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Life cycles of the freshwater, planktonic copepod *Cyclops scutifer* Sars on a north–south gradient in North America

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Abstract

A seasonal cycle longer than one year is exceptional both among marine and freshwater zooplankton, but occurs widely in the freshwater cyclopoid *Cyclops scutifer* Sars. This paper presents the life cycle of this species in eight North American populations in lakes from 42° to 69° N. Five of the populations had life cycles showing a combination of a one and two year cycle. Two populations had a 1-year cycle, and the southernmost had a combination of a 0.5-year and a 1-year cycle. Lengths of cycles increased with latitude and thus inversely with the temperature. Populations in all lakes were divided into a direct and a delayed line of development. Diapause was not documented in any of the lakes.

Introduction

Cyclops scutifer Sars is distributed over a large part of the northern hemisphere (Elgmork & Halvorsen, 1998). In North America it occurs in lakes in New England (Elgmork, 1967) and in Canada (McLaren, 1961, 1964; Reed, 1963). Life histories of *C. scutifer* show extreme variations, ranging from 1-year cycles, combined 1-year and 2-year cycles, and even 3-year cycles both with and without diapause. For reviews of references see Elgmork (1981) and Elgmork & Eie (1989). Life cycle studies, besides two from arctic Canada (McLaren, 1961, 1964) and two from Kamchatka (Nosova, 1970; Kurenkov, 1973), have been so far restricted to Scandinavia, where cycles are known from 50 lakes (Elgmork, in prep.).

The aim of this paper is to present life cycles in eight populations from North America for comparison with cycles in Scandinavia. McLaren (1964) was the first to make such a comparison based on the study of a very few populations. A comparison can now be extended by the present study of eight populations from North America and a large number now available from Scandinavia.

Areas and localities

Locations and characteristics of the sample localities investigated are presented in Figure 1 and Table 1. *Cyclops scutifer* populations were studied in eight lakes situated on a north–south gradient from Victoria Island in arctic Canada to Connecticut in northeastern USA. All lakes were at altitudes lower than 500 m and were relatively shallow, with depths from 6 to 44 m. All lakes, except the monomictic, arctic Keyhole Lake, were dimictic. Periods of ice during winter vary from 3.5 to 9 months among lakes. The southernmost lake was eutrophic, six were oligotrophic, and the northernmost lake also most likely oligotrophic. Further information about the localities is presented under Results.

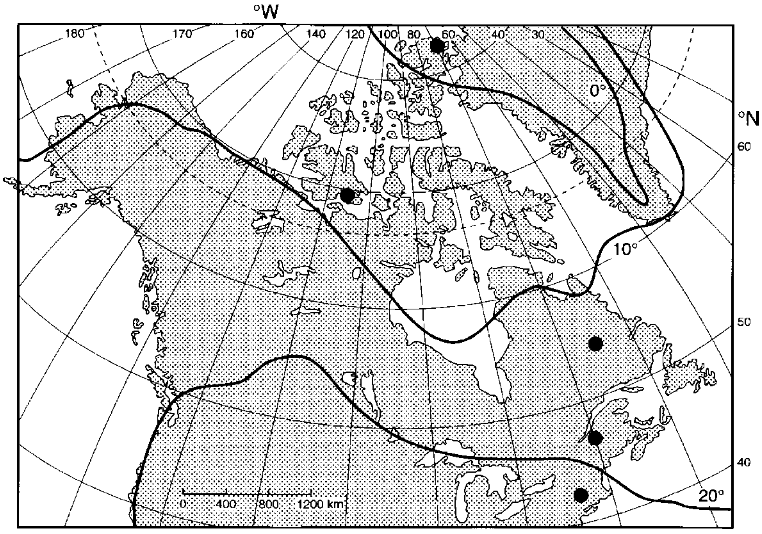

Figure 1. Map of North America showing locations in the following order from south to north: Mt. Tom Pond, Connecticut, two lakes in Maine, four in Quebec, and Keyhole Lake. Also included are the positions of Lake Hazen and Skeleton Pond, Ellesmere Island (McLaren, 1961, 1964). Isotherms indicate mean July air temperature reduced to sea level. Redrawn from Fullard & Darby (1970).

Table 1. Some characteristics of the lakes and populations

Lake	Country	Latitude (degree N)	Altitude (m asl.)	Max. depth (m)	Ice cover (months)	Lake type[a]	Clutch size	Cycle length	Dichotomy	Diapause
1 Mt. Tom Pond	USA	41.50	265	14	3.5	2	28	0.5 + 1	+	0
2 Rangely Lake	USA	45.00	463	44	4	1	22	1	+	0
3 Dodge Pond	USA	45.00	464	15	5	1	20	1	+	0
4 Knob Lake	Canada	54.47	501	15	8	1	24	1 + 2	+	0
5 John Lake	Canada	54.48	502	24	8	1	24	1 + 2	+	0
6 Squaw Lake	Canada	54.50	493	18	8	1	28	1 + 2	+	0
7 Maryjo Lake	Canada	54.48	498	18	8	1	24	1 + 2	+	0
8 Keyhole Lake	Canada	69.20	40	6	9		29	1 + 2	+	0

[a] Lake type: 1, oligotrophic 2, eutrophic.

