between 0.5 and 0.75 mg m⁻³. Two clusters with high *Limacina* spp. abundance, Cluster B of the WE transect and Cluster D of the SN transect, had normal chlorophyll *a* concentration levels with a mean of

Table 5 Abundance and shell diameter of *L. rangii* collected by North Pacific (NORPAC) standard net in three areas of the seasonal ice zone in the Southern Ocean during the Japanese Antarctic Research Expedition (JARE) 38 (1997) to 47 (2006) in March

Station No	Sampling Year	<i>Limacina rangii</i> Abundance (mg m ⁻³)	<i>Limacina rangii</i> Shell diameter (μm)	Chl <i>a</i> (mg m ⁻²)
N1	1997	90.5	168.0 ± 23.1	39.7
	1998	239.8	252.2 ± 73.7	28.9
	2001	351.3	253.2 ± 85.6	25.1
	2004	59.5	160.8 ± 21.0	20.4
	2005	262.6	173.2 ± 29.7	25.7
	2006	636.6	306.6 ± 55.8	49.5
N2	1997	118.9	170.2 ± 25.8	36.3
	2000	379.2	357.8 ± 118.6	15.6
	2001	1847.3	362.6 ± 116.0	15.8
	2002	11.0	269.6 ± 80.6	8.8
	2004	2.6	165.0 ± 27.4	15.9
	2006	55.9	256.0 ± 76.5	20.4
N3	1997	512.7	249.2 ± 99.0	17.8
	1998	611.9	251.0 ± 65.8	16.1
	2000	140.9	447.2 ± 123.0	18.0
	2001	2083.3	267.8 ± 92.4	20.7
	2002	28.9	540.2 ± 144.9	12.8
	2003	75.2	284.4 ± 65.0	N.D
	2004	234.0	201.8 ± 49.1	11.3
	2006	37.8	347.0 ± 245.3	16.2

To enable comparison with *Limacina* data, chlorophyll *a* concentrations (chl *a*) were integrated vertically (0–150 m)

0.57 mg m⁻³ and 0.58 mg m⁻³, respectively (Tables 3, 4). Thus, no relationship was apparent between *Limacina* spp. abundance and chlorophyll *a* concentration; factors other than primary production may have influenced pteropod abundance throughout the sampling area during the sampling periods of this rare event of March 2000.

Limacina abundance and shell size in NORPAC samples

Despite the different sampling layers, NORPAC data obtained simultaneously with CPR data for five stations had similar species compositions, except for foraminiferans and *Limacina* spp. to the north of the SAF (Fig. 5a). Planktonic foraminifera are a large group of protists, and their distribution is highly seasonal and also known to be patchy. They sometimes dominate CPR towing samples, with very high abundances (Takahashi et al. 2010). Recently, finer plankton nets (100 μm) have provided a more realistic view of plankton's ecological significance in the seasonal ice zone of the Southern Ocean (Ojima et al. 2013, 2015; Takahashi et al. 2017). Therefore, it is thought that high foraminiferan

abundance observed only in NORPAC samples was based on the differences in mesh size and timing of sampling.

The abundance of *Limacina* spp. in samples obtained via the CPR decreased sharply in waters bordering the PF, and *Limacina* spp. occurred in low numbers on the northern side. Although NORPAC samples also decreased in waters bordering on the PF, *Limacina* occurred in northern samples with low abundance (Fig. 5b). The same tendency was seen in shell diameter of *Limacina* spp., and shell size decreased by half in the north of the SAF. *Limacina retroversa* is considered to be predominantly a sub-Antarctic species, and to be smaller-sized than *L. rangii*. This species has been reported to occur at low densities or be completely absent south of the PF (Hunt et al. 2008). The station N4 located between PF and SAF had relatively larger mean shell size, but standard deviation was high (Fig. 5b). This may suggest that *Limacina* abundance shifted from *L. rangii* to *L. retroversa* in this region. Because the mean shell size at stations N5 and N6 was < 270 μm, it is clear that the abundance of *Limacina* spp. collected only via the NORPAC net was a result of differences in mesh size.

