

Progress of Chinese zooplankton ecology research in Prydz Bay, Antarctica

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Abstract Zooplankton are considered an important trophic link between primary producers and higher trophic level species in the Southern Ocean ecosystem. Since 1989, when the Chinese Antarctic Zhongshan Station was built, zooplankton have regularly been sampled and investigated in Prydz Bay through oceanographic surveys of each Chinese National Antarctic Research Expedition. This review summarizes the main results from zooplankton ecology studies conducted in Prydz Bay by Chinese researchers. Major topics covered in this review are: (1) a description of the biology and ecology of Antarctic krill (*Euphausia superba*), the key zooplankton species of the Southern Ocean ecosystem; (2) zooplankton community structure, including the horizontal distribution in the epipelagic region and vertical distribution between 0–1500 m; (3) feeding ecology of dominant species such as Antarctic krill, salps and copepods; (4) a short introduction to the molecular research; and (5) prospects for future research.

Keywords zooplankton, Southern Ocean, Antarctic krill, Community, feeding ecology, Chinese research

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1 Introduction

After the Weddell and Ross seas, Prydz Bay is the third largest embayment into the Antarctic land mass with two banks, Fram Bank and Four Ladies Bank, located in the western and eastern ends, respectively. Sea ice covers the bay in winter and spring, although a latent heat-type polynya, which is temporally and spatially variable, is often located in high latitudes near the Amery Ice Shelf (Smith et al., 1984). Multidisciplinary surveys have been conducted in Prydz Bay since 1989, when the Chinese Antarctic Zhongshan Station was built in the Larsemann Hills (Shi et al., 2013). Zooplankton, which link primary production and

higher trophic levels in the Southern Ocean ecosystem, have been studied in Prydz Bay for about 30 years during Chinese National Antarctic Research Expeditions (CHINARE). Zooplankton were collected in the field using Isaacs-Kidd Midwater Trawl (IKMT) nets, North Pacific (Norpac) nets, High Speed Zooplankton Samplers and MultiNet. Biology and ecology of key species (Antarctic krill), zooplankton community structure and feeding ecology of dominant species were studied based on *in situ* experiments and samples. This review describes the main progress of Chinese zooplankton ecology research in Prydz Bay, Antarctica during the past three decades, providing a source of reference for future work. We describe the biology and ecology of the key species (Antarctic krill), zooplankton community structure, feeding ecology of

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dominant species, provide a short introduction of molecular research, and end with prospects for future work.

2 Biology and ecology of the key species, Antarctic krill

2.1 Abundance and distribution

Antarctic krill, *Euphausia superba*, are mainly distributed in the shelf and slope regions of Prydz Bay (Wang and Zhong, 1993; Wang et al., 1993a; Liu et al., 2001; Yang et al., 2010; Liu et al., 2011). The abundance, population structure and distribution of *E. superba* show significant spatial and temporal variation (Wang and Zhong, 1993; Wang et al., 1993a; Liu et al., 2001; Yang et al., 2010; Liu et al., 2011). Adult krill are mainly composed of four age groups (1^+ , 2^+ , 3^+ and 4^+), based on length/frequency distribution data of samples collected using the Isaacs-Kidd Midwater Trawl (IKMT) and Norpac nets during the austral summer of 1989/1990 and 1990/1991 (Wang et al., 1993a). The average abundance of krill was $16.17 \text{ ind} \cdot (1000 \text{ m})^{-3}$ in the austral summer of 1999/2000 and $68.85 \text{ ind} \cdot (1000 \text{ m})^{-3}$ in January 2002, based on IKMT samples (Liu et al., 2001; Liu et al., 2011). The abundance of krill larvae also showed significant interannual fluctuation ($26 \text{ ind} \cdot (1000 \text{ m})^{-3}$ in January of 1990 vs $20113 \text{ ind} \cdot (1000 \text{ m})^{-3}$ in January of 1991) (Wang and Zhong, 1993). Short body length and high sex ratios (Male/Female) were found for krill at high latitudes of Prydz Bay (Wang et al., 1993b). Variation in krill populations may result from differences in water temperature and the effect on krill larvae livability (Wang and Zhong, 1993). During years when ice retreated earlier, concomitant with higher chlorophyll *a* levels, there was greater population recruitment (Wang and Zhong, 1993). Consequently, higher abundance and older developmental stages were usually found in these years (Yang et al., 2010).

