

THE EFFECTS OF LAKE DESTRATIFICATION ON SEDIMENT
OXYGEN CONSUMPTION AND THE OSMOREGULATORY AND
RESPIRATORY ACTIVITIES OF CHIRONOMUS TENTANS
(FABR.), CHIRONOMUS RIPARIUS MEIGEN, AND
CHAOBORUS PUNCTIPENNIS (SAY)

By

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PREFACE

The objectives of this study were to (1) observe the effects of lake destratification on sediment and organism oxygen consumption, maintenance of hemolymph osmotic pressure, and ion concentrations in two benthic dipteran larvae and (2) determine a point at which the interaction of several environmental variables (e.g. temperature, dissolved oxygen, and salinity (NaCl)) caused a negative response in the organisms's ability to respire and osmoregulate.

The author is deeply indebted to Dr. Jerry L. Wilhm, professor, Department of Ecology, Fisheries, and Wildlife, who served as major adviser, for his invaluable advice, supervision, and encouragement in this study. His friendship throughout the past years will remain meaningful for years to come.

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CHAPTER I

INTRODUCTION

Chironomus sp. and Chaoborus sp. occur in large numbers in the anoxic, colder hypolimnetic waters of a lake. These organisms are of interest to investigators due to their physiological and morphological adaptations that enable them to withstand anoxic conditions. The hypolimnion in the summer has lower temperatures, less dissolved oxygen (DO), and more reduced materials such as hydrogen sulfide and ferrous iron. During summer and early fall, a thermocline is present and some benthic invertebrates migrate from the hypolimnion to the epilimnion (Hilsenhoff 1968). Organisms that remain in the hypolimnion survive in the soft bottom mud or in the water above the sediments. The latter instars of Chironomus sp. and Chaoborus sp. generally occur in the sediments of eutrophic lakes.

Benthic invertebrates exhibit physiological changes to seasonal changes in DO and temperature. Reish and Richards (1966) state that perhaps the single most important environmental factor for the growth, reproduction, and survival of aquatic animals is the DO in the water. The maintenance of a normal metabolic rate at low oxygen pressures enables Chironomus sp. and Chaoborus sp. to live under summer stratified conditions. It is reasonable to suppose that these organisms have evolved both respiratory and osmoregulatory specializations which enable them to thrive in the hypolimnion.

The rate of oxygen consumption by sediments from the overlying water is another important physiological measurement in lakes. Hargrave (1969) showed changes in oxygen consumption of the water overlying the sediments were directly correlated with the sediment biological activity and to temperature. The sediment removes DO from the overlying water through biological and chemical respiratory activities (Drury and Gearheart 1975, Fillos 1976, Brewer et al. 1977). The sediments are also a major source of nutrients and reduced substances. Ammonia and various reduced substances are released from the sediments and accumulate in the overlying water causing a further reduction in DO levels (Edwards 1958, Bloesch 1977).

Artificial mixing of a lake by mechanical pumping can eliminate thermal stratification so that the entire body of water is circulated and becomes oxygenated. Artificial mixing of lakes by mechanical pumping of compressed air or epilimnetic water down into the hypolimnetic waters to break up stratification has been accomplished in a number of lakes (Bernhardt 1967, Anon 1971, Biederman and Fulton 1971, Garton et al. 1976). Destratification is a relatively inexpensive technique to use when water quality is poor due to an anoxic hypolimnion (Garton et al. 1979). If artificial destratification is successful, then the benthic organisms must adapt to a new set of physicochemical parameters during summer.

The purpose of the present study was to determine the effects of changes in physicochemical parameters produced by artificial destratification on sediment oxygen consumption and the osmoregulatory and respiratory activities of Chironomus tentans (Fabr.), Chironomus riparius Meigen and Chaoborus punctipennis (Say). Measurements were made on:

- (1) seasonal variation in oxygen consumption of the sediments and oxygen consumption, hemolymph ions (Na^+ , K^+ , Cl^-), and osmotic pressure of C. tentans, C. riparius, and C. punctipennis in Ham's and Arbuckle lakes; and
- (2) the effects of temperature, DO, and salinity on oxygen consumption and the concentration of hemolymph ions of C. riparius and C. punctipennis in controlled laboratory experiments.

CHAPTER II

DESCRIPTION OF LAKES AND PUMPING DESTRATIFICATION

METHODS

Several artificial destratification methods have been used in lakes to improve water quality and extend the vertical distribution of the biota. One method involves bubbling air into the hypolimnion (Riddick 1947, Laverty and Nielson 1978). Other artificial mixing methods involve mechanical pumps which may pump hypolimnetic water to the epilimnion (Hooper et al. 1953, Anon 1971, Biederman and Fulton 1971) or the converse (Steichen 1974, Garton et al. 1976). These methods result in dissolved oxygen (DO) in the hypolimnion throughout the summer when anoxic conditions usually exist (Bernhardt 1967, Kroppert et al. 1970, Anon 1971, Biederman and Fulton 1971, Garton et al. 1979). Changes in other physicochemical conditions and biological parameters have also been measured under destratified conditions (Inland Fisheries Branch 1970, Ferraris and Wilhm 1977, McClintock and Wilhm 1977, Garton et al. 1979).

Two Oklahoma lakes, Ham's and Arbuckle, were selected as the sites for this study. Mechanical pumping was being used to attempt destratification in both lakes (Garton et al. 1976, 1979). Ham's Lake is approximately 8 km W of Stillwater in Payne County (Figure 1). The Soil Conservation Service built the lake in 1965 as a flood detention reservoir. The surface area and volume at the principle spillway level are

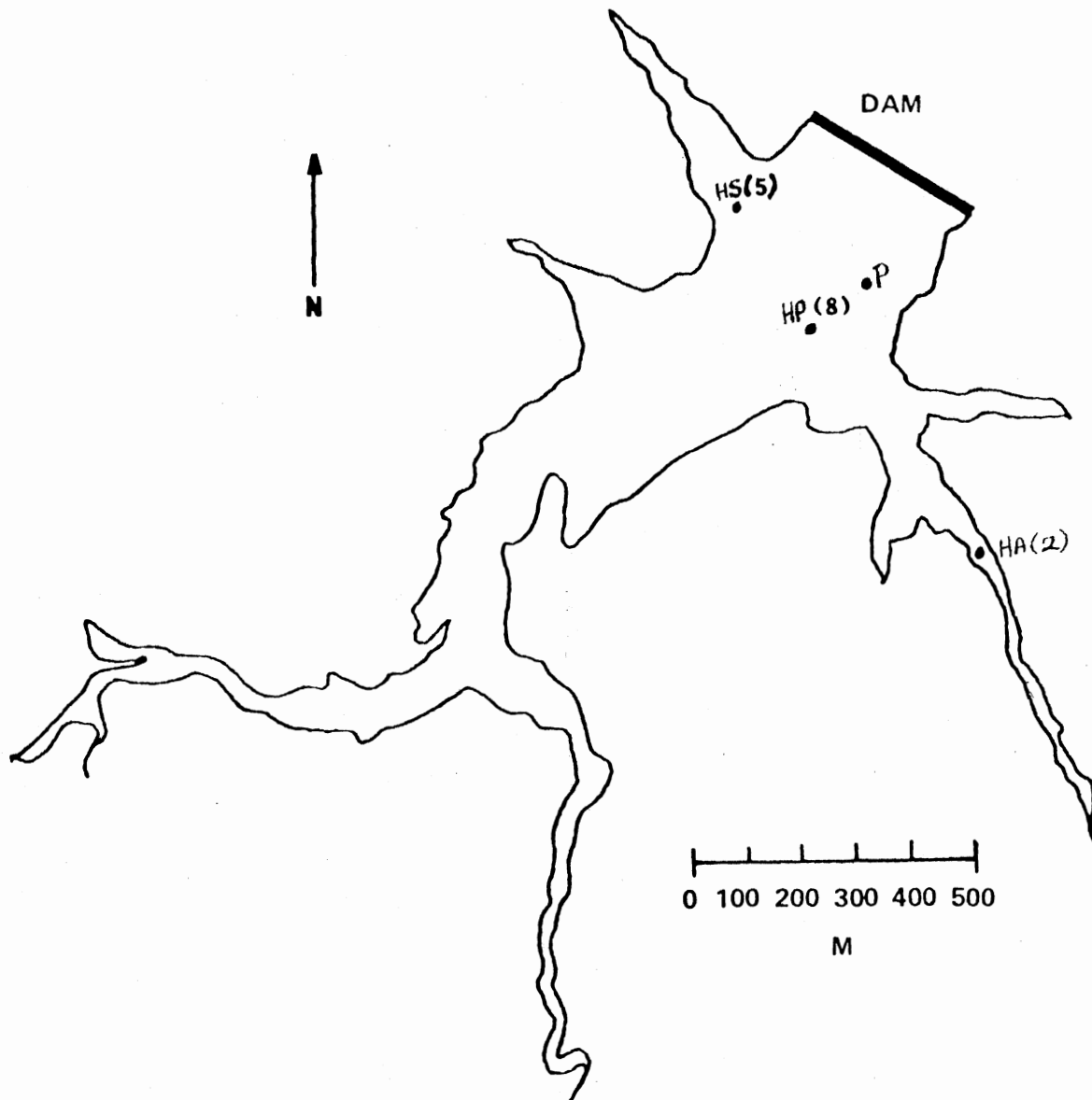


Figure 1. Ham's Lake Showing Sampling Stations (Numbers in Parentheses Denote Depth in Meters; P = Pump)

40 ha and 115 ha-m, respectively (Steichen 1974). The deepest part of the lake is 9.5 m with an average depth of 2.9 m.

Arbuckle Lake, in Murray County, is approximately 9.6 km SW of Sulphur (Figure 2). Arbuckle Lake was created by impounding Buckhorn, Rock, and Sandy creeks in 1965. It provides local municipal water sources, flood control, and recreation (Gomez and Grinstead 1973). The surface area and volume are 951 ha and 8930 ha-m, respectively. The maximum depth at the principle spillway level is 27.4 m, and the average depth is 9.4 m. Arbuckle's area is almost 24 times larger than Ham's Lake.

Mechanical pumps were placed at the surface in the central pool of both lakes to prevent summer stratification. A single Garton axial flow pump consisting of a crop drying fan powered by a 460V, 1.12 kW motor was installed at Ham's Lake. No pumping occurred at Ham's Lake during 1977 and the lake stratified. The pump was activated in May, 1978, and pumping continued until December, 1979. Destratification occurred in Ham's Lake during the summer of 1978. To destratify Arbuckle Lake, a cluster of 16 Garton pumps arranged in an open-centered square were used. Pumping in 1977 was limited due to the late installment of the pumps. Pumps began operating in April, 1978, prior to strong thermal stratification. In mid-May, a storm caused eight pumps to sink to the bottom. The eight operable pumps could not prevent the lake from stratifying. By September, 1978, the 16 pumps were again in operation and may have been successful in lowering the metalimnion but did not oxygenate the hypolimnion.

Sampling sites were selected in both lakes relative to pump location. Samples were taken from 14 April 77-31 December 1978 from three

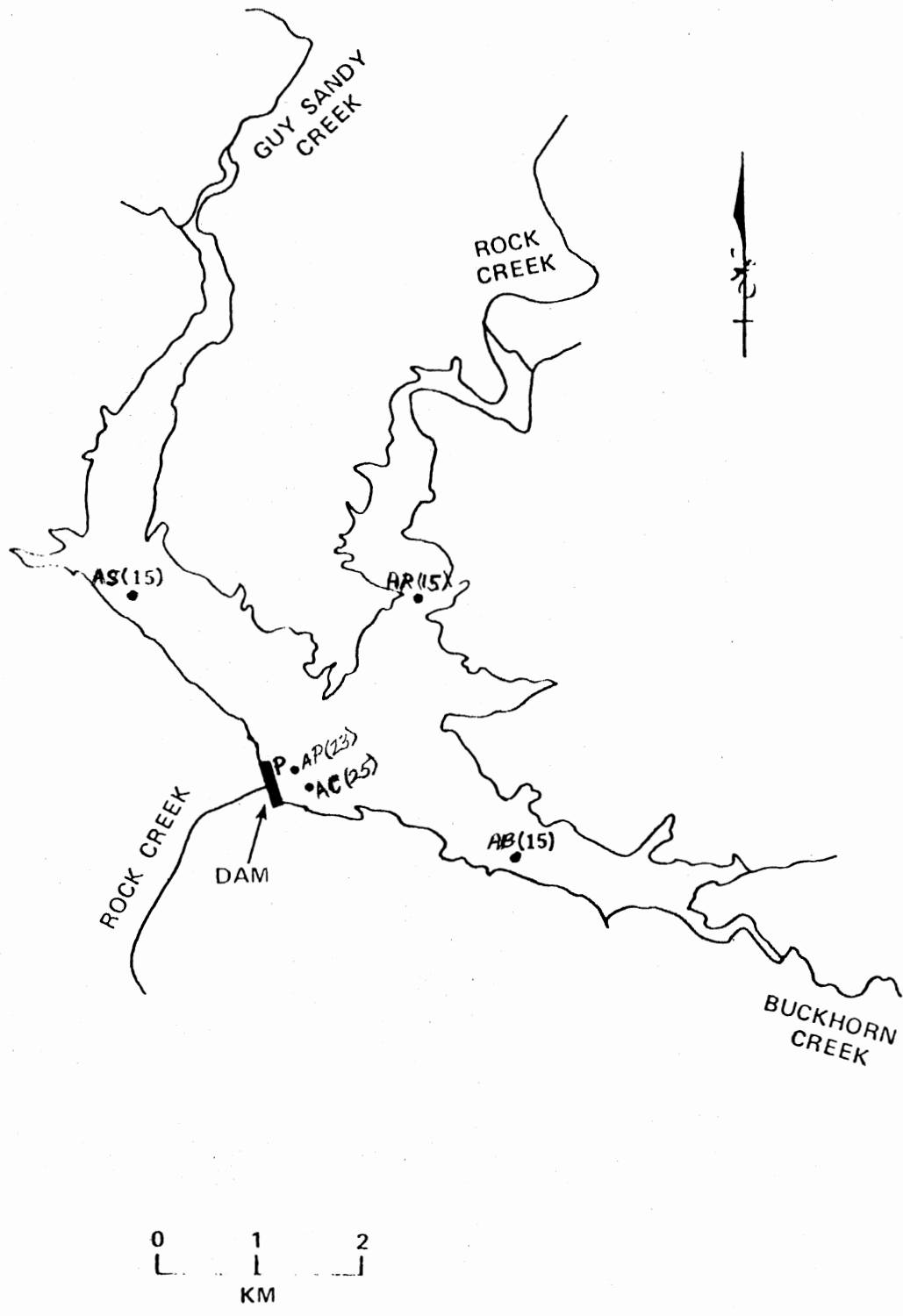


Figure 2. Arbuckle Lake Showing Sampling Stations (Numbers in Parentheses Denote Depth in Meters; P = Pump)

stations in Ham's Lake (Figure 1). The central pool station (HP) was established south of the pump. Another station, HS, approximately 50 m W from station HP, remained stratified due to a submerged dam of a former farm pond which prevented mixing. The east arm station (HA) was also approximately 50 m from station HP and remained destratified during the summer. The depths of stations HP, HS, and HA are 8, 5, and 2 m, respectively.

