

Factors Influencing Seasonal Changes in the Respiration of *Drepanopus bispinosus* (Copepoda: Calanoida) in Burton Lake, a Marine Derived Saline Lake in the Vestfold Hills, Antarctica

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南極，ベストフォードヒルズのバートン湖（塩湖）における
Drepanopus bispinosus（橈脚類）の呼吸量の季節変化におよぼす諸要因

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要旨：東南極の塩湖に生息するかいあし類の一種 *Drepanopus bispinosus* の雌成体の冬季および夏季の酸素消費量を測定した。測定は種々の水温、塩分、溶存酸素量、および餌濃度の実験条件下で行った。呼吸量は水温の上昇とともに増大するが、とくに、生息水温 ($0\pm 2^{\circ}\text{C}$) から致死水温 (13.1°C) 範囲で顕著な呼吸量の増大がみられた。8月から12月にかけての呼吸量の Q_{10} 値は1.65-1.89の範囲にあったが、1月には3.11-3.32に増大した。通常の生息塩分濃度 (37.2-39.5‰) で呼吸量は最も低く、それより高塩分あるいは低塩分で増大した。溶存酸素量および植物プランクトン濃度もまたある程度呼吸量の変化に影響をあたえているらしいことが推測された。8月から1月にかけて *D. bispinosus* の雌成体の呼吸量は連続的に減少する傾向を示した。この呼吸量の減少は繁殖期には繁殖活動の結果によるものであり、繁殖期以降は老衰による生理的機能の低下に起因しているものであることが示唆された。

Abstract: Oxygen consumption of adult females of *Drepanopus bispinosus* living in a marine derived saline lake in East Antarctica was measured under different conditions of temperature, salinity, dissolved oxygen and food concentration both in winter and summer. Variations in respiration paralleled temperature changes, particularly when the animals were in temperatures higher than in the normal habitat ($0\pm 2^{\circ}\text{C}$) and below the upper thermal limit (13.1°C). The Q_{10} values for respiration lay between 1.65 to 1.89 from August to December, but increased to 3.11 and 3.32 in January. Respiration also increased when the animals were subjected to salinities either higher or lower than normal habitat conditions (37.2-39.5‰). Oxygen consumption appeared to be related to the dissolved oxygen content and to some extent to the concentration of phytoplankton cells in the medium. The seasonal variation in respiration of adult females *D. bispinosus* revealed a tendency to decrease continually from August to January. This might have resulted from their reproductive activities during the period of their reproduction. Food concentration, as well as dissolved oxygen, were possible environmental factors influencing oxygen consumption. After

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that, it could have been mainly related to decline of their physiological functions resulting from senescence.

1. Introduction

Burton Lake is the largest of many marine derived lakes in the Vestfold Hills (Fig. 1). Those lakes have limited water exchange with the open sea. Compared with open Antarctic waters, they have a more conspicuous seasonal variation in the main physical and chemical factors such as light, temperature, salinity and dissolved oxygen, which play an important role in controlling nutrient recycling and primary production (WRIGHT and BURTON, 1981; BURTON, 1981; ESLAKE *et al.*, 1991; WANG, 1992). Geographical characteristics of this lake have been described by BAYLY (1986), while seasonal changes of environmental parameters of the lake have been investigated by WANG (1992). The temperature above the chemocline throughout January to May varied between -1.9 to 5°C . From June to December, however, it was stable, ranging between -1.6 and -1.8°C . Salinity in the lake varied with depth and season. It was less than 35‰ above the chemocline before May, increased to 39.5‰ as ice formed in October to November, and decreased again to less than

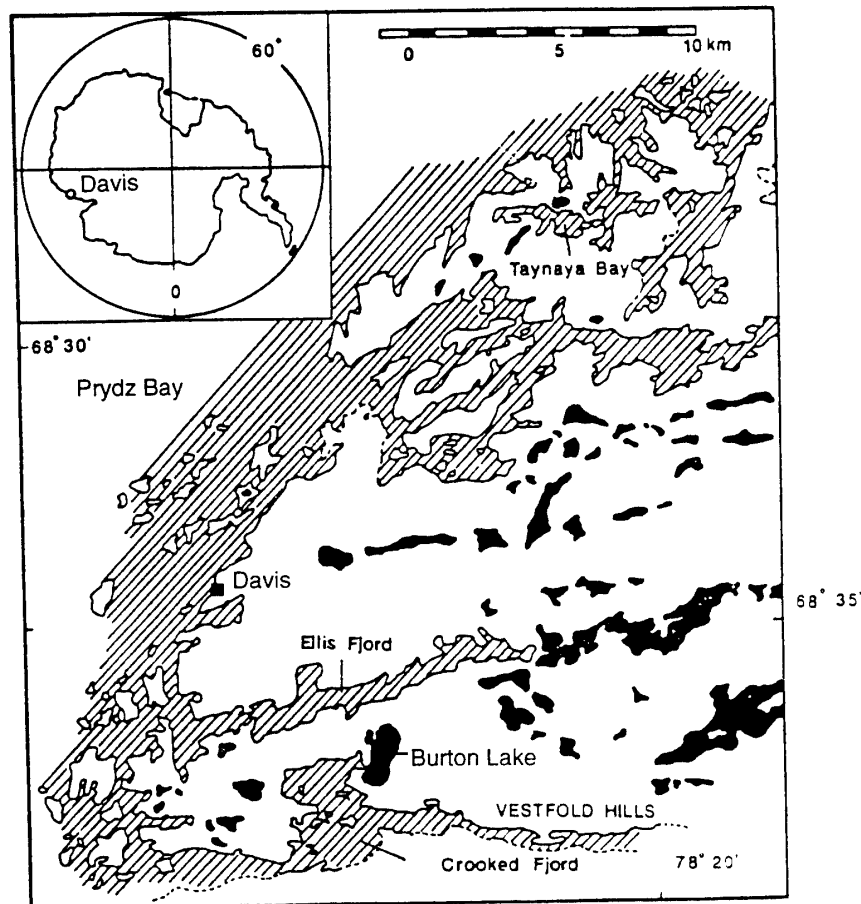


Fig. 1. Map of Burton Lake in the Vestfold Hills, Antarctica.