2.2 Fecundity and spawning

The spawning season of *E. superba* in Prydz Bay began in January and extended to March, one month longer compared with the Atlantic Sector of the Southern Ocean (Wang et al., 1993b). The spawning population mainly consisted of two age groups, 3^+ and 4^+ , with 3^+ being dominant (Wang et al., 1993b). The percentage of males was 34.1% and decreased with increase in body length (Wang et al., 1993b). Most of the gravid females in Prydz Bay spawned once after capture, and the brood size ranged from 225 to nearly 6000 eggs. However, two out of 53 gravid females spawned a second time 5–7 d after the first spawning, with brood sizes of about 500 eggs (Zhong and Wang, 1995). Regeneration of oocytes was not observed within 40 d after spawning. Higher brood size was associated with increasing body weight and body length, though the correlation was poor (Zhong and Wang, 1995). It has been observed that the number of oocytes in gravid females ranges from 2188 to 9263, with an average of 5283

(Zhong and Wang, 1995).

2.3 Growth and diameter of compound eye

Shrinking of *E. superba* due to low food availability was found in both the laboratory and the field (Sun et al., 1995). The number of crystalline cones and body length from samples collected in late summer showed a linear relationship, while eye diameter and body length had an exponential relationship (Figure 1) (Sun et al., 1995; Sun and Wang, 1996). It has been reported that crystalline cone number and the diameter of the compound eye remained relatively unchanged (Sun et al., 1995). Therefore, the crystalline cone number and diameter of the compound eye could be selected as more reliable indicators of age and growth index, compared with body length (Sun et al., 1995).

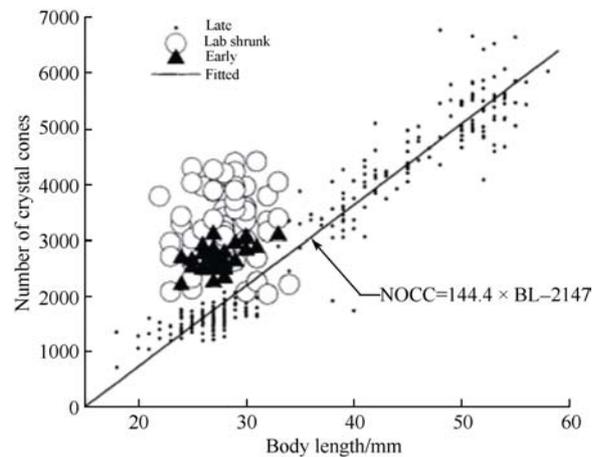


Figure 1 Relationship between body length and the number of crystalline cones in the compound eye of the Antarctic krill for samples collected in high summer (late) (a period of rapid growth), a sample which had been kept in an aquarium (lab shrunk, which leads to shrinking) and a sample collected in spring (early), when the effects of shrinking over winter may still be present (Sun et al., 1995).

2.4 Other krill species

In Prydz Bay, *Thysanoessa macrura* and *E. crystallorophias* were also dominant krill species. *T. macrura* was abundant in the open sea region north of the continental shelf, while *E. crystallorophias* was mainly distributed in the neritic region (Yang et al., 2010). Breeding season of *T. macrura* was reported to start in early October and ended in early January (Zhong and Wang, 1993a). Timing of breeding and developmental stages showed significant interannual variation, dependent on water temperature (Zhong and Wang, 1993a). Based on the larval stage composition, breeding of *E. crystallorophias* seemed to start in early November and end in late December (Zhong and Wang, 1993b). It has been noted that the timing of ice retreating and its effect on food availability could greatly impact breeding and development of krill species in Prydz Bay (Wang and Zhong, 1993).

2.5 Standing crops of krill

The Antarctic krill fishery has been operating since the 1970s, mostly concentrated in the Atlantic Sector. Based on image records from a color fishfinder atlas and targeted sampling using IKMT during the summer of 1990/1991, the standing crop of Antarctic krill off Prydz Bay (68°–108° E, 62°–69° S) was about 2.2×10^7 t with an average density of $32.59 \text{ t}\cdot\text{km}^{-2}$ (Guo et al., 1993). Most of the krill aggregations were found in depths of 40 m with a vertical fluctuation of 10 m (Guo et al., 1993). In the austral summer of 1991/1992, krill standing crops off the Prydz Bay region were 1.69×10^6 t (average density: $22.99 \text{ t}\cdot\text{km}^{-2}$) (68°–103° E, 62°–68° S), and 4.04×10^6 t (average density: $32.15 \text{ t}\cdot\text{km}^{-2}$) in the austral summer of 1992/1993 (58°–83° E, 63°–68° S) (Chen et al., 1996).