Samples were taken from 10 May 77-16 December 1978 from five stations in Arbuckle Lake (Figure 2). Two stations were established in the central pool. One station (AP) was close to the pump while the other (AC) was established 150 m east in the central pool. The average depth of stations AP and AC were 23 and 25 m, respectively. One station each was selected in Buckhorn (AB), Rock (AR), and Sandy (AS) creeks. These stations had an average depth of 15 m. Replicate stations approximately 150 m from each station were sampled from March-June, 1977, at both lakes to measure variation.

CHAPTER III
SAMPLING PROCEDURES AND PHYSICOCHEMICAL
CONDITIONS OF LAKE WATER AND
SEDIMENTS

Sampling Procedures

Benthic Macroinvertebrates

Chironomus tentans, Chironomus riparius, and Chaoborus punctipennis were collected monthly during 1977-78 from Ham's and Arbuckle lakes with a Ekman grab sampler. The sample was washed through a wire-mesh screen (#30) bucket and larvae were placed in jars containing water from the hypolimnion that was collected with a van Dorn water sampler. The jars were placed in ice chests and transported to the laboratory. Organisms were maintained in the laboratory at the same temperature as recorded in the field at the time of sampling. All larvae were used immediately after collecting.

Physicochemical Conditions

Physicochemical conditions of the hypolimnetic water and sediments were measured in Ham's and Arbuckle lakes during 1977 and 1978. Spatial and temporal changes were observed in organic carbon and pH of the sediments and temperature, dissolved oxygen (DO), conductivity, and pH of the bottom water. Temperature and dissolved oxygen were taken with a

Yellow Springs Instrument (YSI) meter (Model 54A) and conductivity with a YSI conductivity meter (Model 33). The pH of the water and sediments was measured using a Corning Model 610 pH meter. Organic carbon was determined by the oxidation procedure of Schollenberger (Black 1968).

Physicochemical Conditions of Lake Water and Sediments

Ham's Lake

The values of the physicochemical conditions of the hypolimnetic water in Ham's Lake during 1977-1978 is shown in Table I. Temperature of the bottom water ranged from 7-32°C. Temperatures at station HS were consistently lower during both summers than those at the central pool station (HP). Little variation existed between stations HP and HA. Seasonal variation among the stations was slight during fall and winter. Pumping during summer 1978 prevented most of the lake from stratifying and the temperature of the hypolimnion was kept lower 1 month longer than in 1977.

Dissolved oxygen (DO) was low in the bottom water in the unmixed area of the lake in both summers (Table I). From 27 May-15 August 1977, DO concentration averaged 0.2 mg ℓ^{-1} at stations HP and HS and 6.5 mg ℓ^{-1} at the arm station (HA). Values exceeded 4.5 mg ℓ^{-1} at all stations from fall to spring. During pumping in summer 1978, values exceeded 2.5 mg ℓ^{-1} in the central pool and were again low in the unmixed area. This variation still existed among stations on 29 October after the lake in the unmixed area had turned over.

Conductivity ranged from 140-580 μ mhos. During stratification in

TABLE I
 MEAN TEMPERATURE, DISSOLVED OXYGEN, CONDUCTIVITY, AND pH OF THE BOTTOM WATER
 IN HAM'S LAKE IN 1977-1978*

Variable	Station (Water Depth in m)	Apr	May	Jun	Aug	Oct	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Dec
		15	27	23	15	26	13	23	25	23	21	23	29	29	2
Temperature (°C)	HA (2)	20	24	29	30	18	7	16	25	25	28	26	23	16	9.5
	HP (8)	21	24	27	32	19	7	16	22	25	26	26	23	16	9.0
	HS (5)	17	19	19	22	16	7	17	18	18	19	24	22	15	9.5
Dissolved Oxygen (mg l ⁻¹)	HA (2)	9.2	5.9	7.8	5.8	8.7	9.0	9.0	6.5	4.5	4.4	4.3	5.4	6.5	8.4
	HP (8)	2.8	1.0	0.0	0.2	7.1	8.4	8.4	5.4	3.5	2.5	4.4	4.5	6.2	8.2
	HS (5)	3.4	0.1	0.0	0.2	6.9	9.0	9.0	4.5	0.2	0.3	0.2	0.2	5.5	8.4
Conductivity (µmhos)	HA (2)	388	355	-	420	295	235	235	355	320	340	349	330	270	225
	HP (8)	380	140	-	300	295	245	245	350	325	355	348	335	280	225
	HS (5)	380	345	-	580	293	250	250	322	335	390	335	310	265	225
pH	HA (2)	-	7.9	8.0	7.7	8.0	8.5	8.5	8.0	8.4	7.9	8.3	8.3	8.2	8.5
	HP (8)	-	7.7	7.8	7.5	7.4	8.5	8.5	8.1	8.5	8.2	8.3	8.4	8.2	8.5
	HS (5)	-	7.6	7.8	7.5	7.7	8.4	8.4	8.0	8.5	8.3	8.4	8.4	8.1	8.6

* Values are the means of three samples.

- Data not measured.

summer 1977, values were lower in the central pool than at stations HA and HS. Little variation existed among stations from 26 October 1977 to the end of the study. Values were generally lower in fall and spring than in summer at all stations.

pH of the bottom water during the study ranged from 7.4-8.6. Little variation existed during both summers although values were lower in 1977 than during other seasons. pH values of the sediment were generally similar to those recorded for the bottom water. The sediment pH became more acidic at all stations during summer 1977 when the lake stratified. During mixing in summer 1978, the sediment pH became more alkaline at stations HP and HA. pH generally increased during winter with a value of 8.5 recorded on 13 March 1978. No significant variation existed among seasons or stations.

Percent organic matter of the sediments in the central pool as determined by the oxidation procedure ranged from 1.0-6.8 (Table II). Organic matter was highest at station HA during summer 1977 under stratified conditions and at station HS during summer 1978. Organic matter measured from a sediment core was generally greater in the 0-1 cm depth than in the 4-5 cm deep sediments.

Arbuckle Lake

Since little variation existed among physicochemical variables measured at the 15 m depths in the arms or between the 23 and 25 m depths in the central pool, data are averaged in Table III. The temperature of the bottom water ranged from 5-26°C. The maximum temperature measured in the central pool was 17°C on several dates and 26°C at the 15 m stations.

TABLE II

PERCENT ORGANIC MATTER OF THE SEDIMENTS IN HAM'S LAKE IN 1977 AND 1978*

Station (Water Depth in m)	Sediment Depth (cm)	Month													
		Apr 15	May 27	Jun 23	Aug 15	Oct 26	Mar 13	Apr 23	May 25	Jun 23	Jul 21	Aug 22	Sep 29	Oct 29	Dec 2
HA (2)	0-1	1.0	-	7.5	7.4	4.2	2.4	3.9	3.7	3.8	4.0	3.9	3.4	3.7	3.8
HP (8)	0-1	3.7	-	6.8	6.8	4.1	3.5	3.1	4.0	4.0	3.6	4.6	4.3	3.9	4.1
	4-5	-	-	-	-	-	-	-	3.8	4.3	4.6	4.0	3.3	4.7	3.8
HS (5)	0-1	4.3	-	5.1	4.6	6.3	4.8	5.7	4.9	5.5	5.6	6.0	5.4	5.5	4.9
	4-5	-	-	-	-	-	-	-	5.0	4.9	4.8	4.8	5.0	4.7	4.7

* Values are the means of four samples.

- Data not measured.

TABLE III

MEAN TEMPERATURE, DISSOLVED OXYGEN, CONDUCTIVITY, AND pH OF THE BOTTOM WATER
IN THE ARMS AND THE CENTRAL POOL OF ARBUCKLE LAKE IN 1977 AND 1978*

Variable	Depth (m)	May 16	Jun 13	Jul 20	Aug 22	Oct 21	Dec 30	Mar 15	Apr 29	Jun 9	Jul 11	Aug 15	Sep 16	Oct 22	Nov 24	Dec 16
Temperature (°C)	15	15	19	21	25	20	8	5	17	19	24	26	26	20	14	8
	24	13	15	15	16	16	8	5	11	14	16	17	17	17	14	8
Dissolved Oxygen (mg l ⁻¹)	15	2.2	0.1	0.1	0.1	7.3	12.0	8.8	5.4	1.0	0.1	0.1	2.3	4.9	-	8.4
	24	0.4	0.1	0.1	0.1	3.8	12.0	8.6	4.7	0.3	0.1	0.1	0.2	2.4	-	7.7
Conductivity (µmhos)	15	388	396	428	497	418	274	310	417	385	423	460	457	425	352	298
	24	380	380	410	485	410	273	315	390	410	422	455	410	422	348	305
pH	15	7.9	8.0	7.6	7.4	7.6	7.9	7.6	8.1	8.0	8.2	8.1	8.1	8.1	8.3	8.4
	24	7.6	8.0	7.7	7.5	7.9	7.6	8.2	7.1	8.2	8.0	8.3	8.0	8.0	8.3	8.4

* Values are the means of three samples at the three 15 m stations (AR, AB, and AS) and two central pool stations (AC-25 m and AP-23 m).

- Data not measured.

Dissolved oxygen values were similar between the 15 and 24 m depths during the study (Table III). DO ranged from 0.1-12.0 mg ℓ^{-1} . Anoxic conditions in the central pool were reached earlier in the spring and remained lower longer in the autumn at the stations in the central pool than at the arm stations.

Conductivity varied from 273-497 μmhos . Little variation existed among the central pool and arm stations. Values were highest at all stations during summer.

Little variation in pH of the bottom water existed among stations. pH values of the hypolimnetic water ranged from 7.1-8.4. Values were generally more alkaline in 1978 than in 1977. pH of the sediments ranged from 6.6-8.4. No consistent trends existed among stations in pH values of the bottom water and sediments.

Spatial and temporal variation in percent organic matter was not significant during the sampling period (Table IV). The range in percent organic matter was 4.0-6.8%. Organic matter was higher in 1978 than in 1977 and was generally greater in the surface sediments than at the 4-5 cm depth.

TABLE IV
 PERCENT ORGANIC MATTER OF THE SEDIMENTS IN ARBUCKLE LAKE IN 1977 AND 1978*

Water Depth (m)	Sediment Depth (cm)	May 5	Jun 13	Jul 18	Aug 18	Oct 20	Dec 30	Mar 15	Apr 29	Jun 9	Jul 11	Aug 13	Sep 16	Oct 22	Nov 24	Dec 16
15	0-1	4.8	4.6	4.7	4.8	6.0	4.4	6.7	4.7	5.2	5.1	5.3	5.8	5.9	5.9	5.2
	4-5	-	-	-	-	-	-	-	-	5.4	5.0	5.0	5.6	5.3	5.6	5.2
24	0-1	4.3	4.7	4.0	4.5	6.6	6.5	6.8	5.8	6.0	6.4	6.8	6.2	6.7	6.3	6.3
	4-5	-	-	-	-	-	-	-	-	5.6	6.0	6.2	6.4	6.4	5.5	6.2

* Values are the means of four samples at the three 15 m stations (AR, AB, and AS) and two central pool stations (AC-25 m and AP-23 m).

- Data not measured.

CHAPTER IV

SEDIMENT OXYGEN CONSUMPTION

Introduction

The rate of consumption of dissolved oxygen (DO) from the overlying water by undisturbed sediments is a rapid and sensitive index of benthic community metabolism (Hargrave 1969). DO is removed from the overlying water by bacterial and benthic invertebrate respiratory activities in the aerobic layer and by the immediate oxygen demand of the reduced substances from the deeper anaerobic layers.

Early workers found that the respiration rate generally was independent of oxygen concentration until the oxygen concentration of the water was depleted to some threshold value below which the respiration rate decreased (Harrison 1972). A linear relationship exists between oxygen concentration and rate of oxygen consumption by the sediment and hypolimnetic water (Longmuir 1954, Edwards and Rolley 1965, Edberg 1976, Fillos 1976, Graneli 1976, Brewer et al. 1977). Seasonal variation in sediment oxygen consumption has been observed to be more dependent on the temperature of the system than the oxygen concentration (Baity 1938, Gardner et al. 1965, Hargrave 1969).

Bacterial densities fluctuate in response to the DO levels in the water. Bacterial densities increase linearly with increasing DO levels in the hypolimnion (Drury and Gearheart 1975). Generally,

bacterial densities decrease in the deeper layers of the sediment column. Zobell and Stadler (1940) found that sediment bacteria multiply much less as oxidizable organic matter becomes limiting. Since anaerobic metabolism generally increases in the sediment column below 5 cm due to the accumulation of reduced substances, chemical oxygen consumption increases (Pamatmat et al. 1973).

