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DATED *March 29*.....1972

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THE ROLE OF WETLAND
HETEROGENEITY IN THE REGULATION
OF DUCK POPULATIONS IN
EASTERN ONTARIO

by

James Howard Patterson, B.Sc., M.Sc.

A thesis submitted to the Faculty of
Graduate Studies in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Carleton University

Ottawa, Ontario

March, 1972

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ABSTRACT

Both behavioural spacing of breeding pairs, and the availability of energy resources have been proposed as major regulatory mechanisms of duck populations. In order to compare the relative importance and interaction of the two mechanisms, the distribution of duck populations was determined in a heterogeneous system of beaver ponds.

The study area was located approximately 20 miles west of Ottawa, Ontario, in the vicinity of a contact of the Ottawa-St. Lawrence Lowland and the Precambrian Shield. Ponds were selected from a number of geological substrates, so that within a relatively small geographical area a wide variety of chemical conditions were represented.

All pond waters were of the calcium bicarbonate type, with the cation composition generally being of the order $\text{Ca} > \text{Mg} > \text{Na} > \text{K}$. In the hard water sedimentary ponds the concentrations of all major ions were highly variable, in response to the composition and solubility of the local bedrock. In the more dilute Precambrian ponds, calcium was the only major ion which appreciably varied from pond to pond.

The seasonal fluctuations and stratification of ions were more pronounced in the harder water ponds. This variability was attributed to the greater biological activity in the chemically rich ponds producing anaerobic conditions in the lower main column, and thereby facilitating nutrient release from the sediments. In the soft water ponds, fluctuations of major ions were relatively independent of the sediments.

The production of submerged aquatic macrophytes was determined by seasonal biomass changes in four ponds, representing the range of water chemical conditions in the study area. Maximum annual production was found to be similar in each pond, however, growth rates from spring minima varied as a function of water hardness. In the hardest water pond maximum macrophyte biomass was reached in May, while in the softest the biomass peak was in July. It is postulated that the differences in macrophyte growth rates are of major ecological significance with regards to nutrient cycling, and the provision of a resource base for consumer organisms.

Numbers of breeding pairs, broods and fledged ducks were independently related to the chemical and physical characteristics of the ponds. Breeding pair numbers were found to be dependent only on the amount of surface water available, indicating that the major population regulatory mechanism was behavioural spacing. Fledged ducks, on the other hand, were found to select fertile wetlands regardless of size, indicating that populations were regulated by the availability of energy resources. Regulation of brood numbers was intermediate, as behavioural escape cover and food availability were important.

It is postulated that the different environmental requirements of the three life history stages are an evolutionary adaptation to a temporally unpredictable environment. The adaptations allow duck populations to maintain equilibrium in a temporally heterogeneous environment, and attain high population size in a spatially

heterogeneous environment. In conclusion, the findings of this study are used as a basis of the concept that not only species diversity, but all dimensions of system heterogeneity can affect the stability of ecosystems.

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INTRODUCTION

One of the more widely accepted generalizations of waterfowl biology is that duck populations are regulated by habitat fertility. Biologically productive wetlands located in edaphically rich areas usually support large duck populations while wetlands in edaphically poor areas support only sparse populations.

The recognition of the importance of habitat fertility has mainly been a result of extensive regional waterfowl studies. Moyle (1956) in Minnesota and Jahn and Hunt (1964) in Wisconsin have shown that breeding populations of ducks are much higher in sedimentary regions where wetlands are of the hard water type than in the soft water Precambrian Shield regions. Such regional disparities in breeding duck densities and production are clearly interpreted as population regulation by food availability. Jahn and Hunt (1964) conclude that Wisconsin's mineral poor waters have low waterfowl capacity. In these waters plant production and nutritional quality are poor, so that duck populations are regulated by the available energy resources.

Hawkins (1964) states that "Food abundance and waterfowl distribution go hand in hand." Based on the assumption that the energy requirement is high at all stages of a duck's life, he concludes that a great abundance of high quality food must be readily available at all times.

