ARCTIC
VOL. 66, NO. 1 (MARCH 2013) P. 37–42

The Freshwater Copepod *Limnocalanus macrurus* in the Canadian Arctic Archipelago: Numbers, Weights, and Respiration Observed from September 1961 – July 1962

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(*Received 10 June 2011; accepted in revised form 19 June 2012*)

ABSTRACT. Numbers, weights, and oxygen consumption of the copepod *Limnocalanus macrurus* were measured through the winter 1961–62 under the ice of Immerk Lake on Devon Island, Arctic Canada. Maximum abundance was 2361 animals per m^3 found under ice in mid June, average adult wet weight was 65 µg, and hourly oxygen consumption per adult ranged from 0.26 µg in late summer to 0.03 µg in early winter. The results are compared with results from Char Lake and Resolute Lake on Cornwallis Island, Arctic Canada. The Immerk population was more stable than those at the other lakes, and weights and oxygen consumption appear to be comparable. The seasonal breeding cycle at Immerk Lake was different from that at Char Lake and similar to that at Resolute Lake. A comparison of Immerk Lake data from 1961–62 and 1972–73 showed almost identical levels of total oxygen metabolism. Immerk Lake copepod oxygen consumption was 6.5% of the total lake metabolism, while that at Char Lake was 6%. These data may assist in future assessment of climate or anthropogenic changes.

Key words: *Limnocalanus macrurus*, Arctic lake copepod numbers, weights, respiration, Arctic lake metabolism

RÉSUMÉ. Le nombre, le poids et la consommation d'oxygène du copépode *Limnocalanus macrurus* ont été prélevés au cours de l'hiver 1961-1962 sous la glace du lac Immerk, sur l'île Devond, dans l'Arctique canadien. L'abondance maximale se dénombrait à 2 361 animaux par m^3 sous la glace au milieu de juin, tandis que le poids humide moyen d'un copépode adulte s'élevait à 65 µg, et que la consommation horaire d'oxygène par adulte variait entre 0,26 µg en fin d'été et 0,03 µg en début d'hiver. Les résultats ont été comparés aux résultats obtenus au lac Char et au lac Resolute sur l'île Cornwallis, dans l'Arctique canadien. La population du lac Immerk était plus stable que celle des autres lacs, tandis que le poids et la consommation d'oxygène de cette population semblaient comparables. Au lac Immerk, le cycle de reproduction saisonnier différait de celui du lac Char, mais il s'apparentait à celui du lac Resolute. La comparaison des données recueillies au lac Immerk en 1961-1962 ainsi qu'en 1972-1973 a affiché des taux quasi identiques sur le plan du métabolisme de l'oxygène total. La consommation d'oxygène chez le copépode du lac Immerk correspondait à 6,5 % du métabolisme total du lac, tandis qu'au lac Char, ce taux s'élevait à 6 %. Ces données pourraient aider à évaluer le climat à l'avenir ou à déterminer les changements de nature anthropique.

Mots clés : *Limnocalanus macrurus*, nombre de copépodes des lacs de l'Arctique, poids, respiration, métabolisme des lacs de l'Arctique

Traduit pour la revue *Arctic* par Nicole Giguère.

INTRODUCTION

The High Arctic is a region rich in freshwater lakes. Evidence from diatom remains in lake sediments from this region indicate that unprecedented biological change has occurred in many of these lakes over the 20th century, likely as a result of climate change (Smol et al., 2005). While these changes in algae are well documented, much less is known about how organisms higher in the food chain, such as zooplankton, are responding to climate change across this region, largely because only a few studies have examined the basic physiology (Roff, 1973; Rigler et al., 1974) and ecology (Minns, 1977; Strecker et al., 2008) of these organisms in the Arctic.

