

THE EFFECT OF THE WINTER ICE COVER ON ODNATA LARVAE
IN A POND NEAR PETERBOROUGH, ONTARIO*

David Beresford
Trent University, Peterborough, Ontario
(presented at the Conference by Margo Shaw)

Abstract

Dragonfly nymphs were sampled from a small (3 ha.) pond southwest of Peterborough, Ontario during the fall and winter of 1982/83. The purpose of this study was to examine how winter cover affects the spatial distribution of these insects in ponds. It was hypothesized that ice and snow cover could affect the nymphs directly by invading their habitat, or indirectly due to a change in the nature of the pond environment.

Odonata larvae were sampled in the fall to determine their initial distribution, and in late winter. Air and surface water temperatures and precipitation were monitored throughout the sampling period. During freeze-up the ice cover was monitored daily until permanent cover appeared, at which time measurements of ice thickness were recorded after each major precipitation event.

The winter of 1982/83 was very unusual as abnormally high amounts of rainfall and low amounts of snowfall were recorded. This resulted in a complex pond cover consisting of alternate white and black ice layers with a minimal snow cover. Initial freezing of the pond occurred during high water levels, so that when these levels declined, air became trapped between the water and ice layers. This provided a unique opportunity to observe the indirect effects of the ice on Odonata larvae.

The autumnal distribution of dragonfly nymphs was variable but organisms were found throughout the pond. Samples taken under late winter cover showed that the larvae had migrated to the shallow shoreward regions of the pond.

The most probable effect of the ice cover which initiated this response was the reduction of oxygen in the deep regions of the pond. Other possible causes of migration include the death of vegetation and resultant lack of suitable habitat for some Odonata species, and the increase in hydrogen sulfide at low water depths. The results of this study support the findings of Lawton (1970) who also found that Odonata larvae migrated shoreward during the winter.

Introduction

Dragonfly nymphs are often the dominant predators in littoral zones of water bodies. Their presence has a profound effect on prey species which include insects, molluscs, tadpoles and even minnows and fry (Benke, 1978). In order to fully understand their role in ponds, their spatial distribution must be understood. Although some work has been done on spring, summer and fall distributions, (Corbet, 1962; Lawton, 1970; Macan, 1964), little is known about their distribution under ice cover in winter. This paper is an examination of the way in which the winter cover (snow and ice) of a pond affects the spatial distribution of Odonata larvae.

The hypothesis is that winter cover does affect the spatial distribution of dragonfly nymphs. This effect can be either direct: ice actually invading the nymphs' habitat, or indirect: the presence of the winter cover changing the nature of the pond environment. The direct response to the ice was thought to be either through horizontal migration into deeper regions or vertical migration down to or into the sediments or else through larvae being trapped in the ice and frozen solid. Corbet, 1962, felt that the first response occurred. Lawton, 1970, having observed junior Pyrrhosoma nymphula larvae at the base of

* Winner of Student Prize, 1983. This paper was based on an undergraduate Honours thesis submitted to the Departments of Biology and Geography, Trent University, Peterborough, Ontario, in the spring of 1983.

vegetation at pond edges in winter, suggested this as an example of the second response to ice. The third foreseen behavioral effect caused by the presence of ice was that if no escape was attempted, the larvae would be frozen solid in the ice. Corbet, Longfield and Moore (1960) report finding large nymphs trapped in ice, which swam away unharmed upon thawing. These findings were rare, not enough to suggest that this was the usual way of over-wintering.

The indirect effects of winter cover are the blocking of light from the unfrozen body and the related lowering of oxygen concentration. This could either affect the larvae directly or it would affect their prey which would in turn affect the dragonfly distribution. Also, the death of aquatic plants under the ice could force some larvae to seek more suitable habitats.

Literature Review

Literature on the effects of winter cover on invertebrate distributions is not extensive. In part, this is due to the regretful tendency for workers to discontinue sampling over the winter months and to concentrate mainly on spring, summer and fall distributions. Macan (1964) gave careful attention to the April through December distribution of Odonata nymphs, but made only passing comments on the winter distributions. Corbet (1962) indicated that larvae seem to retire to deeper regions of the pond when cold weather begins in the fall. Norton (1970) discovered that the damselfly nymph *Pyrrhosoma nymphula* Sulzer over-wintered close to shore. This last is the only reference which provides quantitative data about over-winter distributions.

Despite this sparsity of literature on winter distribution of invertebrates, there is a range of related material which can be adapted to the present study. Adams and Prowse (1977) state that the winter cover of lakes acts as a lid effectively preventing atmosphere-water interaction. This is analogous to a closed system, where no oxygen can enter the pond or lake through the ice cover. Jackson (1979) compared a lake in winter to a B.O.D. bottle, where the organisms gradually decrease the oxygen concentration in the unfrozen water body.

Since up to one metre of black ice, in the absence of snow cover, can allow enough photosynthesis to take place to satisfy oxygen demands (Wright, 1964; Schindler, 1971), the actual physical barrier that the ice creates is less important than the fact that the cover is often opaque, reducing light penetration and photosynthesis. Greenbank (1945) found that 84% of surface light penetrated 9 cm of black ice and Wetzel (1975) notes that 72% of surface insolation passed through 43 cm of black ice.

White ice inhibits light penetration, 24 cm of it blocking all but 22% of incoming light according to Greenbank, 1945 (see also Gerdel, 1948). However, it is snow that stops most incoming light. Gravelle (1949) found that 30 cm of snow allowed only 7% transmittance and Outerbridge (1981) found that 20 cm of snow only allowed 1% of the light to penetrate. Maguire (1975) found that 10 cm of snow "effectively inhibits net photosynthesis" but he went on to say that a black ice cover in the absence of both snow and white ice can so effectively transmit light that it can cause oxygen supersaturation in the unfrozen water body. Relationships between different types of ice and snow and the light regime of lakes are treated in some detail by Adams et al (1983) and Adams and Roulet (1983).

Thus, as Sagriff (1979) stated, increased snow depth causes decreased photosynthesis. This, coupled with the findings of Adams and Prowse (1981) that snow and white ice are thickest in the littoral zone of water bodies, suggests that oxygen production will be less in such littoral locations than in deeper parts of the water body. Sagriff (1979) observed that during the winter, as snow depth increased, phytoplankton ascended vertically to take advantage of any available light passing through the cover. Highest densities of phytoplankton were just under the ice in the relatively snow and white ice free centre of the lake. The decay of dead organic matter and the respiration of the biotic community cause oxygen to be lost most rapidly in the deeper regions of lakes and ponds. In the case of lakes, this loss may result in fish kill (e.g. Jackson, 1979). Lasenby (personal communication) observed that *Chaoborus* migrate upwards as oxygen concentrations drop in the deeper parts of the lake.

Besides such indirect effects of ice cover, the actual physical presence of the ice influences lake and pond margins. McClellan (1971) cites examples of damaged vegetation

caused by ice push at Gillies Lake. Adams and Mathewson (1975) also noticed much damage around the shore of the same lake resulting from ice movement. Wassen (1966) gives detailed examples of the physical effects of ice at lake margins, including the ripping up of vegetation entrapped in the ice during spring break-up.

Specifically relating to dragonflies, Corbet (1980) noted that dragonflies need to over-winter in a cold-resistant stage. This takes the form of eggs or nymphs. Temperature and photoperiod play an important role in synchronized emergence in the spring. Lutz (1968, 1974) has shown that decreased temperature and photoperiod cause northern species to enter a diapause state of suppressed development. Ingram (1975) found that "spring-like conditions" of high temperature and/or long photoperiods cause larvae to leave the diapause state.

While all of the above suggest that winter cover is important in changing the environment of pond communities, few conclusions can be drawn from the literature as to how the distribution of nymphs is affected by ice and snow on a pond. Among other things, the winter cover of such small water bodies seems to have received much less attention than that of others.

Study Site

Study was undertaken at a pond located in Meyer's Garden Centre, Peterborough, Ontario. The pond has an area of 3 hectares and is 100 metres long, east-west and 30 metres wide, north-south. Two 1.75 metre deep regions exist, divided by a 0.4 metre deep ridge (Fig. 1).

At the northeast corner of the pond is an island surrounded by a moat 0.6 metres deep. A 2-storey house, east of the pond, blocks easterly winds and provides some shelter. The north shore is largely barren of cover, while the south shore is protected by a stand of 15-20 high pine trees. The west end of the pond degenerates into a wetland and saturated field. The pond is fed via the water-table and responds almost overnight to rainfall events. Pond sediments are silt and/or muck. Cattails surround the north, west and south shores of the pond; the east end is bordered by a domestic lawn. In the autumn of the study in 1982, the bottom of the pond was covered with the algae Oscillatoria which also was the dominant plant on the north side. Nostoc occurred around the edges. Spirogyra was abundant throughout but mostly along the south bank and at the west end of the pond (Otto and Towle, 1969).