3 Zooplankton community structure

3.1 Horizontal distribution

Zooplankton could easily be affected by climate change because of their short lifespans and weak swimming ability (Beaugrand et al., 2002). Significant dynamics of zooplankton communities have been observed in West Antarctica, with a noticeable decline of *E. superba* and an increase of salps (*Salpa thompsoni*), attributed to the decrease in sea ice (Atkinson et al., 2004). Since 1978, macrozooplankton have been collected using rectangular midwater trawls (RMT 8) in Prydz Bay, and three latitudinally distributed communities (the neritic, the oceanic and the krill-dominated), have been identified (Hosie and Cochran, 1994; Zhang and Sun, 2000); however, RMT 8 under-samples mesozooplankton. Interannual dynamics of zooplankton communities were analyzed based on samples collected using Norpac nets from 1999 to 2006 (Yang et al., 2011a).

Oceanic and neritic communities were consistently separated in all cruises (Figure 2) (Yang et al., 2011a). Zooplankton assemblages showed good correspondence with indicator analysis, which has previously been shown in macrozooplankton studies (Hosie and Cochran, 1994). *E. crystallorophias* and *Stephos longipes* were the indicator species in the neritic community and formed neritic assemblage. Indicator species for the oceanic community like *Haloptilus ocellatus*, *Heterorhabdus austrinus*, *Rhincalanus gigas* and *Thysanoessa macrura* formed the oceanic assemblage. *E. superba*, *S. thompsoni* and *P. antarcticum* (postlarval stage) were usually separated from other species in zooplankton assemblage studies because of their patchy distribution.

Significant interannual dynamics of zooplankton communities were found in oceanic and neritic communities, with more obvious changes in the latter (Yang et al., 2011a). Community variation and population dynamics corresponded with sea ice conditions. The timing and extent of ice retreat (polynya appearance) and their effects on food availability, influenced interannual

dynamics of zooplankton communities (Yang et al., 2011a). For the oceanic community, higher abundance of younger copepodites of large copepods occurred during years with earlier ice retreat and extra time for phytoplankton bloom; whereas for the neritic community, higher abundance of earlier stage *E. crystallorophias* and large copepods occurred when the extent of polynya was larger (Yang et al., 2011a). In years with later ice retreat and smaller polynya with less time for phytoplankton bloom, the abundance of copepods was lower and the population was mainly composed of older stages (Yang et al., 2011a).

Long-term dynamics in ice concentration may result from atmospheric or oceanic circulation effects. Sea ice could have an important role in connecting climate change and the dynamics of zooplankton communities in the Southern Ocean (Yang et al., 2011a).

3.2 Vertical distribution

Vertical distribution of zooplankton is important for understanding the role of zooplankton in biogeochemical cycles and the impact of environmental variables (Schmidt et al., 2011; Schulz et al., 2012). In the Southern Ocean, there have been several studies on the vertical profiles of the entire zooplankton community (Atkinson and Peck, 1988). Many factors, such as food availability, properties of water masses and vertical migrations could greatly influence zooplankton vertical distribution (Atkinson and Peck, 1988).

To date, most zooplankton community studies have focused on samples collected in epipelagic zones (Hosie and Cochran, 1994; Zhang and Sun, 2000), while communities in mesopelagic and bathypelagic regions have been less studied (Hosie and Cochran, 1994). Knowledge of zooplankton in the mesopelagic zone, such as abundance and vertical distribution, is important to better understand their role in the Prydz Bay ecosystem.

Yang et al. described the vertical profiles of zooplankton communities between 0 and 1500 m based on samples collected at 11 stations using a Hydro-Bios MultiNet (200 μm mesh, 0.5 m^2 mouth size) during the austral summer of 2012/2013 (Yang et al., 2017). Depth was the strongest factor influencing zooplankton vertical structure. Four zooplankton communities, belonging to various water strata, were divided using cluster analysis: Group 1 was comprised of samples from surface water (< 100 m) of shelf and neritic stations, and mainly included early copepodites CI-III of *Calanus propinquus* and the small copepods *Oithona similis*, *Oncaea curvata* and *Ctenocalanus citer*; Group 2 contained samples collected from upper layers (0–200 m) of the oceanic and neritic and shelf regions (<500 m), and was characterized by high proportions of *Euphausia crystallorophias*, *Metridia gerlachei* and the small abundant copepods *C. citer*, *O. similis*, *O. curvata* and *Scolecithricella minor*; Group 3 consisted of samples from the mesopelagic and upper bathypelagic zones (200–1500 m) of shelf and oceanic stations, and was characterized by high proportions of