The copepod *Limnocalanus macrurus* is a cold-water stenotherm found in post-glacial lakes in north temperate and Arctic latitudes of North America, Europe, and Asia. It is also found and is quite common in low-salinity coastal seas of Canada, Alaska, and Russia (Roff and Carter, 1972; Hirche et al., 2003). The distribution and abundance of this species have been investigated in lakes on Cornwallis Island (Roff and Carter, 1972) and Ellesmere Island (Van Hove et al., 2001; Strecker et al., 2008). Minns (1977) measured the abundance of the copepod in Immerk Lake on Devon Island

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in August 1973. Given that *L. macrurus* adults overwinter (Roff and Carter, 1972), physiological measurements of this species during ice-covered conditions will also provide useful data for future comparisons.

This paper reports data collected throughout the winter of 1961 – 62 on the numbers, weights, and oxygen consumption of the only copepod, *L. macrurus*, in Immerk Lake on Truelove Lowland (75˚33′ N, 84˚40′ W), devon Island, Arctic Canada as part of a research program of the Arctic Institute of North America. Some comparisons are made with *L. macrurus* in Char Lake, which is smaller but deeper (27.5 m) than Immerk Lake, and nearby Resolute Lake (22 m); both lakes are on Cornwallis Island (74˚42′ N, 94˚50′ W) some 300 km west-southwest of Immerk Lake.

Site Description

The environmental circumstances and rich vegetation of the terrain surrounding Immerk Lake are reported in detail in several papers in Bliss (1977). The morphometry of Immerk Lake is shown by Minns (1977). The lake is quite shallow, with a mean depth of 3.24 m, a maximum depth of 8 m, and a calculated volume of 3107 × 10 m^3. There are two basins in the lake; the northern basin is much smaller and shallower (≈ 3.4 m) than the southern basin. The two basins are separated by a sill about 1 m below the surface. At maximum thickness of ice, the northern basin is cut off from the southern basin. The total unfrozen volume of the lake was thereby reduced by ≈ 7%.

METHODS

The copepod *Limnocalanus macrurus* was collected on 13 occasions from a hole through the ice between 30 September 1961 and 15 June 1962, by slow vertical tows of a #20 mesh (76 µm) net and a #10 mesh (158 µm) bucket with a diameter of 30 cm and a length of about 1 m. Tows were made from 5 m near the deepest part of the lake. The net was towed twice on each occasion and the contents were combined. When towed through 354 cm of water, the two tows together filtered about 0.5 m^3. All the animals were counted under a binocular microscope, and nauplius, copepodite, and adult stages were noted. Because of the net mesh, nauplii and younger copepodites were probably under-sampled by an unknown amount. The actual number of animals taken per 0.5 m^3 was doubled to approximate animals per m^3. This approximate number of animals per m^3 was then adjusted for decreasing lake volume by comparing the depth (354 cm) that filtered 0.5 m^3 of water with the length of net tow. When the depth of free water and the length of the tow were greater than 354 cm, the filter depth, the numbers of animals per m^3 was reduced by the ratio of filter depth to tow length. When the free water depth was less than 354 cm, the number of animals per m^3 was increased by the ratio of filter depth to tow length. The numbers per m^2 were estimated by multiplying the numbers per m^3 by the average depth (3.24 m) of the lake. Additional tows were made to collect animals for respiration trials.

On 4 October and on 12 February, five sets of animals, each consisting of 50 stage VI copepods, were weighed, and the average weights were calculated. The total wet weight of all animals was measured after they had rested on absorbent paper and then been placed on pre-weighed filter paper. Weights were measured on a chemical balance (Voland & Sons, Inc., Model 100; sensitivity: 0.1 mg). Oxygen consumption by the copepods was measured on 12 occasions between 29 September and 8 July. Copepods were suspended in 155 ml glass-stoppered bottles at 5 m for about 48 hours. Oxygen was measured by the standard Winkler titration method (Barnes, 1959) at the beginning and end of each trial. All animals were counted, and the total weight of all animals combined was measured except for June and July. Water samples for temperature and oxygen measurements were collected by a Van Dorn sampler at four depths (down to 6 m) on 29 occasions from 10 September to 5 June. Temperatures were measured with a thermometer in the water bottle as soon as it reached the surface. All work on the lake surface was performed from a small sampling hut.