The water weed Ceratophyllum echinatum Gray occurred along the Ridge as did Potamogeton L. (see Fig. 2). The north shore has regularly received fertilizer from the nursery which used to operate there. The pond itself was smaller until twenty years ago when it was widened and deepened.

The animal life is typical for such ponds in this area. One point of interest is the presence of crayfish Orconectes immunis, which of late has been declining in numbers around Peterborough. Large populations of Chaoborus, Chironomidae, Daphnia magna, some Mayfly larvae, caddisfly larvae and water beetles occur in the pond.

Methodology

Data were obtained from a series of 3 transects in the fall, across the 2 deep holes and the ridge and also from 2 transects at peak ice time across the same location. Samples were taken at 1 metre intervals along the transects near the margin and every 2 metres in the middle of the pond (see Fig. 3). The net used had a square face 25 x 24 cm, was 20 cm deep and had a 1.6 m handle. The mesh was 2 mm x 1.5 mm. At each sample site, the net was drawn across the bottom perpendicular to the transects for a distance of 1 metre with the lower lip of the net including the top 1-2 cm of sediment (Beresford, 1983). By this process, some weeds and algae were often pulled up by the net even though they were not actually in it. These were included in the sample. Each sample was bagged and numbered, and sorted later in the lab. The larvae caught in each sample were preserved in separate envelopes, enabling the whole transect to be preserved intact for future identification and counting.

The identification of the dragonfly larvae was done using Needham and Westfall's keys (1955). The damselfly larvae were identified using Walker's keys (1953).

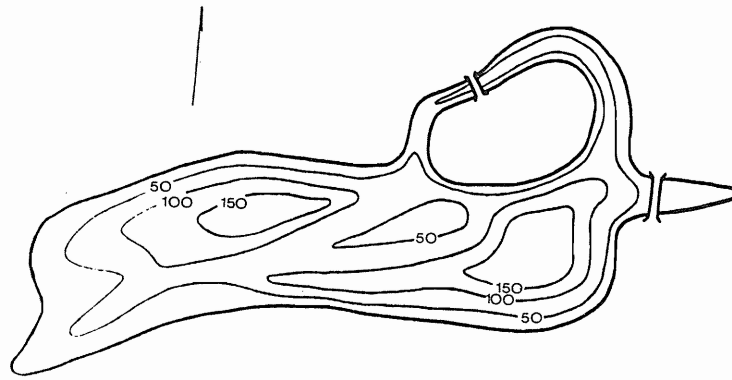


Fig.1. Bathymetry of Meyer's Pond.

Depths in centimetres

10m

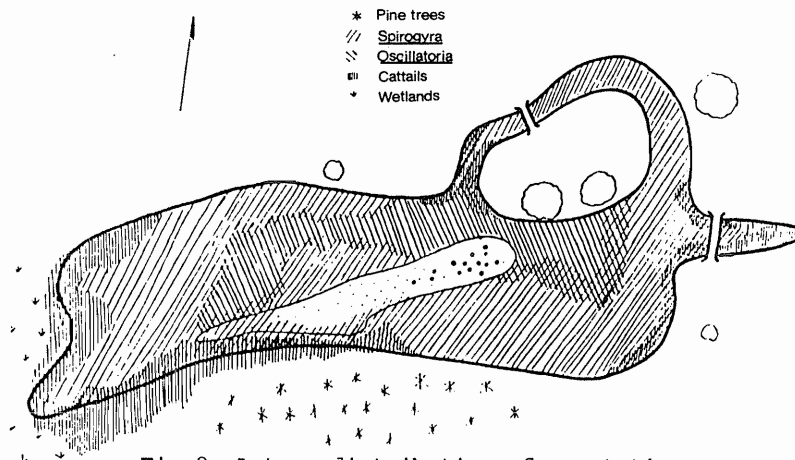


Fig.2. Autumn distribution of vegetation.

10m

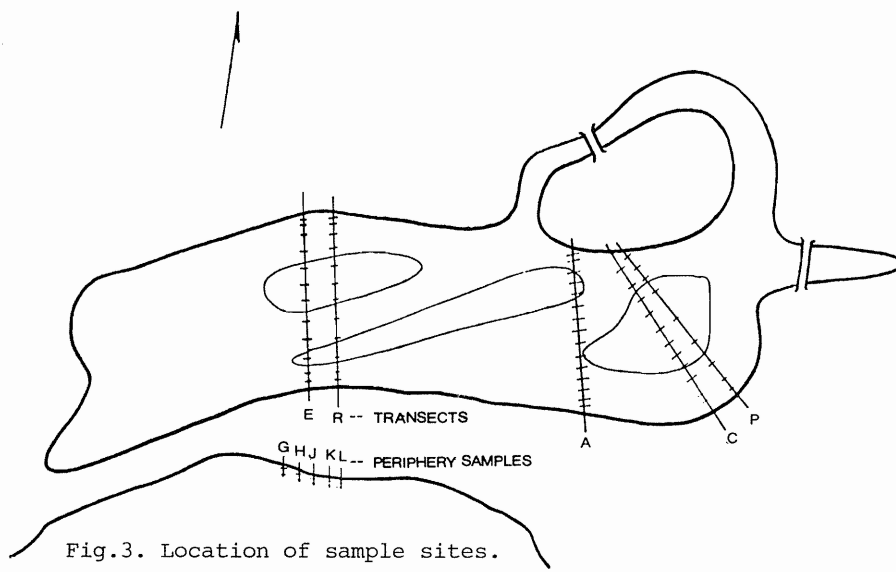


Fig.3. Location of sample sites.

10m

The square-faced net was a considerable improvement on the round nets used by Macan (1964) and Lawton (1970).

As the ice developed, the perimeter of an adjacent pond in which the same species were present, was sampled to monitor any migration into deeper water. This was done in order not to disturb the winter cover on Meyer's Pond since considerable holes through the ice were needed for each sample. Air temperatures from the Airport, 3 km away, were used in the study after it was discovered that, during the fall, there was no difference in temperature between the 2 sites. Surface water temperature and hydrostatic water level were recorded using a mercury thermometer and a staff gauge respectively. The staff gauge was a stake driven into the sediments (Bruce and Clark, 1980). Precipitation data were also obtained from the Airport.

During freeze-up, ice cover was monitored daily until the permanent cover appeared. A time lapse camera was established in January to record spatial patterns of snow on the pond or any melt that might have occurred. These photographs were not available early enough to be incorporated into the study.

A number of tests were made to complement the pond study itself. Larvae were frozen in the laboratory to see if they could survive after thawing. An outdoor pond, 1 metre x 2 metres x 5 metres with a gentle slope on 1 side, was filled with larvae, weeds and water and allowed to freeze half way down to discover any horizontal movement away from the ice (see Beresford 1983). Observations of larvae in an aquarium were also made.

For the winter, the transects were sampled, often in concentrations for both east and west deep holes at a depth of 0.1 and 1.5 metres were analyzed using the Winkler technique.

Results

The results for 5 transects were given in Table 1. The values per sample were multiplied by 4 to get per square metre values, since each sample represents approximately 25 cm x 100 cm. Transects A, C and E sampled October 8, November 6 and October 31, 1982 respectively, represent the autumnal distribution. Transects P and R, obtained March 5 and 19, 1983, represent the peak ice distribution of larvae.

The larvae present in the lake are Leucorrhinia intacta, Libellula quadrimaculata, Anax junius, Aeshna juncea and damselflies of the genus Enallagma. Of the above, only L. intacta, L. quadrimaculata and Enallagma were abundant enough to be adequately sampled by the methods used.

Anax junius and Aeshna juncea were present largely in conjunction with the water weeds along the ridge. As can be seen from Table 1, and Figures 4, 5, 6 and 7, the other three larvae were present in all regions of the pond. Although L. quadrimaculata appears to be distributed sparsely, subsequent sampling in all areas of the pond show that they were present, in low densities, throughout both the deep and shallow sections.

Transects P and R (see Fig. 7 & 8) show the winter distribution of larvae. Note the absence of larvae in the deeper regions. This absence could not be disproved by subsequent diligent searching with the net.

The results of the winter perimeter samples are tabulated in Table 2. As can be seen, no horizontal migration occurred away from the ice.

Table 3 summarizes the physical data.