Waterfowl investigations carried out within edaphically homogeneous regions have indicated another major regulatory mechanism of duck populations, that of behavioural spacing. Mendall (1958) suggested that territorialism limited pair populations of ring-necked ducks on certain streams in Maine. In a prairie pothole region of South Dakota, Evans and Black (1956) could not find any relationships between breeding pairs and measurable factors of pond quality such as food or cover. They concluded that pairs sought only space and freedom interference, and thus were evenly dispersed over the available habitat.

In a recent review of the waterfowl literature, Dzubin (1969) states that "Intolerance and hostile behaviour between pairs as a possible population density control has been largely speculative with no concrete evidence yet presented to show that pair interactions consistently interfere with pair settling...." He suggests that spacing mechanisms help place an upper limit on pair densities although upper densities themselves would vary with habitat units. Dzubin cautions that enumeration of breeding pairs only may lead to erroneous conclusions about the ability of that habitat to support duck populations. Habitats which can support breeding pairs may not be adequate for the survival of young. Similarly, Jahn and Hunt (1964) suspect that pairs which nest in poorer quality habitats may be less efficient in producing ducklings.

Although there is a considerably body of knowledge concerning duck populations, and their relationships to specific environmental factors, very little is known about their over-all environmental requirements. This fact is strongly pointed out in the transactions of the Saskatoon Wetlands Seminar published in 1969. Contributors repeatedly ask the question of what are the over-all environmental requirements of duck populations. In the summary, Jahn (1969) states that for progress to be made in waterfowl research "Seasonal needs of the birds must be related to the physical, chemical and biotic features of the ecosystem."

In a discussion of intertrophic level species Slobodkin, Smith and Hairston (1967) note that many seed eaters are also carnivorous, especially during the breeding season when demand on the general food supply is greatest. They further state that "... these species often show evidence of food-limitation, or else show an evolutionary response (e.g., territoriality) to what must have been intraspecific competition for resources in the past."

Both territorial spacing and direct food limitation have been proposed as major regulatory mechanisms to the density and distribution of ducks. As a group they provide a good example of omnivorous organisms which, according to Slobodkin, Smith and Hairston, should be directly or indirectly resource-limited.

If densities of duck populations could be determined in a geographically small, but spatially

heterogeneous system of wetlands which had recognisable variations in food supply, it should be possible to evaluate the relationships of the two population control mechanisms. Furthermore, it should provide a means of evaluating the value of environmental heterogeneity.

The physical characteristics of an area west of Ottawa, Ontario, suggested that it would provide an excellent location for this type of research investigation. The presence of numerous beaver ponds overlying a wide variety of geological substrates provides a natural outdoor laboratory, where ponds of different edaphic quality and morphometry could be selected from within a geographically small area.

The present research program was initiated in 1966. Most of the research effort was directed to the analysis of the interrelationships, and the spatial and temporal variations in the abiotic and biotic components of the pond ecosystems. It was assumed that the emphasis on the pond ecosystems, rather than duck populations, would provide a stronger basis for the evaluation of the environmental requirements of the ducks.

The results of the 1966 and 1967 pond habitat research have been presented previously (Patterson, 1969). This study is based primarily on the field investigations of 1969 and 1970, but includes the duck population and related habitat data from 1966 and 1967.

THE STUDY AREA

Geology and Pond Location

Field investigations were conducted in March and Huntley Townships, Carleton County, Ontario, in an area bounded by $75^{\circ}55'$ to $76^{\circ}05'$ west longitude and $45^{\circ}15'$ to $45^{\circ}25'$ north latitude. The study areas are located in the western portion of the Ottawa-St. Lawrence Lowland close to its contact with the Canadian Shield. The sedimentary geology of the area has been described by Wilson (1946). The Lowland is underlain by rocks of Ordovician age with the exception of the basal sandstones which may be Cambrian. The geology of the study area and the location of all study ponds are shown in Figure 1.

