Study on the metabolism of two dominant copepods: Calanoides acutus and Metridia gerlachei collected in summer from the marginal ice zone of the Prydz Bay, Antarctica

Li Chaolun (李超伦), Sun Song (孙 松), Zhang Guangtao (张光涛) and Ji Peng (吉 鹏) Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China

Received September 10, 2001

Metabolic rates (oxygen consumption and ammonia excretion) of two dominant copepods, Calanoides acutus and Metridia gerlachei, were measured during the austral summer (December 1998 - January 1999), in the marginal ice zone of the Prydz Bay. Their elemental compositions (C and N) were also analysed through these metabolic experiments. The results showed that C. acutus was 48.4% - 48. 6% of dry weight in carbon content and 6.1% - 6.5% of dry weight in nitrogen content. Metridia gerlachei was 47.1% - 50.1% and 5.9% - 7.4%, relatively. Oxygen consumption rates of C. acutus were variant in the different areas (0.226 to 0. 774 μ lO₂mg⁻¹h⁻¹). And its ammonia excretion rates ranged from 0. 014 to 0. 105 ugNmg⁻¹h⁻¹. The ratio between the rates (O∶N) exhibited a large difference (5 - 6 times). For Metridia gerlachei, oxygen consumption rates were 0.488 - 0.644 $\mu lO_2 mg^{-1}$ and ammonia excretion rates were 0.015 - 0.034 $\mu gNmg^{-1}h^{-1}$. From the results of metabolic rate measurements and elemental analyses, daily losses of body carbon and nitrogen were estimated to be 0.59% - 1.99% and 0.44% - 3.27%, respectively. The metabolic carbon requirements accounted for 0.6% - 29.2% of primary production per day, and their excretion of ammonia occupied 0.2% - 38.0% of daily phytoplankton nitrogen demand.

Key words Calanoides acutus, Metridia gerlachei, metabolism, Prydz Bay.

1 Introduction

The Southern Ocean belongs to one of the peculiar marine ecosystem in the world, where the seawater temperatures is close to or below 0°C throughout the year. The day light lasts nearly for 24 h in summer and it is of complete darkness in winter, with the result of ceasing of primary production during the latter period (Knox 1970). Despite these rigorous conditions, zooplankton biomass in the Antarctic Ocean is generally far greater than that in oceanic area of low latitudes (Hopkins 1971). Integrated information on the metabolic activities of zooplankton can advance our understanding of the ecological mechanisms in the Antarctic pelagic ecosystem. Up to now, available information in this field is limited. If done, the studies were mostly concentrated on the krill. But sometimes other zooplankton, such as copepods, can also form the important component of the zooplankton biomass (Conover and Huntley 1991).

In general, a low concentration of inorganic nutrient salt in the euphotic zone

has been linked with low phytoplankton biomass and low phytoplankton production, while a high concentration of these nutrients has been linked with high phytoplankton production. Nevertheless, the Southern Ocean was reported to have low phytoplankton productivities, although the levels of NO_3^- , PO_4^{3-} and $Si(OH)_4$ were relatively higher in the waters as compared with those of other world oceans. To explain this discrepancy, it has been proposed that phytoplankton production was limited by conditions of cold temperature, low light, water column instability and lack of microelement. Some investigations of ^{15}N nitrogenous uptake in the Antarctic Ocean suggested that NO_3^- is not utilized as the sole or even the preferential nitrogen source by phytoplankton, rather, NH_4^+ is preferred, which is the principle nitrogenous waste excreted by zooplankton and micronekton (Mayzaud 1973; Harris 1973).

The work presented here gives preliminary results of metabolic rates (oxygen consumption and ammonia excretion) of two dominant copepods, *Calanoides acutus* and *Metridia gerlachei*, in the Prydz Bay region, which were obtained during the R/V Xuelong cruise in austral summer of 1998/1999. The major objective of this study was to measure the metabolic rates of zooplankton and their potential contribution to the nitrogen requirements for primary production of phytoplankton at the seasonal ice zone of the Prydz Bay region.