Oxygen consumption has been correlated with the amount of organic matter (Hargrave 1972). The uptake of dissolved organic matter (DOM) appears to be primarily a bacterial process in the sediment. Bacteria use DOM to meet their energy requirements and for synthesis of new cell materials (Sepers 1977). The concentration of organic matter decreases with sediment depth (Shapiro et al. 1971). As organic matter increases, the oxygen demand of the aerobic bacteria at the sediment interface increases. The total amount of organic matter in the sediment does not necessarily indicate its availability to either the microorganisms (Waksman and Hotchkiss 1938) or the benthic invertebrates (Hargrave 1970a). Some authors show no relation between DOM of the sediment and bacterial oxygen consumption (Andersen 1939, Edwards and Rolley 1965).

The purpose of the present study was to determine the effects of physicochemical parameters brought about by artificial destratification on seasonal variation in sediment oxygen consumptions in Ham's and Arbuckle lakes.

Materials and Methods

An Ekman grab sampler was used to collect sediment. Sediment samples were obtained by inserting core tubes vertically into an undisturbed dredge sample. Corks were placed in the tube ends and

returned in an ice chest to the laboratory.

A profile of sediment oxygen consumption was determined by subsectioning core tubes into 0-1, 4-5, and 9-10 cm fractions. Oxygen consumption was measured on a Gilson respirometer within 24 h after collection. All consumption measurements were made at the same temperature as that recorded in the field. To each reaction flask, 3 g wet weight of sediment and 2 ml of bottom lake water were added. One reaction flask contained 2 ml of lake water as a control. After an initial incubation of 15 min, sediment consumption tests were run 3 h (Liu 1973). Then, 500 μl of 2% Formalin was added to each flask to differentiate between biological and chemical oxidative processes (Hargrave 1972).

Rates of oxygen consumption were determined on three cores from each site and means are recorded in this paper.

Results

Ham's Lake

Oxygen consumption of the sediments varied from 0.05-0.95 $\mu\text{l O}_2$ g dry wt⁻¹ h⁻¹ (Appendix, Table X). Since little variation existed between consumption of the surface sediment at the two Stations HP and HA, means of the two stations are shown on Figure 3. Oxygen consumption was consistently greater at Station HS than at Stations HP and HA. This difference was significantly greater ($p = 0.05$) in summer and fall. Oxygen consumption tended to decrease through summer at the two stations in the central pool, while values remained high at Station HS. Measurements increased between August and October and decreased in November at

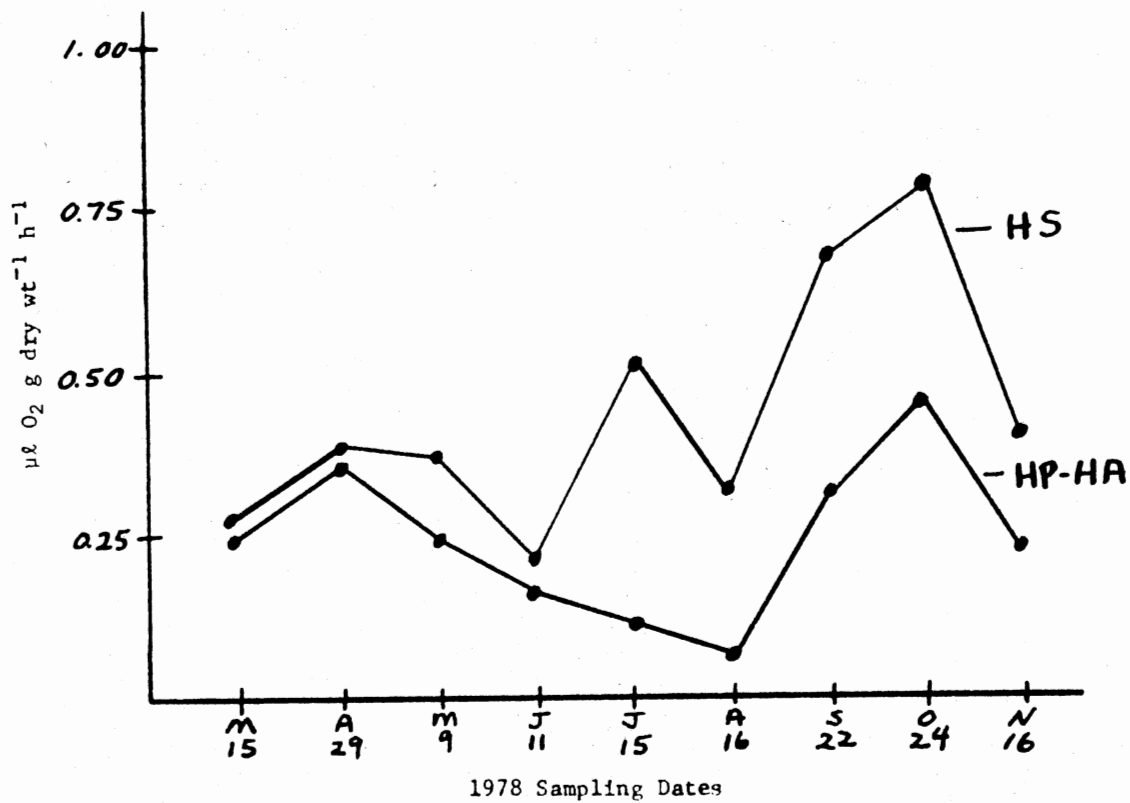


Figure 3. Mean Oxygen Consumption Rates of the Surface Sediment in Ham's Lake in 1978

all stations. No consistent trend existed in the variation of oxygen consumption of sediment among depths of 0-1, 4-5, and 9-10 cm.

Arbuckle Lake

Mean sediment oxygen consumption rates ranged from 0.07-1.20 $\mu\text{l O}_2$ g dry wt⁻¹ h⁻¹ (Appendix, Table XI). Since little variation existed in consumption rates of the surface sediments between the two stations in the central pool or among the three stations in the arms, means of the central pool and the arm stations are presented in Figure 4. Oxygen consumption was consistently greater at Stations AC and AP than at stations in the arms. This difference was significantly greater ($p = 0.05$) in summer and fall. Values at Stations AC and AP tended to increase through 11 July 1978 and then decline through 16 September 1978. In contrast, the arm stations showed a progressive decline in consumption rates through summer with an increase occurring in fall. No significant differences existed in consumption rates among sediment depths at Stations AC, AS, AR, and AB (Appendix, Table XI).

Discussion

The rates at which sediments consume oxygen vary widely. Issac (1962) obtained consumption rates of 0.78-0.91 g O₂ m⁻² day⁻¹ and Brewer et al. (1977) observed a similar range of 0.31-0.98 g O₂ m⁻² day⁻¹ for sediments from a eutrophic lake. A range of 0.15-1.06 g O₂ m⁻² day⁻¹ existed for lake surface sediments (Hayes and MacAulay 1959). Oxygen consumption rates ranged from 0.05-0.95 and 0.07-1.20 $\mu\text{l O}_2$ g dry wt⁻¹ h⁻¹ in Ham's and Arbuckle lakes, respectively, which are similar to the range reported by other investigators.

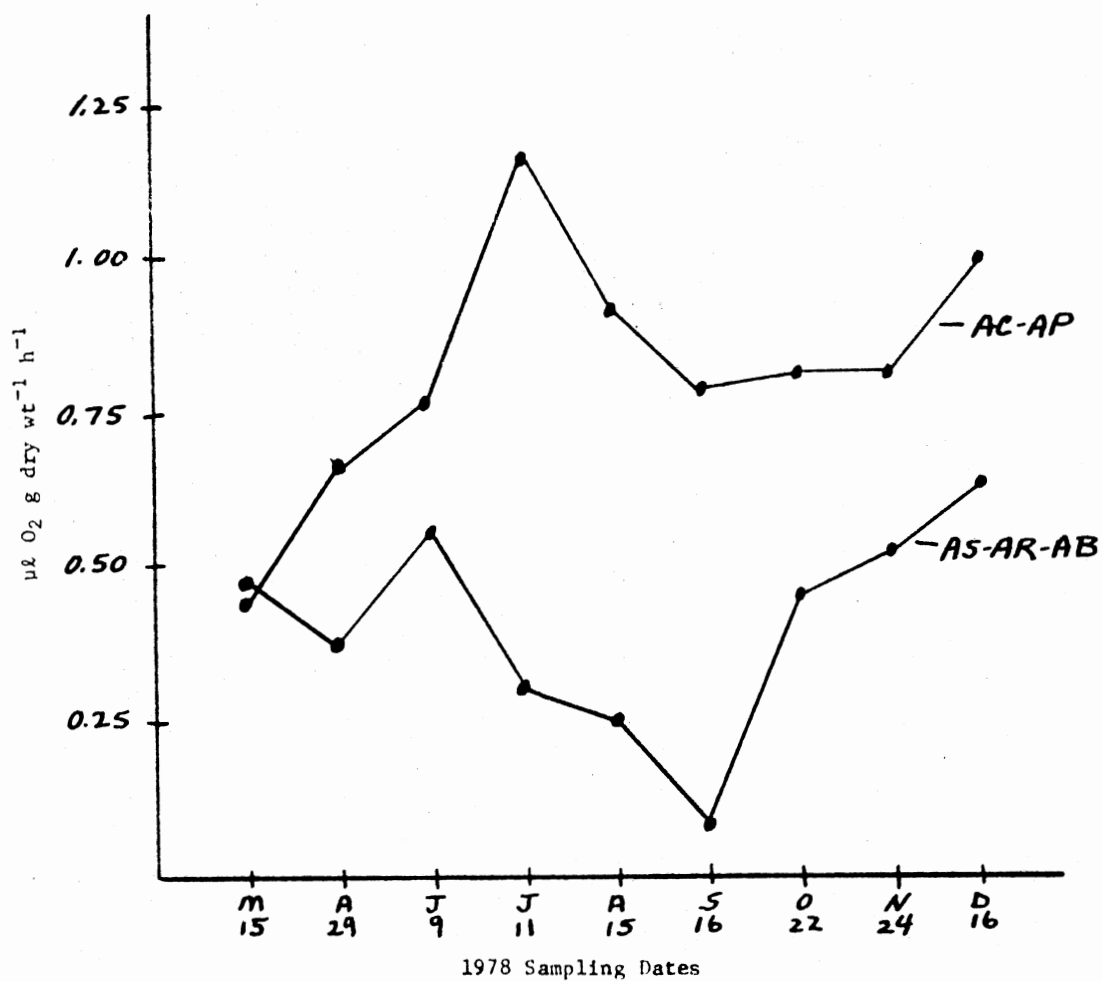


Figure 4. Mean Oxygen Consumption Rates of the Surface Sediment in Arbuckle Lake in 1978

Oxygen consumption by the sediments is primarily a surface phenomenon. Several authors noted highest consumption rates in the top 1 cm of sediment which correlates with maximum densities of bacterial populations and organic material (Hayes 1959, Liu 1973, Yarushek 1973). However, Hargrave (1969) observed no significant effect of depth on sediment oxygen consumption. No significant correlation existed between the depth in the sediment column and oxygen consumption in the present study.

Respiration rates may have been inflated due to exposure of reduced substances such as iron and sulfides to aerobic conditions which made them oxidize immediately giving higher consumption values. These oxidation reactions may mask biological respiration. Formalin was added to each sediment sample to differentiate between biological and chemical processes. Reduced compounds are produced in the sediment by the metabolic activities of anaerobic organisms and oxidize immediately under aerobic conditions. The decline in oxygen consumption rates in the presence of Formalin demonstrated that oxygen removal by sediments from the overlying water in Ham's and Arbuckle lakes is mainly a biological process. Consumption values obtained at the stratified stations in Ham's and Arbuckle lakes exhibited 15% chemical respiration in the upper 5 cm of sediment.

Time-dependent changes in consumption rates by the sediment can be expected as labile substances are oxidized. Substances which may cause the initial increase in consumption rates may be reduced minerals such as ferrous iron and ferrous carbonate. Slower rates of oxygen consumption over a longer period of time may be due to microbial oxidation of organic material and acid-insoluble iron sulfide minerals (Gardner and

Lee 1965). This trend in consumption rates has been observed with various types of sediment (Anderson 1939, Kate 1956, Rybak 1969, DiSalvo 1971). Hargrave (1972) observed maximum rates of oxygen consumption in short-term experiments which reflect rates occurring in nature if samples are taken from well-aerated areas. Time-dependent changes in oxygen consumption rates were observed in the present study. Maximum consumption was observed during the first hour and a progressive decrease existed during the remaining 3 h.

Early workers found that respiration rate generally was independent of the oxygen concentration until the concentration decreased to some threshold value below which the respiration rate decreased. Surface sediments taken from a eutrophic lake exhibit maximum consumption rates during anoxic conditions in summer (Brewer et al. 1977, DeVol 1978). Adaptive metabolic changes in microorganisms occur in response to anoxic conditions which produce higher consumption rates (Johnson 1967, DeVol 1978). Temperature and the oxygen concentration of the bottom water affect the rate of diffusion of oxygen and reducing compounds across the mud-water interface and the respiration of organisms in the sediment (Hargrave 1969). Sediment oxygen consumption in the present study was highest in both lakes at stations with anoxic hypolimnions during summer (Figures 3 and 4).

A positive correlation existed in the present study between percent organic matter of the sediments and its respiration rate. The percent organic matter was significantly greater at the stratified than at the destratified stations in both lakes during summer (Tables II and IV). Brewer et al. (1977) observed a direct relationship between bacterial populations and organic matter of the sediments. The higher consumption

rates observed in the present study at the stratified stations may be due to a proliferation in bacterial populations in response to increased amounts of organic material.