Planktonic cyclopoids

At northern latitudes and in high mountain lakes in Scandinavia *C. scutifer* is the dominant and often the only cyclopoid in the lake zooplankton, as documented for example for northern Sweden (Lindström, 1952, 1958; Lötmarker, 1964) and for south central Norway (Langeland, 1972, Halvorsen, 1980). Cyclops scutifer was also found to be dominant in the North American lakes, including two high arctic lakes (McLaren, 1961, 1964). In Keyhole Lake *C. scutifer* was dominant, with a very few other unidentified cyclopoids present. In the Quebec lakes *C. scutifer* was by far the dominant planktonic cyclopoid co-occurring only with a few *Diacylops* spp. In the Maine lakes *Mesocyclops edax*, and in Mt. Tom Pond *M. edax*, *Acanthocyclops vernalis*, *Orthocyclops molestus*, and *Eucyclops speratus* were also present.

Methods

Studies of the seasonal cycles were based on samples collected by standard plankton nets with openings of about 30 cm and with mesh widths of 90 μm. The same type of net was used in all localities during the entire sampling period from

1963 to 1982, except in Keyhole Lake, where net specifications are lacking. Qualitative plankton samples were taken by vertical net hauls from the bottom to the surface over the deepest part of the lake. This will secure representative samples of the population, even with *C. scutifer*, which often concentrates at deeper levels (Elgmork, 1967; Halvorsen & Elgmork, 1876). Samples were taken during the whole year except in Keyhole Lake, where sample dates ranged from July to November. Sampling times are presented as vertical stippled lines in the diagrams in Figures 2–9.

Ample presence of the earliest nauplii shows that the mesh size used was sufficiently small. In the best-studied locality, Mt. Tom Pond, quantitative samples with a 1.5 l Friendinger water sampler were also taken to supplement the net samples and study vertical distributions (Elgmork, 1967). Two to seven replicate samples were taken each time, and preserved in 4% formalin.

In the laboratory copepodids and adults were identified and counted under a binocular microscope on a counting slide (Elgmork, 1959). A minimum of 200 individuals was counted in each sample. Identification of the copopodids were made using previous descriptions of the instars of the related *Cyclops strenuus* (Elgmork, 1959).

Nauplii were identified to instar (using Elgmork & Langeland, 1970) in a sample of 50 individuals from each sampling date by use of an ordinary microscope. Identification to species level was assured by comparisons of nauplii with those hatched from different species, as well with specimens from localities where *C. scutifer* was the only cyclopoid in the plankton. The same procedure was also used for the earlier copepodids. Since *C. scutifer* is greatly dominant over other cyclopoids in all the localities studied, a few possible misidentifictions should therefore be negligible.

Sediment samples were taken by the mud sampler described by Elgmork (1962a), except in the Canadian lakes where an Ekman grab was used. The water close above the bottom was in the field decanted and examined for copepodids of *C. scutifer*. After the mud samples were brought to the laboratory in thermos bottles, water was added to the mud and repeatedly decanted. The residue was filtered each day until no more individuals emerged

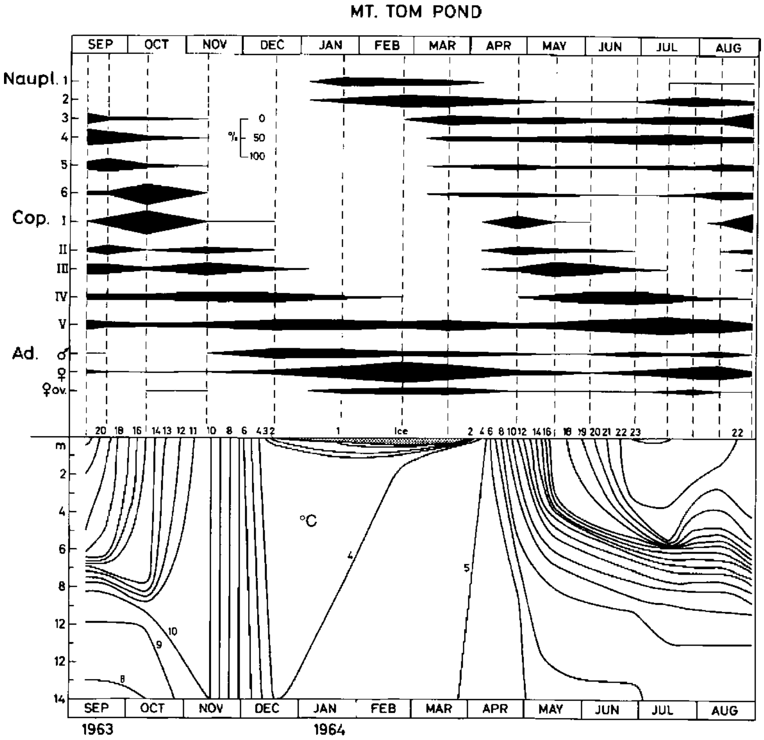

Figure 2. Seasonal cycle of *C. scutifer* in Mt. Tom Pond, Connecticut (top) and water isotherms (bottom).