From Fig. 9, it is obvious there was much more rainfall than usual in November. Also, this particular autumn was warmer than the previous 10 autumns (Fig. 10 & 11). This delayed freeze-over until 28 December 1982.

As a result of the abnormally high rainfall in November and December, the pond water level rose, causing freeze-up to occur when the water table was high. Usually freeze-up occurs at lower levels (Fig. 12). This resulted in an ice cover that was virtually high and dry around the littoral zones, as the water level dropped after the permanent ice cover appeared (Fig. 13).

During January and February three rainstorms resulted in water running into the pond from the surrounding area. This became perched above the original ice layer. This new

Table II

Perimeter Sampling, Results

Sampling site	G	H	J	K	L
Date	Jan. 8	Jan. 22	Jan. 29	Feb. 5	Mar. 5
Distance from shore	125	125	125	125	125
L. quadrinaculata	1	6	2	1	0
L. intacta	0	0	1	1	0
Enallagma	7	12	16	4	5

Table I.a

Number of larvae per sample

Distance from South shore metres	Transsects											
	A	B	C	D	E	F	G	H	I	J	K	L
1	0	0	26	0	6	13	0	2	19	0	1	4
2	0	0	15	1	0	11	0	2	30	1	6	65
3	0	0	7	0	2	9	3	3	1	0	0	0
5	0	0	12	0	0	20	1	3	5	0	0	0
7	0	1	24	0	0	13	0	0	12	0	0	0
9	0	1	39	0	0	18	0	2	12	0	0	0
10	1	0	16	0	0	5	0	0	4	0	0	0
11	0	2	5	0	0	27	0	0	0	0	0	0
12	0	0	9	0	0	11	1	2	17	0	0	0
13	0	0	33	0	1	9	3	4	18	0	0	0
14	1	0	1	0	1	23	0	4	22	0	0	0
15	1	1	16	0	0	0	0	0	0	0	0	0
16	0	1	11	0	2	83	0	7	14	0	0	0
17	0	6	23	0	2	82	0	4	82	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0

q.---L. quadrinaculata
i.---L. intacta
E.---Enallagma

Table I.b

Total number of larvae per transect

	Transects			
	A	C	E	P
L. quad.	84	88	172	168
L. intacta	24	8	36	36
Enallagma	1856	1144	1392	1540
Total	1964	1240	1600	1744

Table III
Weather Data, Meyer's Pond, 1982-83

	Mean Temperature °C		Rainfall mm		Snowfall cm		Total Precipitation mm	
	Month	Normal	Month	Normal	Month	Normal	Month	Normal
September	13.3	13.3	85.0	72.9	nil	nil	86.0	86.0
October	8.5	7.9	63.5	59.0	Trace	1.1	63.5	63.5
November	3.1	2.1	109.2	52.8	2.0	15.9	111.2	111.2
December	-1.8	-6.0	76.2	40.5	12.4	38.6	88.2	88.2
January	-6.7	-9.3	19.0	14.2	17.7	35.3	36.3	36.3
February	-4.7	-8.5	32.2	21.1	17.1	31.5	46.8	46.8

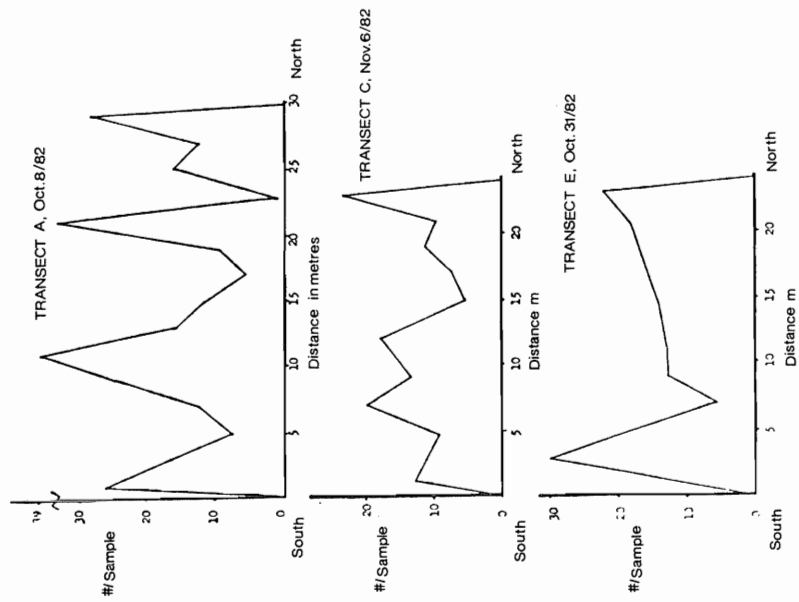


Fig.4. Autumn distribution of Libellula quadrimaculata.

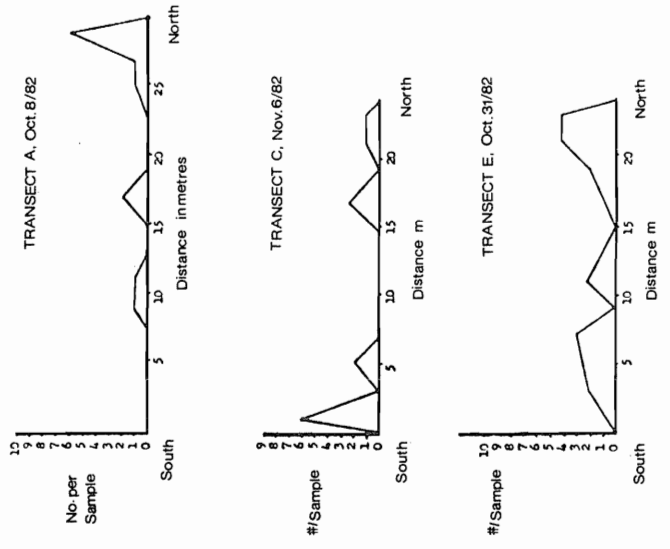


Fig.5. Autumn distribution of Leucorrhinia intacta.

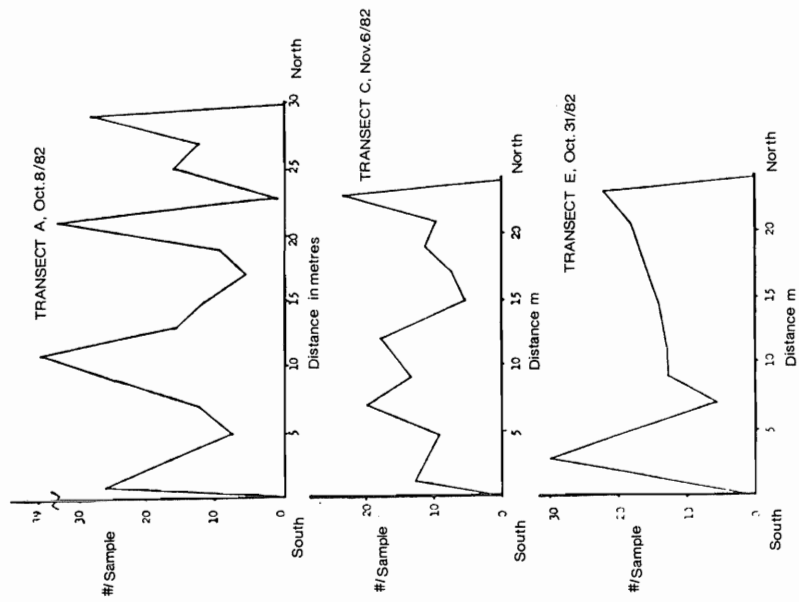


Fig.6. Autumn distribution of Enallagma.

Transect P, March 5/83

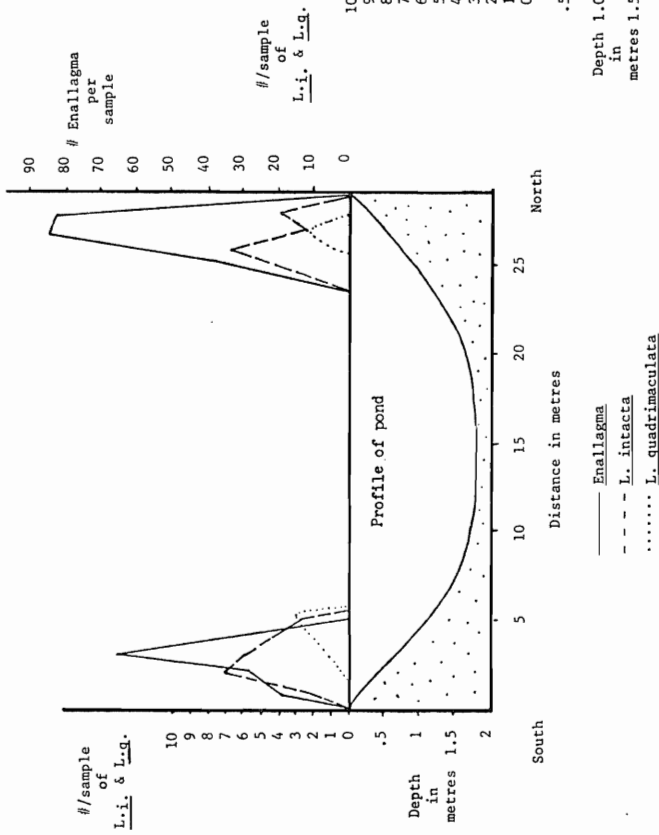


Fig.7. Winter distribution, transect P.