37°C in January. Snow and ice melting lowered the salinity down to a depth of 5 m. Seasonal factors which resulted in the fluctuation of dissolved oxygen included ice growth or melting, photosynthesis and the density of heterotrophs in the lake. Dissolved oxygen concentration decreased steadily in winter. The lowest average value (3.4 ml/l) above the chemocline was recorded in November. It was rising rapidly, and increased to 15–21 ml/l (above 5 m) in January, while the ice melted and phytoplankton began to bloom.

Drepanopus bispinosus is a common stenothermal calanoid copepod occurring in Antarctic and sub-Antarctic waters (BAYLY, 1982; TUCKER and BURTON, 1990). The animals have been also found in Burton Lake throughout the year (WANG, 1988). The reproduction and population dynamics of this species have been studied in detail by BAYLY (1986) and WANG (1992). The population life cycle appears to be 20–21 months. Their reproductive activities extend from winter to early summer. The mature males appeared mainly in June and disappeared mostly after releasing their spermatophores in July–August. The adult females appeared mostly in late June and constituted most of the winter and summer populations with the larvae. They disappeared mostly in late January–February. The tolerance of the adult female to temperature and salinity has been investigated as well (WANG *et al.*, 1990; WANG, 1991). This paper reports the seasonal respiration of *D. bispinosus*, and its related factors, particularly with the variations of environmental parameters in Burton Lake.

2. Materials and Methods

2.1. Sample collection

Samples were collected from the center of the northern part of Burton Lake (depth 16 m) from August 1984 to January 1985. A collapsible plankton net (mesh size 210 μm) described by BAYLY (1986) and KIRKWOOD and BURTON (1987) was used for zooplankton collection. The net was pushed and hauled through a 10 cm diameter hole cut through the ice with a SIPRE corer. Under the ice, the net was opened and hauled vertically through the water above the chemocline for living material, and the entire height of the chemocline for other biological studies (WANG, 1992). Living copepods for physiological experiments were sorted from the samples immediately after collection, and kept in transparent 200 ml polyethylene wide mouth jars (approximately 100 animals per jar), and filled with lake water collected at the same time. Because of the weather, the sampling dates were not so regular. Field work had to be done two or three times for physiological experiments each month, and there was an interval of more than twenty days between two monthly collections. The animals used for physiological experiments were maintained at $0 \pm 5^\circ\text{C}$ in the laboratory before the experiment. The samples for biological measurements were collected in the same months as above, then were preserved in a 5% formaldehyde/seawater solution immediately after collection.

2.2. Respiratory measurement

Since the adult males had mostly disappeared by August, only adult females

were used for respiration measurements. Each measurement was carried out within 6–48 hours after capture, in order to reduce the possible influence on animal respiration of capture or of acclimation to laboratory conditions (IKEDA, 1977; IKEDA and SKJOLDAL, 1980; SKJOLDAL *et al.*, 1984). In the experiments, 150–200 unhurt adult females were used in each measurement. Before testing, the animals were sorted and placed into 5–6 glass bottles (vol. 50 ml filled with unfiltered lake water, 30–35 animals in each) and allowed to acclimate for 3 hours under the respective experimental conditions. The groups of animals were then immediately removed carefully into 5–6 incubators (125 ml DOC bottle), where they were kept for 12 hours under the designed conditions. Considering mortality, animals were kept for 8 hours when the salinity was less than 26°C and temperature at 10°C.

The procedure for respiration experiments was as follows: (1) Seasonal changes in oxygen consumption by adult females. The measurements were made once a month from August to January under 6 different temperatures (–3, –1.5, 0, 2, 5, and 10°C) and habitat salinity. (2) Oxygen consumption by adult females under different salinities. The measurements were made in August and December. The salinities used for these experiments were 26.8, 30.6, 33.3, 37.3, 44.6 and 57.1‰ in August, and 24.9, 29.6, 34.1, 39.2, 45.9 and 56.2‰ in December, with the temperatures at –1.5, 0 and 2°C. (3) Oxygen consumption by adult females under different dissolved oxygen concentration at temperatures of –1.5, 0, 2 and 5°C and habitat salinities. The measurements were made in August, November and January. (4) Oxygen consumption by adult females with filtered and non-filtered lake water. The measurements were made in August, November and January, at temperatures of –1.5, 0, 2 and 5°C and monthly lake salinities. (5) Three bottles without animals and filled relevant medium were used as the blank in each measurement.

WHATMAN-1 filters were used in all of the experiments to remove phytoplankton cells in the medium, except when a non-filtered medium was needed. The pore size of this filter was $0.97 \mu\text{m}$ ($SD \pm 0.033$, $n = 10$). It was quite effective in removing most of the algal and microalgal cells (cell size 20–200 μm) and even some nanoplankton (cell size 2–20 μm) (OMORI and IKEDA, 1984) from the medium. The efficiency of filtering was $95 \pm 2.5\%$ in August to September, $96 \pm 2.5\%$ in October to November and $92 \pm 3.0\%$ in December to January (with relevant flow speed of 50 ml/cm² min, $p = 700$ mm Hg). Thus, few micro or nanoplankton cells remained in the experimental medium. The errors affecting oxygen measurement could be neglected, particularly when the experiments were done in the dark.