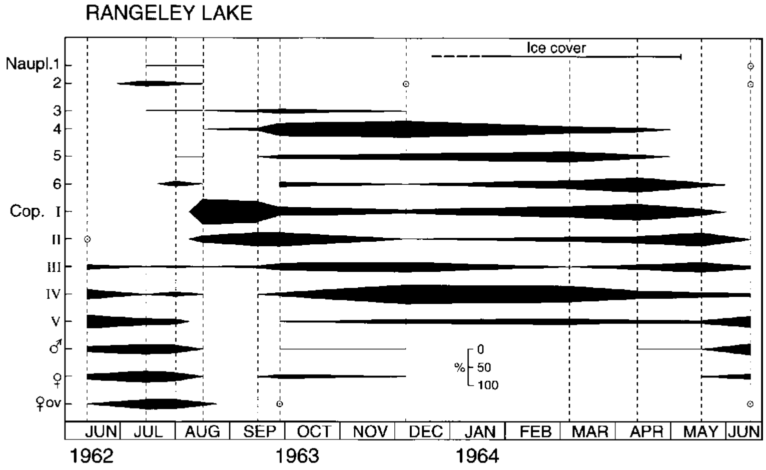

Figure 3. Seasonal cycle of *C. scutifer* in Rangeley Lake, Maine.

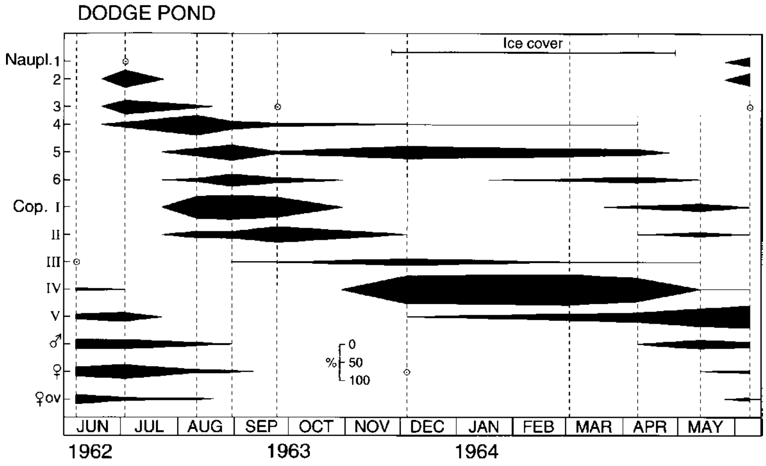

Figure 4. Seasonal cycle of *C. scutifer* in Dodge Pond, Maine.

(Elgmork, 1959, 1981). Examination of samples of the mud after the decanting was completed showed that no more individuals were left in the mud. In some cases, without repeated decanting, the mud itself was dispersed in water and small fractions studied directly under the binocular microscope.

The variation in population composition is presented as percentage curves (Figs 2–9 and 11) where the percentages of nauplii are calculated from the total population, whereas percentages of copepodids and adults are calculated from the sum of these later stages. This was done because a sudden, large input of newborn nauplii at times of very active reproduction will otherwise reduce the apparent percentages of the other stages considerably (Elgmork, 1959). In the diagrams horizontal complete lines indicate a percentage <5%, and circles indicate an isolated sample with a percentage <5%. Horizontal dashed lines indicate samples with too few individuals to calculate percentages, and shows only that the instar was present.

The seasonal cycles in the Maine and Quebec lakes are based on results from parts of two different years (Figs 6 and 8). For the Maine lakes, results from June to the middle of September 1962 are combined with results from late September 1963 to June 1964. For the Quebec lakes, results from December 1963 to June 1964 are combined with results from July to November 1982. This amalgamation is defensible as cycles based on samples from different years show a high degree of concordance, as shown, for example, in

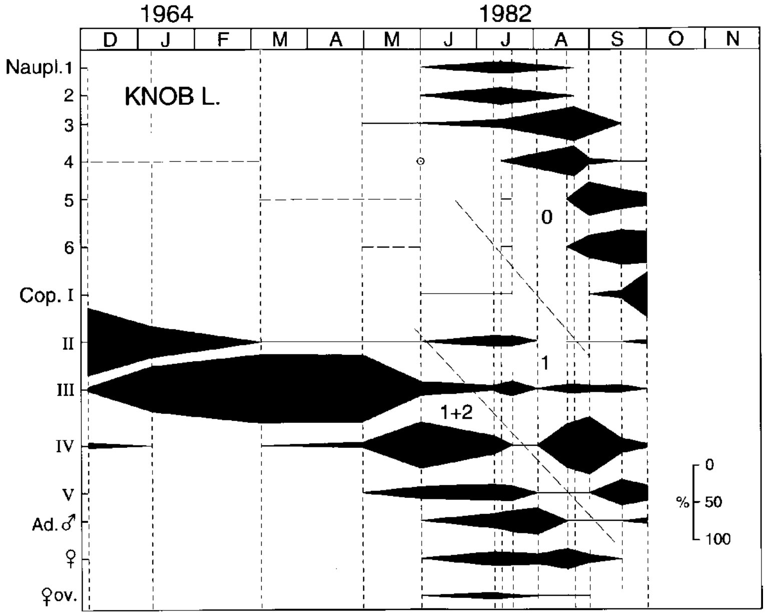

Figure 5. Seasonal cycle of *C. scutifer* in Knob Lake, Quebec.