Waksman and Hotchkiss (1938) found that sand consumed less oxygen than mud and that most of the uptake occurred within the first few days. An inverse relationship has been shown between particle size and oxygen consumption (Hargrave 1972, Yarushek 1973). Particle size in Ham's and Arbuckle lakes varies inversely with depth and tended to decrease as the lakes stratified (Clay 1978).

This study presented evidence that oxygen removal by the sediments in Ham's and Arbuckle lakes is greatest in an anoxic hypolimnion. During stratification, organic material in the sediment increased and the oxygen demand of the bacterial population probably increased. The subsequent consequence would be an additional stress on the oxygen-poor hypolimnion.

CHAPTER V

OXYGEN CONSUMPTION IN CHIRONOMUS TENTANS (FABR.),

CHIRONOMUS RIPARIUS MEIGEN, AND CHAOBORUS

PUNCTIPENNIS (SAY)

Introduction

Diffusion of dissolved oxygen (DO) in aquatic insects occurs cutaneously or involves specialized structures (e.g. gills or anal papillae). Chironomid larvae normally respire through anal papillae located on the last two segments of the body. The posterior part of the body displays rhythmical undulating movements which insures a renewal of fresh water surrounding the organism. Chironomus plumosus L. and Chironomus dorsalis Meigen come to the surface when the oxygen supply is low; however, Chironomus tentans (Fabr.) has limited swimming abilities which restricts migratory movements (Cole 1921).

Hemoglobin is present in the hemolymph of chironomids. The hemoglobin has three functions: (1) aids normal activity of the larva when oxygen levels are low, (2) acts in oxygen transport at low tensions permitting continuous respiratory movements, and (3) allows more rapid recovery from anaerobiosis (Walshe 1947 a, b; 1949; 1950). Chironomus sp. blood has a comparatively low oxygen capacity which may be due to the hemoglobin being less concentrated (Leitch 1916, Florkin et al. 1941, Fox 1945, Walshe 1950). The larvae cannot transport oxygen in well-aerated waters since the hemoglobin cannot unload (Ewer 1942).

Chironomids normally displays filterfeeding, respiratory movements, and resting in well-aerated water. When oxygen becomes limiting, respiratory movements are nearly continuous. At higher oxygen levels, the original consumption rate is resumed. A return to normal consumption activity is aided greatly by the presence of hemoglobin. Species rich in hemoglobin tend to occur in water of lower oxygen content than pale or colorless species (Walshe 1951).

Aquatic insects generally show an oxygen consumption that is independent of the ambient oxygen content (Hiestand 1931). A chironomid survived anoxic conditions from 3 to 120 days under laboratory conditions (Ssinitza 1937, Lindemann 1942). Chironomids in Lake Mendota survived 3 wk without oxygen (Cole 1921). Hemoglobin and anaerobic metabolism enables chironomids from lentic habitats to survive prolonged exposure to anoxia (Eggleton 1931, Ssinitza 1937, Harnisch 1936; 1939, Von Brand 1944, Walshe 1950).

Oxygen consumption is also influenced by water temperature. In laboratory studies, oxygen consumption increased linearly with rising temperatures in Chironomus dorsalis, Chironomus riparius Meigen, and Chaoborus flavicans Meigen (Edwards 1958, Buck 1965, Berg and Jonasson 1965). However under field conditions, C. riparius had a higher oxygen consumption in summer than in autumn at 20°C (Edwards 1958).

The literature on the effects of salinity on respiration is conflicting. Many authors have found that oxygen consumption increased under osmotic stress (Flemister and Flemister 1951, Rao 1958, Dehnel 1960, Lance 1965, Ramamurthi 1967). Other investigators have found no significant changes in respiration rate which may be correlated with salinity (Gilchrist 1956, MacFarland and Pickens 1965, Palmer 1968).

The purpose of the present study was to determine the effects of changes in physicochemical parameters brought about by artificial de-stratification on the respiratory activities of Chironomus tentans, Chironomus riparius, and Chaoborus punctipennis. Measurements were made on seasonal variation in oxygen consumption of these organisms from Ham's and Arbuckle lakes. Laboratory experiments were also conducted to measure the independent effects of temperature, DO, and salinity on oxygen consumption.

Materials and Methods

Chironomus tentans, Chironomus riparius, and Chaoborus punctipennis were collected from the lakes as previously described in Chapter III. Oxygen consumption of fourth instar larvae of uniform size were measured on a Gilson respirometer. Five replicates of 10 chironomid or 20 chaoborid larvae per flask were placed in 5 ml of lake water in 15 ml reaction flasks. For carbon dioxide absorption, 0.2 ml of a 10% KOH solution and a strip of Whatman No. 1 filter paper were added to the center well of each flask. The flasks were attached to the respirometer with temperature of the water bath equal to the lake water from which the organisms were collected. The flasks were shaken at a constant, moderate speed to allow the larvae to respire without making the characteristic wriggling movements (McFarland and McLusky 1972). Oxygen consumption was measured between 1200 and 1800 h to minimize the influence of possible circadian respiratory patterns (Buffington 1968). The flasks were kept in darkness. Several flasks contained 5 ml of lake water to correct for oxygen uptake by factors other than the larvae (Umbreit et al. 1972). After an initial incubation period of 30 min,

readings were taken every 30 min for 4 h.

After the oxygen consumption measurements, the larvae in each flask were placed in tared aluminum weighing pans, dried for 24 h at 105°C, and weighed. Results are expressed in $\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$.

Controlled laboratory oxygen consumption experiments were conducted on C. riparius and C. punctipennis collected from Ham's Lake. Oxygen consumption rates were determined for three replicates each of larvae exposed to different temperatures, dissolved oxygen (DO), and salinity levels after a 48 h acclimation in 500 ml of the treated lake water. Oxygen consumption was measured at seven temperatures (3, 8, 12, 17, 22, and 32°C) in a controlled-temperature water bath. The larvae were exposed to DO concentrations of nondetectable, 5, and 10 mg ℓ^{-1} . Mineral oil on the water surface created anoxic conditions, while the other levels were maintained by aerating the water for different times. Dissolved oxygen concentrations were checked every 8 h using a YSI DO probe. Oxygen consumption was determined on larvae exposed to five sodium chloride (NaCl) levels (deionized water, 0.1, 0.3, 0.5, and 0.8% NaCl). Temperature exhibited the greatest influence on oxygen consumption above 17°C. Thus, the interaction of temperature at 17, 22, and 24°C and the other two variables were examined.

Results

Chironomus tentans (Fabr.)

Chironomus tentans was collected only in March and April, 1978, from Arbuckle Lake. Oxygen consumption values were similar for these months at all stations. No significant differences in oxygen

consumption were observed between the central pool (AC and AP) and arm (AS, AR, AB) stations. Mean oxygen consumption values in April for the central pool and arm stations were 2.0 and 2.3 $\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$, respectively.

Chironomus riparius Meigen

Oxygen consumption in Chironomus riparius from Ham's lake in 1978 ranged from 1.0-9.9 $\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$ (Table V). Variation among seasons and between the central pool (HP) and stratified arm (HS) stations was significant. Oxygen consumption at Station HP increased linearly through 23 June and then decreased abruptly to 2.5 $\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$ on 21 July. The maximum oxygen consumption rate was recorded in August at Station HP. Station HA exhibited similar trends to those recorded at Station HP. Little seasonal variation existed in consumption rates during the sampling period at Station HS. Consumption values were lower in spring and summer at Station HS than those at Stations HP and HA.

Chaoborus punctipennis (Say)

Oxygen consumption rates in Chaoborus punctipennis from Arbuckle Lake in 1978 ranged from 0.9-12.6 $\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$ (Table VI). Maximum consumption rates were generally recorded in fall, while the lowest rates occurred in spring. Similar oxygen consumption trends occurred among the arm stations with values increasing significantly from 15 March to 29 April and decreasing to a mean of 2.0 $\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$ on 15 August. A linear increase occurred from September through December. Oxygen consumption rates recorded from the central pool

TABLE V

MEAN OXYGEN CONSUMPTION RATES* ($\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$) OF CHIRONOMUS RIPARIUS MEIGEN
AND CHAOBORUS PUNCTIPENNIS (SAY) FROM HAM'S LAKE IN 1978

Organism	Station (Depth in m)	Mar 13	Apr 23	May 25	Jun 23	Jul 21	Aug 22	Sep 29	Oct 29	Nov 30
<u>Chironomus riparius</u>	HS (5)	1.8	1.5	-	1.4	1.3	-	2.4	-	3.6
	HP (8)	2.3	3.2	4.0	5.0	2.5	9.9	2.0	-	-
	HA (2)	1.3	-	2.2	-	9.0	8.6	1.8	-	-
<u>Chaoborus punctipennis</u>	HS (5)	3.4	-	-	4.6	4.6	6.4	2.6	-	1.5
	HP (8)	2.0	1.4	1.7	2.5	3.2	6.0	1.6	-	5.1
	HA (2)	3.9	-	-	-	-	2.2	1.8	-	4.7

* Mean value obtained from five replicates.

- Data not measured.

TABLE VI
 MEAN OXYGEN CONSUMPTION RATES* ($\mu\text{l O}_2 \text{ mg dry}$
 $\text{wt}^{-1} \text{ h}^{-1}$) OF CHAOBORUS PUNCTIPENNIS (SAY)
 FROM ARBUCKLE LAKE IN 1978

Station (Depth in m)	Mar 15	Apr 29	Jul 11	Aug 15	Sep 16	Oct 22	Dec 16
AC (25)	-	1.1	-	9.4	4.0	9.2	9.3
AP (23)	2.6	1.2	-	4.3	7.8	12.6	10.8
AS (15)	1.2	8.1	-	1.9	1.4	4.9	9.1
AR (15)	1.2	8.2	3.4	1.7	1.3	5.3	11.1
AB (15)	0.9	-	8.0	2.3	2.6	2.8	7.1

* Mean value obtained from five replicates.

- Data not measured.

stations were significantly different ($p = 0.5$) from one another from August through October. A linear consumption rate was recorded during this period at Station AP.

The range of oxygen consumption rates in C. punctipennis from Ham's Lake in 1978 was 1.4-6.4 $\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$ (Table V). Consumption values were generally higher at the stratified station than at the central pool and arm stations. An increase in consumption rates occurred from 23 April-22 August at Station HP. Values at Station HS increased significantly in August. A decrease in consumption rates occurred on 29 September at all stations. Seasonal trends were not evident at Station HA.

Laboratory Experiments

Oxygen consumption of Chironomus riparius in laboratory experiments increased from 0.2-3.0 $\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$ as temperature increased from 3-22°C (Appendix, Table XII). Consumption decreased at 28°C. A similar trend was observed for Chaoborus punctipennis except the maximum uptake reached 6.2 $\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$ at 22°C. Since consumption peaked around 22°C, subsequent studies of the effects of dissolved oxygen and salinity on consumption were examined at 17, 22, and 24°C.

Oxygen consumption of both species increased as dissolved oxygen increased from 0-10 mg l^{-1} at all three temperatures (Appendix, Table XIII). Although no significant differences were observed between consumption at 5 and 10 mg l^{-1} , differences were significant between 0 mg l^{-1} and the high DO levels at every temperature. The mean consumption rate at 0 and 10 mg l^{-1} over all temperatures was 2.0 and 2.7 $\mu\text{l O}_2 \text{ mg}$

dry wt⁻¹ h⁻¹ for C. riparius and 2.0 and 5.0 µl O₂ mg dry wt⁻¹ h⁻¹ for C. punctipennis.

A linear increase in oxygen consumption in systems containing 10 mg l⁻¹ was observed in both organisms through 0.3% NaCl and a significant decrease occurred at 0.5% NaCl at all temperatures (17, 22, 24°C) (Appendix, Table XIV). Maximum consumption values were observed at 0.3% NaCl at 22°C. Mean consumption rates averaged over all the temperatures at 0.3% NaCl were 3.2 and 6.0 µl O₂ mg dry wt⁻¹ h⁻¹ for C. riparius and C. punctipennis, respectively. The significant simple effects were temperature × DO between the 0 and 10 mg l⁻¹ levels and temperature × salinity at 0.5% NaCl.

Since data on the simple effects of temperature, dissolved oxygen, and salinity on oxygen consumption suggested that interactions may be significant, a factorial experiment was designed. Oxygen consumption varied from 1.0-3.5 and from 1.2-9.0 µl O₂ mg dry wt⁻¹ h⁻¹ in C. riparius and C. punctipennis, respectively (Table VII). In both species oxygen consumption values and trends were similar at DO concentrations of 5 and 10 mg l⁻¹ and values are averaged on the table. An increase in consumption occurred through 0.3% NaCl followed by a significant decrease. Significant differences (p = 0.05) existed in oxygen consumption in both species at the DO concentration of 0 mg l and the 5 and 10 mg l levels. A linear increase was observed in consumption rates in C. riparius and C. punctipennis at 0 mg l⁻¹ through 0.3% NaCl at 17 and 22°C and at all temperatures at the higher DO levels. In contrast, an inverse relationship between consumption and salinity existed at 0 mg l⁻¹. Temperature × salinity was significant except at 24°C and 0 mg l⁻¹.

TABLE VII
 THE EFFECTS OF DISSOLVED OXYGEN, SODIUM CHLORIDE,
 AND TEMPERATURE ON THE OXYGEN CONSUMPTION*
 ($\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$) OF CHIRONOMUS
RIPARIUS MEIGEN AND CHAOBORUS
PUNCTIPENNIS (SAY)**

DO mg ℓ^{-1}	NaCl (%)	Temperature ($^{\circ}\text{C}$)		
		17	22	24
0	0.0	2.0 (3.0)	2.1 (2.6)	2.0 (3.4)
	0.1	2.1 (3.2)	2.0 (3.0)	2.0 (3.0)
	0.3	2.6 (3.4)	2.6 (3.8)	1.7 (2.4)
	0.5	2.0 (3.0)	2.2 (2.4)	1.7 (1.9)
	0.8	2.1 (2.8)	1.6 (2.0)	1.0 (1.2)
$\bar{X}_{5,10}$	0.0	2.4 (5.2)	2.3 (4.4)	2.3 (5.4)
	0.1	2.3 (7.2)	2.7 (6.2)	2.8 (5.8)
	0.3	2.8 (6.8)	3.5 (9.0)	3.5 (6.2)
	0.5	2.2 (6.1)	2.1 (3.8)	1.7 (2.4)
	0.8	2.1 (4.3)	1.5 (2.9)	1.0 (2.0)

* Mean value obtained from three replicates.