Transect R, March 19/83

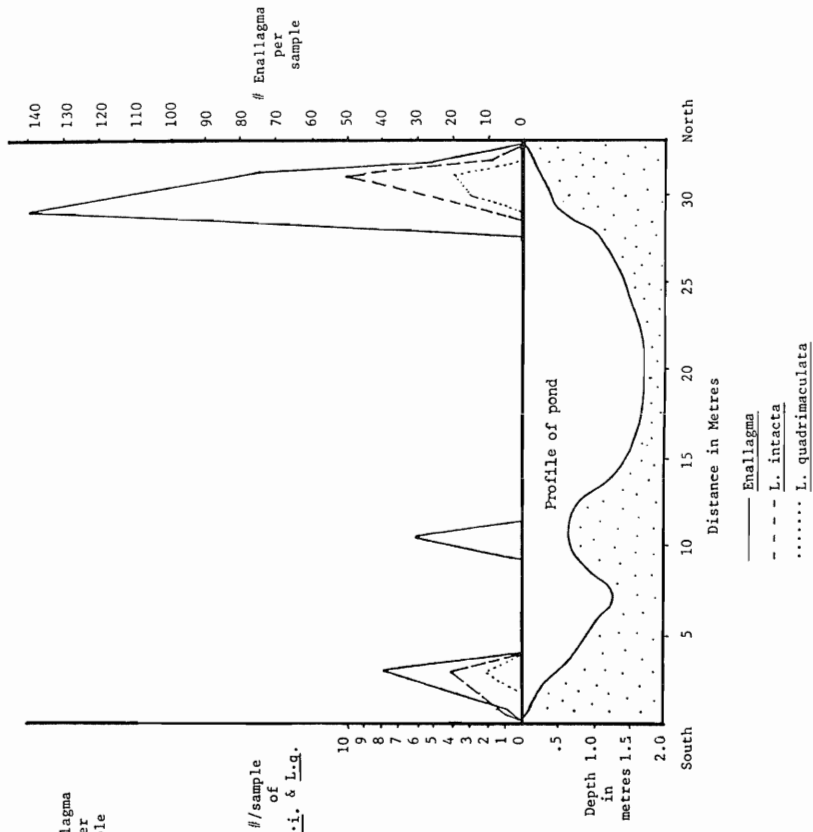


Fig.8. Winter distribution, transect R.

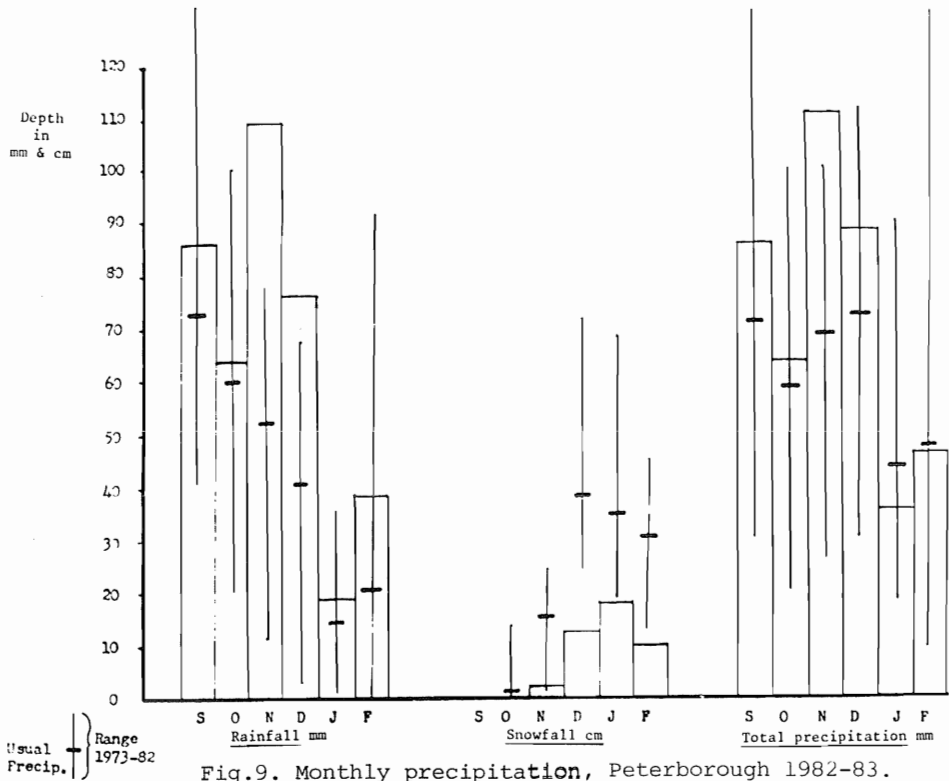


Fig.9. Monthly precipitation, Peterborough 1982-83.

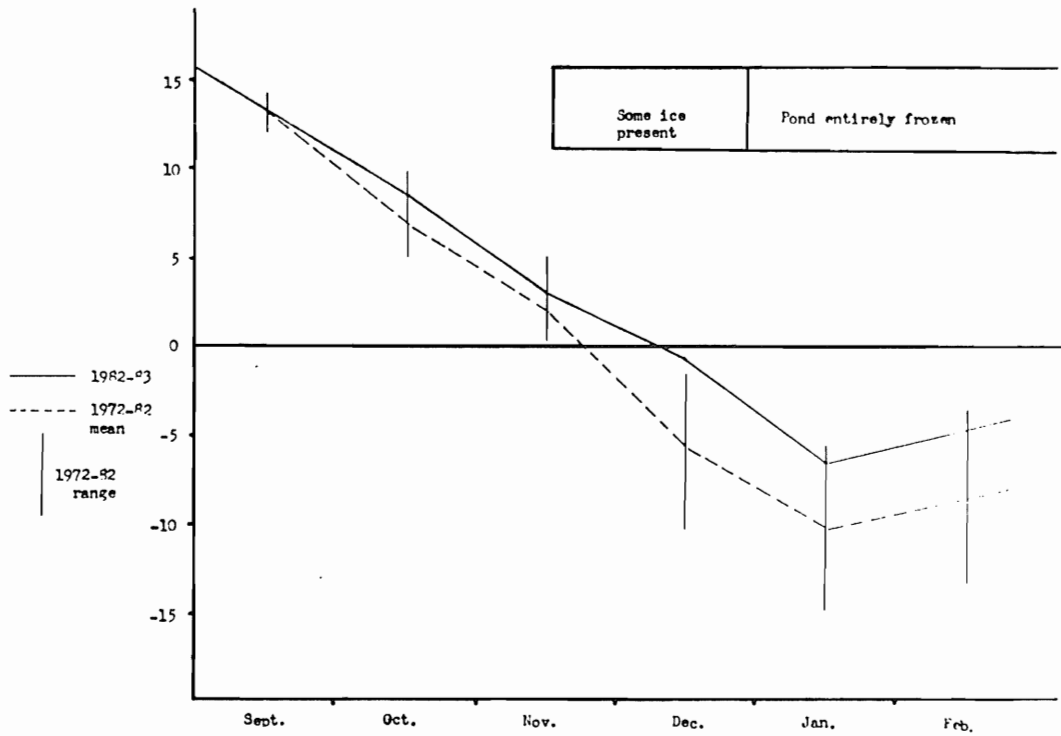


Fig.10. Peterborough mean monthly temperatures, 1972-1983.