Ponds C-1 and C-3 are located on the Oxford formation. Although the influent drainage to C-1 and C-3 originates in the Precambrian upland to the south, most of its length is confined to the sedimentary lowland. Ponds C-2, C-4 and C-5 are located on a contact of the Oxford and March formations. However, influent drainage to the three ponds is primarily from the March formation. Ponds C-6 and C-7 are situated within the Ottawa formation and their drainage basins are confined to this rock type.

The March formation lies between the Nepean sandstone and the Oxford dolomite. Locally it lies unconformably on the Precambrian but normally both contacts are conformable. The March strata consist of alternating grey sandstone and sandy dolomite, or blue-grey dolomite. The sand grains are generally large, rounded and loosely

FIGURE 1

Map showing the bedrock geology of the study area and the location of the 21 beaver ponds. After Wilson (1946).

cemented. The dolomite beds can contain pockets of calcite crystals.

The Oxford formation lies above the March and is succeeded by the Rockliffe. In the northwest part of the Lowland where the study area is located, the Oxford is thought to overlap the Nepean and March, and lie unconformably upon the Precambrian. The Oxford is mostly a thick-bedded rusty weathering dolomite. As in the March formation, some of the lower beds contain pockets of calcite crystals. Where the Oxford lies against or overlaps the Precambrian the dolomite contains pebbles and boulders of quartz up to 12 inches long.

The Ottawa formation is dominantly limestone but includes some shale and sandstone at the base. A small amount of shale persists upward as shaley partings.

The Precambrian study area is located north of Carp, Ontario, on a long prong of Precambrian rock within the Palaeozoic basin. This southeasterly trending prong reaches elevations of 425 to 450 feet. It connects with the Canadian Shield at Morris Island and extends across Torbolton and March to Nepean Township. The northern boundary of the prong is suspected of being an angular unconformity, while on the southern boundary the Precambrian rocks are in fault contact with Palaeozoic rocks along the Hazeldean fault.

The detailed geology and the location of ponds in the Precambrian study area are shown in Figure 2. The geology of the area has been described by Livingstone et al. (1969). The rocks north of Carp in the prong are

FIGURE 2

Map showing the bedrock geology of the Precambrian study area, the location of the 14 beaver ponds, and the pond drainage patterns. After Livingston, Hill and Kirwan (1969).

most red granitic gneisses (3a) which are intercalated with subordinate mafic gneiss and schist. Ponds PC-2, PC-5, PC-12 and PC-14 are all contained in this subunit. South of pond PC-2 is a calcic subunit (3b) containing green, coarse-grained diopside pyroxenite layers up to 10 feet thick, and lenses of coarse-grained pink marble usually less than 10 feet across. Subunit 3b interfingers with the non-calcic granitic gneiss. PC-13 lies within subunit 3c which is composed of feldspathic quartzite and quartzofeldspathic gneiss. These fine-grained quartz-rich rocks grade imperceptibly into the medium-grained granitic gneiss.

Midway between the two monzonite stocks is a small unit (2) composed of intercalated biotite-hornblende bearing schists and gneisses which are interlayered with marble.

At the eastern edge of the study area is an intruded stock of red syenite (4). It is composed predominantly of medium-grained microcline with plagioclase, scattered microperthite and minor pyroxene, hornblende and biotite. PC-1, PC-3 and PC-4 lie on the southern contact of the syenite and the granitic gneiss.

Two monzonite stocks are present in the study area as shown by map unit 5. They are composed of coarse-grained perthitic feldspar, plagioclase, orthoclase and minor microcline, augite, subordinate sphene, apatite, ilmenite and magnetite.

The northern and largest monzonite stock has been described by Nesbitt (1968) and demonstrated to be far from uniform in composition. Nesbitt found variations within the stock in which the mafic mineral content increases to 50

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per cent and the plagioclase feldspar has a high calcium content, so that locally the stock is a diorite. Also, in the vicinity of pond PC-8 are zones of scapolite and epidote rock with a high calcium and carbonate content. Considerable interstitial calcite is present through these rocks. PC-7, PC-8, PC-9, PC-10 and PC-11 are all located within the monzonite stock, and PC-6 is on the contact of the stock and the granitic gneiss.