** Values for Chaoborus punctipennis are in parentheses.

Discussion

Consumption rates were highest in Chaoborus punctipennis from Ham's and Arbuckle lakes at stratified stations during summer. In several trichopteran larvae, ventilation becomes continuous with decreasing oxygen content of the water and the respiration rate increases (Edwards 1953). Since higher consumption rates were observed in the present study under anoxic conditions, then maintenance of this metabolic rate must require oxygen. If the water is depleted of oxygen, then the organism must rely on an internal source. Glycogen within the body is broken down anaerobically producing energy in Chironomus plumosus (Cole 1921, Harnisch 1938, Walshe 1947, Augenfeld 1967). Glycogen usage is higher initially under anoxic conditions and then levels off (Tessler and Domogalla 1931). Where pumping maintained at least $2.0 \text{ mg } \ell^{-1}$ of dissolved oxygen in the hypolimnetic water at the destratified stations in Ham's and Arbuckle lakes, a low respiratory rate was observed in C. punctipennis which would conserve what limited oxygen is available.

In contrast to the trend observed for C. punctipennis, C. riparius maintained a low respiratory rate during anoxic conditions in summer in Ham's Lake. This reduced metabolic rate during prolonged exposure to anoxia is in agreement with the literature (Ewer 1942, Walshe 1948). At the destratified central pool station, consumption increased linearly through June and dropped significantly on 21 July and 29 September. Since conditions were not anoxic on either of these dates, the decrease might be associated with prepupal formation. A decrease in metabolic

rate has been associated with ecdysial activities (Walshe 1947, Edwards 1958).

In controlled laboratory experiments, the range of consumption values observed for C. riparius was 0.2-3.0 $\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$. A similar range has been reported by other authors for Chironomus sp. (Walshe 1947, Edwards 1958, Buck 1965, McFarland and McLusky 1972). Consumption values in C. punctipennis ranged from 0.2-6.2 $\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$ which is similar to values in the literature (Berg and Jonasson 1965, Ransom et al. 1970). Oxygen consumption rates of C. riparius and C. punctipennis increased linearly with temperature to 22°C with a subsequent decline in values occurring at 28°C. Tombes and Sigman (1975) observed an increase in oxygen consumption in C. punctipennis with increasing temperatures and considerable mortality at 30°C. In the present study, a temporary heat paralysis caused C. riparius and C. punctipennis to become lethargic at 28°C and an increase in mortality occurred. A slight increase in consumption rates did occur above 28°C which may be attributed to the death process. Keister and Buck (1964) have speculated that an insect could be shifting from one isozyme to another as the inactivation temperature of the first isozyme is reached and the optimum temperature for the second isozyme is approached. Additional work must be done with these larvae to determine if this is happening at 28°C.

A decline in oxygen consumption rates was observed in both species as the oxygen level decreased to a nondetectable concentration. A similar trend in oxygen consumption in relation to DO levels was demonstrated for C. plumosus (Ewer 1942).

A linear increase in consumption values in C. riparius and C.

punctipennis occurred through a 0.3% NaCl solution. The respiratory rate decreased significantly at 0.5% NaCl. A metabolic shift probably occurs within the organism and energy is diverted from other life functions to assist in osmoregulation. Thus, the energy requirements for osmoregulation processes would be increased under osmotic stress, but no overt change in oxygen consumption could be detected.

The interactions of temperature, salinity, and DO in relation to oxygen consumption has not been investigated extensively. Several authors (Dehnel 1960, Dimock and Groves 1975) have shown that the response of oxygen consumption to salinity is affected significantly by higher temperatures and lower DO levels. These investigators have demonstrated an increase in respiration rates in conditions in which stronger osmoregulation must take place. In the present study, C. riparius and C. punctipennis appear to reach their isosmotic point in approximately a 0.3% NaCl solution as indicated by the maximum consumption values. At the higher salinities of 0.5 and 0.8% NaCl, respiratory rate declines. Since both species were unable to maintain osmotic equilibrium in a 0.5% NaCl solution, physiological stress must have been induced as evidenced by the declining consumption rates. An inverse relationship in oxygen consumption occurred at 24°C and 0 mg ℓ^{-1} DO over the entire salinity range. This combination of DO, temperature, and sodium chloride was apparently too great for the organisms to cope with as demonstrated by the inverse consumption and high mortality rates at 24°C.

CHAPTER VI

OSMOREGULATION IN CHIRONOMUS TENTANS (FABR.),

CHIRONOMUS RIPARIUS MEIGEN, AND

CHAOBORUS PUNCTIPENNIS (SAY)

Introduction

Aquatic insects are able to regulate the composition of their hemolymph under internal and external environment stress (Winogradskaja 1936, Wigglesworth 1938a, Wright 1975). The overall composition of the hemolymph in an insect represents a steady state between influxes of salts, heavy metals, organic materials, and water obtained through the cuticle or by ingestion and lost through secretion, excretion, and respiration.

Sodium (Na^+), potassium (K^+), and chloride (Cl^-) are the most important inorganic ions of the hemolymph. The concentrations of Na^+ and K^+ in the hemolymph is variable. In all aquatic species examined by Sutcliffe (1962b), the Na^+ concentration was high (69-155 mM) and exceeded that of K^+ (2-31 mM) which is often low. In several species of Chironomus, hemolymph cation (Na^+ , K^+) concentrations remain constant during instar stages, but increase at each ecdysal period (Firling 1970, Schin and Moore 1977). The hemolymph Cl^- concentration is low relative to the other ions present and is usually half the concentration of sodium (Boné 1947, Sutcliffe 1962b).

Conflicting views are reported in the literature with respect to

the organism's ability to regulate internal ion concentrations in relation to the external medium's ion concentration or osmotic pressure. Hemolymph Na^+ regulation in Aedes aegypti L. has been shown to follow the same trends as those of the hemolymph osmotic pressure (Ramsay 1953a, Shaw and Stobbart 1963). Therefore, the regulation of the hemolymph osmotic pressure is dependent on the regulation of the hemolymph electrolytes. If ion regulation is dependent, then hemolymph Na^+ and Cl^- concentrations are kept well below the external Na^+ and Cl^- levels especially at higher external concentrations. However, some investigators have observed an independent regulation in the hemolymph Na^+ and Cl^- concentrations. The Cl^- concentration did not parallel the Na^+ concentration or the total osmotic pressure of the hemolymph when organisms were exposed to various external NaCl concentrations (Wigglesworth 1938, Beadle 1939, Ramsay 1951, 1953a).

The hemolymph osmotic pressure is made up largely of electrolytes and provides an estimate of the concentration of solutes in the hemolymph. Osmotic pressure is usually determined quantitatively by freezing point depressions (Ramsey 1949, Frick and Sauer 1973). Determining the osmotic pressure of the medium and the hemolymph is the usual procedure to assess the regulatory capacity of the organism. Various culicid larvae have osmotic pressure values ranging from 0.3-0.8 osmoles (Winogradskaja 1936, Wigglesworth 1938a, Beadle 1939, Frick and Sauer 1973). Higher osmolarity values have been observed in these larvae previous to molting (Richards and Meier 1974, Firling 1977).

The hemolymph osmotic pressure can be used to estimate rapidly the adaptive response of the organism to various environmental conditions. In general, most freshwater insect larvae do not survive well in

solutions exceeding 1% NaCl (Beadle 1943). When subjected to solution exceeding 1% NaCl, hemolymph ion regulation breaks down with subsequent isosmotic conditions occurring between the hemolymph and medium. When an isosmotic condition occurs, the organism will usually become lethargic and eventually expire. A few culicid larvae show excellent control over their internal ion/osmotic regulation. Aedes aegypti L., Culex pipiens Say, and Chironomus thummi Meigen are able to regulate their osmotic pressure to avoid iso-osmotic conditions when subjected to external salinities exceeding 1% NaCl (Wigglesworth 1938a, Neumann 1961, Richards and Meier 1974).

Little work has been done on changes in hemolymph ion concentrations and osmotic pressure in relation to stressful environmental conditions. Water temperature affects hemolymph ion concentrations. A slight decrease in Na^+ ions was observed from 21-24°C with a subsequent increase in Na^+ around 26°C in Chironomus tentans (Fabr.) (Wright 1975). Asphyxiation has been shown to increase hemolymph osmotic pressure in A. aegypti (Wigglesworth 1938a). Osmotic pressure of the blood will also increase in overwintering larvae of Anopheles sp. (Winogradskaja 1936). These osmotic and ionic changes in response to various environmental conditions are probably due to an accumulation of metabolites, a failure of some active osmoregulatory process, or a change in cuticle permeability. More emphasis should be placed on investigating interactions of several environmental variables and their effects on the osmoregulatory abilities in aquatic organisms.

The purpose of the present study was to determine the effects of physicochemical parameters brought about by artificial destratification on the osmoregulatory abilities of Chironomus tentans (Fabr.),

Chironomus riparius Meigen, and Chaoborus punctipennis (Say). Measurements were made on seasonal variation in osmoregulation of these organisms from Ham's and Arbuckle lakes. Laboratory experiments were also conducted to measure the independent effects of temperature, dissolved oxygen, and salinity on osmoregulation.

Materials and Methods

Chironomus tentans, Chironomus riparius, and Chaoborus punctipennis were collected from the lakes as previously described in Chapter III. Fourth instar larvae, selected on the basis of uniform size, were used in all the osmoregulatory experiments.

For collection of hemolymph samples, larvae were surfaced dried with Kimwipes and secured to masking tape on a microscope slide. A dorsal mesothoracic puncture was made with an insect pin under a dissecting microscope. Hemolymph issuing from the puncture was collected in disposable glass micropipettes (Microcaps, Drummond Scientific Co.). Samples were discarded if they became contaminated with other body tissues. Samples were analyzed immediately after collection since freezing alters hemolymph composition (Stephen and Johnson 1962).

Measurements of sodium (Na^+) and potassium (K^+) were made on individual larvae. Hemolymph Na^+ and K^+ samples ($0.5 \mu\text{l}$) were transferred into $500 \mu\text{l}$ of deionized water for analysis on a Beckman 440 atomic absorption spectrophotometer. Chloride (Cl^-) analysis was made directly without dilution and measured with a Fiske Marius Microchlor-o-counter. Ten microliters of hemolymph was required from 10 chironomids and 20 chaoborids for a Cl^- analysis.

Ion assays were made on $1 \mu\text{l}$ of lake water from each sampling

station. The concentrations of cations (Na^+ , K^+) and the anion (Cl^-) were determined with an atomic absorption spectrophotometer and microchlor-o-counter, respectively.

The osmotic pressure of the hemolymph and lake water was determined by freezing point depressions measured with a Clifton Technical Physics Nanoliter Osmometer, sensitive to the nearest 0.001°C (Frick and Sauer 1973). Less than $0.1 \mu\text{l}$ of hemolymph and lake water was used for each assay. Seasonal ion concentrations and osmolarities were determined for five replicates of each organism and lake water per sampling station.

Controlled laboratory osmoregulation experiments were conducted on C. riparius and C. punctipennis collected from Ham's Lake. Hemolymph ion analyses and osmolarities were determined for five replicates each of larvae exposed to different temperatures, dissolved oxygen (DO), and salinity levels after a 48 h acclimation in 500 ml of the treated lake water. Ion concentrations were measured at seven temperatures (3, 8, 12, 17, 22, and 32°C) in a controlled-temperature water bath. The larvae were exposed to DO concentrations of nondetectable, 5, and 10 mg l^{-1} . Mineral oil was added to the water surface to create anoxic conditions, while the other levels were maintained by aerating the water for timed intervals. Dissolved oxygen concentrations were checked every 8 h using a YSI DO probe. The larvae were also exposed to five sodium chloride (NaCl) levels (deionized water, 0.1, 0.3, 0.5, 0.8% NaCl). Temperature exhibited the greatest influence on hemolymph ion concentrations and its osmolarity above 22°C . Thus, the interactions of temperature at 22, 24, and 26°C and the other two variables were examined.

Results

Chironomus tentans (Fabr.)

The range of Na^+ ions in the hemolymph of Chironomus tentans in Arbuckle Lake was from 49-172 mM (Table VIII). Although the ranges were similar at the arm stations and in the central pool, values were generally greater in the arms. The mean concentrations were 97 and 112 mM, respectively. Variation between values measured at the two central pool stations and among values at the three arm stations was not significant. Since the species was not commonly collected in the central pool and at the arm station AS and AR in 1977, trends could not be observed (Appendix, Table XV). C. tentans was commonly collected at all stations in 1978. The concentration of Na^+ exhibited considerable seasonal fluctuation in 1978 reaching minima on 9 June and 15 August and maxima on 11 July (Appendix, Table XVI).

Hemolymph K^+ in C. tentans in Arbuckle Lake ranged from 2-11 mM and averaged 7 mM (Table VIII). Little variation existed between the central pool and arm stations. In both years values tended to be higher in summer and early fall than in spring (Appendix, Tables XV and XVI).

The range of Cl^- ions in Arbuckle Lake was from 16-80 mM and the average was 46 mM (Table VIII). Concentrations at the arm stations and in the central pool were similar. In 1977 values were generally higher on 10 May than during summer (Appendix, Table XV). In 1978 the concentration of Cl^- exhibited considerable fluctuation. The maxima were measured at most stations on 11 July and minima on 15 August.