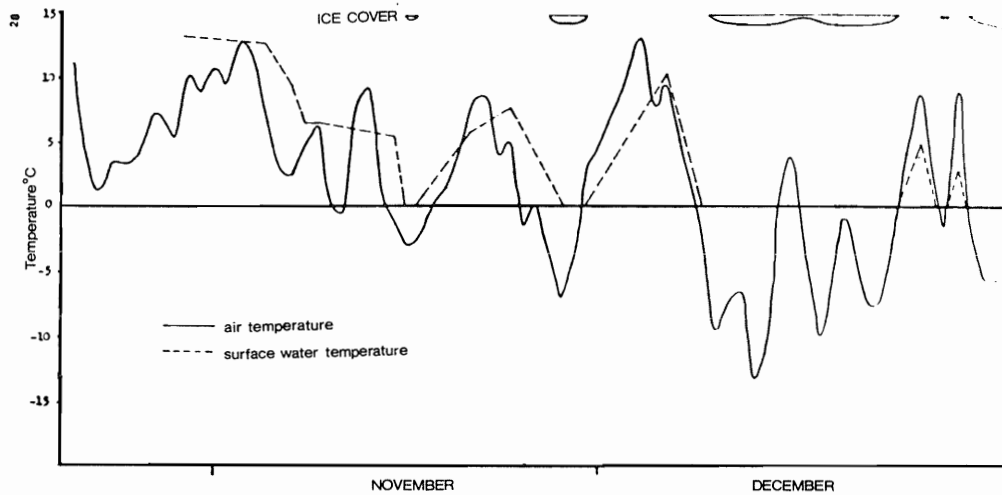


Fig.11. Air and surface water temperatures, Meyer's Pond.

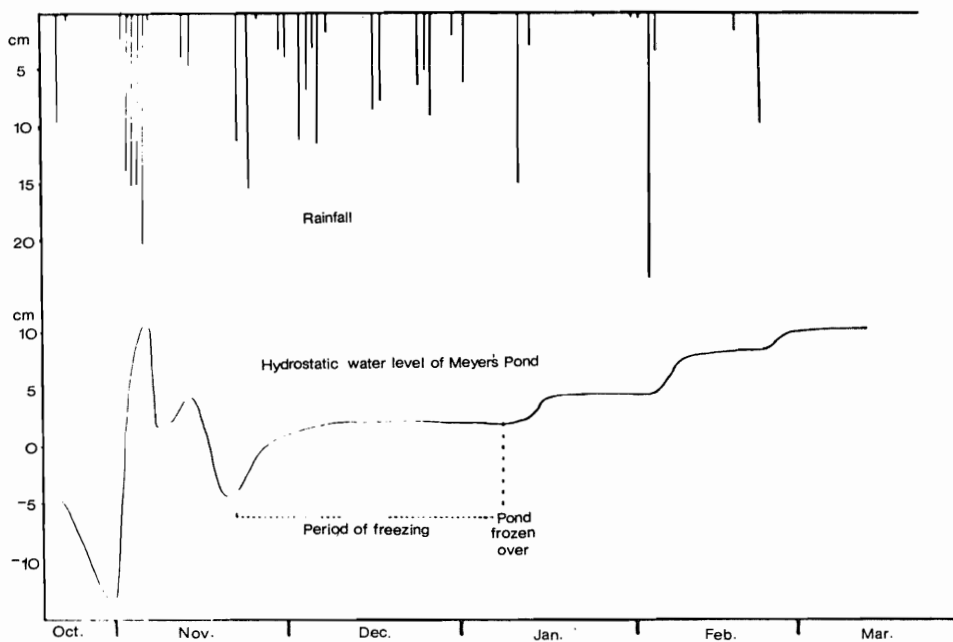


Fig.12. Rainfall-hydrostatic water level response.

layer of ice was 12 cm thick at the time of the first storm, January 10, 1983, and never grew thicker. All subsequent freezing occurred in this perched layer.

As the perched runoff began to freeze downward, the original ice layer floated upward slowly, as some of the water seeped below into the unfrozen pond (see Fig. 14). Thus the ice cover composed of alternate black and white ice layers (see Fig. 15).

The temperature and conductivity profiles of the pond, taken October 24, November 20, 1982 and March 9 and March 14, 1983 indicate that the pond was not stratified but turning over during the autumn months. However, it was very stratified by late winter (see Fig. 16). As a result of the turnover, oxygen concentration was the same at all depths but in early March it can be seen that oxygen concentration decreased with depth in the west and east deep holes (see Fig. 17). The laboratory work indicated that larvae, when frozen and thawed, die. No exceptions were found to this, whether frozen rapidly or slowly (over a period 3-4 hours). This agrees with Corbet et al, 1960, who found that only large, robust, larvae could survive being frozen. The larvae frozen in the laboratory were L. intacta, L. quadrimaculata, and Enallagma, none of which is large or robust.

The results of the outdoor artificial pond are inconclusive. Thirty larvae were placed among the weeds on the gently sloping side. The pond, which was 0.5 metres deep, was allowed to freeze until the ice was 30 cm thick. After removing the ice, 9 larvae were still alive, 13 were dead in the water and 2 were frozen in the ice. No trace of the remaining 6 could be found.

Observations from the aquarium indicated that larvae remained in the weeds and on the sediments while the water stayed fresh. After 4 or 5 days in the same water, larvae began to cling to the sides of the aquarium. After 12 to 14 days, all larvae were found in the top 3-4 cm of the aquarium, and some larvae ventured above the water level. Corbet (1962) found that oxygen concentrations of 2 mg/l would drive larvae to the surface to breathe air by extending their anal appendages above the water. Enallagma, after 2 days in the aquarium, stopped active movement and began to wave their caudal lamellae back and forth to breathe (see Fig. 18).

Discussion

The autumn and winter of this study were most unusual in terms of weather. Fig. 9 indicates the higher than usual rainfall. Note that November and December received more rain than the 1973-81 range. The expected mean monthly rainfall usually decreases as the fall progresses, resulting in a corresponding drop in the water table. This year the large amount of rain caused the water table to be high during freeze-up (see Fig. 4, 12).

The high temperatures delayed ice formation (see Fig. 4, 10, 11). The higher than normal mean monthly temperatures coupled with frequent rainfalls caused the ice cover to virtually grow upwards away from the larval habitat. Fig. 12 shows the ice layer just before the rainfall event of January 10. Note the air space between the ice and the water surface, below which is the larval habitat. After the rainfall of January 10, all freezing downward ceased and the perched runoff froze. Also the original ice floated upwards. Thus this year, no ice penetrated into the larval habitat. At worst (from the point of view of the larvae), algae floating to the surface were frozen. In this study, only 2 Enallagma were found frozen, in spite of extensive searching for larvae trapped in the ice.

As a result of the most unusual weather, no conclusions could be drawn as to the physical effect of the ice on the larval habitat. The lack of observable migration from the perimeter is indicative of this (Table II). Nevertheless, this year provided an excellent opportunity for observing the indirect effects of the winter cover on larval distribution.

As can be seen from Fig. 4, 5 & 6, the autumnal distribution L. intacta, L. quadrimaculata and Enallagma across the pond are relatively constant, albeit the great deal of variation. The winter distribution is slightly different as Fig. 7 & 8 illustrate. All larvae are absent from deep water. This result is similar to that of Lawton (1970) in Durham, England, with Pyrrhosoma nymphula (Fig. 19). It is apparent from Table I that this shoreline concentration of larvae represents a migration, not a kill of larvae, in the deep water. The number of larvae per square metre in winter along the shore is over twice that of the fall. Also from Table 1b, it can be seen that the total larval popula-

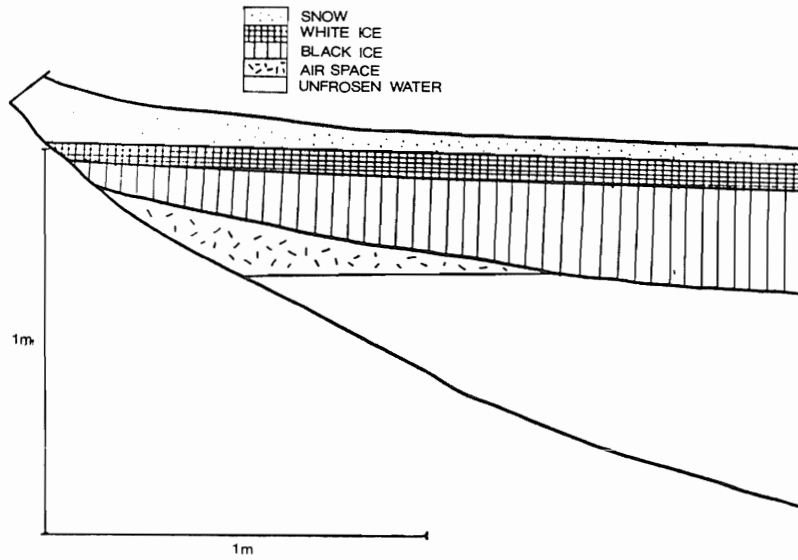


Fig.13. Profile of perched ice.