2 Materials and methods

The metabolic rates (oxygen consumption and ammonia excretion) of copepods were measured at five stations from December 1998 to January 1999 (Fig. 1). According to the satellite images, the research area was a typical marginal ice zone during the study period. The northern edge of fast-ice is about at 69°05′S. There was an open-water area between 68°56′S to 67°44′S. The float ice zone almost reached to 62°S. The stations selected for experiments were located at different ice-covering conditions. Sampling time, temperature of surface water and ice-covering condition of each station were showed in Table 1.

Table 1. Experimental time, temperature and conditions

Station	Time	Temperature of surface water/ °C	Condition
FI	98. 12. 16	- 2.0	Fast ice zone
III–2	98. 12. 22	- 1.0	Edge of pack ice zone(ice-covering < 10%)
III - 4	98. 12. 19	- 1.1	Pack ice zone(ice-covering: 50%)
III–13	99. 01. 12	1.7	Reocurring polynia
IV_9	98. 12. 25	- 1, 5	Pack ice zone(ice-covering: 80%)

Zooplankton samples were collected by a trawl net with the mesh size of 333 μ m from the depth of 200 m to surface. A flowmeter was mounted in the center of the net mouth to measure the volume of water filtered. Samples were preserved in the 5% formalin-seawater solution for quantitative analyses of species composition and biomass. Samples for metabolic experiments were captured using the same net but with a sealed cod-end. Immediately after the collection, undamaged specimens were gently transferred into 2 litre glass bottles filled with 0.45 μ m filtered sea water to empty their gut. Rates of oxygen consumption and ammonia excretion were measured simultaneously by a water bottle method as Ikeda and Skjoldal (1989). Briefly, 20

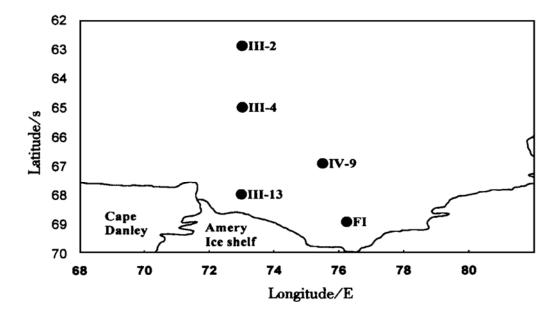


Fig. 1. Map showing the positions of the metabolic experiments.

30 living individuals were picked and cultured in a 500 ml bottle filled with 0.45 μm filtered sea water, then the bottle was kept in dark and bathing in a constant–temperature water bath set to the surface seawater temperature. Three duplicate bottles were used in each experiment. Control bottles without zooplankton were prepared concurrently. Experiments run for 10 $^-$ 20 h. At the end of the incubation, two 150 ml and two 25 ml water samples were siphoned out for duplicate measurements of dissolved oxygen and ammonia, respectively. The copepod specimens were removed from the experimental bottles, and frozen at - 20 $^{\circ}$ C for later weighing and elemental analyses ashore. Dissolved oxygen was determined by a Winkler titration method and ammonia by a modified phenol–hypochlorite method as described in National Criterion of Marine Investigation (GB 12763. 4–01). All analyses were made immediately after each experiment. Frozen copepod specimens were weighed after drying at 60 $^{\circ}$ C for 24 h. Carbon and nitrogen content were measured with a elemental analyzer (PE240C).

At each experiment station, CTD, nutrients (N, P, Si), chlorophyll a (fluorescence) and primary production (14 C) were measured simultaneously.

3 Results

3. 1 Quantitative distribution and chemical composition

Both Calanoides acutus and Metridia gerlachei are the dominant copepods in the study area. The mean abundance of Calanoides acutus was 6. 7 ind. m⁻³. On a regional scale, northern edge of the float ice zone (III-2) and reocurring polynia area (III-13) had high biomass (13. 7 ind. m⁻³). By comparison, biomass of Calanoides acutus at fast ice zone (FI) was low (< 1 ind. m⁻³). The mean abundance of Metridia gerlachei was 4.5 ind. m⁻³. The lowest biomass was found at III-2. There was no substantial variability among the other stations.

The contents of carbon and nitrogen were expressed as percent of dry weight. Carbon contents of *Calanoides acutus* ranged between 48. 4% and 48. 6% and

nitrogen contents, ranged between 6.1% and 6.5%. Carbon and nitrogen contents of $Metridia\ gerlachei$ range 47.1% $^-$ 50.1% and 5.9% $^-$ 7.4%, respectively. There was no local difference in carbon and nitrogen composition of both copepods.