Osmotic pressure of the hemolymph in C. tentans ranged from 0.119-0.629 $-\Delta^\circ\text{C}$ and averaged 0.332 $-\Delta^\circ\text{C}$ (Table VIII). The pressure was

TABLE VIII

RANGE AND (MEAN) ION CONCENTRATION AND OSMOTIC PRESSURE OF THE HEMOLYMPH OF ORGANISMS COLLECTED IN ARBUCKLE AND HAM'S LAKES IN 1977-1978

Organism	Lake* Area	Ion (mM)			Osmotic Pressure (-Δ°C)
		Na ⁺	K ⁺	Cl ⁻	
<u>Chironomus tentans</u>	AC-AP	49-169 (97)	4-11 (7)	20-80 (42)	0.127-0.602 (0.293)
	AS-AR-AB	48-172 (112)	2-10 (7)	16-72 (48)	0.119-0.629 (0.350)
<u>Chironomus riparius</u>	HS	87-129 (110)	5-10 (7)	35-64 (52)	0.266-0.366 (0.337)
	HP	87-141 (115)	5-10 (8)	35-69 (50)	0.259-0.454 (0.360)
	HA	81-159 (120)	5-9 (7)	35-65 (50)	0.248-0.465 (0.366)
<u>Chaoborus punctipennis</u>	AC-AP	60-141 (90)	4-17 (7)	24-66 (44)	0.250-0.607 (0.355)
	AS-AR-AB	45-145 (108)	4-13 (8)	15-60 (43)	0.214-0.605 (0.411)
	HS	85-180 (121)	5-13 (8)	40-82 (53)	0.330-0.628 (0.497)
	HP	94-150 (121)	5-12 (8)	40-60 (52)	0.309-0.598 (0.488)
	HA	79-144 (105)	5-12 (8)	32-60 (47)	0.206-0.560 (0.420)

* Arbuckle Lake: AC-AP (central pool, 24 m), AS-AR-AB (arms, 15 m).

Ham's Lake: HS (stratified arm, 5 m), HP (central pool, 8 m), HA (arm, 2 m).

significantly greater in organism taken from the arm stations than from the central pool. In 1977, values were generally high at all stations on 10 May. Insufficient organisms were taken from Stations AP, AS, and AR from 10 June-22 October to enable measurements, hence no trends could be observed. In 1978, values were similar in the central pool until late summer and were higher on 22 October and 16 December (Appendix, Table XVI). Osmotic pressure of C. tentans in the arms peaked on 11 July, while low values were measured on 15 March and 16 December.

Chironomus riparius Meigen

Hemolymph Na^+ ions ranged from 81-159 mM and averaged 115 mM in Chironomus riparius in Ham's Lake (Table VIII). Values were generally larger at station HA than the deeper water stations. Organisms were not commonly collected in 1977 and no trends were observed (Appendix, Table XVII). In 1978, values tended to increase in spring at all stations, reach peak concentrations in summer, and decrease during the rest of the study (Appendix, Table XVIII). The stratified station, HS, and the mixed station, HP, were not significantly different in summer during mixing except for a significantly lower value at the stratified station on 23 June.

Little variation existed among stations in hemolymph K^+ concentration in C. riparius in Ham's Lake (Table VIII). Values ranged from 5-10 mM. In 1978, values tended to be higher during summer than during spring.

Hemolymph Cl^- concentrations varied from 35-69 mM and averaged 50 mM (Table VIII). Variation among stations was slight. Minimum values occurred on 13 March 1978. Values increased at all stations

between 13 March and 23 April, while maximum values were recorded on 22 August. Pumping in summer did not result in variations in ion concentrations of Cl^- .

The range of osmotic pressure of the hemolymph in C. riparius was less than that for the other species (Table VIII). Values ranged from 0.266-0.465 $-\Delta^\circ\text{C}$. Values were significantly less at the stratified station than at Stations HS and HP. Values tended to increase from minimum values measured on 13 March 1978 to maxima in late spring or summer (Appendix, Table XVIII). During summer pumping, values were significantly greater at the mixed station than at the stratified station. Hemolymph osmotic pressure decreased during the remainder of the study.

Chaoborus punctipennis (Say)

The range of Na^+ ions in the hemolymph of C. punctipennis in Arbuckle Lake ranged from 45-145 mM and averaged 97 mM (Table VIII). The variation among the three arm stations and between the two central pool stations was not significant. Values in the arms were generally greater than values in the central pool. No trends were observed in 1977, although values were significantly lower on 10 June and 15 August (Appendix, Table XIX). In 1978 hemolymph Na^+ ions generally decreased from 15 March-9 June, remained low during anoxic conditions, and then increased during fall (Appendix, Table XX). In Ham's Lake, Na^+ ions in C. punctipennis ranged from 79-180 mM and averaged 116 mM (Table VIII). Values were significantly lower at the 2 m station (HA) than Stations HS and HP during the entire study. In 1977, when no pumping was

conducted, little variation existed between Stations HS and HP. Values tended to decrease from 20 May-December 14 (Appendix, Table XVII). In 1978, Na^+ concentration increased from spring to summer, peaked on 22 August, and decreased through 30 November. Values were not significantly different in 1978 except during pumping in summer when the concentration was significantly greater in organisms in the stratified arm (Appendix, Table XVIII).

The concentration of K^+ ions in the hemolymph of C. punctipennis in Arbuckle Lake ranged from 4-17 mM (Table VIII). Little variation existed between the arms and the central pool. In 1977, the concentration was greater in summer and fall than in other seasons, while in 1978 maximum concentration were recorded in fall (Appendix, Tables XIX and XX). Hemolymph K^+ values were similar in Arbuckle and Ham's lakes. In 1978, little seasonal variation existed and a variation among stations was not measured as was observed with Na^+ .

The range of Cl^- ions in the phantom midge in Arbuckle Lake was from 15-66 mM (Table VIII). Little variation existed between the central pool and arm stations. The seasonal trends were similar to those observed for Na^+ ions (Appendix, Tables XIX and XX). Values were significantly lower on 10 June and 15 August 1977 and in 1978 were generally low during anoxic conditions. Hemolymph Cl^- ions were generally greater in organisms in Ham's Lake than in Arbuckle Lake. Chloride values in Ham's Lake averaged 51 mM and were generally lower at the 2 m station than the 5 and 8 m stations. Little seasonal variation existed in 1977; however, values tended to increase in 1978 and reach maximum values during summer. During pumping in 1978 the Cl^- ion concentration was significantly greater at the stratified station than at the mixed

station on 22 August, but not on 23 June and 21 July.

Osmotic pressure of the hemolymph of C. punctipennis in Arbuckle Lake ranged from 0.214-0.607 $-\Delta^{\circ}\text{C}$ and averaged 0.387 $-\Delta^{\circ}\text{C}$ (Table VIII). Little variation existed between the two stations in the central pool and among the three stations in the arms. In 1977 values for the central pool were greater than those for the arms; whereas, the reverse was true in 1978 (Appendix, Tables XIX and XX). Osmotic pressure was erratic in 1977 reaching minimum values on 10 June and 15 August as was observed for Na^+ concentration in the hemolymph. In 1978 values decreased in spring, remained low in summer, and increased in the fall. Although the range of osmotic pressure of the hemolymph of C. punctipennis was similar in Ham's and Arbuckle lakes, the mean of 0.468 $-\Delta^{\circ}\text{C}$ was considerably larger in Ham's Lake (Table VIII). As was observed for Na^+ ions, osmotic pressure was less in organisms taken from the 2 m station than from the deeper water stations. Little variation generally existed between stations HP and HS and no effect can be attributed to pumping (Appendix, Tables XVII and XVIII).

Laboratory Experiments

Hemolymph ion concentrations of Chironomus riparius and Chaoborus punctipennis tended to increase linearly as temperature increased from 3-38 $^{\circ}\text{C}$ (Appendix, Table XXI). The hemolymph sodium (Na^+) concentration for this temperature range varied from 92-205 and 80-196 mM in C. riparius and C. punctipennis, respectively. The potassium (K^+) concentration remained low in both species, 4-9 mM, through 22 $^{\circ}\text{C}$ and increased abruptly at higher temperatures. The hemolymph chloride (Cl^-) concentration also exhibited a pronounced increase between 22 and 28 $^{\circ}\text{C}$ in both

species. Chloride concentrations were intermediate to the values of Na^+ and K^+ . Since hemolymph ion concentrations increased significantly between 22 and 28°C, subsequent studies of the effect of dissolved oxygen (DO) and salinity (NaCl) on ion concentrations were examined at 22, 24, and 26°C.

Ion concentrations of both species decreased as dissolved oxygen increased from 0-10 mg ℓ^{-1} at all three temperatures (Appendix, Table XXII). Although no significant differences were observed between ion concentrations at 5 and 10 mg ℓ^{-1} , values were significantly smaller at these concentrations than at 0 mg ℓ^{-1} . The Na/Cl concentration at 0 and 10 mg ℓ^{-1} averaged over all temperatures was 166/71 and 143/49 mM, respectively, for C. riparius and 159/60 and 134/47 mM for C. punctipennis. In the two species, K^+ ions ranged from 11-22 mM at 0 mg ℓ^{-1} and 7-14 mM at 10 mg ℓ^{-1} .

A linear increase in hemolymph ion values was observed in both species from 0.0-0.8% NaCl at all temperatures (Appendix, Table XXIII). Although no significant differences were observed between ion concentrations at 22 and 24°C over the NaCl concentrations, differences were significantly ($p = 0.05$) greater at 26°C than at the lower temperatures in both species. Mean hemolymph Na/Cl concentrations for C. riparius at 26°C ranged from 152/46 mM at 0.0% NaCl to 190/150 mM at 0.8% NaCl. The Na/Cl range for C. punctipennis was similar to that measured for C. riparius. The concentration of K^+ in the hemolymph of the organisms exceeded 40 mM at a salinity of 0.8% at all temperatures. The significant simple effects were temperature \times DO levels and temperature \times salinity.

Since data on the simple effects of temperature, dissolved oxygen,

and salinity on hemolymph ion concentrations suggested that interactions may be significant, a factorial experiment was designed (Table IX). The concentration of ions in the hemolymph was generally greater than values measured in previous laboratory experiments. Values of Na^+ reached 240 mM in both organisms, while the concentration of Cl^- reached 180 mM in C. riparius and 190 mM in C. punctipennis. In both species ion concentrations and trends were similar at DO concentrations of 5 and 10 mg l^{-1} and values are averaged on Table IX. Significant differences existed in ion concentrations in both species between the DO level of 0 mg l^{-1} and the 5 and 10 mg l^{-1} levels. As was observed in previous experiments, values increased with increasing temperatures and were higher at lower DO levels. A linear increase in Na^+ and Cl^- ions occurred in both species from 0.3-0.8% NaCl at all temperatures and DO concentrations. The interactions between DO \times salinity and DO \times temperature were significant ($p = 0.05$) in both species.

Discussion

Knowledge of changes in hemolymph inorganic ions, specifically Na^+ , K^+ , and Cl^- , is important in osmoregulation studies of the bloodworms Chironomus tentans and Chironomus riparius, and the phantom midge, Chaoborus punctipennis, since the hemolymph is the direct extracellular environment from which the cells acquire necessary substances to function. Changes in hemolymph ion concentrations might alter the physiological function of many tissues and organs surrounded by this medium. The problem of maintaining a constant homeostatic state within these larvae is of interest with respect to the fluctuations in physiocochemical parameters. Attempts to correlate ion regulation with physiocochemical

TABLE IX

THE EFFECTS OF DISSOLVED OXYGEN, SODIUM CHLORIDE, AND TEMPERATURE ON THE MEAN*
HEMOLYMPH SODIUM (Na^+) AND CHLORIDE (Cl^-) CONCENTRATIONS (mM) IN
CHIRONOMUS RIPARIUS MEIGEN AND CHAOTORUS PUNCTIPENNIS (SAY)

Organism	DO (mg l^{-1})	Ion	22°C			24°C			26°C		
			NaCl (%) =			NaCl (%) =			NaCl (%) =		
			0.3	0.5	0.8	0.3	0.5	0.8	0.3	0.5	0.8
<u>Chironomus riparius</u>	0	Na^+	165	172	189	180	189	206	196	210	240
		Cl^-	100	107	116	110	131	150	120	150	180
	$\bar{X}_{5,10}$	Na^+	152	161	178	162	168	181	182	194	200
		Cl^-	65	100	120	88	105	128	110	126	140
<u>Chaoborus punctipennis</u>	0	Na^+	165	184	192	196	210	230	196	230	240
		Cl^-	94	136	149	110	142	185	120	160	190
	$\bar{X}_{5,10}$	Na^+	143	160	182	160	178	186	185	196	209
		Cl^-	68	97	112	88	113	132	103	131	154

* Mean value obtained from five replicates.

parameters of the overlying water in the present study were unsuccessful in both lakes.

The range of Na^+ ions in the hemolymph of C. tentans as measured by several authors is rather small, 92-120 mM (Boné 1945, Firling 1970, Wright 1975). Wright (1975) found that the level of Na^+ is rather constant at 102 mM in C. tentans. Although a similar mean was measured for C. tentans in Arbuckle Lake in the present study, Na^+ ion concentration ranged from 48-172 mM. The larger range probably resulted from the longer duration of the present study which was 18 months compared to 7-120 days for the other investigations.

Hemolymph K^+ and Cl^- values in C. tentans from Arbuckle Lake exhibited slight fluctuations in concentration. Potassium remained relatively low. This trend agrees with data showing that hemolymph Na^+ and Cl^- content is consistently higher than potassium (Sutcliffe 1962b, Wright 1975, Schin and Moore 1977). Similar ranges for K^+ and Cl^- were reported in the literature for these ions (Sutcliffe 1962b, Firling 1970, Schin and Moore 1977).