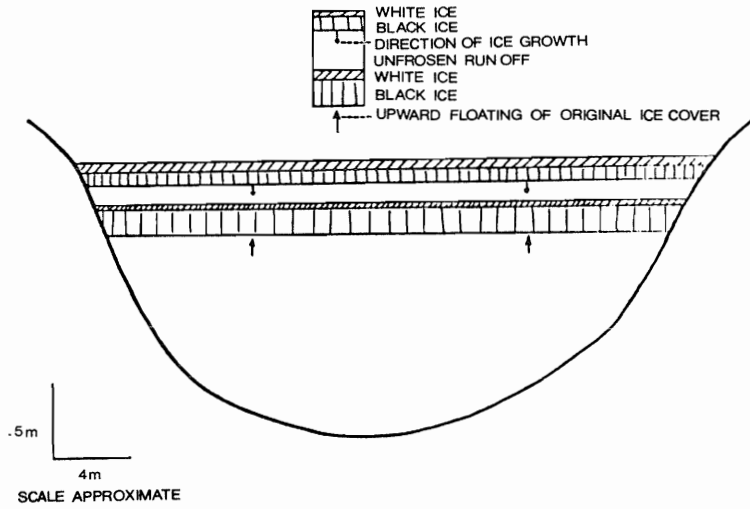


Fig.14. Freezing of perched runoff.

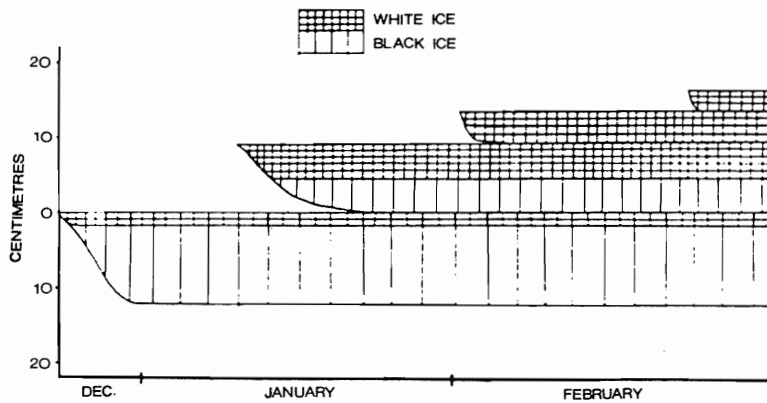


Fig.15. Growth of the ice cover of Meyer's Pond, 1983.
 Each new layer was in response to a rainfall event.

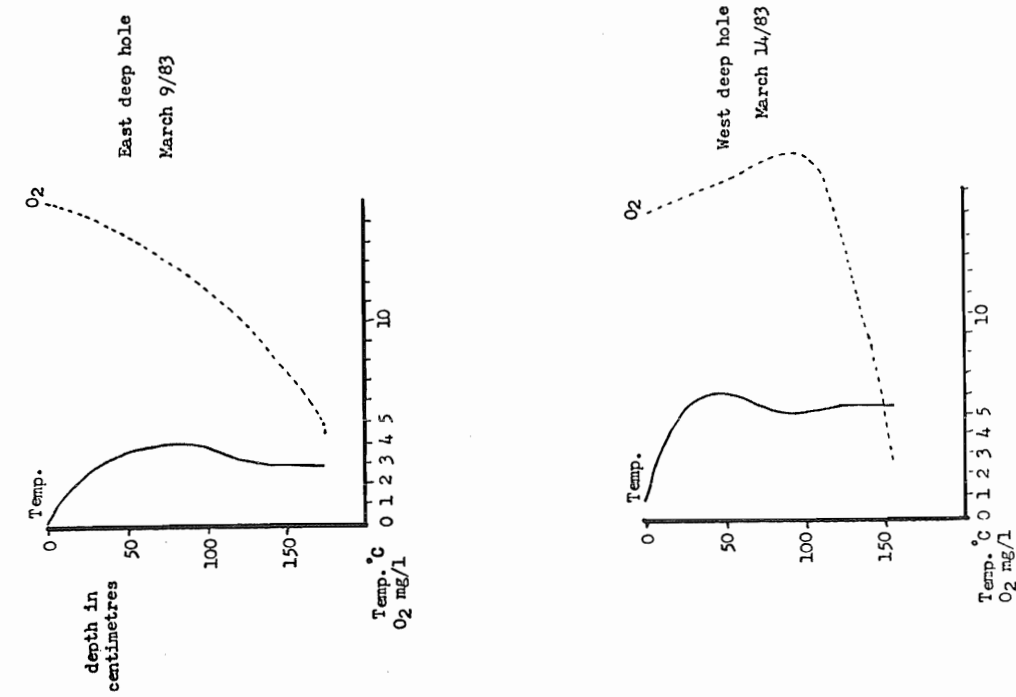


Fig.16. Temperature, conductivity profiles.

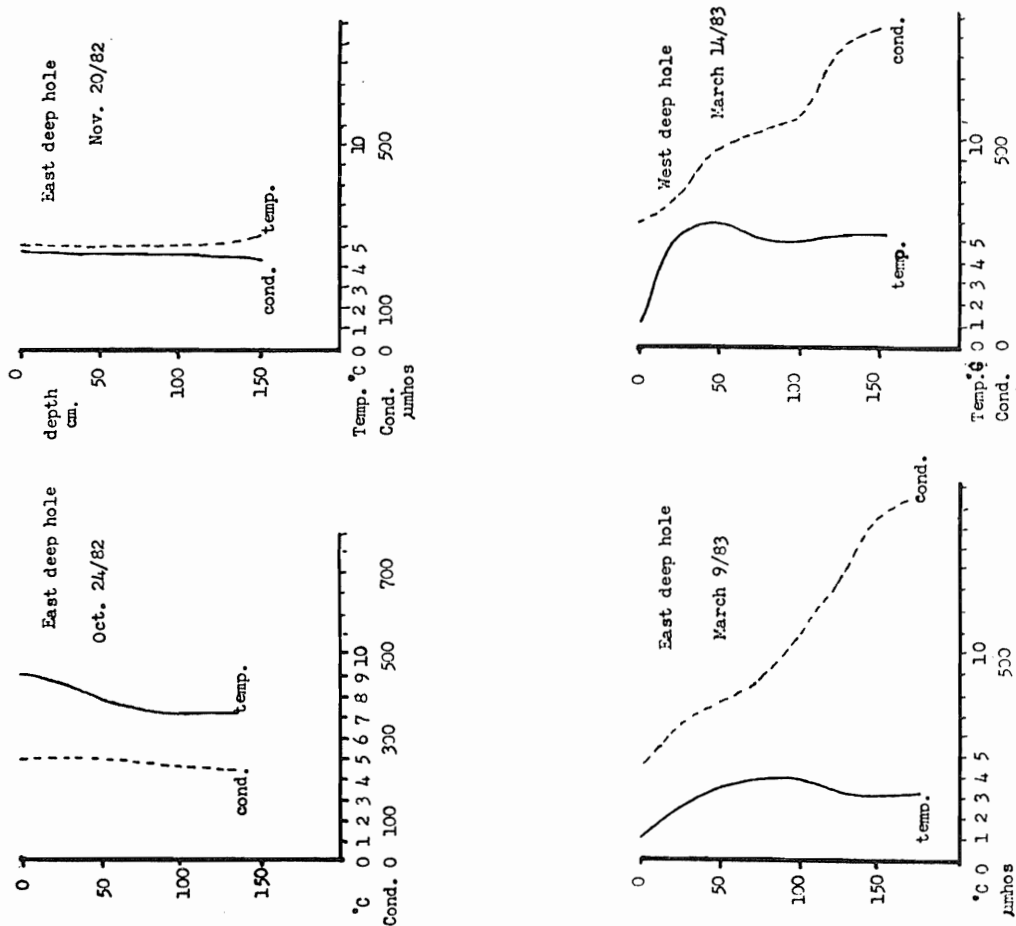


Fig.17. Temperature and oxygen profiles.