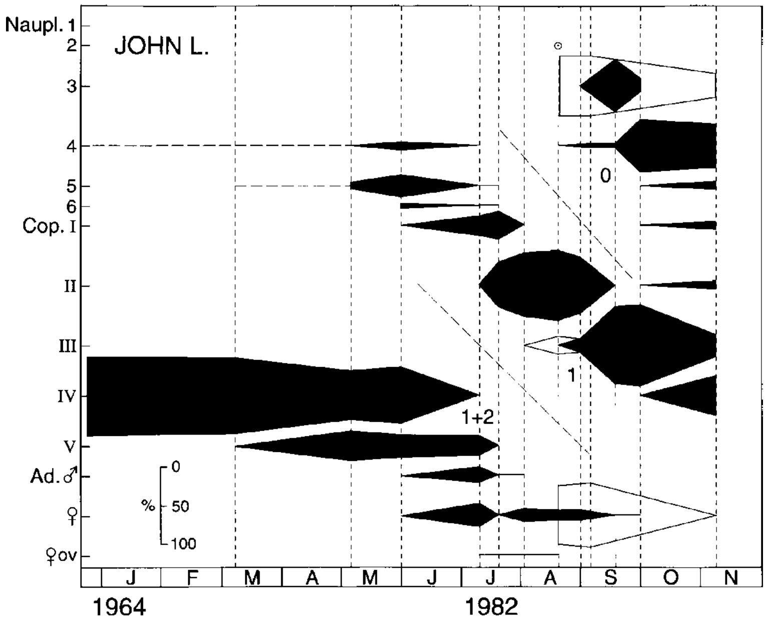

Figure 6. Seasonal cycle of *C. scutifer* in John Lake, Quebec. Open diagrams: results from 1964 included in the 1982-series.

two large oligotrophic lakes (Fig. 11) (Halvorsen & Elgmork, 1976), and in two high mountain lakes (Elgmork & Eie, 1989). In a few autumn samples from two of the Quebec lakes, the results from two years were different, as indicated by open diagrams in Figures 6 and 8.

Abbreviations used in the figures are: Naupl. 1–Naupl. 6 for first to sixth naupliar instars; Cop. I–Cop. V the five copepodid stages; Ad. indicates adults. Lengths of life cycles are indicated in the text as 1-year, 2-year, etc., with a 1 + 2-year cycle indicating that life cycles lasting both one and two years occur in the same population.

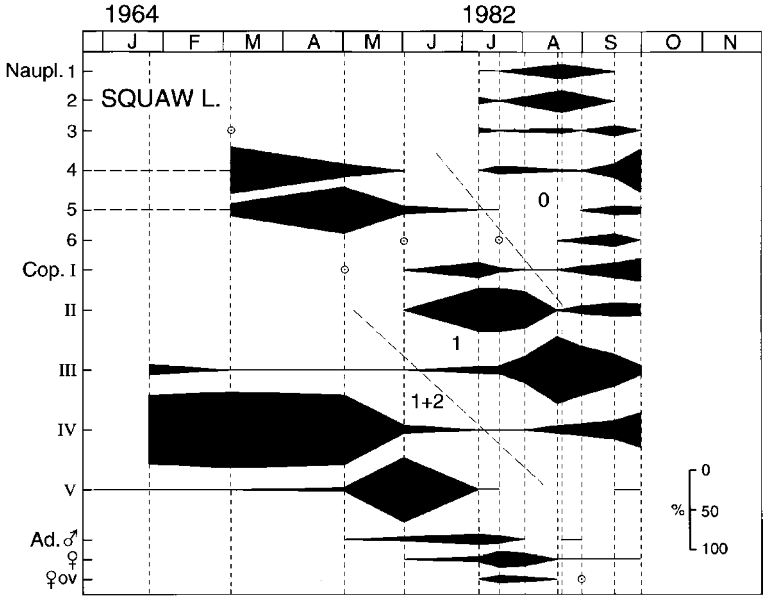

Figure 7. Seasonal cycle of *C. scutifer* in Squaw Lake, Quebec.