3.2 Ammonia excretion, oxygen consumption and O: N ratio

The experiment results of Calanoides acutus were shown in Table 2. Local difference in oxygen consumption was evident among the stations. The highest value was found at station III-2 ((0.774 \pm 0.085) μ IO₂mg⁻¹h⁻¹). At station II-4, the oxygen consumption rate of Calanoides acutus was only (0.226 \pm 0.014) μ IO₂mg⁻¹h⁻¹. The ammonia excretion rates ranged between 0.014 and 0.105 μ gNmg⁻¹h⁻¹. The highest value was measured at float ice zone and the lowest value at fast ice zone. Because the sea water temperature was close, the relationship between the metabolic rates and temperature was not observed. But the ratio between the rates (0:N) exhibited a large difference among the stations(5-6 times).

Because there were not enough specimens, the metabolic activities of *Metridia* gerlachei were only measured at two stations (III-13 and IV-9). The results were shown in Table 2. Both oxygen consumption and ammonia excretion at III-13 were higher than those at IV-9. But the O: N ratios were similar between two stations.

Table 2. Experimental results of copepod metabolism in the marginal ice zone of the Prydz Bay,

minarctica in	Summer				
Species	Station	Temperature /°C	Oxygen consumption rate / \(\mu \) O \(\text{org}^{-1} \) h^{-1}	Ammonia excretion rate	o:N
	FI	- 2	0.558 ± 0.035	0.014 ± 0.002	32. 7
Calanoides	III–2	- 1	0.774 ± 0.085	0.105 ± 0.004	5. 9
acutus	∭-4	- 1	0.226 ± 0.014	0.023 ± 0.001	8. 0
	III – 13	2	0.670 ± 0.107	0.053 ± 0.006	10.0
	IV -9	- 2	0.520 ± 0.028	0.062 ± 0.001	4.0
Metridia	III-13	2	0.644 ± 0.128	0.034 ± 0.003	15. 0
gerlachei	IV -9	- 2	0.488 ± 0.287	0.015 ± 0.006	15. 1

3.3 Daily metabolic losses of body C and N

According Ikeda and Bruce (1986), for protein metabolism, the daily metabolic loss of carbon was estimated as follows: oxygen consumption rate × 0. 97 × 12/22. 4, where 0. 97 is RQ, 12/22. 4 is carbon weight in 1 mol of CO₂. The daily metabolic loss of nitrogen was calculated assuming that ammonia is the only end-product of protein metabolism. In marine zooplankton, ammonia is known to constitute the major fraction (70%) of soluble nitrogen excreta (Corner and Davies 1971). Thus, the daily metabolic losses of Calanoides acutus are estimated to range from 0. 58% to 1. 99% for body carbon and from 0. 44% to 3. 27% for body nitrogen. Those of Metridia gerlachei were less than Calanoides acutus at the same station, ranging from 1. 25% to 1. 66% for body carbon and from 0. 47% to 1. 06% for body nitrogen (Table 3).

T 11 2	C 1	1 '1	. 1 1 1	ı c	1 1	1	1	· • • • • • • • • • • • • • • • • • • •
Table 3.	Copepod	daily	metabolic	loss of	-pod	v carboi	n and	nitrogen

С :	G:	Metabolic loss/%d ⁻¹			
Species	Station	C	N		
	FI	1.43 ± 0.09	0.44 ± 0.06		
Calanoides	III – 2	1.99 ± 0.22	3.27 ± 0.12		
acutus	III -4	0.58 ± 0.04	0.72 ± 0.03		
	III – 13	1. 72 ± 0.28	1. 65 ± 0.19		
	IV_9	1.34 ± 0.07	1.93 ± 0.03		
Metridia	III–13	1. 66 ± 0.03	1. 06 ± 0.09		
_gerlachei	IV-9	1.25 ± 0.07	0.47 ± 0.19		

Compared with the data of primary production, the daily metabolic loss of body carbon for *Calanoides acutus* accounted for 10.1% of primary production on average, ranging from 0.6% to 23.6% (Table 4). Carbon requirements of *Metridia gerlachei* were less than those of *Calanoides acutus* (6.4%).

The potential contribution of the excreted nitrogen to the primary production was 14.2% for *Calanoides acutus* and 3.5% for *Metridia gerlachei*, respectively (Table 4).