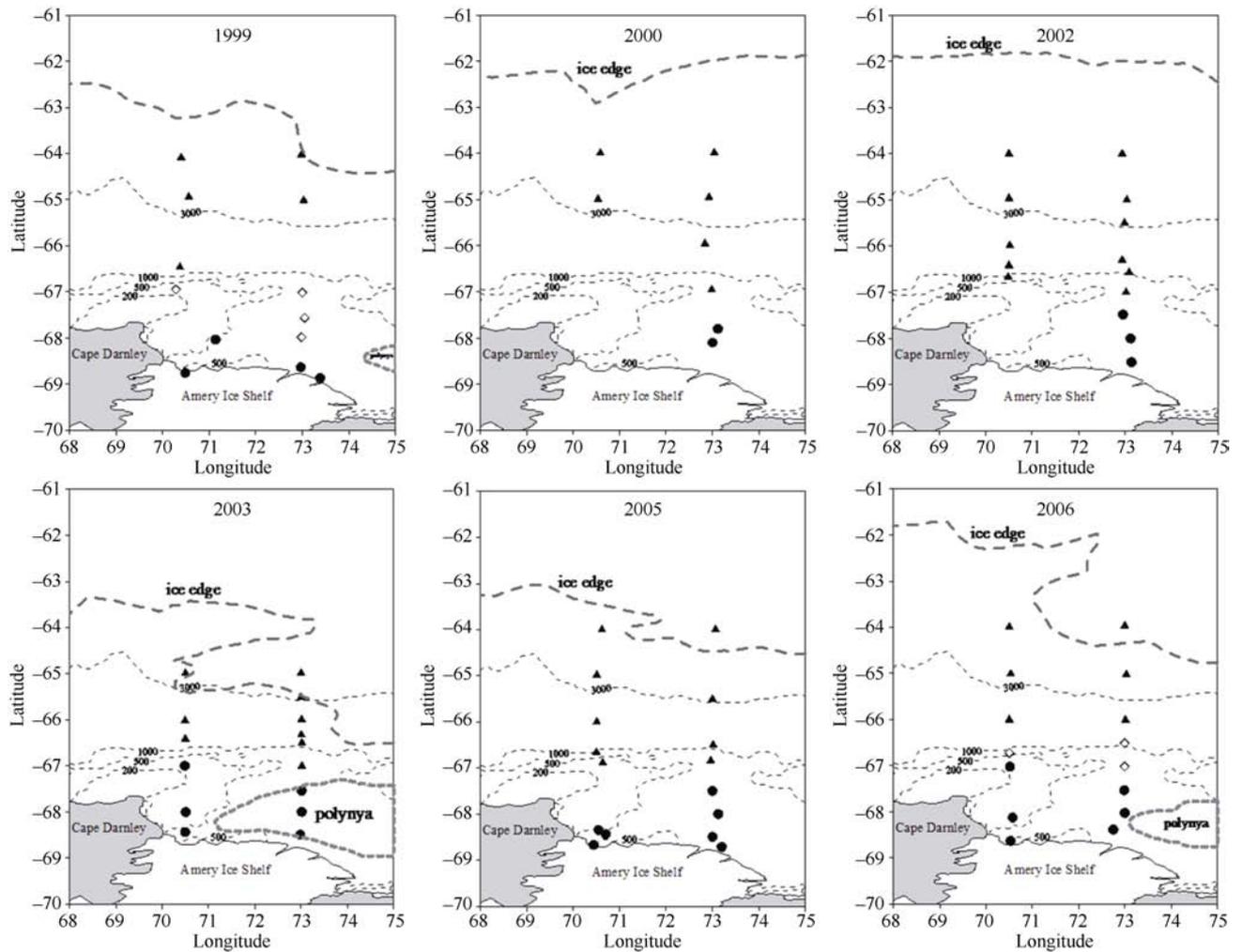


Figure 2 Station groupings identified by intraannual cluster analysis using the full species list from all cruises. Filled triangles, open diamonds and filled circles represent the oceanic, transitional and neritic groups, respectively. Ice edge and polynya position on 15 December (about 1 month before plankton sampling) are shown by the wide broken line (Yang et al., 2011a).