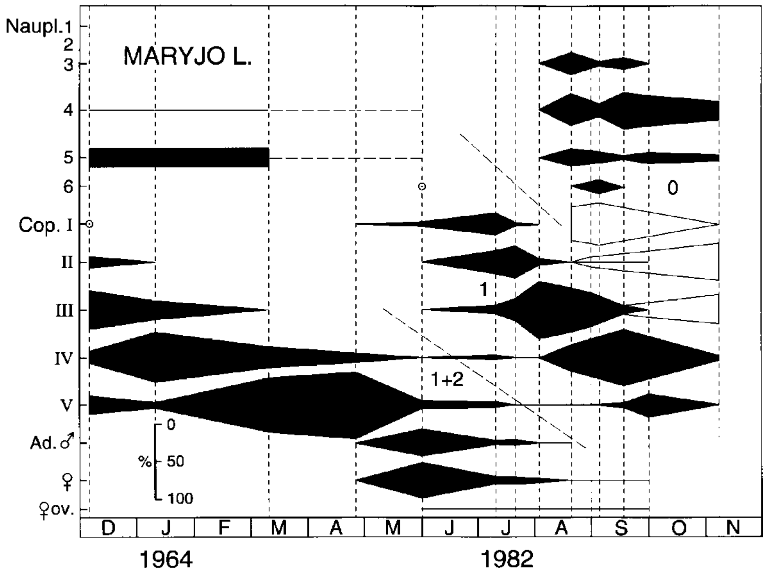

Figure 8. Seasonal cycle of *C. scutifer* in Maryjo Lake, Quebec. Open diagrams: see Fig. 6.

Results

Mt. Tom Pond, Connecticut

Environment

This lake is situated in forested areas in the northwestern corner of Connecticut in the coldest part of the state (Elgmork, 1967). Surface temperature during summer goes well above 20 °C (Fig. 2). Winter shows a regular inverse stratification with temperatures from 1 to 4–5 °C near the bottom. Maximum ice thickness was 40 cm at the end of February 1964. Oxygen in the lake was depleted during summer and autumn in the lower water

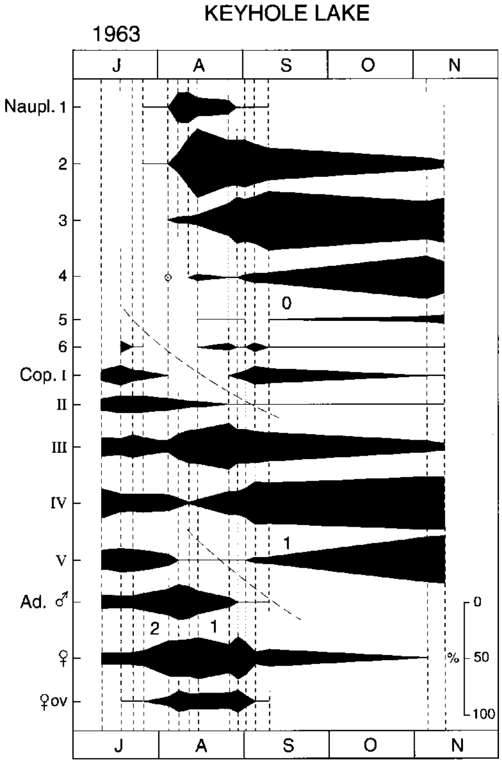

Figure 9. Seasonal cycle of *C. scutifer* in Keyhole Lake, Victoria Island.

layers (Elgmork, 1967) in accordance with the lake's eutrophic status.

Seasonal cycle

The seasonal cycle (Fig. 2) is extraordinary, as the main period of reproduction occurred during winter with a smaller one during summer (Elgmork, 1991). The development from nauplii born during winter diverged into two lines in April. One went directly in about half a year to reproducing adults in summer, whereas about 20% of nauplii were delayed in instars 3 and 4 and only reached the adult stage next winter when a year old. Animals from the delayed fraction mixed with those from the direct line in autumn and they reproduced together during next winter. The Mt. Tom population thus has a life cycle composed of a 0.5-year-old fraction and a smaller 1-year-old fraction.

Sediment samples ($n = 21$) were taken on four dates from September to March with negative results for *C. scutifer*, whereas diapause was documented in *Mesocyclops edax* and *Acanthocyclops vernalis* (Elgmork, 1996). Also, the vertical distribution of *C. scutifer* Elgmork (1967) and examination of the water close to the mud surface, indicated no concentration of copepodids in the water close to the bottom mud, as is often found accompanying diapause (Elgmork, 1981; Elgmork & Langeland, 1980; Elgmork & Lie, 1998).

Maine lakes

Environment

C. *scutifer* is very common in large lakes in the Rangeley area in Maine (Elgmork, 1967). The localities studied there were Rangeley Lake and Dodge Pond situated only about 500 m apart in the western part of the state. These two lakes were chosen to include a range of lake sizes, as Rangeley Lake is much larger in area and deeper than Dodge Pond (Table 1). Both lakes were temperate lakes situated in forested areas. Maximum ice thickness was 90 cm in Rangeley Lake and 60 cm in Dodge Pond measured in the beginning of April 1964.

Seasonal cycle

Rangeley Lake – A new generation was produced in July (Fig. 3). One fraction quickly developed into copepodids in August, whereas another fraction of about the same proportion postponed development throughout autumn and winter, and developed slowly to copepodids during winter and early spring. Also the fraction with the direct development was delayed during winter, predominantly as copepodid IV. The two fractions mixed with each other in late spring and reproduced together during the summer. The Rangeley Lake population thus showed a 1-year cycle divided into two fractions during the non-reproductive period of the year.

Sediment samples ($n = 9$) taken on four dates from September 1963 to April 1964 produced no emerging diapause stages.