Snow depths and ice thickness on the lake were measured 23 times from 13 September to 15 April, when the ice reached its maximum thickness of 2 m. On each occasion, five measures of snow and ice were made using standard measuring equipment from SIPRE (Snow, Ice and Permafrost Research Establishment, later Cold Regions Research and Engineering Laboratory), and these measures were then averaged.

RESULTS

Ice Cover

Ice thicknesses and percentages of frozen lake volume are shown in Table 1. Snow in the spring of 1962 was 10 – 12 cm, about 50% that of 1961 and 66% that of 1963. This 1962 depth was about 33% that of 1973 (Minns, 1977). At its maximum thickness, ice occupied 60% of lake volume. Because the least snow cover occurred in 1961 – 62, this maximum ice volume may be greater than normal.

Numbers of Animals

Table 2 records the actual numbers of *Limnocalanus macrurus* collected on each sampling date through the winter. The numbers adjusted for increasing ice thickness and expressed as animals per m^3 and m^2 are also listed in Table 2. The copepod apparently increased in numbers from 30 September (515 animals per m^3) to 29 January (1578 animals per m^3). The lake volume was 30% frozen by 1 December and 60% frozen at the end of March. Decreasing volume of unfrozen water and thus increasing concentrations of animals may account in part for the apparently increasing numbers of animals. There was no apparent

TABLE 1. Ice thickness on Immerk Lake, 1961 – 62.

Date	Ice thickness (cm)	% lake volume frozen
September 13	5	
October 5	25	
October 20	50	30
October 30	61	
November 16	86	
December 30	137	
January 21	146	52
February 11	172	
March 4	178	
March 11	188	
March 18	197	60
April 15	205	

trend in numbers from March into May, when ice growth was minimal, until mid June, when a total of 1018 animals were counted (calculated as equivalent to 2361 animals per m^3). The average number per m^3 for the sampling period September – July was 1177 (± 586). Copepodite stages II and III were found only on 30 September, one stage IV was found in October, and stage V copepodites were found in decreasing numbers until 1 March. Nauplii were found in early May under snow-covered ice and in early July under snow-free melting ice. Although nauplii and young copepodites were very likely under-sampled, the data do indicate the seasonal pattern of reproduction.

Weights of Animals

The average wet weight of individual adult animals was 63.8 (± 0.62) µg in October 1961 and 62.8 (± 0.49) µg in February 1962. Further, the average weight of animals in eight trials for respiration during 29 September – 24 May was 69 (± 17.4) µg. The average weight per animal from all data combined was 64.15 (± 14.5) µg. Weight declined from 29 September (80 µg) through mid October (66 µg). The lowest value (33 µg) was found on 24 March, and the highest value (99 µg) on 24 May. The high September and May values raise the average weight per animal for the winter from about 64 to 69 (± 17.4) µg. No weights were estimated in June, when all adults had full guts.

Respiration

Oxygen consumption by copepods from September into July is shown in Table 3. The hourly consumption per animal ranged from 0.03 µg to 0.26 µg. Values tended to decline from the highest value at the end of summer (0.26 µg in September) through October, and to rise from late March (0.10 µg) into June (0.18 µg), when water temperatures began to rise and feeding began. These trends were similar to those in the weights of animals. The mortalities in June (Table 3) could have been a consequence of greater densities of animals in combination with increased feeding and higher temperatures in the respiration trial bottles. Unfortunately, when the mortalities were observed in the bottles, no final oxygen measurements were made.