Distilled water was added to reduce salinity, and NaCl to increase salinity. The salinity was determined from chlorinity measurements using a DIONEX-10 liquid chromatograph. Temperatures in the tests were controlled by a closed cycle LAUDARN-35 thermostat (acc. 0.01°C). In the experiments, the test bottles were placed in a covered chamber, which was part of the closed cycle system, for keeping out the light. Oxygen concentration was determined by the Winkler titration method. After testing, the group of animals was placed on filter paper to blot them dry, then sealed in special aluminum containers. The wet weight of test animals was subsequently measured.

2.3. *Biological measurements*

In the laboratory, the prosome length and wet weight of adult females were measured. The specimens had been preserved in a 5% formaldehyde/seawater solution for 12-18 months after collection. Fifty adult females were used in each measurements. BAYLY (1986) compared dry weights of two groups of *D. bispinosus*, which had been preserved for 45 months and 3-5 months in formalin respectively. The result does indicate that initial weight loss does not continue progressively with time. Thus, it is reasonable to believe that there was no significant difference in wet weight between the specimens preserved for 12 months and 18 months.

3. Results

3.1. *Seasonal changes in respiration*

The monthly mean weight-corrected oxygen consumption values of adult females

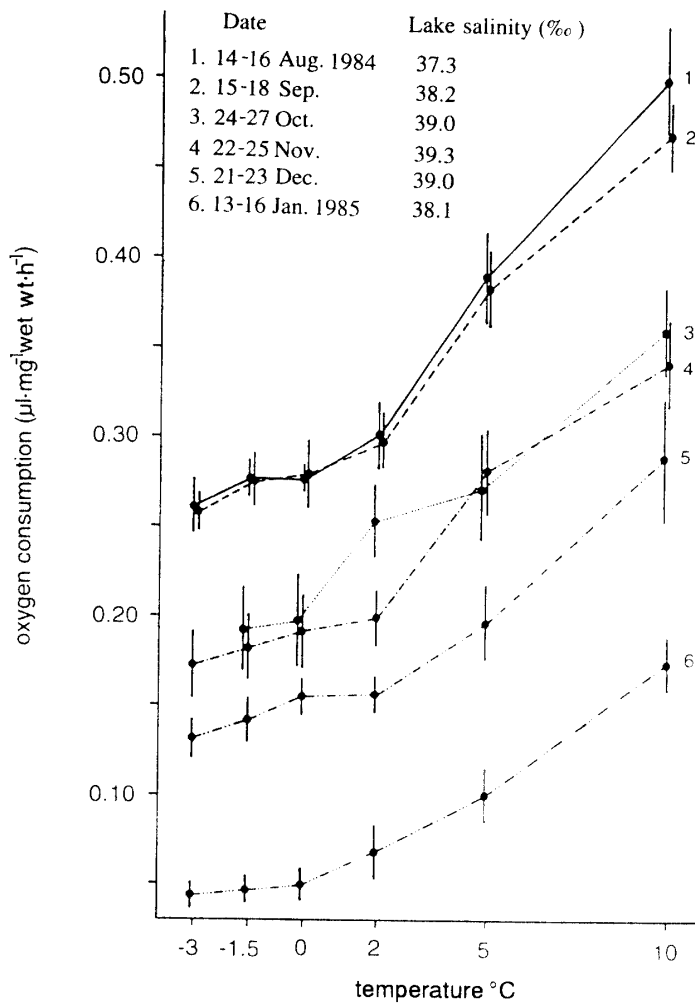


Fig. 2. Seasonal changes in oxygen consumption by adult female *D. bispinosus* in Burton Lake from August 1984 to January 1985.

Table 1. Regression equations for log oxygen consumption in $\mu\text{l}\cdot\text{mg}^{-1}\text{ wet}\cdot\text{wt}\cdot\text{h}^{-1}$ on temperature for *D. bispinosus* in different seasons.

Month	Equation	R
August 1984	$\log\text{O}_2 = 0.0251 (T) - 0.6057$	0.97
September	$\log\text{O}_2 = 0.0209 (T) - 0.6019$	0.98
October	$\log\text{O}_2 = 0.0240 (T) - 0.7479$	0.97
November	$\log\text{O}_2 = 0.0244 (T) - 0.7785$	0.98
December	$\log\text{O}_2 = 0.0262 (T) - 0.8977$	0.98
January 1985	$\log\text{O}_2 = 0.0463 (T) - 1.3905$	0.98

Table 2. Rate of decrease (%) of oxygen consumption by adult female *D. bispinosus* within two months in Burton Lake from August 1984 to January 1985.