Dodge Pond – The seasonal cycle (Fig. 4) was fundamentally the same as in Rangeley Lake with reproduction in July, divergence into two fractions in autumn that were delayed during winter, and united in spring into a common reproducing pool in summer. The division into the two fractions was more clearly expressed in Dodge Pond than in Rangeley Lake. The delayed fraction of nauplii represented less than 20% in Dodge Pond, compared with about 50% in the deeper and colder Rangeley Lake. The delayed instars were primarily in nauplius 4 in Rangeley Lake, but nauplius 5 in Dodge Pond.

Sediment samples ($n = 13$) taken on three dates from September 1963 to March 1964 produced no diapause stages of *C. scutifer*.

Quebec lakes

Environment

The Quebec lakes are situated in a sub-arctic region dominated by open lichen woodland. Samples were taken in four lakes in the Knob Lake basin: Knob, John, Maryjo, and Squaw lakes (Table 1). Knob Lake is isolated whereas rivers connect the others in the above sequence, making gene flow possible among their populations. The lakes are at about 500 m altitude and are relatively shallow, depths ranging from 11 to 24 m. All four lakes are oligotrophic. *Cyclops scutifer* must be very common in the area, since it was present in all four arbitrarily chosen lakes.

Seasonal cycle

The seasonal cycle was similar in all the Quebec lakes (Figs 5–8). Reproduction occurred during July and August, and one fraction of the nauplii developed directly during autumn and winter to late copepodids, reaching maturity and reproduction next summer as 1-year olds. Another fraction was delayed as nauplii and reached copepodid 1 next summer. These 1-year olds developed during the second summer to late copepodids that passed the second winter and reached the adulthood during the early second summer as 2-year olds.

The relatively few nauplii present 1964 in all the Quebec lakes during winter may be due to a sampling or technical error not known to the author, who did not take the samples. Copepodids developed from these nauplii were, however, abundant and the nauplii showed normal numbers in samples taken in 1982.

Sediment samples from all four lakes in December 1963 and in January 1964 produced no diapause stages of *C. scutifer*.

Keyhole Lake, Victoria Island

Environment

This is an arctic lake situated on barren ground and is the shallowest of the lakes studied, with a maximum depth of only 6 m (J.G. Hunter, Fisheries and Oceans Canada, pers. comm.). The 9-month duration of ice cover was extremely long. The temperature was below 2 °C under the ice in June, and below 5 °C in July. The lake circulated during the ice-free period in summer with temperatures from 7 to 9 °C. *Cyclops scutifer* was the only cyclopoid in the plankton.

Seasonal cycle

The seasonal cycle of *C. scutifer* in Keyhole Lake was based on samples taken only from July to November 1963 (Fig. 9). This reduces the reliability of the results, although fairly reasonable interpretations have been made in arctic regions based on shorter sampling times, down to one summer month in the high-arctic Skeleton Pond (McLaren, 1961, 1964). A realistic interpretation of the life cycle in Keyhole Lake is that it began with a period of reproduction and subsequent nauplii in August. These developed during autumn to nauplius 4. They reappeared in July next year as copepodids and a fraction reached the adult stage in August, including females with eggs. At the same time another fraction of the original cohort was delayed in development and passed the autumn and the following winter as late copepodids. This fraction reached adulthood in July as 2-year olds. These adults mixed with the 1-year olds in a common pool of reproducing adults as indicated by the short period with egg-bearing females and nauplii production. The life history in Keyhole Lake thus combines a 1-year and 2-year cycle.

The few nauplius 6 and copepodid I instars in August–September may be interpreted as the beginning of a direct line in a dichotomy that developed further to late copepodids and merged with the delayed fraction in autumn.

Sediment samples taken in November 1963 yielded no diapause stages of cyclopoids.

Discussion

Qualitative sampling with vertical net hauls has yielded reliable results in a number of studies of the life cycle of *C. scutifer* and other cyclopoids (e.g., Elgmork, 1959, 1981, 1985; Halvorsen & Elgmork, 1976; Nilssen & Elgmork, 1977; Elgmork & Langeland 1980; Elgmork & Eie 1989; Elgmork & Lie, 1998). Often minute, statistically non-significant differences in the frequencies of an instar prove by later samples to be real. The gradual changes in the relative frequencies of the instars usually show logical sequences: e.g. later instars occur after earlier, males before females, etc. This supports the reliability of the method.

The eight populations of *C. scutifer* studied here have a life cycle ranging from combined 0.5 + 1, 1-year, and combined 1 + 2 years. The localities range in latitude from 42° to 69° N. On Ellesmere Island at about 82° N, this species has a 2-year cycle in lake Hazen (McLaren, 1961, 1964). Located in the same area is the very shallow Skeleton Pond, with a maximum depth of only 3.5 m and an area of 1.5 ha (Mclaren, 1964). For a high-arctic area, the pond was relatively warm, being isothermal on August 4 at 11 °C, and was thought to mix irregularly during summer.