DISCUSSION

Numbers of Animals

The total numbers of *L. macrurus* in Immerk Lake through the winter suggest a quite stable population consistent with the observation of Rigler et al. (1974:644) that the mortality rate in Char Lake was "surprisingly low." The average number of copepods throughout the sampling period, 1961 – 62, was 1177 per m^3, and the highest was 2361 per m^3 on 15 June, still under snow and thick ice. These values compare to 1740 per m^3 found by Minns (1977) on 3 August, his only sampling date in Immerk Lake. (In the

TABLE 2. Numbers by stages of *Limnocalanus macrurus* collected in Immerk Lake in 1961 – 62. Numbers per m^3 are adjusted for decreasing lake volume (cf. First paragraph of METHODS).

Date	Nauplii	I	II	III	IV	V	Male	Female	Total #	# per m^3	# per m^2
September 30			2	3		22	151	185	363	515	1668
October 23					1	12	160	191	364	574	1860
November 17						4	175	163	342	588	1905
December 1						3	290	236	529	941	3049
December 23							327	292	619	1176	3810
January 13							393	357	750	1470	4763
January 29						1	438	350[1]	789	1578	5113
February 13							77	90[2]	167	354	1147
March 1						1	521	410	932	2050	6642
March 16							186	173	359	833	2699
April 6							352	301	653	1515	4908
May 5	59						295	225	579	1343	4351
June 15	8						396	614[1]	1018[3]	2361	7650
July 8	100										
Average # animals							**284**	**276**	**574**	**1177**	**3813**

[1] Three spermatophores.

[2] One spermatophore.

[3] All adults with full guts.

TABLE 3. Oxygen consumption by *Limnocalanus macrurus* in Immerk Lake, September 1961 to July 1962.

Date	No. of animals	µg per animal	µl O_2 per hour	Hourly O_2 intake per animal (µg)	T°C
September 29	20	80	3.75	0.26	1.15
October 1	56	75	3.90	0.10	1.15
October 6	61	65	1.04	0.03	1.20
October 14	71	66	2.50	0.05	1.30
October 16	114	73	3.13	0.04	1.30
October 19	101	63	5.20	0.07	1.30
March 24	91	33	6.38	0.10	1.16
May 24	450	99	43.1	0.13	1.58
June 2	438	–	43.5	0.14	1.61
June 6	239	–	20.0	0.12	1.61
June 9	350	–	46.8	0.18	–
June 16	all died	–	–	–	3.10
June 20	all died	–	–	–	–
July 8	361[1]	–	28.9	0.15	3.10

[1] 261 adults, 100 naupli.

same study, Minns found no *Limnocalanus* in two nearby lakes.) A corresponding number for zooplankton in Char Lake is about 2500 per m^3 (Rigler et al., 1974; Minns, 1977). The highest total population of the copepod found in Char Lake, which is much deeper (27.5 m) than Immerk Lake, was 61 680 per m^2, including nauplii and copepodite instars (Roff and Carter, 1972). From February until May, the adult population in Char Lake fluctuated from 300 to 800 per m^2.

Males and females of *L. macrurus* in Immerk Lake in 1961 – 62 appeared to be approximately equal in numbers, in contrast to the results of Roff and Carter (1972), who found significantly greater numbers of females than males in Char Lake over two years. A higher ratio of females to males was also found in ultraoligotrophic Upper Dumbell Lake in northern Ellesmere Island (Apollonio and Saros, unpubl. data), which is similar to Char Lake. Immerk Lake is more productive than Char Lake (Minns, 1977). We may speculate that the higher ratios of females to males may be an energy-allocation strategy used by females in ultra-oligotrophic lakes to ensure egg production sufficient for species survival. Dawson (1978) also suggested that the high female-to-male ratio he observed among copepods in the central Arctic Ocean was a reproductive strategy used to increase fecundity and selective advantage. More productive lakes may be able to support a higher ratio of males to females.

The variability in total numbers of *L. macrurus* through the winter in Immerk Lake may result from nonrandom population distribution. Roff and Carter (1972:368) found all instars in Char Lake "distinctly aggregated" for much of the year. They cited wind-induced mixing in open-water months as a mechanism accounting for some of the aggregation, but they apparently also found such nonrandom distribution under ice cover in October. Wind could not be a factor for aggregation under the ice cover of Immerk Lake during the present study.