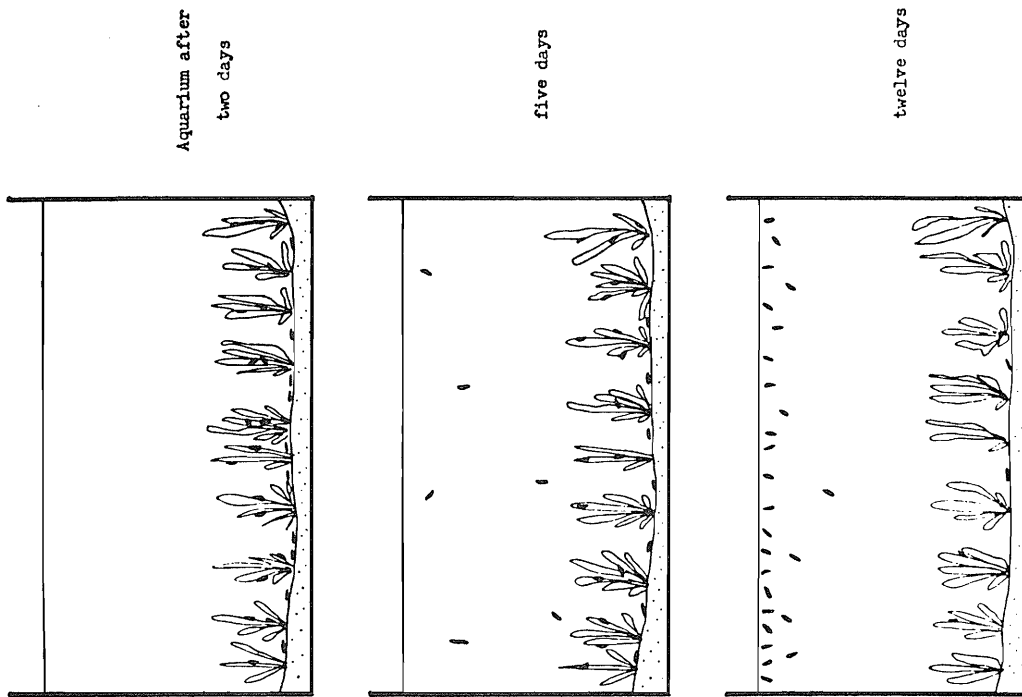


Fig.18. Stagnant aquaria showing larval distribution.

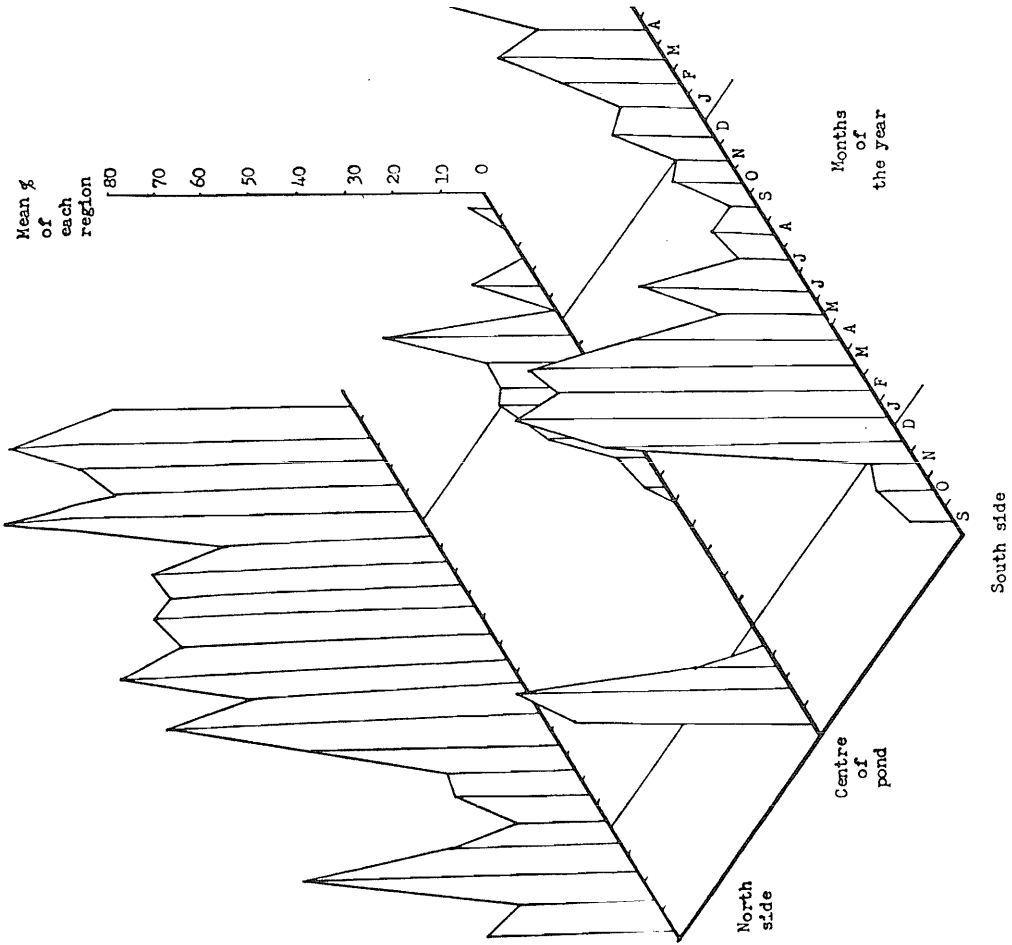


Fig.19. Seasonal distribution of dragonfly larvae (Lawton, 1970).

tion across the transects remains constant in autumn and winter. Transects A, C and D have mean populations of L. intacta of 115 and, L. quadrimaculata of 23 and Enallagma of 1464. Transects P and R have mean transect populations for the 3 above species of 158, 34 and 1720 respectively. These values were obtained by taking the areas under the curves in Fig. 4, 5, 6, 7 and 8.

The migration occurred in response to 1 of 3 possible factors. These are lack of vegetation, lack of prey or lack of oxygen in the deeper regions.

There is some evidence in favour of the first of these possibilities (Fig. 2). L. intacta and Enallagma are weed dwellers. Corbet et al (1960) categorize L. intacta as a "specialized weed dweller". Thus, as the macroalgae and weeds die at the end of their growing season (Wetzel, 1975), L. intacta and Enallagma could be forced to migrate shoreward to find suitable weeds to cling to, the dead plants having fallen to the bottom.

This would not be the case with L. quadrimaculata. Corbet et al (1960) categorize Libellula as a "highly specialized mud dweller". The lack of macroalgae in its environment would not affect Libellula. Thus the shoreward migration of L. quadrimaculata must be attributed to another cause.

It appears that the lack of vegetation, rather than causing the migration of larvae cover, is simply an effect of another condition that exists under the ice. Although this cannot be substantiated in the case of L. intacta and Enallagma, it does remain true for L. quadrimaculata.

The second suggested factor, the lack of prey, can be easily dismissed. Norton et al (1980) felt that starvation did not cause mortality in the field, larvae having a diverse diet including other larvae. Also, they note that larvae can survive "long periods" without food at 16°C. The usual diet of larvae is a reflection of the most common prey available (Pritchard, 1964). Benke (1978) found that these were Chironomids, of the midge larvae and mayfly. Pritchard (1964) also found that Chironomids were the most frequent prey of Anisopterous larvae (Fig. 21). Macan (1964) made the same observation with regard to the Zygoptera present in his fish pond.

The deep regions of Meyer's Pond contain more than 20 Chironomids per scoop. Availability of prey obviously did not necessitate the shoreward migration.

The third proposed explanation of the winter migration was the lack of oxygen in deeper regions (see Fig. 17). The oxygen concentration of the bottom of the west deep hole was 2.6 mg/l. At the east deep hole, 4.2 mg/l. Corbet (1962) noted that 2 mg/l oxygen was the lower threshold for dragonfly larvae at which concentration the larvae ascended above the surface "gasping" for air. The observations in the aquaria, in this study, support this (Fig. 18). Here the larvae climbed closer to the surface as the water was allowed to stagnate.

As an aside, it has been suggested that increasing concentrations of hydrogen sulphide at the bottom of the pond, that is produced by decaying organic matter, could be the cause of migration shoreward. Again, it is this author's opinion that the hydrogen sulphide is symptomatic of the true cause of migration, which appears to be the low oxygen concentrations at the bottom of the pond. Nevertheless, an actual migration shoreward did occur in response to the winter cover of ice and snow. Thus, the original hypothesis of this study is supported.

Acknowledgments

This work was supervised by Drs. W.P. Adams and M. Berrill of the Watershed Ecosystems Program, Trent University. The paper was read at the Eastern Snow Conference by M. Shaw. The great assistance of these persons is gratefully acknowledged.

References

- Adams, W.A., W.P. Adams, P.A. Flavelle, N.T. Roulet, 1983. Variability of light beneath a modified portion of the snow and ice cover of a lake. Verein. Int. Verh. Limnol. (in press)
- Adams, W.P., 1976. Classification of freshwater ice. Musk-Ox 18: 99-102.
- Adams, W.P. and S.A. Mathewson, 1976. Approaches to the study of ice-push features with reference to Gillies Lake, Ontario. Rev. Geogr. Montreal, XXX (Proc. of 1st International Symposium on the Geological Actions Floating Ice, 1976), 1-2: 187-196.