Month	T (°C)					
	-3	-1.5	0	2	5	10
August-September	1.5	0.1	-1.0	1.8	2.1	6.6
September-October	-	30.3	28.9	14.7	28.7	22.8
October-November	32.5*	5.0	3.2	18.9	-7.4	5.3
November-December	24.1	23.1	19.1	24.2	32.8	14.9
December-January	66.9	66.9	67.9	56.1	44.7	39.9

*Decrease rate from September to November.

of *D. bispinosus*, measured from August to January, at designed temperatures and habitat salinity are plotted in Fig. 2. It was evident that oxygen consumption decreased from winter to summer. Under natural T-S conditions, the average was 0.28 ($\mu\text{l}\cdot\text{mg}^{-1}\text{ wet}\cdot\text{wt}\cdot\text{h}^{-1}$) in August, and 0.14 in December. It then decreased rapidly to 0.05 in January. The temperature-respiration relationship in Fig. 2 is not linear. The regression equations for log oxygen consumption on temperatures from August to January are listed in Table 1. The largest slope (0.0463), in the equation for January, means that the temperatures produces the greatest change in oxygen consumption in January. The decrease in percentage rate of oxygen consumption during different months in this period is shown in Table 2. There are significant differences in the respiration between monthly results. The mean percentage rate in decrease of oxygen consumption from August to September was 2.42 (SD \pm 2.46, $n=5$, $r=0.1-6.6$); from September to October it was 25.1 (SD \pm 6.48, $n=5$, $r=14.7-30.3$); from October to November it was 9.73 (SD \pm 7.27, $n=5$, $r=3.2-18.9$); from November to December it was 23.1 (SD \pm 5.99, $n=6$, $r=14.9-32.8$); and it was 57.1 (SD \pm 12.32, $n=6$, $r=39.9-67.9$) from December to January. It is likely that there are three large changes in the respiration of adult females during and after their overwintering period, particularly in January.

3.2. Respiratory responses to external factors

3.2.1. Temperature

The results from monthly oxygen measurements indicate that the respiration of *D. bispinosus* increased with temperature rise. Oxygen consumption increased when the animals were subjected to temperatures higher than habitat conditions ($-1.7 \pm 0.1^\circ\text{C}$, above the chemocline, from August to January). Figure 3 shows that the variation in oxygen consumption was low at temperature less than 2°C in all months except January. The value of oxygen consumption at temperature -1.5 , close to the habitat condition, can be regarded as the normal (or standard) respiratory rate. Compared with this, oxygen consumption declined when the animals were at the supercooling temperature of -3°C . Evidently, oxygen consumption increased at temperatures higher than -1.5 . The average percentage increase rate in oxygen consumption from August to January was 3.2, when the temperature increased from -1.5 to 0°C . Furthermore, it was 13.4 from August to December when the temperature increased to 2°C , and 46.5 for 5°C . In January, however, the increase rate was much higher than before as temperatures rose from 2 to 10°C .

Table 3 shows Q_{10} values over the ranges -3 to 5°C and 0 to 10°C . Q_{10} in the lower temperature range was lower than in the higher temperature range. The values

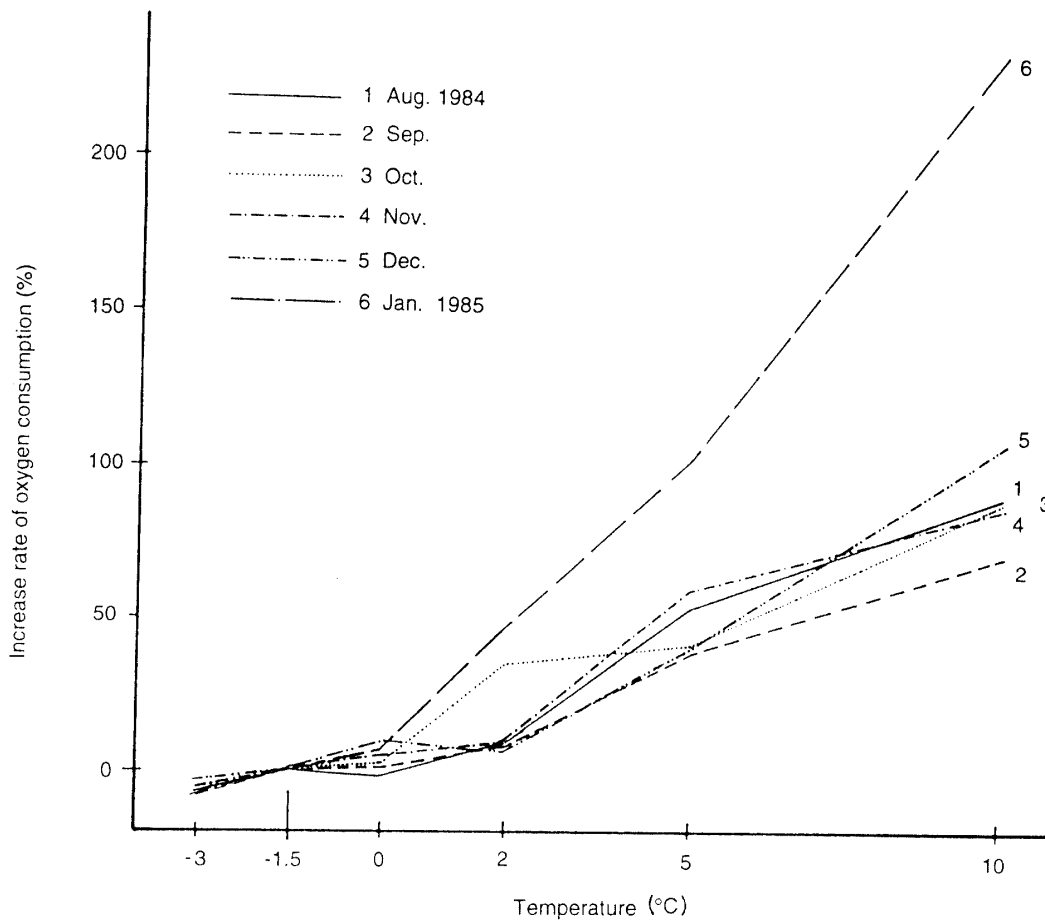


Fig. 3. Percentage increase on oxygen consumption by adult female *D. bispinosus* from Burton Lake with changing temperature against lake temperature (standard $T -1.5^\circ\text{C}$) from August 1984 to January 1985.