Aetideopsis minor, *Bathycalanus richardi*, *Megacalanus princeps*, the late copepodite stages of *C. acutus* and *R. gigas*, *P. antarctica*, *M. gerlachei*, *Eukrohnia hamate*, *Alacia* spp. and small copepods; and Group 4 mainly comprised samples collected in the 1000–1500 m water stratum of three northern oceanic stations with indicator species *A. minor*, *B. richardi* and *M. princeps* (Yang et al., 2017). Zooplankton abundance, rather than species composition, was the main difference among the four groups. Zooplankton in pelagic zones showed higher species abundance and more pronounced dissimilarity within groups compared with those distributed in deeper zones, based on SIMPER analysis (Yang et al., 2017). Depth-related characteristics of environmental factors may have significant effects on vertical zooplankton community structure; however, this is based on data from a single cruise and a definitive conclusion cannot be made. More frequent sampling of zooplankton, especially in the mesopelagic and bathypelagic zone, should be conducted in Prydz Bay to systematically analyze zooplankton distribution and the

impact of environmental factors.

4 Feeding ecology of dominant zooplankton species

With seasonal cycles in sea ice, the Southern Ocean ecosystem is unique because primary production is restricted in austral spring and summer and regions with ice retreat. Research on the zooplankton community in Prydz Bay showed significant interannual variation, with sea ice retreat and appearance of polynya contributing to zooplankton community dynamics by affecting food availability (Yang et al., 2011a). The phytoplankton bloom associated with ice retreat could favor zooplankton feeding and reproduction.

4.1 Grazing of zooplankton species based on gut pigment analysis

E. superba was considered a major grazer on phytoplankton based on krill swarms with high biomass. Gut pigment

analysis showed that the average ingestion rate of sub-adult and adult krill on chlorophyll *a* could reach 180 ng to 464 ng (Zhong 1995). Li et al. (2001) analyzed the grazing impact of dominant zooplankton species, such as copepods and salps, on phytoplankton standing stock at the seasonal ice zone of Prydz Bay during the austral summer of 1998/1999. Their results showed that the grazing impact of the most common copepods in the Southern Ocean, *Calanoides acutus* and *Metridia gerlachei*, accounted for

less than 1% of phytoplankton standing stock, even though individual ingestion rates were high (Table 1) (Li et al., 2001). *S. thompsoni* could graze 72% of primary production at the northern station (Li et al., 2001), while grazing impact of microzooplankton could account for 10%–65% of phytoplankton standing stock (Li et al., 2001). Nitrogen excretion by microplankton ($0.44\text{--}1.75\text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$) supported 6.8%–53.6% of phytoplankton nitrogen demand (Li et al., 2000).

Table 1 Phytoplankton biomass, primary production and grazing pressure by copepods in Prydz Bay during December 1998/January 1999 (Li et al., 2001)

Station	Copepod		Chlorophyll <i>a</i> / (200 m-integ. $\text{mg}\cdot\text{m}^{-2}$)	Primary production/ ($\text{mg}\text{ C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	Daily grazing rate		Grazing pressure	
	Species	Abundance/ (200 m-integ. $\text{ind}\cdot\text{m}^{-2}$)			$\text{/(mg pigment}\cdot\text{m}^{-2}\cdot\text{d}^{-1})$	$\text{/(mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1})$	chl. $\text{/(}\%$)	Primary production $\text{/(}\%$)
F	<i>Calanoides acutus</i>	61	135.1	No data	0.006	3.7	< 0.1	No data
	<i>Metridia gerlachei</i>	133	135.1	No data	0.002	1.9	< 0.1	No data
III-2	<i>C. acutus</i>	2197	35.7	254.2	0.156	26.2	0.4	10.3
III-4	<i>C. acutus</i>	254	45.2	167.6	0.015	6.4	< 0.1	3.8
III-13	<i>C. acutus</i>	1206	374.5	401.1	0.462	50.3	0.1	12.5
	<i>M. gerlachei</i>	710	374.5	401.1	0.110	21.3	< 0.1	5.3

4.2 Feeding of zooplankton species based on *in situ* incubation

The gut fluorescence technique could not detect the proportion of ciliates in zooplankton diet (Li et al., 2001). Zooplankton in the Southern Ocean could switch to an omnivorous diet to survive periods of phytoplankton shortage (Kruse et al., 2009). Using field incubation experiments, Yang et al. (2013) investigated feeding behavior of dominant zooplankton species in neritic, slope and oceanic regions of Prydz Bay during the austral spring and summer of 2009/2010. They found distinct spatial and temporal variation in ingestion and filtration of dominant zooplankton species. *C. acutus* was inactive and had a low ingestion rate ($1.30\text{ }\mu\text{g}\text{ C}\cdot\text{ind}^{-1}\cdot\text{d}^{-1}$) during late spring, before ice retreat. *E. crystallophias*, *C. acutus*, *M. gerlachei* and *Ctenocalanus citer* had high ingestion rates during early summer when diatom blooms, dominated by *Thalassiosira* spp. and *Fragilaria* spp., occurred in the neritic region. Copepods mainly ingested ciliates as the main food during late summer in regions with lower microplankton concentrations (Figure 3) (Yang et al., 2013).