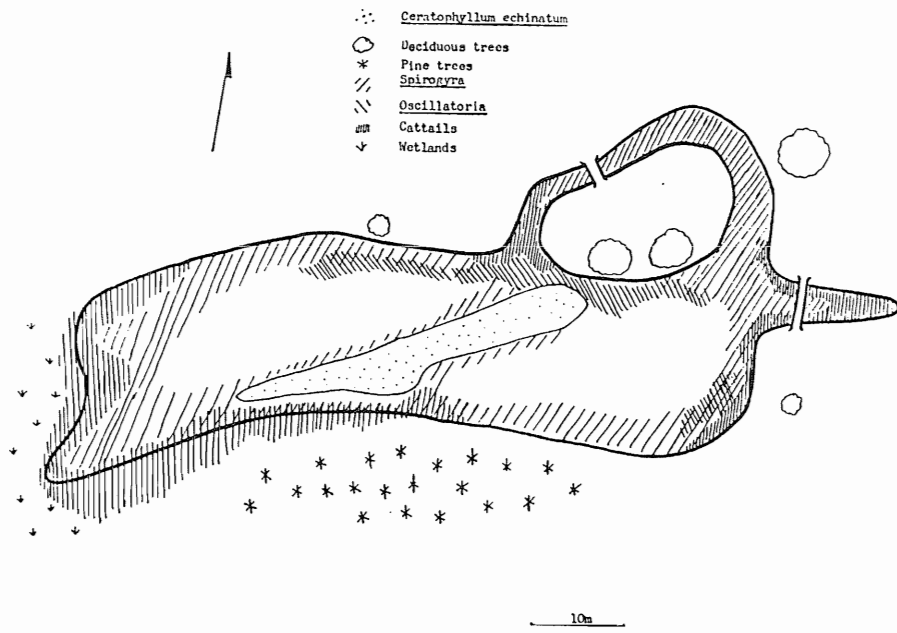


Fig.20. Winter distribution of vegetation.

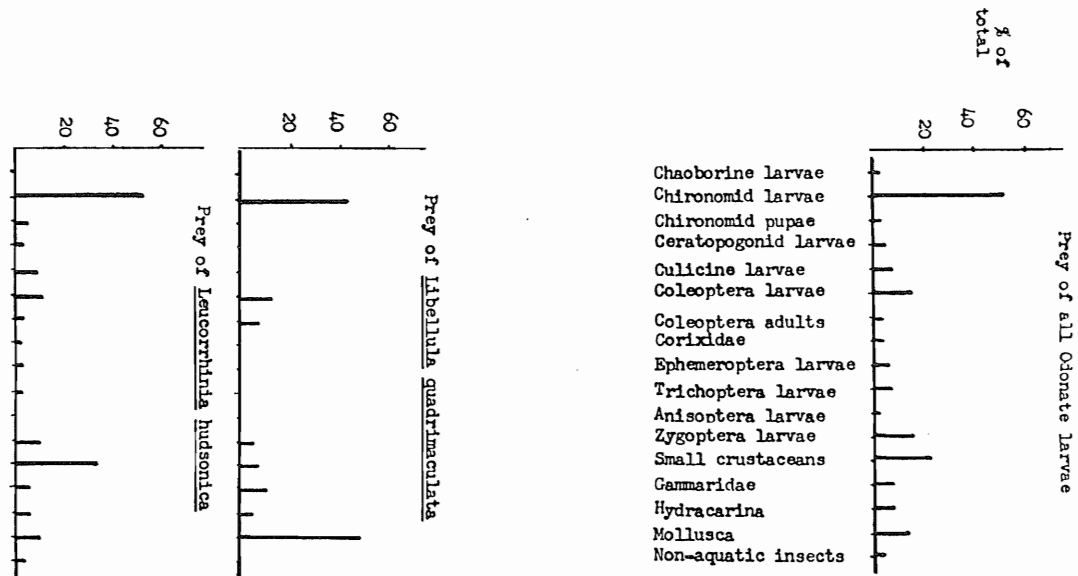


Fig.21. Prey of dragonfly nymphs (Pritchard, 1964).

- Adams, W.P. and T.D. Prowse, 1981. Evolution and magnitude of spatial patterns in the winter cover of temperate lake. Fennia, 159: 343-359.
- Adams, W.P. and N.T. Roulet, 1983. Light under a snowdrift on Lake St. George. Proc. Eastern Snow Conference, 40 (in press).
- Benke, A.C., 1978. Interactions among co-existing predators - a field experiment with dragonfly larvae. J. Anim. Ecol. 47: 335-350.
- Beresford, D., 1983. The effect of the winter ice cover on Odonata larvae in Meyer's Pond. Hons. B.Sc. Thesis, Biology-Geography, Trent University, Peterborough, Ontario, 48 p. + appendices.
- Bruce, J.P. and R. Clark, 1978. Introduction to Hydrometeorology. Pergamon Press, Toronto.
- Corbet, P., 1962. A Biology of Dragonflies. Witherby Ltd., London.
- Corbet, P., 1980. Biology of Odonata. Ann. Rev. of Ent. 25: 189-218.
- Corbet, R., Cynthia Longfield and N.W. Moore, 1960. Dragonflies. Collins, London.
- Gerdel, R.W., 1948. Penetration of radiation into the snowpack. Trans. Amer. Geophysical Union, 29: 366-374.
- Greenbank, J.T., 1945. Limnological conditions in ice-covered lakes, especially as related to winterkill of fish. Ecol. Monogr. 15: 343-392.
- Ingram, B.R., 1975. Diapause termination in two species of damselflies. J. Insect Physiol. 21: 1909-16.
- Jackson, M.B., 1979. Winter oxygen loss in three southern Ontario lakes. M.Sc. thesis, Biology-Geography, Trent University, Peterborough, Ontario.
- Lasenby, D.C. 1983. Professor of Biology, Trent University, Peterborough, Ontario (personal communication).
- Lawton, J.H., 1970. A population study on the larvae of the damselfly Pyrrhosoma nymphula (Sulzer). Hydrobiologia. 36: 33-52.
- Lutz, P.E., 1968. Effects of temperature and photoperiod on larval development in Lestes eurinus. Ecology. 49: 637-44.
- Lutz, P.E., 1974. Effects of temperature and photoperiod on larval development in Tetragoneuria cynosura. Ecology. 55: 370-77.
- Macan, T.T., 1964. The Odonata of a moorland fishpond. Int. Revue ges Hydrobiol. Hydrogr. 49: 325-360.
- Maguire, J., 1975. Effect of ice and snow on transmission of light in lakes. Scientific Series No. 54. Inland Waters., Environment Canada.
- McClellan, A.G., 1971. Ambiguous "glacial" striae formed near water bodies. Can. J. Earth Science. 8: 477-479.
- Needham, J., M. Westfall, 1955. Dragonflies on North America. Univ. Calif. Press, California.
- Otto, J. and A. Towle, 1969. Modern Biology. Holt, Rinehart and Winston, Inc., Toronto.
- Outerbridge, K., 1981. Transmission of light through a snow cover. Honours thesis, Dept. of Geography, Trent University, Peterborough, Ontario.
- Pritchard, G., 1964. The prey of dragonfly larvae in ponds in northern Alberta. Can. J. Zool. 42: 785-800.
- Prowse, T., 1977. The importance of winter lake cover to underwater production. Ecology Bulletin, Dept. of Biology, Trent University, Peterborough, Ontario. 3: 8-15.
- Sagriff, L., 1979. Temporal and spatial variability of phytoplankton in an ice covered lake. Honours thesis, Biology-Geography, Trent University, Peterborough, Ontario.
- Schindler, D.W., 1971. Light, temperature and oxygen regimes of selected lakes in the experimental lake area, northern Ontario. J. Fish Res. Bd. Can. 28: 157-169.
- Walker, E., 1953. The Odonata of Canada and Alaska. Univ. of Toronto Press, Toronto.
- Wassen, G., 1966. Vegetation and flora eines lapplandischen Seeufers. Gardiken. Stockholm. Kungliga Svenska Vetenskapsakademiens avhandlingar i naturskyddsarenden 222. 144 p.
- Wetzel, R.G., 1975. Limnology. Saunders College Pblg. Philadelphia.
- Wright, R.J., 1964. Dynamics of a phytoplankton community in an ice covered lake. Limnologica, Oceanographica 9: 163-178.