Examination by Minns (1977) of gut contents of Arctic char (*Salvelinus alpinus*), the only fish in Immerk Lake, gave no indication of predation or impact upon the numbers of *L. macrurus*; chironomids were the principal prey of char during the period (mid May to mid August) of sampling by Minns. Similar results were found in Char Lake, and with empty stomachs much more frequent, but with some crustacean remains for the rest of the year (Roff and Carter, 1972; Minns, 1977).

Reproductive Season

The reproductive season for *L. macrurus* in Immerk Lake began in mid-winter with the appearance of spermatophores in late January and February and hatching of nauplii in late April and early May. A few late-stage copepodites were still present in September and October. This pattern contrasts to those of Char Lake, where reproduction starts in October, and nearby Resolute Lake, where it begins in June (Roff and Carter, 1972). Roff and Carter note that the season of reproduction of *L. macrurus* is quite variable: in Char Lake, it began two weeks earlier in 1970 than in 1969, and apparently began two weeks earlier still in 1971. Such shifts over the years may cause the reproductive seasons in different lakes to come into and go out of synchrony and may be considered normal for this species.

Weights of Animals

Wet weight of *L. macrurus* in Resolute Lake was reported to be four times that of dry weight (Roff, 1973). The wet weights of four copepod species in the Barents Sea were also reported (Ikeda and Skjoldal, 1989; Mauchline, 1998) as four times their dry weights. Roff (1973) cited an upper dry weight of 27.5 µg for adult *L. macrurus* in Resolute Lake, a wet weight equivalent of 110 µg, somewhat higher than any weight found in Immerk Lake. Roff (1973) measured weights in spring, summer, and early fall, but did not measure weights in winter, comparable to those from Immerk Lake. Given the seasonal variations of copepod weights, this seasonal difference of sampling could explain the higher weights reported by Roff.

The highest wet weight in Immerk Lake found in late May 1962, when the copepod presumably had begun feeding, was 99 µg, or 24.75 µg dry weight, which is similar to Roff's (1973) highest value. Hirche et al. (2003:724) found *L. macrurus* in the Kara Sea to be considerably heavier (females 102–293 µg "dry mass") than those of Resolute Lake, with an "enormous lipid content" that resulted from feeding on a phytoplankton bloom; even though *L. macrurus* is an omnivore, it has strong carnivore tendencies (Vanderploeg et al., 1998). The present study and others cited throughout this paper indicated that prior to 1975, adult weight of High Arctic *Limnocalanus macrurus* ranged from 15.88 µg (dry weight equivalent) in Immerk Lake to 27.5 µg (dry weight) in Resolute Lake. As part of a study of the elemental composition and dry mass of *L. macrurus* conducted in 2006 in eight High Arctic lakes, including Char and Resolute Lakes, Chételat et al. (2012) reported high values of dry mass from Immerk Lake. These values for males and females (34.6–37.6 µg) are three to four times as great as those from the other Arctic lakes. These high Immerk Lake values, apparently found in mid summer in ice-free water and at a high temperature (4.9˚C), are about 1.5 times our highest dry weight found in late May under snow and ice. This apparent summer increase in mass is comparable to that (1.6 times) found for *L. macrurus* from mid June to mid July and at comparable temperatures (2˚–7˚C) in the hypolimnion of Lake Michigan (Vanderploeg et al., 1998).

The variation in weights of *L. macrurus* through the seasons in Immerk Lake may well be accounted for by variations in the weight of stored lipids, most of which are wax esters, storage of which is unusual for freshwater copepods but common in marine copepods (Vanderploeg et al., 1998; Dahlgren et al., 2012). Copepods can survive long periods of starvation and derive energy for reproduction using wax esters (Hirche et al., 2003). Vanderploeg et al. (1998) note the constancy of body length, body volume, and concentration of lipid-free dry mass per unit volume; they note that almost all variation in body mass was related to stored lipids and that herbivorous copepods store higher levels of wax esters than omnivorous copepods. They found changes (1.6 times) of total lipids from mid June to mid July as a result of the beginning of feeding in the spring. Dahlgren et al. (2012) found a tripling of wax ester content from April to September in preparation for winter survival. They note that use of lipid reserves during winter is common among high-latitude marine copepods.