According to McLaren (1964) the *C. scutifer* population in Skeleton Pond in 1958 had a combined 1-year and 2-year cycle. A new interpretation by the present author indicates that the cycle was instead a combination of 2-year and 3-year fractions. The presence of the 3-year fraction is supported by the population distribution on July 31 with four maxima: nauplii, early copepodids, late copepodids, and adults, indicating a 3-year cycle. That some 2-year-old late copepodids would soon have developed to adults is probable, because there was a marked development of early copepodids during the summer of sampling, thus giving a combined 2- and 3-year cycle. This interpretation (agreed to by I.A. McLaren, pers. comm.), if accepted, is the first example of a combined 2-year and 3-year cycle among more than 60 populations of *C. scutifer* so far investigated (Elgmork, in prep.).

For the ten populations in N. America (including the two on Ellesmere I.), there is a clear positive relation between length of the cycle and latitude (Fig. 10). The north–south temperature gradient is substantial (Fig. 1). Mean air temperature for July is around 20° for Connecticut and Maine, close to 13 °C for the Quebec localities, slightly below 10 °C for Keyhole Lake, and below 0 °C for Lake Hazen and Skeleton Pond on Ellesmere Island (Fulland & Darby, 1970). Temperature therefore emerges as the paramount factor regulating lengths of life cycles. But other environmental factors as shallowness, abundance of food, and presence of predators may locally influence the length and type of life cycle.

The short, half-year cycle and winter reproduction in Mt. Tom Pond are exceptional (Elgmork, 1991). Since Mt. Tom Pond is the warmest and southernmost known *C. scutifer* locality, it might be inferred that winter reproduction is related to high temperatures. But winter reproduction has also been demonstrated in Lake Blankvatn in Norway (Elgmork & Langeland, 1980; Elgmork, 1991), which is a much deeper and colder lake than Mt. Tom Pond. Temperature is apparently not the only factor inducing winter reproduction.

An interesting aspect of this study is the striking similarity in lengths and types of seasonal cycles in *C. scutifer* between lakes in North America and in Scandinavia. Except for the very short cycle in Mt. Tom Pond, lengths of cycles are of the same

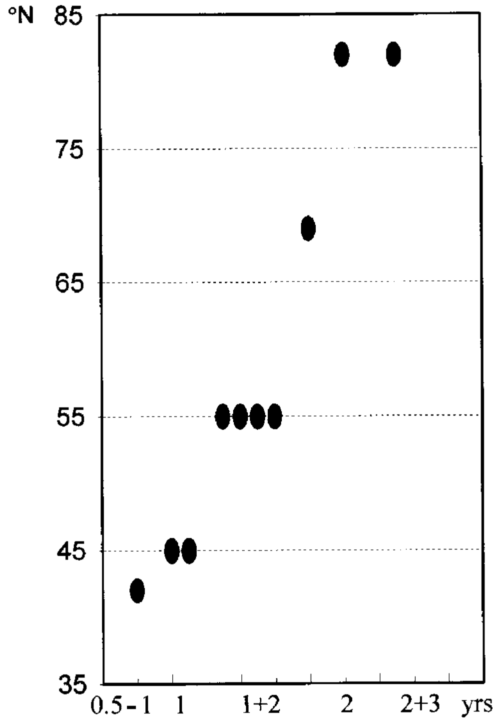

Figure 10. Relation between life-cycle length and latitude in North American lakes. The localities are arranged as in Figure 1. The two upper circles are from Lake Hazen and Skeleton Pond (McLaren, 1961, 1964).

magnitude, including 1, 1 + 2, 2, and even 3-year cycles as found in Norway. The most common cycle among the North American populations was a combined 1 + 2-year cycle found in five of eight populations (Table 1). This is also a common cycle in Scandinavia. (Halvorsen & Elgmork, 1976; Elgmork et al., 1978; Elgmork & Eie, 1989; Elgmork et al., 1990; Elgmork, in prep.). The Scandinavian populations studied are mostly situated in regions with a mean July air temperature of about 15 °C. This corresponds well with the July temperatures for the Quebec localities (Fig. 1), where all four lakes investigated had 1 + 2-year cycles.

A difference between the two continents appears to be the absence of diapause in the North American *C. scutifer* populations so far studied. Mud samples were taken by a method that has revealed large number of diapausing *C. scutifer* in a number of other lakes. For example, a density of 3.7 million diapaused copepods per m^2 has been documented in one locality in Norway (Elgmork, 1962b, 1981). Sediment samples were taken in the North American localities during autumn and winter. This is the best period for detection of diapause, since in all 11 Norwegian lakes known to have diapaused *C. scutifer*, five were in diapause from July to the following April (Elgmork, in prep.), whereas in six other lakes diapause was documented from December to April (Elgmork, 1962a, b; Elgmork, et al., 1990). Both the method and time of sampling therefore support the conclusion that diapause did not occur in the North American populations. Only a very small number of lakes, however, have been investigated.

Dormancy is characteristic of diapause, but other indications of diapause may occur without dormancy in the condition called 'active diapause' (Elgmork, 1980; Krylov, et al., 1996). These include arrested development, lack of significant gut contents, and presence of large, orange lipid droplets in the body cavity (Elgmork, 1962b). The possibility of an active diapause in the N. American localities can be tested against these criteria.