Table 3. Temperature coefficient (Q_{10}) influence on metabolic rate of adult female *D. bispinosus* in Burton Lake (August 1984–January 1985).

Month	1984					1985
	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.
Q_{10} ($-3\sim 5^{\circ}\text{C}$)	1.77	1.68	1.71	1.69	1.67	3.11
Q_{10} ($0\sim 10^{\circ}\text{C}$)	1.90	1.69	1.83	1.80	1.89	3.32

Van't Hoff's formula: $\log Q_{10} = (\log R_2 - \log R_1) \cdot 10 / (T_2 - T_1)$.

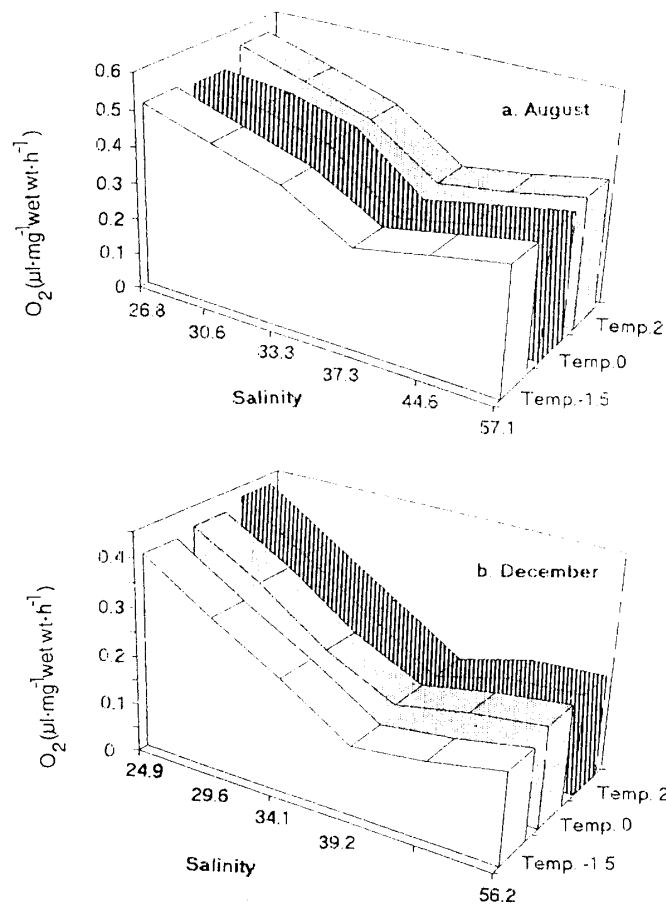


Fig. 4. Oxygen consumption by adult female *D. bispinosus* from Burton Lake at different salinities in temperature range of -1.5 to 2°C (1984).
a. August 16–19. b. December 30–31.

from August to December lie between 1.65 and 1.77 in the temperature range -3 to 5°C , and 1.69–1.89 in the range 0 to 10°C . In January, however, they increase to 3.11 and 3.32 in the same temperature ranges.

3.2.2. Salinity

Figure 4 shows oxygen consumption by adult females *D. bispinosus* measured at different salinities. In August (Fig. 4a), the lowest oxygen consumption was 0.28

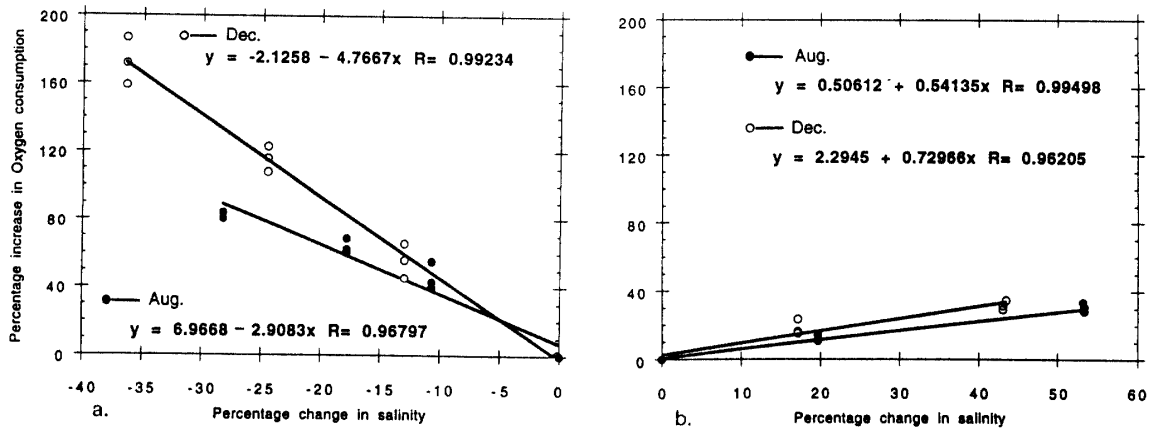


Fig. 5. Percentage increase in oxygen consumption by adult female *D. bispinosus* from Burton Lake with salinity variations (%) in temperature range of -1.5 to 2°C (August 16–19, and December 30–31, 1984). a. Salinity diluted. b. Salinity increased.