Table 4. The relationship of copepod daily carbon requirement and ammonia excretion with primary

production							
Station	Percent of primary production for carbon requirement/%			Potential contribution of N excreted			
	C. acutus	M . gerlachei	Sum	C. acutus	M. gerlachei	Sum	
$_{ m FI}$	0.6	_		0. 2	_		
III–2	11. 2	_		19. 5	_		
III-4	2. 6	_		3. 4	_		
III-13	12. 4	7. 2	19. 6	12. 5	4. 8	17. 3	
IV_9	23. 6	5. 6	29. 2	35. 8	2. 2.	38. 0	

4 Discussion

Ikeda and Hing (1981) reported that the oxygen consumption rate ranged between 0.086 and 0.398 μ lO₂mg⁻¹h⁻¹ for *Calanoides acutus* and between 0.183 and 1.500 μ lO₂mg⁻¹h⁻¹ for *Metridia gerlachei*. The ammonia excretion rate of *Calanoides acutus* was 0.0049 μ gNmg⁻¹h⁻¹. The results from Ross Sea indicated that the ammonia excretion rate of zooplankton was 1.6 μ gNg⁻¹ wet weight h⁻¹ on average in summer (Biggs 1982). Ikeda and Mitchell (1982) published that oxygen consumption and ammonia excretion of *Metridia gerlachei* were 0.183 - 1.208 μ lO₂mg⁻¹h⁻¹ and 0.118 μ gNmg⁻¹h⁻¹, respectively. Our results of oxygen consumption fell in with the data reported by other literatures. But ammonia excretion rates were lower than previous reports.

The continuous or seasonal presence of sea ice results in a low phytoplankton productivity environment during most time a year. Only with the ice melting during the short summer period, the developing phytoplankton productivities provide abundant food to zooplankton growing. Adapting to this unique environment, zooplankton usually go down to the deep sea in winter and back to surface water for seeking food in summer (Conover and Huntley 1991). Consequentially, zooplankton have seasonal varieties in their metabolic activities. They can shut down their respiration to conserve energy when there is no apparent source of nutriment for a prolonged period. When zooplankton mainly put reliance on stored lipid, utilization

of oxygen will be increasing with relation to nitrogen excretion. The O: N ratio by atoms is therefore a potential index of metabolic substrate being utilized. Based on the known data, a pure protein substrate should yield an O: N ratio between 3 and 16, and equal utilization of protein and lipid should yield the O: N ratio between 50 an 60 (Mayzand and Conover 1988). During this study period, phytoplankton production well developed at most stations. Energy for copepod metabolism mainly depended on the phytoplankton. So the O: N ratios fell in with the range between 3 and 16. Only station FI was an exception. Maybe it was because the phytoplankton bloom had not developed in the fast ice zone, unlike to other areas. The lipid still occupied a great proportion in the metabolic substrate. Summarizing the chemical compositions and daily metabolic losses of 14 Antarctic zooplankton species, Ikeda and Mitchell (1982) reported that the C and N contents of Antarctic zooplankton accounted for 4. 7% - 47. 5% and 1. 2% - 12. 5%, respectively. Daily metabolic losses accounted for 0. 4% - 2. 8% of body carbon and 0. 6% - 2. 5% of body nitrogen. These data were similar to our results.

The primary production transferred to high trophic levels by the herbivorous food web plays an important role on the material and energy cycling in marine ecosystem. This role can be evaluated by the ratio of energy required for zooplankton growth and metabolism to total primary production. This ratio varies widely in different seasons and areas. The studies in the Bransfield Strait showed that the metabolic carbon requirements of zooplankton only represented about 4.5% of primary production, and mainly contributed by salps. The contribution of copepods was less than 1%. In this study, for the single species Calanoides acutus, the daily consumption of carbon accounted for 10.0% of primary production in the investigative area. which was higher than the results of Alcaraz et al. (1998). Especially at station IV-9, the proportion was up to 23.6%. Even at the north of the investigative area (III-2), where the salps were relatively abundant, the daily carbon consumption of Calanoides acutus population occupied 12.4% of primary production. Only the results from the fast ice zone (FI) were similar to Alcaraz et al. (1998). In addition, the metabolic rates of copepods may be underestimated in the present study because the specimens were incubated in a non-food environment and other copepods, such as Paracalanus spp., Oithona. spp. and Calanus propinggus, were not included. Therefore copepods play an important role in the planktonic food web at the marginal ice zone of the Prydz Bay in summer.