4.3 Feeding strategies of copepods based on biomarkers

Along with traditional approaches, such as gut pigment analysis and field incubation experiments, biomarkers (e.g. fatty acids and stable isotopes) have frequently been used in

feeding ecology studies (Wang et al., 2014). Some indicator fatty acids characteristic of specific microplankton groups, could be used as dietary signatures with little modification after incorporating into consumers; while $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values are usually used to study carbon sources and trophic levels in food web analyses (Schmidt et al., 2003). Based on fatty acid and stable isotopic analyses, Yang et al. (2016a) investigated feeding strategies and dietary preferences of dominant zooplankton species sampled during austral summer in Prydz Bay. Their results showed regional differences in microplankton abundance, fatty acid biomarker content and stable isotopic values, with higher concentrations in the neritic region and lower values in the oceanic region (Yang et al., 2016a). Similar to food sources, regional differences in fatty acids and isotopic signatures were reflected in copepod species. Species in the neritic region showed higher dinoflagellate fatty acids and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Figure 4) (Yang et al., 2016a). Additionally, copepods showed interspecies differences in fatty acid and stable isotopic values. *C. acutus* and *C. propinquus* showed higher proportions of long chain unsaturated fatty acids, 20:1n-9 and 22:1n-9, while DHA was higher in *M. gerlachei* (Figure 5). Based on $\delta^{15}\text{N}$ isotopic approaches, *C. acutus* occupies the highest trophic level compared with the other three copepod species (Yang et al., 2016a). Yang et al. (2016) showed that dominant zooplankton species had flexible diets because of fluctuating environments during ice retreat in Prydz Bay (Yang et al., 2013, 2016a, 2016b).

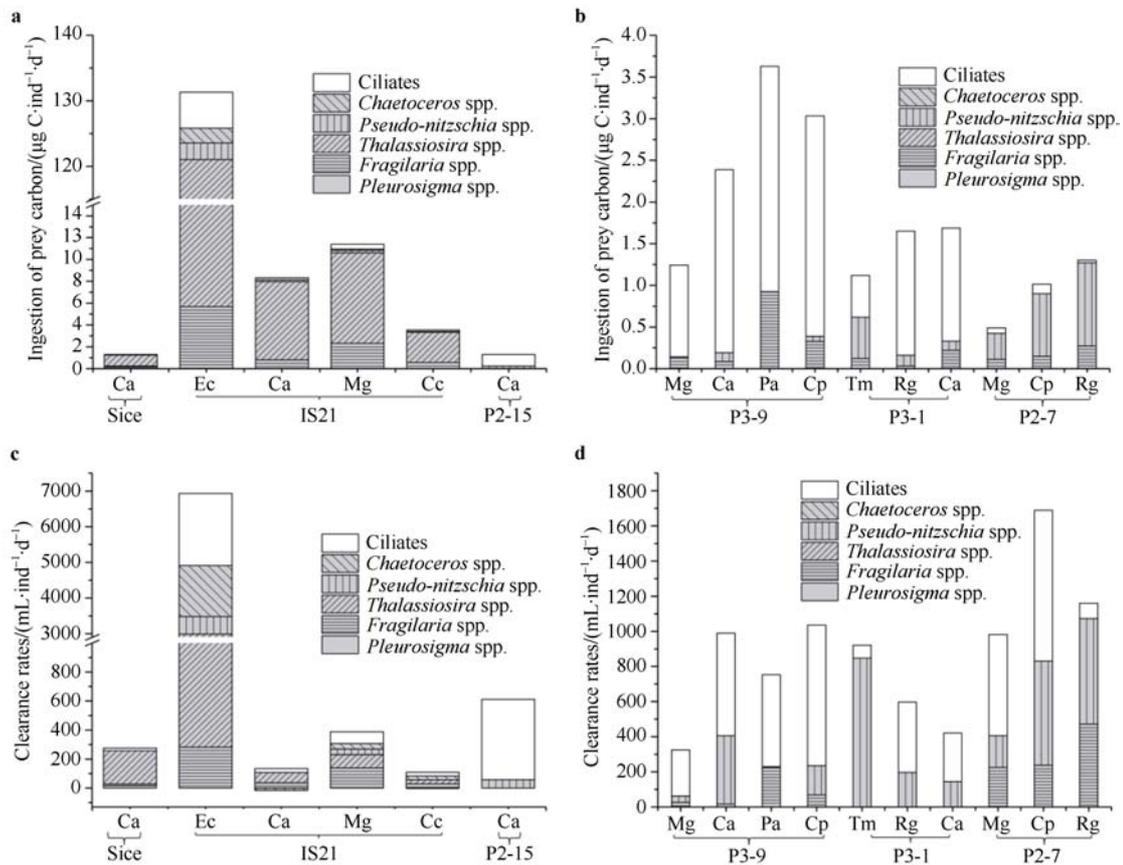


Figure 3 Ingestion rate and clearance rate of predominant zooplankton species in the neritic (a, c) and shelf and oceanic stations (b, d) (Yang et al., 2013).