($\mu\text{l}\cdot\text{mg}^{-1}$ wet wt $\cdot\text{h}^{-1}$) with salinity 37.3‰ at temperatures of -1.5 to 0°C , which closely resembles the T-S conditions in Burton Lake (WANG, 1992). In December (Fig. 4b), it was minimal in salinity of 39.2‰. Oxygen consumption increased while animals were kept in salinities above or below the lake conditions (37–38‰ in August and 38.5–39.5‰ in November and December above the chemocline). Figure 5 shows the percentage increase in oxygen consumption against the change in salinity. For example, at -1.5°C in August, the increase of oxygen consumption was 69.3% in salinity of diluted 17.8% (equivalent to 30.6‰) (Fig. 5a), and it was 17.7% only in salinity of increased 19.8% (equivalent to 45.9‰) (Fig. 5b). At same temperature in December, animals were less adaptable to lower salinity than in August. However, there was a little difference in respiratory response to higher salinities between August and December.

3.2.3. Dissolved oxygen

Oxygen consumption of adult females under different dissolved oxygen stress in

Table 4. Oxygen consumption of adult female *D. bispinosus* in different dissolved oxygen levels.

Date	T ($^{\circ}\text{C}$)	-1.5		0		2		5	
		Os	Oc	Os	Oc	Os	Oc	Os	Oc
17 August	37.3	7.52	0.27	7.49	0.27	7.50	0.29	7.44	0.46
23 August	37.3	6.13	0.217	6.13	0.24	6.10	0.29	5.96	0.40
21 November	39.1	7.51	0.17	7.52	0.18	7.32	0.20	7.24	0.24
	39.1	5.12	0.14	5.10	0.15	5.08	0.16	5.10	0.21
29 November	39.3	5.67	0.17	5.68	0.17	5.95	0.19	5.91	0.24
	39.3	7.87	0.19	7.81	0.19	7.77	0.22	7.43	0.24
10 January	38.2	5.99	0.04	6.02	0.04	6.06	0.04	6.10	0.06
	38.5	7.81	0.04	8.05	0.05	7.56	0.05	7.78	0.06

Os: dissolved oxygen in water sample (ml/l).

Oc: oxygen uptake ($\mu\text{l}\cdot\text{mg}^{-1}$ wet wt $\cdot\text{h}^{-1}$).

habitat salinity at 4 temperatures is shown in Table 4. It is apparent that the oxygen consumption was variable following changes of dissolved oxygen concentration. Compared with that in higher dissolved oxygen concentration, the animals had lower oxygen consumption when they were in lower dissolved oxygen stress. In August, for example, at -1.5°C , while the dissolved oxygen concentration decreased from 7.52 (ml/l) to 6.13 (equal to the rate of decrease of 18.5%), their oxygen consumption was 0.05 less than before (equal to the rate of decrease of 22.7%). On November 21, the rate of decrease in oxygen consumption was 17.7%, corresponding to 32% decrease in dissolved oxygen concentration. The oxygen consumption by animals seems also to increase as dissolved oxygen concentration rises. The rate of increase in oxygen consumption was 11.8%, corresponding to 38.8% increase in dissolved oxygen concen-

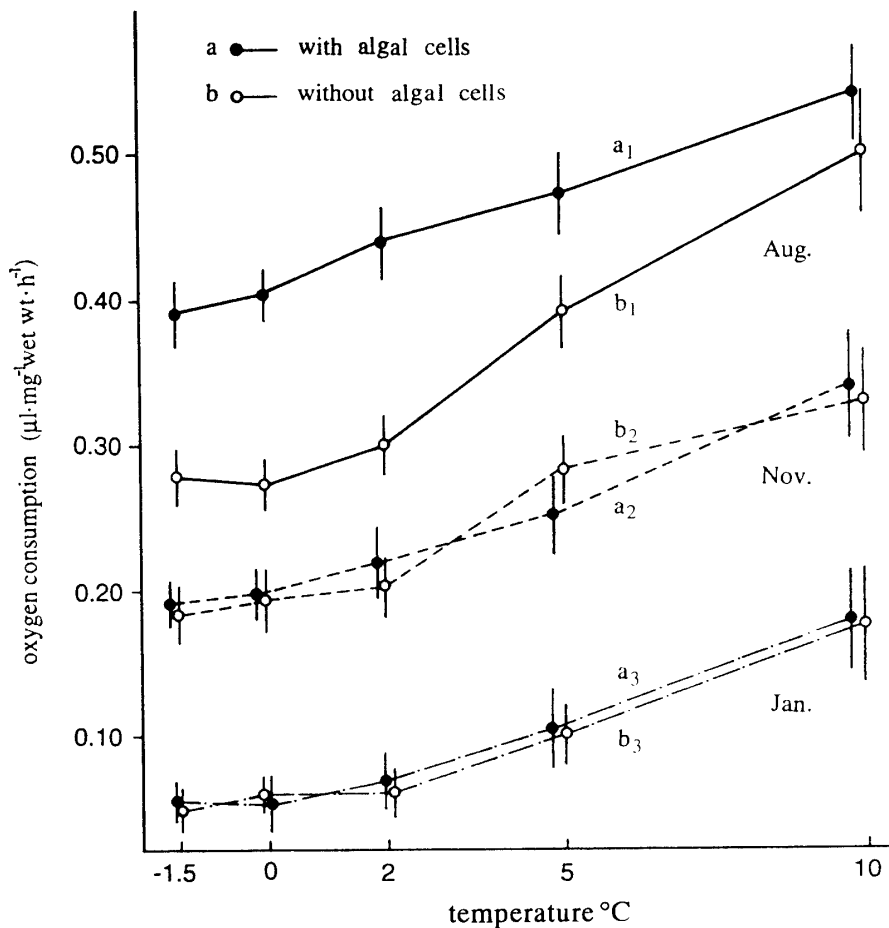


Fig. 6. Comparison of oxygen consumption by adult females *D. bispinosus* between groups from Burton Lake cultured in medium (a) with algal cells and (b) without algal cells.