The proportion of phytoplankton nitrogen requirement depending on zooplankton metabolism is of considerable ecological interest in marine ecosystem. Banse (1995) indicated that the metabolic rates of zooplankton directly affected the whole ocean production in oligotrophic sea. Although the Southern Ocean was known as eutrophic sea in the word, the nitrogen excreted by zooplankton is important as introduced at the beginning of this paper. Ammonia excretion of copepods only accounted for 0.2% – 38.0% of daily phytoplankton nitrogen requirement during our study. This result was higher than those from Bransfield Strait and Ross Sea (Alcaraz *et al.* 1998; Biggs 1982). But its potential contribution to primary production was very lower as compared with those in subtropical and tropical oligotrophic seas (35% – > 100%; Alcaraz *et al.* 1994).

Acknowledgements This research was supported by Innovation Project of CAS (KZCX2–303) and National Key Project (98–927–01). We thank Captain Yuan Shaohong and the crew of the R/V *Xuelong* for invaluable assistance in collecting zooplankton samples and in doing experiments on board ship.

References

- Alcaraz M, Saiz E, Estrada M (1994): Excretion of ammonia by zooplankton and its potential contribution to nitrogen requirements for primary production in the Catalan Sea (NW Mediterranean). Mar. Biol., 177: 163 170.
- Alcaraz M, Saiz E, Fernandez JA, Trepat I, Figuerias F, Calbet A, Bautista B (1998): Antarctic zooplankton metabolism: carton requirements and ammonium excretion of salps and crustacean zooplankton in the vicinity of the Bransfield Strait during January 1994. Journal of Marine Systems, 17: 347 359.
- Banse K (1995): Zooplankton: Pivotal role in the control of ocean production. ICES J. Mar. Sci., 52: 265 277.
- Biggs DC (1982): Zooplankton excretion and NH⁺ cycling in near-surface waters of the Southern Ocean. I. Ross Sea, austral summer 1977 – 78. Polar Biol., 1: 55 – 67.
- Corner RJ, Davis AG(1971): Plankton as a factor in the nitrogen and phosphorus cycls in the sea. Adv. Mar. Biol., 9:101 204.
- Conover RJ, Huntley M (1991): Copepods in ice-covered seas distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. Journal of Marine Systems, 2: 1 41.
- Harris RP (1973): Feeding, growth, reproduction and nitrogen utilization by the harpacticoid copepod, Tigropus brevicornis. J. Mar. Biol. Assoc. UK, 53: 785 800.
- Hopkins TL (1971): Zooplankton standing crop in the Pacific sector of the Antarctic. In: Llano GA, Wallen IE ed., Biology of the Antarctic Seas IV. Washington D. C.: American Geophysical Union. 347 - 362.
- Ikeda T, Bruce B (1986): Metabolic activity and elemental composition of krill and other zooplankton from Prydz Bay, Antarctic, during early summer (November December). Mar. Biol., 92: 545 555.
- Ikeda T, Hing FE (1981): Metabolic activity of zooplankton from the Antarctic Ocean. Aust. J. Mar. Freshwater Res., 32: 921 930.
- Ikeda T, Mitchell AW (1982): Oxygen uptake, ammonia excretion and phosphate excretion by krill and other Antarctic zooplankton in relation to their body size and chemical composition. Mar. Biol., 71: 283 298.
- Ikeda T, Skjoldal HR(1989): Metabolism and elemental composition of zooplankton from the Barents Sea during early Antarctic summer. Mar. Biol., 100: 173 183.
- Knox GA (1970): Antarctic marine ecosystems. In: Holdgate MW ed., Antarctic Ecology, London: Academic Press, 1: 69 97.
- Mayzaud P (1973): Respiration and nitrogen excretion of zooplankton. II. Studies of the metabolic characteristics of starved animals. Mar. Biol., 21: 19 28.
- Mayzand P, Conover RJ (1988): O: N atomic rate as a tool to describe zooplankton metabolism. Mar. Ecol. Progr. Ser., 45: 289 302.