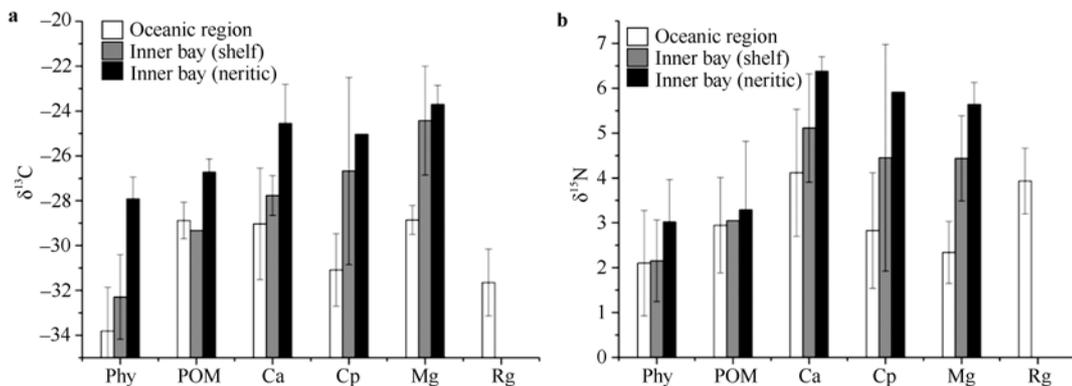


Figure 4 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm SE) of phytoplankton (Phy), particulate organic matter (POM), *Calanoides acutus* (Ca), *Calanus propinquus* (Cp), *Metridia gerlachei* (Mg) and *Rhincalanus gigas* (Rg) in the oceanic, shelf and neritic regions (Yang et al., 2016a).

5 Mitochondrial genome and DNA barcoding

Gene organization, gene rearrangement and codon usage in the mitochondrial genome of Prydz Bay Antarctic krill were analyzed (Shen et al., 2010). *E. superba* had a large mitochondrial genome (more than 15000 bp) where duplicates of one tRNA (trnN) and translocation of four tRNAs (trnL1, trnL2, trnW and trnI) were found. The

mitochondrial genome of *E. superba* showed regional differences between samples collected in Weddell Sea and Prydz Bay, and segregating sites were found in nad2 and nad5 genes (Shen et al., 2010).

Using DNA barcoding approaches, Cheng et al. (2014) established a reference library for 32 zooplankton species in Prydz Bay. The base-pair region of mtCo1 gene (mitochondrial cytochrome c oxidase) ranged from 830 to 1050, and the average intraspecific variation was 0.67% (Cheng et al., 2014). DNA barcoding was determined an