A significant decrease in hemolymph ions of C. tentans at all stations in Arbuckle Lake was observed on 9 June and 15 August 1978. Schin and Moore (1977) found Na^+ and K^+ to be constant during the fourth instar in C. thummi except at the beginning of the fourth instar when elevated Na^+ and K^+ concentrations were observed. Previous to molting, a significant decrease in hemolymph ions and osmotic pressure occurs in C. thummi. Similar cation increases are noted around each ecdysial period for C. tentans (Schin and Moore 1977). Perhaps the fluctuations in hemolymph ions and osmotic pressure in C. tentans in the present study are due to physiological activities associated with molting and

growth rather than related to the effects of destratification.

The range of ion values of Chironomus riparius from Ham's Lake were lower than those of C. tentans in Arbuckle Lake. The range of hemolymph osmotic pressure in C. riparius is smaller than that observed in C. tentans. The more stable osmotic pressure of C. riparius may be due to an increase in proteins in the blood associated with the production of ecdysone and juvenile hormone (Firling 1977).

In Ham's Lake, ion values were highest in C. riparius at the stations mixed by pumping in the central pool. A gradual increase in ion concentrations was noted during summer 1978 at all stations although values were significantly lower at the anoxic station (HS). Again, the effects of destratification may not be responsible for the depressed values at Station HS but rather due to physiological development in that instar. Anoxic conditions may produce a stressful condition in which a retarded growth pattern could be occurring in this species due to a shift in metabolic energy from one life process to another.

The range of Na^+ ions in C. punctipennis from Arbuckle Lake was 45-145 mM. Potassium remained relatively constant and varied from 4-17 mM. The Cl^- concentration was also within the range reported in the literature (Sutcliffe 1962b). Ion concentrations were not significantly different between stations. A seasonal trend in the fluctuations of ions occurred at all stations during 1977. A significant decrease occurred on 10 June and 15 August 1977. This apparent decline may have been associated with molting physiology. In 1978, no apparent seasonal trend was observed at any station. Ion values were significantly lower at the anoxic central pool stations. This suppression of ion values in

relation to anoxic conditions was also seen in C. tentans and C. riparius.

C. punctipennis from Ham's Lake showed lower ion values at all stations which were anoxic during summer 1977. However, ionic values were significantly higher in this species at the anoxic station (HS) during summer 1978. As observed in the previous oxygen consumption study, C. punctipennis had maximum consumption rates under anoxic conditions. Perhaps the increase in ion concentrations was due to a failure in the active osmoregulatory process since oxygen was being diverted to its respiratory function.

In controlled laboratory experiments, Na^+ , K^+ , and Cl^- ranges are in agreement with other studies on dipteran larvae (Florkin et al. 1949, Ramsay 1949, Roeder 1953, Treherne 1954b, Stobbart 1960, Sutcliffe 1962b, Firling 1970, Wright 1974). Ion values of C. riparius and C. punctipennis increased linearly with temperature from 3-38°C. Potassium concentrations remained constant at lower temperatures but increased abruptly between 22 and 28°C. Chloride concentrations, although approximately one half the concentration of Na^+ , paralleled the trends observed for the Na^+ concentration which suggests similar regulation of these ions. Since fluctuations are so slight in K^+ , its regulation is probably independent of other hemolymph cations and anions. Osmoregulation appears to break down in both species in this study at its upper tolerated temperature range of 38°C. Therefore, temperature did affect the metabolism in these organisms.

A decline in ion concentrations was observed in both species as the DO level increased. The larvae appear to regulate their hemolymph composition efficiently at 5 and 10 mg ℓ^{-1} DO as noted by no significant

differences in ion values between these DO concentrations. Since oxygen consumption was lowest at 0 mg l^{-1} for these species in the controlled studies previously, oxygen is probably being diverted from its respiratory function to help maintain functioning of the active transport mechanisms associated with osmoregulation to insure survival under anoxic conditions.

Trends in the Na^+ and Cl^- data suggest that both species are able to regulate sodium up to an external medium concentration of 0.5% NaCl (85.5 mM) at temperatures of 22 and 24°C. At 26°C, the larvae are only able to regulate Na^+ and Cl^- up to an external medium concentration of 0.3% NaCl (51.3 mM). The osmotic response of C. riparius and C. punctipennis to various concentrations of NaCl solutions are typical of the responses in other freshwater dipteran larvae (Harnish 1934, Wigglesworth 1938a, Ramsay 1953a, Treherne 1954b, Stobbart 1960, Thornton and Sauer 1972). These experiments have demonstrated that both species are able to maintain a rather constant hemolymph composition over a considerable range of salinities.

The interactions of temperature, salinity, and DO in relation to maintenance of hemolymph ion concentrations has not been reported in the literature for dipteran larvae. In the present factorial experiment, both species were unable to survive in water at higher temperatures and less DO. Ion values continued to increase linearly in NaCl solutions from 0.3-0.8% at all temperature and DO combinations. Anoxic conditions were most lethal to both species at 24 and 26°C from 0.3-0.8% NaCl.

C. riparius and C. punctipennis appear to have an equal ability to regulate and survive in various freshwater environments. They differ

in their tolerance of high osmotic pressures and somewhat in their ability to regulate Na^+ . From the controlled saline and factorial studies, it seems that death will occur when the response curve crosses the isosmotic line.

CHAPTER VII

SUMMARY

1. Oxygen consumption by the sediments is mainly a biological process. The respiratory rate was greatest in the summer and fall and at the stratified stations in Arbuckle and Ham's lakes. No consistent trend existed in oxygen consumption among sediment depths of 0-1, 4-5, and 9-10 cm.
2. No significant differences were observed in oxygen consumption values in Chironomus tentans collected from the central pool and arm stations at Arbuckle Lake in 1978. Chironomus riparius from Ham's Lake maintained a higher respiratory rate in the mixed central pool area of the lake during the summer, while lowest values were observed at the stratified station. Oxygen consumption in Chaoborus punctipennis from both lakes was highest during summer at the stratified stations.
3. In laboratory studies, the oxygen consumption of C. riparius and C. punctipennis increased linearly with temperature, dissolved oxygen, and salinity. Both species appear to reach their isosmotic point in a 0.3% NaCl solution as indicated by the maximum consumption values. At higher salinities of 0.5 and 0.8% NaCl, the organisms lose their ability to osmoregulate and the respiratory rate declines. An inverse relationship in oxygen consumption occurred at 24°C,

0 mg ℓ^{-1} dissolved oxygen, from 0.3-0.8% NaCl. The interactions of temperature \times salinity and temperature \times DO were significant.

4. Hemolymph ion concentrations and osmotic pressure in C. tentans and C. riparius from Arbuckle and Ham's Lakes, respectively, were significantly lower at the stratified stations than at the mixed stations as was noted for oxygen consumption. In Arbuckle Lake, hemolymph ion values in C. punctipennis were generally lower during anoxic conditions. Ion concentrations in C. punctipennis from Ham's Lake were significantly lower at the mixed stations than at the stratified station which was the same relationship observed for oxygen consumption.
5. Hemolymph ion concentrations in laboratory experiments of C. riparius and C. punctipennis tended to increase linearly as temperature increased from 3-38°C. Ion concentrations of both species decreased as DO increased from 0-10 mg ℓ^{-1} at 22, 24, and 26°C. A linear increase occurred as NaCl increased from 0-0.8%. The interactions between DO \times salinity and DO \times temperature were significant.

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APPENDIX

TABLE X
 MEAN OXYGEN CONSUMPTION RATES ($\mu\text{l O}_2 \text{ g dry wt}^{-1} \text{ h}^{-1}$) OF SEDIMENTS AT
 THREE STATIONS IN HAM'S LAKE IN 1978*

Station (Depth in m)	Core Depth (cm)	Mar 13	Apr 23	May 25	Jun 23	Jul 21	Aug 22	Sep 29	Oct 29	Nov 30
HS (5)	1	0.27	0.38	0.38	0.22	0.53	0.34	0.69	0.79	0.41
	5	0.40	0.62	0.61	0.21	0.50	0.29	0.36	0.58	0.39
	10	-	-	0.00	0.20	0.49	0.23	0.35	0.76	0.60
HP (8)	1	0.23	0.35	0.28	0.16	0.13	0.09	0.30	0.58	0.36
	5	0.52	0.50	0.33	0.15	0.07	0.09	0.22	0.56	0.59
	10	-	-	0.30	0.27	0.15	0.11	0.20	0.72	0.95
HA (2)	1	0.26	0.38	0.23	0.16	0.12	0.06	0.23	0.33	0.13
	5	0.39	0.55	0.25	0.10	0.09	0.05	0.14	0.51	0.25

* Means obtained from three replicates.

- Data not measured.

TABLE XI

MEAN OXYGEN CONSUMPTION RATES ($\mu\text{l O}_2 \text{ g dry wt}^{-1} \text{ h}^{-1}$) OF SEDIMENTS AT
FIVE STATIONS IN ARBUCKLE LAKE IN 1978*

Station (Depth in m)	Core Depth (cm)	Mar 15	Apr 29	Jun 9	Jul 11	Aug 15	Sep 16	Oct 22	Nov 24	Dec 16
AC (25)	1	0.44	0.76	0.77	1.36	0.89	0.82	0.73	0.84	0.95
	5	0.51	0.77	0.72	1.03	1.18	0.86	0.57	0.74	0.61
	10	-	-	0.75	1.20	0.89	0.98	0.63	0.70	0.90
AP (23)	1	0.45	0.62	0.81	0.99	0.97	0.77	0.90	0.80	1.07
	5	0.53	0.82	0.86	0.54	1.03	0.87	1.10	0.65	0.64
	10	-	-	1.20	1.09	0.43	0.59	0.94	0.63	0.63
AS (15)	1	-	0.37	0.70	0.46	0.25	0.07	0.44	0.49	0.70
	5	-	0.80	0.64	0.47	0.15	0.11	0.45	0.45	0.70
	10	-	-	0.66	0.40	0.13	0.09	0.27	0.48	0.58
AR (15)	1	-	0.38	0.62	0.32	0.38	0.10	0.61	0.70	0.41
	5	-	0.58	0.75	0.28	0.12	0.09	0.42	0.69	0.34
	10	-	-	0.65	0.22	0.11	0.09	0.70	0.62	-
AB (15)	1	0.49	0.41	0.40	0.19	0.17	0.09	0.36	0.44	0.83
	5	0.62	0.65	0.40	0.16	0.13	0.07	0.21	0.44	0.85
	10	-	-	0.46	0.15	0.07	0.07	0.35	0.37	0.76

* Means obtained from three replicates.

- Data not measured.

TABLE XII

THE EFFECTS OF TEMPERATURE ON OXYGEN CONSUMPTION*†
 ($\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$) OF CHIRONOMUS RIPARIUS
 MEIGEN AND CHAOBORUS PUNCTIPENNIS (SAY)

Organism	Temperature ($^{\circ}\text{C}$)							
	3	8	12	17	22	28	32	38
<u>Chironomus riparius</u>	0.2	1.7	2.4	2.6	3.0	0.33	1.0	1.2
<u>Chaoborus punctipennis</u>	0.6	0.78	1.9	4.2	6.2	1.7	2.2	2.4

* Mean value obtained from three replicates.

† All experiments conducted with DO concentration of $10 \text{ mg } \ell^{-1}$.

TABLE XIII

THE EFFECTS OF DISSOLVED OXYGEN ON OXYGEN
 CONSUMPTION* ($\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$)
 OF CHIRONOMUS RIPARIUS MEIGEN AND
CHAOBORUS PUNCTIPENNIS (SAY)

Organism	DO (mg l^{-1})	Temperature ($^{\circ}\text{C}$)		
		17	22	24
<u>Chironomus</u> <u>riparius</u>	0	2.0	2.2	1.8
	5	2.4	2.8	2.0
	10	2.8	3.4	2.0
<u>Chaoborus</u> <u>punctipennis</u>	0	3.0	2.0	1.2
	5	4.4	5.0	4.2
	10	4.6	6.0	4.4

* Mean value obtained from three replicates.

TABLE XIV

THE EFFECTS OF SODIUM CHLORIDE ON OXYGEN
 CONSUMPTION*† ($\mu\text{l O}_2 \text{ mg dry wt}^{-1} \text{ h}^{-1}$)
 OF CHIRONOMUS RIPARIUS MEIGEN AND
CHAOBORUS PUNCTIPENNIS (SAY)

Organism	NaCl (%)	Temperature ($^{\circ}\text{C}$)		
		17	22	24
<u>Chironomus riparius</u>	0.0	2.4	2.4	2.3
	0.1	2.4	2.6	2.8
	0.3	2.8	3.6	3.3
	0.5	2.0	2.5	1.8
	0.8	2.0	1.9	1.0
<u>Chaoborus punctipennis</u>	0.0	4.3	6.0	4.0
	0.1	4.9	6.4	4.8
	0.3	5.6	6.9	5.4
	0.5	3.8	4.2	3.6
	0.8	3.2	3.5	3.0

* Mean value obtained from three replicates.

† All experiments conducted with DO concentration of 10 mg l^{-1} .

TABLE XV

MEAN HEMOLYMPH ION CONCENTRATIONS (mM) AND OSMOTIC PRESSURE ($-\Delta^{\circ}\text{C}$) OF
CHIRONOMUS TENTANS (FABR.) FROM ARBUCKLE LAKE IN 1977*

Station (Depth in m)	Ion	May 10	Jun 10	Jul 17	Aug 15	Sep 18	Oct 22	Dec 30
AP (23)	Na ⁺	169	-	-	49	-	-	90
	K ⁺	5	-	-	4	-	-	11
	Cl ⁻	80	-	-	36	-	-	56
	O.P.	0.602	0.258	-	0.127	-	-	0.257
AS (15)	Na ⁺	166	-	172	57	-	-	94
	K ⁺	5	-	9	7	-	-	9
	Cl ⁻	72	-	60	36	-	-	50
	O.P.	0.597	0.257	0.629	0.152	-	-	0.271
AR (15)	Na ⁺	155	70	-	-	-	-	94
	K ⁺	6	3	-	-	-	-	10
	Cl ⁻	56	44	-	-	-	-	40
	O.P.	0.551	0.226	-	-	-	-	0.271
AB (15)	Na ⁺	165	104	127	58	132	-	94
	K ⁺	6	3	2	4	7	-	9
	Cl ⁻	56	44	48	16	70	-	45
	O.P.	0.607	0.306	0.452	0.119	0.457	-	0.279

* Mean value obtained from five replicates.