In the seasonal ice zone south of 59°E, in which we found a high *Limacina* spp. abundance in the JARE–41 CPR samples, we examined the variability of abundance and shell size of *Limacina* for the 10 years from 1997 to 2006 (Fig. 6). Based on the shell height/diameter ratio, abundant *Limacina* larvae south of 59°E in our survey were most likely those of *L. rangii*. This species is typical of Antarctic waters, and its abundance increased towards lower Southern Ocean latitudes (Hunt et al. 2008; Mackey et al. 2012; Bednaršek et al. 2012b). *Limacina rangii* spawns primarily in late summer to autumn (Hunt et al. 2008), and its larval stages are sometimes a major contributor to the zooplankton community in the seasonal ice zone during autumn (Brierley and Thomas 2002).

In the present study, a mean shell diameter < 270 μm was observed in 13 of 20 samples. *Limacina* individuals < 300 μm in size are in the veliger stage (Lalli and Gilmer 1989). Thus, it was clear that *Limacina* veliger abundance was underestimated in CPR samples with mesh size of 270 μm. A comparative study of 76-μm, 202-μm, and 330-μm mesh nets demonstrated *Limacina* spp. abundance in the 76-μm mesh of 21.96 ind. m⁻³, while they were completely absent in the 202-μm and 330-μm mesh nets (Hopkins 1971). To evaluate veliger abundance more accurately, it is necessary to use a suitable mesh size for larger microzooplankton (100–200 μm).

In another data set for JARE zooplankton monitoring using NORPAC in March, Nishizawa et al. (2016) measured samples collected at 110° E and 64° S from 1987 to 2008. The mean shell diameter of *Limacina* spp. was 209.2 ± 33.8 μm, and there was no significant fluctuation in the shell size over the 20-year study period. In March

2000, when high abundance was widely observed via CPR, *L. rangii* abundances were low compared with other years (Fig. 6). However, relatively large-sized individuals were found in N2 (mean 357.8 μm) and N3 (mean 444.7 μm) (Table 5). It is thought that the CPR was able to catch the large-sized individuals that were dominant during CPR towing in March 2000. At each sampling site, there was no association between *Limacina* abundance, shell size, and environmental factors, such as chlorophyll *a* concentration and sea surface temperature, at the time of sampling. The timing of reproduction and the growth of the new generation by a year may have influenced *Limacina* abundance and shell size throughout the sampling area. Long-term observations in the western Antarctic Peninsula have revealed sea ice to be the dominant driver of pteropod abundance (Thibodeau et al. 2020). The model proposed by Thibodeau et al. (2020) indicates that earlier sea-ice retreat in the austral spring leads to rapid pteropod growth, with more open water combining with warmer waters of sea surface temperature. It is also possible that the rare event that we report for March 2000 was because of early sea-ice retreat producing an environment conducive to pteropod growth.

Thecosome pteropods are major components of polar food webs, and they can dominate zooplankton communities in the Southern Ocean seasonal ice zone. Because these pteropods are a major aragonite-producing group, they are vulnerable to the effects of ocean acidification (Orr et al. 2005; Fabry et al. 2008). Accordingly, two Southern Ocean *Limacina* species have been proposed as indicators of acidification (Manno et al. 2012; Mekkes et al. 2021; Johnston et al. 2022). Early life stages are more susceptible to the effects of climate change than adults (Dupont and Thorndyke 2009; Gardner et al. 2018). The *Limacina* collected in our study were either veligers or juveniles. Because larval shells form relatively quickly (Bednaršek et al. 2012b; Thibodeau et al. 2020; Weldrick et al. 2021), larval stages may be more sensitive to environmental changes than those of adults. An understanding of population dynamics, and the accumulation of fundamental biological data for these larval stages, is therefore necessary to more fully evaluate recruitment and long-term population viability in response to environmental change such as ocean acidification. Long-term monitoring of *Limacina* abundance and growth characteristics at a fixed location, and high-resolution annual time series data on population structure at multiple locations, would enable accurate determination of species' lifespans and responses to environmental change.

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Author Contributions KTT directed the JARE monitoring program and wrote the manuscript. HU carried out field sampling aboard the icebreaker *Shirase* and processed the samples.

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Data availability All raw data on which this study is based are available at the Australian Antarctic Data Centre via the home page of the Southern Ocean Continuous Plankton Recorder (SO-CPR) Survey (<http://data.aad.gov.au.aadc/cpr/>).

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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