Average total algal cell content:

(a₁) 107×10^3 cells/l (17–18 August 1984).

(a₂) 595×10^3 cells/l (22–23 November 1984).

(a₃) 3025×10^3 cells/l (10–11 January 1985).

Salinity: (a₁,b₁) 37.3, (a₂,b₂) 39.1 and (a₃,b₃) 38.4.

Filter coefficient (%)

(b₁) > 92.5.

(b₂) > 93.5.

(b₃) > 89.0.

tration at -1.5°C on November 29. A similar tendency can be seen at temperatures of 0 to 5. In comparison with August and November, however, the variability of oxygen consumption by animals under different dissolved oxygen stress might be smaller, in particular it was very slight in January.

3.2.4. Food concentration

The differences of oxygen consumption by animals between the groups cultured in filtered and non-filtered lake water are shown in Fig. 6. Algae cell concentration in non-filtered lake water was 107×10^3 cells/l in August, 610×10^3 cells/l in November, and 7025×10^3 cells/l in January respectively. The results showed that the animals had higher respiration in the medium with algae than in that without algae. In August, at -1.5°C , the oxygen consumption by animals was 0.39 ($\text{SD} \pm 0.0179$, $r = 0.37-0.41$, $n = 5$) and 0.28 ($\text{SD} \pm 0.0129$, $r = 0.260-0.291$, $n = 5$) respectively, when the animals were in media with and without algae. The body weight of the former after testing with algae was about 2-6% heavier than that without algae; translucent clean guts could be seen in the body of the latter. Compared with in August, there were very slight differences in oxygen consumption between the animal groups cultured in filtered and non-filtered lake water after November ($0.005-0.025 \mu\text{l}$, in temperature range of -1.5 to 2°C , for example on November 22), particularly in January. No

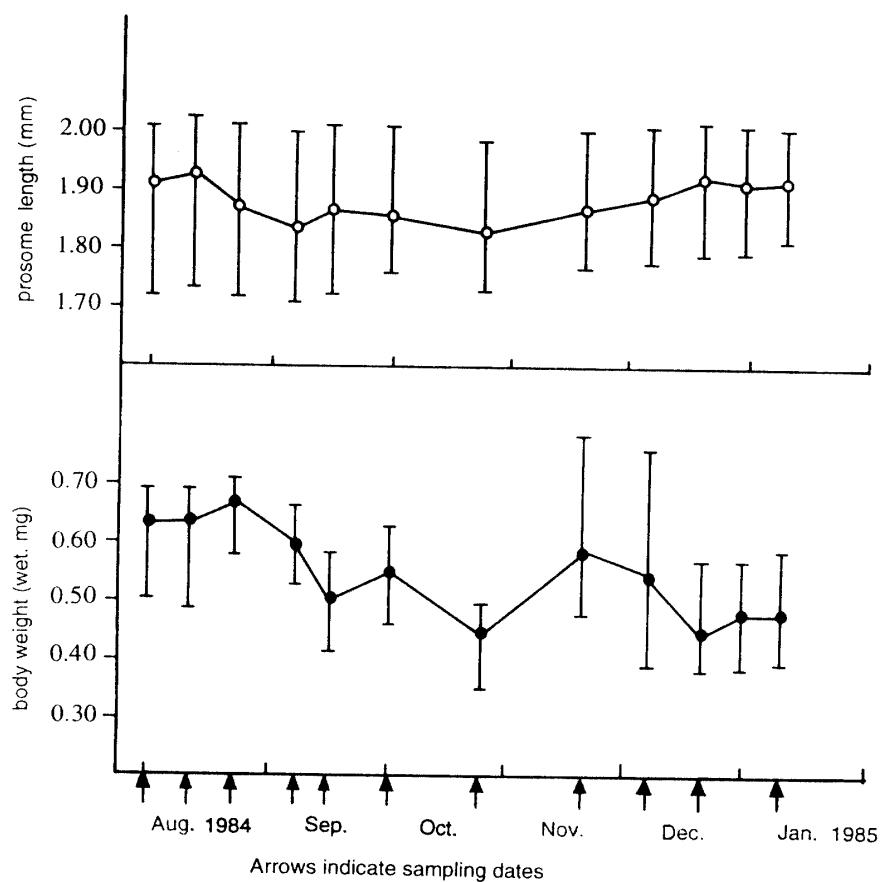


Fig. 7. Seasonal changes in body weight (wet) and prosome length (mm) of adult female *D. bispinosus* in Burton Lake (August 1984–January 1985).

significant differences of body weight were found between the two groups after tests.

3.3. *Biological measurements*

Seasonal changes in body weight and the prosome length of adult females are shown in Fig. 7. The prosome length did not change much from August to January, but the body weight fluctuated considerably during this period. The first decrease occurred in September, with an average individual drop in weight of 25.4% from August. It reached the lowest levels (average 0.44 mg wet/ind.) on October 26. After a short increase in November, it drooped again in December and January. Meanwhile, the ranges of body weight were wider in November and December than that in other months. There were about 55% fatter individuals of adult female with full guts contents and about 25% thinners with translucent clean guts in population component on November 23, the latter increased to about 57% and 89% on December 21 and January 8.