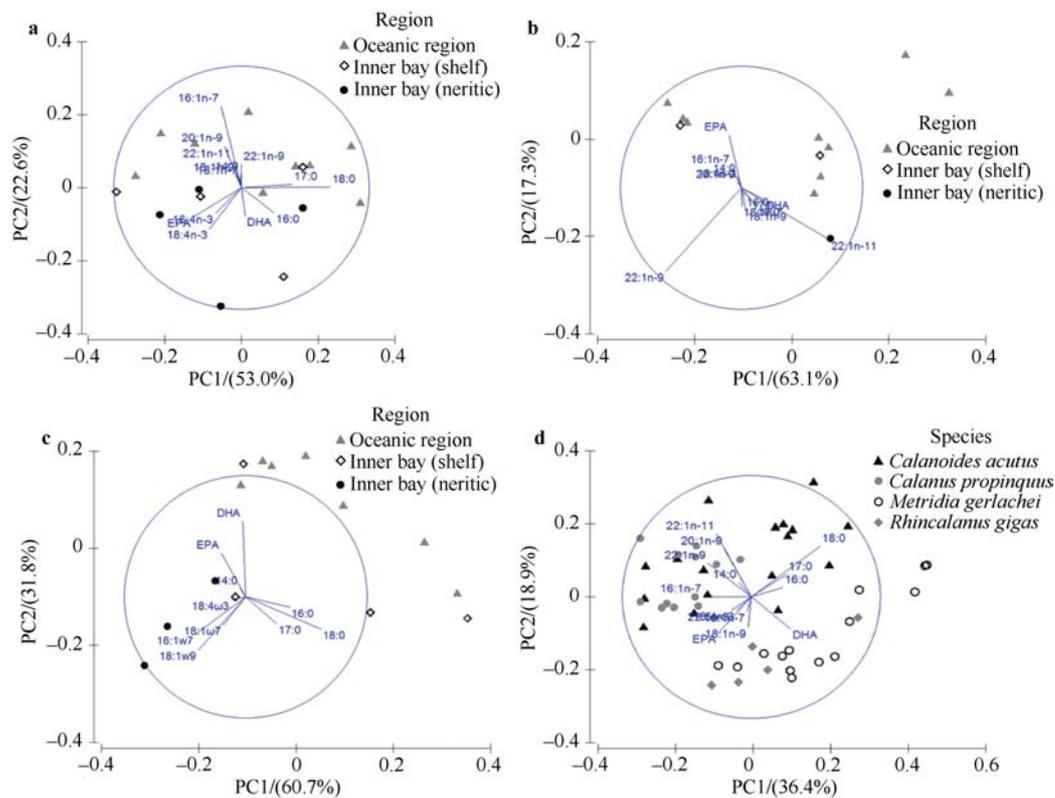


Figure 5 Principal component analysis of (a) *Calanoides acutus*, (b) *Calanus propinquus*, (c) *Metridia gerlachei* and (d) all copepod samples based on relative fatty acid compositions (Yang et al., 2016a).

efficient approach for zooplankton identification in future research because of the smaller intraspecific genetic divergence compared with interspecific genetic divergence.

6 Prospects

After nearly 30 years of sampling and field experiments, China has contributed knowledge of zooplankton ecology in Prydz Bay, specifically in the understanding of krill shrinkage, community variation, population dynamics and feeding ecology of dominant species (Zhong and Wang, 1995; Zhang and Sun, 2000; Yang et al., 2011b, 2016b, 2017). However, because of limited ship time during expeditions, many aspects of zooplankton ecology remain unknown and need to be further studied.

Dominant zooplankton species, such as krill and copepods, showed flexible feeding strategies to cope with food availability in Prydz Bay (Yang et al., 2013, 2016a). Recently, the Southern Ocean environment has been changing. Ocean acidification, caused by increasing atmospheric CO₂ concentrations, could have great effects on zooplankton species — not only calcifying organisms, but also crustacean-like krill and copepods. Ecophysiological responses of these zooplankton species to environmental changes such as warming and ocean acidification should be investigated to better understand the adaptation of zooplankton to climate change. This could

provide better understanding of the influence of climate change on the zooplankton community and Southern Ocean ecosystem.

The majority of zooplankton studies in Prydz Bay have focused on species in the epipelagic region, with field work conducted in austral summer. Zooplankton composition, community structure and feeding ecology in the mesopelagic and bathypelagic zone should be further studied (Yang et al., 2017). Moreover, new instruments aimed at long-term monitoring (e.g. Acoustic Zooplankton Fish Profiler (AZFP) and sediment traps) should be used to identify zooplankton dynamics in ice-covered areas and in other seasons. Understanding the seasonal abundance and distribution of zooplankton can allow us to understand lifecycles of dominant species in response to sea ice dynamics and climate change.

As trophic links that transfer carbon and energy from primary producers to higher trophic levels in the food web, zooplankton play a key role in the “biological pump” of the Southern Ocean ecosystem through passive sinking (corpse and molt), fecal pellets, diel vertical migration and consumption of sinking particles. Faced with climate change and sea ice dynamics, knowledge of the contribution of passive sinking and fecal pellets from different zooplankton groups to midwater is necessary to predict the control mechanisms of zooplankton for “biological pump” efficiency, and the effect on deep sea and benthic food webs

of Prydz Bay and other regions of the Southern Ocean.

Zooplankton researchers from China deserve broader recognition for advancing knowledge of Prydz Bay and other regions of the Southern Ocean over the past 30 years. However, zooplankton research in remote polar regions with severe field conditions cannot be properly conducted by a single country. International cooperation has been, and should continue to be conducted in zooplankton research of Prydz Bay and the Southern Ocean. Zooplankton scientists from China should take an active part in international research hotspots such as the network of large-scale Marine Protected Areas (MPA) around Antarctica and the construction of the long-term Southern Ocean Observation System.

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