- Data not measured.

TABLE XVI

MEAN HEMOLYMPH ION CONCENTRATIONS (mM) AND OSMOTIC PRESSURE ($-\Delta^{\circ}\text{C}$) OF
CHIRONOMUS TENTANS (FABR.) FROM ARBUCKLE LAKE IN 1978*

Station (Depth in m)	Ion	Mar 15	Apr 29	Jun 9	Jul 11	Aug 15	Sep 16	Oct 22	Dec 16
AC (25)	Na ⁺	93	95	-	-	70	100	119	120
	K ⁺	5	6	-	-	8	9	8	9
	Cl ⁻	40	44	-	-	23	42	45	50
	O.P.	0.264	0.261	-	-	0.246	0.316	0.358	0.358
AP (23)	Na ⁺	93	95	70	117	60	95	110	105
	K ⁺	4	6	5	7	5	6	8	7
	Cl ⁻	40	45	44	52	20	38	40	42
	O.P.	0.262	0.264	0.244	0.350	0.235	0.264	0.312	0.306
AS (15)	Na ⁺	97	114	73	138	84	124	115	96
	K ⁺	4	7	5	9	6	8	8	4
	Cl ⁻	40	57	46	60	35	50	46	35
	O.P.	0.279	0.310	0.246	0.458	0.248	0.365	0.352	0.281
AR (15)	Na ⁺	84	114	90	139	96	130	125	90
	K ⁺	3	7	8	8	6	9	7	5
	Cl ⁻	40	58	47	54	37	56	51	32
	O.P.	0.246	0.352	0.256	0.460	0.263	0.452	0.451	0.276
AB (15)	Na ⁺	84	114	116	145	88	141	129	93
	K ⁺	3	7	8	10	7	10	10	4
	Cl ⁻	41	60	47	65	31	55	56	34
	O.P.	0.243	0.352	0.356	0.440	0.250	0.460	0.453	0.279

* Mean value obtained from five replicates.

- Data not measured.

TABLE XVII

MEAN HEMOLYMPH ION CONCENTRATIONS (mM) AND OSMOTIC PRESSURE ($-\Delta^{\circ}\text{C}$) OF
CHIRONOMUS RIPARIUS MEIGEN AND CHAOBORUS PUNCTIPENNIS (SAY)
 FROM HAM'S LAKE IN 1977*

Organism	Station (Depth in m)	Ion	May 20	Jun 20	Aug 1	Sep 10	Oct 15	Dec 14
<u>Chironomus riparius</u>	HS (5)	Na ⁺	-	-	-	-	113	87
		K ⁺	-	-	-	-	8	5
		Cl ⁻	-	-	-	-	38	35
		O.P.	-	-	-	-	0.354	0.259
	HP (8)	Na ⁺	-	-	-	-	100	87
		K ⁺	-	-	-	-	6	5
		Cl ⁻	-	-	-	-	35	35
		O.P.	-	-	-	-	0.313	0.260
	HA (2)	Na ⁺	-	-	133	124	-	87
		K ⁺	-	-	6	6	-	5
		Cl ⁻	-	-	52	41	-	35
		O.P.	-	-	0.450	0.424	-	0.248
<u>Chaoborus punctipennis</u>	HS (5)	Na ⁺	154	131	136	97	126	94
		K ⁺	8	9	13	8	8	5
		Cl ⁻	52	48	44	55	40	47
		O.P.	0.628	0.553	0.556	0.408	0.514	0.330
	HP (8)	Na ⁺	137	129	118	97	126	94
		K ⁺	9	10	12	8	8	5
		Cl ⁻	52	48	44	42	43	40
		O.P.	0.598	0.537	0.510	0.396	0.510	0.350
	HA (2)	Na ⁺	118	110	79	58	117	79
		K ⁺	8	12	12	6	8	5
		Cl ⁻	56	56	32	33	37	35
		O.P.	0.490	0.445	0.321	0.206	0.486	0.255

* Mean value obtained from five replicates.

- Data not measured.

TABLE XVIII
 MEAN HEMOLYMPH ION CONCENTRATIONS (mM) AND OSMOTIC PRESSURE ($-\Delta^{\circ}\text{C}$) OF
CHIRONOMUS RIPARIUS MEIGEN AND CHAOBORUS PUNCTIPENNIS (SAY)
 FROM HAM'S LAKE IN 1978*

Organism	Station (Depth in m)	Ion	Mar 13	Apr 23	May 25	Jun 23	Jul 21	Aug 22	Sep 29	Oct 29	Nov 30
<u>Chironomus riparius</u>	HS (5)	Na ⁺	90	115	129	91	125	120	115	118	115
		K ⁺	5	7	10	6	9	8	8	7	7
		Cl ⁻	49	58	55	46	56	64	58	55	53
		O.P.	0.256	0.352	0.449	0.263	0.366	0.358	0.346	0.354	0.350
	HP (8)	Na ⁺	92	100	129	141	133	130	125	120	110
		K ⁺	5	7	9	9	9	10	7	8	7
		Cl ⁻	39	53	53	54	58	69	54	50	52
		O.P.	0.262	0.313	0.454	0.445	0.440	0.442	0.361	0.355	0.315
	HA (2)	Na ⁺	96	81	104	154	154	149	129	118	106
		K ⁺	5	6	8	9	9	9	8	8	8
		Cl ⁻	38	46	47	58	61	65	52	54	54
		O.P.	0.297	0.251	0.310	0.460	0.463	0.465	0.369	0.350	0.310
<u>Chaoborus punctipennis</u>	HS (5)	Na ⁺	85	-	113	137	166	180	130	121	110
		K ⁺	5	-	9	7	8	12	6	6	8
		Cl ⁻	45	-	53	62	70	82	47	52	48
		O.P.	0.332	-	0.452	0.552	0.565	0.590	0.550	0.491	0.442
	HP (8)	Na ⁺	84	111	116	139	150	150	120	126	120
		K ⁺	6	7	9	9	7	9	9	8	7
		Cl ⁻	47	59	54	58	70	70	52	48	48
		O.P.	0.338	0.450	0.458	0.554	0.564	0.562	0.500	0.496	0.490
	HA (2)	Na ⁺	80	-	104	144	103	129	121	115	119
		K ⁺	5	-	8	7	7	7	9	7	8
		Cl ⁻	43	-	46	60	51	56	56	51	45
		O.P.	0.309	-	0.398	0.560	0.430	0.534	0.491	0.451	0.500

* Mean value obtained from five replicates.

- Data not measured.

TABLE XIX

MEAN HEMOLYMPH ION CONCENTRATIONS (mM) AND OSMOTIC PRESSURE ($-\Delta^{\circ}\text{C}$) OF
CHAOBORUS PUNCTIPENNIS (SAY) FROM ARBUCKLE LAKE IN 1977*

Station (Depth in m)	Ion	May 10	Jun 10	Jul 17	Aug 15	Sep 18	Oct 22	Dec 30
AP (23)	Na ⁺	94	-	126	87	141	127	94
	K ⁺	5	-	17	7	13	8	9
	Cl ⁻	56	-	48	40	66	45	35
	O.P.	0.345	-	0.513	0.356	0.607	0.514	0.374
AS (15)	Na ⁺	145	65	115	58	117	127	74
	K ⁺	7	7	6	11	12	9	9
	Cl ⁻	56	34	46	30	54	50	27
	O.P.	0.546	0.341	0.464	0.226	0.514	0.467	0.270
AB (15)	Na ⁺	98	45	125	73	101	110	69
	K ⁺	9	7	12	13	11	9	9
	Cl ⁻	36	15	40	30	48	48	36
	O.P.	0.353	0.214	0.519	0.255	0.408	0.447	0.273

* Mean value obtained from five replicates

- Data not measured.

TABLE XX

MEAN HEMOLYMPH ION CONCENTRATIONS (mM) AND OSMOTIC PRESSURE ($-\Delta^{\circ}\text{C}$) OF
CHAOBORUS PUNCTIPENNIS (SAY) FROM ARBUCKLE LAKE IN 1978*

Station (Depth in m)	Ion	Mar 15	Apr 29	Jun 9	Jul 11	Aug 15	Sep 16	Oct 22	Dec 16
AC (25)	Na ⁺	87	95	70	-	65	60	110	86
	K ⁺	4	6	5	-	8	5	7	7
	Cl ⁻	40	48	45	-	24	26	40	34
	O.P.	0.358	0.352	0.251	-	0.250	0.250	0.445	0.356
AP (23)	Na ⁺	107	85	70	74	70	73	94	83
	K ⁺	4	5	5	6	5	8	7	6
	Cl ⁻	52	44	44	40	42	42	46	39
	O.P.	0.440	0.352	0.249	0.259	0.248	0.262	0.351	0.340
AS (15)	Na ⁺	116	141	70	75	88	101	136	90
	K ⁺	4	8	5	5	6	9	9	8
	Cl ⁻	53	53	44	41	42	40	50	44
	O.P.	0.465	0.605	0.248	0.260	0.353	0.406	0.545	0.342
AR (15)	Na ⁺	126	103	100	93	98	110	132	84
	K ⁺	4	6	7	8	8	9	10	5
	Cl ⁻	56	53	46	42	41	42	53	39
	O.P.	0.513	0.400	0.401	0.350	0.354	0.445	0.540	0.354
AB (15)	Na ⁺	111	-	-	117	86	108	120	76
	K ⁺	4	-	-	9	6	8	9	5
	Cl ⁻	53	-	-	42	36	40	52	38
	O.P.	0.446	-	-	0.465	0.350	0.442	0.510	0.254

* Mean value obtained from five replicates.

- Data not measured.

TABLE XXI
 THE EFFECT OF TEMPERATURE ON MEAN HEMOLYMPH SODIUM
 (Na^+), POTASSIUM (K^+), AND CHLORIDE
 CONCENTRATIONS (mM) OF CHIRONOMUS
RIPARIUS MEIGEN AND CHAOBORUS
PUNCTIPENNIS (SAY)*†

Organism	Ion	°C							
		3	8	12	17	22	28	32	38
<u>Chironomus</u> <u>riparius</u>	Na^+	92	98	110	120	132	164	188	205
	K^+	4	4	6	6	9	19	28	39
	Cl^-	32	38	40	40	42	60	84	89
<u>Chaoborus</u> <u>punctipennis</u>	Na^+	80	95	112	115	125	156	174	196
	K^+	4	5	8	8	9	14	18	24
	Cl^-	30	32	39	42	46	59	68	92

* Mean value obtained from five replicates.

† All experiments conducted with DO concentration of 10 mg ℓ^{-1} .

TABLE XXII

THE EFFECTS OF DISSOLVED OXYGEN ON MEAN* HEMOLYMPH
 SODIUM (Na^+), POTASSIUM (K^+), AND CHLORIDE
 (Cl^-) CONCENTRATIONS (mM) OF CHIRONOMUS
RIPARIUS MEIGEN AND CHAOBORUS
PUNCTIPENNIS (SAY)†

Ion	DO ($\text{mg } \ell^{-1}$)	°C		
		22	24	26
Na^+	0	145 (140)	168 (160)	184 (176)
	5	134 (130)	142 (136)	159 (152)
	10	130 (124)	142 (130)	156 (148)
K^+	0	11 (11)	23 (13)	19 (22)
	5	8 (8)	8 (10)	13 (11)
	10	8 (7)	8 (11)	14 (10)
Cl^-	0	60 (49)	69 (62)	84 (70)
	5	42 (44)	54 (49)	59 (54)
	10	40 (42)	50 (48)	57 (50)

* Mean value obtained from five replicates.

† Values for Chaoborus punctipennis are in parentheses.

TABLE XXIII
 THE EFFECTS OF SODIUM CHLORIDE ON MEAN* HEMOLYMPH
 SODIUM (Na⁺), POTASSIUM (K⁺), AND CHLORIDE
 CONCENTRATIONS (mM) OF CHIRONOMUS
RIPARIUS MEIGEN AND CHAOBORUS
PUNCTIPENNIS (SAY)**†

% NaCl	Ion	22°C	24°C	26°C
0.0	Na ⁺	132 (126)	140 (132)	152 (150)
	K ⁺	8 (8)	9 (10)	11 (11)
	Cl ⁻	41 (40)	46 (46)	46 (50)
0.1	Na ⁺	138 (134)	148 (135)	160 (158)
	K ⁺	8 (8)	12 (16)	17 (20)
	Cl ⁻	49 (46)	60 (62)	65 (82)
0.3	Na ⁺	148 (140)	160 (165)	178 (176)
	K ⁺	19 (21)	20 (30)	32 (34)
	Cl ⁻	65 (69)	75 (80)	101 (100)
0.5	Na ⁺	160 (159)	163 (172)	180 (184)
	K ⁺	24 (26)	23 (41)	42 (46)
	Cl ⁻	100 (98)	101 (110)	140 (132)
0.8	Na ⁺	172 (174)	178 (180)	190 (196)
	K ⁺	40 (40)	40 (49)	50 (53)
	Cl ⁻	130 (110)	136 (140)	150 (154)

* Mean value obtained from five replicates.

** Values for Chaoborus punctipennis are in parentheses.

† All experiments conducted with DO concentration of 10 mg l⁻¹.

VITA²

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Doctor of Philosophy

Thesis: THE EFFECTS OF LAKE DESTRATIFICATION ON SEDIMENT OXYGEN CONSUMPTION AND THE OSMOREGULATORY AND RESPIRATORY ACTIVITIES OF CHIRONOMUS TENTANS (FABR.), CHIRONOMUS RIPARIUS MEIGEN, AND CHAOBORUS PUNCTIPENNIS (SAY)

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