The most detailed study was of Mt. Tom Pond, where development occurred during the entire seasonal cycle with no periods of delayed development (Fig. 2). The instars capable of diapause in *C. scutifer* are copepodids II–V (Elgmork, 1962b), and these had some gut contents during the entire winter. Lipid droplets increased in size from November to February, when they were well developed, evidently forming a food reserve built up during the winter. The continuing development during winter shows that there was no active diapause in Mt. Tom Pond.

Populations in the Maine lakes showed a more delayed development as nauplii and late copepodids. The delay was most evident in Dodge Pond with a retarded development during several months in winter as Naupl.5 and Cop.IV. These instars had many large lipid droplets in the body cavity and very reduced gut contents. These observations all indicate an active diapause in the Maine lakes, especially in Dodge Pond.

In the four Quebec lakes there was a clear delayed development during winter except in Maryjo Lake (Figs 5–8). In this locality a development proceeded during winter, but with a slight tendency for an accumulation of Cop.IV during late winter. That a development took place in Maryjo Lake, was also corroborated by the presence of many exoskeleton casts. In the other three populations there was a conspicuous halt in development during winter as Cop.III in Knob and as Cop.IV in John and Squaw Lakes. Gut contents were examined only in Knob and Maryjo Lakes, and little or none was found. Lipid droplets also varied, being present in Knob and very prominent in Maryjo Lake, but were sparse in the others. The delayed development, large and many lipid droplets, and sparse gut contents indicate an active diapause in the Quebec lakes.

A halted development and lack of gut contents could also result directly from low temperature and inadequate nutrition. There is thus a gradient from halted development induced directly by adverse environmental conditions (quiescence), through active diapause without dormancy, to diapause with dormancy. Except for the dormant state, exact limits are difficult to draw.

A special aspect of the life cycle of *C. scutifer* is the phenomenon first demonstrated in Swedish lakes by Lindström (1952, 1958) under the term 'dualism,' followed by Lötmarker (1964), and called 'dimorphism' by Axelson (1961), and since then found in a large number of *C. scutifer* populations in Norway (Elgmork, in prep.). Since both these terms have been used to mean other things in

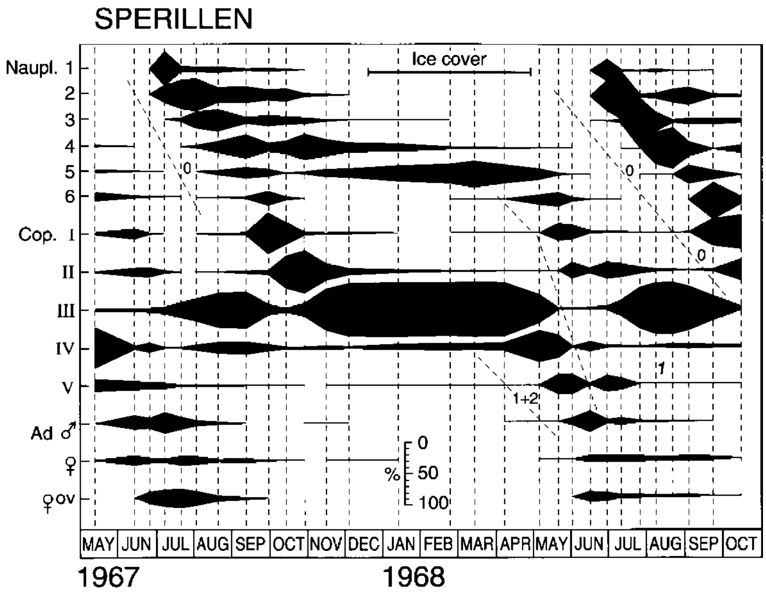

Figure 11. Seasonal cycle of *C. scutifer* in the Norwegian Lake Sperillen, showing typical dichotomy and a 1 + 2 year cycle. (Redrawn from Halvorsen & Elgmork (1976)).

life-history studies, the phenomenon is here called ‘dichotomy.’ A typical example is shown from the Norwegian Lake Sperillen (Fig. 11). Dichotomy is characterised by a division of the nauplii population into two lines in autumn. One line develops directly to copepodids, pauses in development during winter, and develops further into reproducing adults next summer. The other line develops slowly as nauplii and passes the winter in this stage. In spring, part of this line may develop to adults and merge with the adults from the direct line as 1-year-olds, while a delayed fraction may develop more slowly and pass another winter before reproducing in summer as 2-year-olds.

In the American populations presented here, dichotomy is most prevalent in Dodge Pond, but is also seen in Rangeley Lake, in the Quebec lakes, and in Keyhole Lake. Also in the southernmost Mt. Tom Pond there is a split in the nauplii population, not in autumn, but in spring (Fig. 2), unlike all other populations in which dichotomy has been found.

The types of life cycle of *C. scutifer* in the American populations are thus in detail parallel to many life cycles on the other side of the Atlantic Ocean, including the phenomenon of dichotomy.

An adaptive significance of prolonged life cycles in arctic regions may be that in multi-annual populations the presence of younger developmental stages throughout the year ensure reproduction in the following year(s), whereas with annual cycles, a lack in reproduction in one year could be catastrophic.

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