4. Discussion

4.1. *Environmental factors affecting respiration*

In some previous literature the causative factor for seasonal changes in respiration of marine zooplankton species has mostly related to the thermal history of the animals (SIEFKEN and ARMITAGE, 1968) or seasonal variations in sea water temperature (GEE, 1985). In Burton Lake, the distribution of *D. bispinosus* depended on salinity and they occurred in the entire water column above the chemocline from July to December. In January, the adult females were mostly found below the depth of 3 m (WANG, 1992). Since there was only a slight variation in temperature ($-1.7 \pm 0.1^\circ\text{C}$) in the lake from August to December, and in January (below the depth of 3 m) (WANG, 1992), the animals did not experience a thermal history during this period. This is a similar phenomenon has been observed with other animals such as *Limnocalanus* in an Arctic lake (ROFF, 1973). The monthly decrease in oxygen consumption by adult females from August to January was not much related to the temperature change in the lake during this period.

The respiration of adult females could be highly responsive to changes in ambient salinity (see Fig. 4). In comparison with the response under diluted salinity stress, the respiration was much less elevated when the animals were in higher salinity (see Fig. 5). In Burton Lake, because of melting ice, the salinity was much diluted from December to January (WANG, 1992). The percentage rate of changes in salinity below a depth of 3 m was less than 5% (about 39–37‰) in this period (WANG, 1992), which could induce the animals to have about 20% increase in their oxygen consumption as in Fig. 5a. In fact, the oxygen consumption of adult females in the lake still decreased in this period (Fig. 2). Thus, the salinity dilution in Burton Lake in this period did not much promote respiration by animals.

As in former studies (VERNBERG and VERNBERG, 1972), the respiration of adult females depended on oxygen concentration in the medium (Table 4). The dissolved oxygen decreased from July and reached its lowest value (less 3.5 ml/l) in November

in Burton Lake. This could actually induce the animals to decrease their respiration during this period, in order to survive in low oxygen tension in winter. It seems that the low respiration might represent one of the overwintering strategies of this species. However, the effect on respiration of decreasing dissolved oxygen was limited, particularly after November (Table 4).

IKEDA and SKJOLDAL (1980) and SKJOLDAL *et al.* (1984) believed that starvation was the dominant factor causing the decrease in respiratory rates. COMITA (1968) found that oxygen uptake by fed females of *Diaptomus* was higher than in starved ones. The results from the present study show that adult females revealed higher oxygen consumption in the medium with algae before January (see Fig. 6). This is in agreement with COMITA (1968). In January, however, there were no significant differences in oxygen consumption by *D. bispinosus* between filtered and non-filtered water (Fig. 6). Despite there being many more algae in the medium, the body weights of tested animals were close to those of groups without algae after testing. This might demonstrate that the animals had less feeding activity during late period in their life cycle because of senescence (see Section 4.2). In practice, the increase both of phytoplankton cells and dissolved oxygen as algae bloom in the lake in January did not much stimulate the increase of respiration by animals (see Fig. 2). Thus, the decrease in oxygen consumption of adult females after December must depend on other important factors.

4.2. Physiological factors

D. bispinosus is a univoltine inhabitant in Burton Lake. Generally, most adult females laid their eggs during September and November (BAYLY, 1986; WANG, 1992). The adult females occurred mainly from September to October, coinciding with the highest density of eggs (12847.5/m³, on October 1) (WANG, 1992). The first great decrease in respiration in October might result in an apparent metabolic cost for their reproductive activities (*e.g.* egg production, TISELIUS *et al.*, 1987). Many adult females died soon after their reproductive activities, and this caused a large decline of population density (BAYLY, 1986; WANG, 1992). Similarly, the second great decrease in respiration in December corresponded to the late peak of reproductive activity (in November) and large decline of population density (in December). Thereafter, the adult females, including nonproductive individuals, were mostly in the last stage of their life cycle before dying in January to February (WANG, 1992). Despite the increase in abundance of algae and oxygen concentration in the lake from December to January, the adult females in this period lost weight, but in their prosome length (Fig. 7). Fatter individuals, which had heavier weight, increased shortly in November, then the thinners, which were lighter, rapidly increased after December. Thus, more differences of body weight came out in different animal groups mixed with fatter and thinner individuals, and caused larger areas in body weight (Fig. 7). It is reasonable to extrapolated that the thinners had less feeding activity than before, so that food would not be an important factor to bring out the increase in respiration during this period. On the other hand, the higher Q_{10} values in January (see Table 3) indicated that animals became more susceptible to tempera-

ture change (this variance was identical with that of declining thermal tolerance, e.g. their upper thermal limit dropped from 14.7°C in July to 13.1 in December), and had a high mortality in the diluted medium after over wintering (WANG *et al.*, 1990). Furthermore, the sharp decrease in density of adult females (from 510.4/m³ on December 6 to 33.2/m³ on January 22) resulted in the death of adult females in this period (BAYLY, 1986; WANG, 1992). When the adult females were in the last stage of life (after December), they may change in their physiological function and some biological features, and exhibit great failure in adaptation to environmental stress, such as weakening in response to temperature and salinity changes, respiratory decrease, and weight loss, which should be considered as more important features for determining animal senescence (PROSSER, 1961; MARSHALL and ORR, 1972; WANG *et al.*, 1990). Therefore, it is reasonable to suggest that senescence could be an important physiological factor to influence the respiration of adult females before they died in summer.

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