Respiration

Roff (1973) listed many factors that may be expected to influence the rate of copepod respiration, including temperature and food concentrations. Our results from Immerk Lake seem to be consistent with those of Roff (1973) in Resolute Lake in winter after 5–10 hours of trials, and they are considerably higher than Roff's animals in September and in the spring. Immerk Lake appears to be more productive than Char Lake; Minns (1977) estimated chlorophyll in Immerk Lake to be 1.78 times that of Char Lake. Better feeding conditions in Immerk Lake may account for the differences in respiration, as well as in weights, from Char Lake.

Hourly oxygen consumption per animal reported here ranged from a low of 0.03 µg to a high of 0.26 µg. This range is similar to the seasonal range for several species of marine copepods reported by Marshal and Orr (1958). There seems to be a trend in copepod respiration in Immerk Lake from the highest value at the end of summer (September) to consistently low values in late autumn to increasing values in late spring (May). Weights of animals seemed to reflect this cycle. Chlorophyll was found to be high (0.5 mg per m^3) in May 1973, when Minns (1977) began sampling. Its highest value (≈ 1 mg per m^3 in early July) was followed by a decline in mid August to half the peak values of July. All our copepods had full guts in mid June 1962. Immerk *L. macrurus* weights and respiration appear to respond to the availability of phytoplankton food, as did those recorded by Hirche et al. (2003).

Lake Metabolism

Wolfe and Smith (2004) noted that detailed studies of Arctic lake metabolism are sparse. Minns (1977) used oxygen data collected by this project in 1961–62 to estimate Immerk Lake metabolism, giving an annual value of 69.4 g of oxygen per m^2. This is almost identical to the annual value (69.2 g oxygen per m^2) calculated by Minns for 1972–73, suggesting little change in lake metabolism in that eleven-year period. Welch (1974) concluded that lake metabolism is a conservative property and will exhibit only a slow response to alterations of the condition of a lake. The data for 1961–62 indicate annual oxygen consumption by *L. macrurus* of 4.5 g per m^2 or about 6.5% of whole lake metabolism. Welch (1974) estimated Char Lake total annual consumption at 40.1 g per m^2 and Rigler et al. (1974) calculated *L. macrurus* consumption to be 6% of total Char Lake metabolism.

Implications for Climate Change

Arctic freshwater systems—lake, ponds, and rivers—are among the most sensitive ecosystems on the planet (Schindler and Smol, 2006) and are especially vulnerable to climate change, which has greatly accelerated during the 20th century. Polar and alpine lakes are undergoing particularly rapid climate-induced change and therefore may be among the most sensitive monitors of climate change (Williamson et al., 2009). However, Schindler and Smol (2006) note that a paucity of long-term monitoring data poses a significant challenge to environmental assessments. These data from Immerk Lake could aid in assessing the ecological effects of climate and anthropogenic changes on invertebrates in Arctic lakes.

ACKNOWLEDGEMENTS

This work was part of the larger Devon Island Expedition (1960–63) of the Arctic Institute of North America. The expedition was supported by funds and supplies from the Arctic Institute, the Defence Research Board of Canada, the National Research Council of Canada, the Royal Society, the United States Steel Foundation, the Hudson's Bay Company, the Office of Naval Research (USA), the National Science Foundation (USA), Massey-Ferguson Ltd., the United States Weather Bureau, the Meteorological Branch of the Department of Transport (Canada), and the Quartermaster Corps of the United Sates Army, among other institutions, as well as a large number of private individuals and companies. We thank anonymous reviewers for constructive suggestions and relevant references.

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