Surficial Geology

Gadd (1962) found evidence for only one episode of southward-moving glaciation in the Ottawa area. This ice sheet derived its material from local bedrock and consequently the glacial till and related sediments reflect the composition of the underlying and nearby bedrock. The major bedrock types in the carbonate study area are covered by glacial till which is shallow and full of stones from the underlying material. Shallow non-marine clay is extensive and sandy material occurs locally.

A small sandy ridge occurs in the vicinity of ponds C-2, C-4 and C-5. This deposit was not mapped by Gadd but is noted on the Soil Survey Map of Carleton County (1938). Because it is a non calcareous fine sand and is associated with an abandoned river channel, it is probably high terrace alluvium.

Clay deposits occur in both the Precambrian and carbonate study areas. The clay is of non-marine origin and was probably derived in great part from older unconsolidated sediments by wave and current action during the

last stages of the Champlain Sea and during subsequent estuarine and fluvial action (Gadd, 1962).

Bedrock in the Precambrian study area is well exposed as a result of erosion by wave action of the Champlain Sea. Depressions between outcrops are filled with sediments composed of till and the fresh-water clay described above. The till is a heterogeneous mixture of all sizes, from clay to large boulders, but generally sandy (Gadd, 1962).

Soils

The soils of the Ottawa area are derived from superficial deposits of Pleistocene and Recent ages. Hills (1961) describes the regional soil type as a grey-brown podzol except in areas of stoney limestone till (and where limestone gravel is near the surface). In these latter areas brown forest soils are common.

Ponds C-1 and C-3 overlie a contact of the Rideau Clay and the Farmington Soil Series. The Rideau Clay, a humic gleysol, has formed on the lacustrine clay deposits. It is composed of light brown and grey clay over a grey-brown clay. Mottling occurs below 18 inches and the profile is stone free.

The Farmington series is a shallow soil overlying the Oxford dolomite. There is little differentiation in colour or texture within the weathered portion of the profile. The surface soil is a loam and commonly contains free carbonates. This series is most probably related to the Brown Forest soils.

Pond C-2 overlies Rideau Clay, but is surrounded by the Nepean Sand Series. All influent drainage is off of the Nepean. The Nepean Series is composed of shallow sandy soils with sandstone bedrock within three feet of the surface.

Ponds C-4 and C-5 overlie the Farmington and the Uplands Sand Series. However, influent drainage is primarily off of the Nepean Sand. The Uplands Series is a well drained soil formed on sand and sandy loam. Developed on low lime materials and under predominantly coniferous vegetation, it exhibits a well developed podzol profile.

Ponds C-6 and C-7 and their drainage basins are within the Farmington Series. As in the C-1 and C-3 area the soil is shallow and outcrops are numerous. In this case, however, bedrock is the Ottawa limestone.

Soils in the Precambrian study area are of the Podzolic and Gleysolic Great Groups. In the drier areas having good drainage an Orthic Podzol of the Wendigo Series develops on the granitic outwash sand. Gleyed Orthic Podzols and Orthic Gleysols occur respectively in areas of imperfect and poor drainage (Hoffman, Mathews and Wicklund, 1964).

Regional Climate

Eastern Ontario is placed in the Humid mesothermal climatic zone of the Thorthwaite climate classification (Hills, 1961). Putnam and Chapman (1938) describe the region as having a climate of temperature extremes, with very cold snowy winters and warm summers with adequate

rainfall and little likelihood of drought. Precipitation in the vicinity of the study areas averages between 30 and 40 inches per annum. The mean annual temperature is 42°F.

General Forest Vegetation

Rowe (1959) includes the area in which the study ponds are located in the Upper St. Lawrence Section of the Great Lakes-St. Lawrence Forest Region. In the Ottawa Valley the extent of this region coincides with the distribution of the Palaeozoic rocks of the Ottawa-St. Lawrence Lowland. The physiognomic boundary of the section is characterized by a vegetational change from predominantly deciduous forest within to mixed deciduous and coniferous forest without.

Study Ponds

In the course of the investigation, field studies were conducted on a total of 21 beaver ponds. Seven ponds were located in the sedimentary lowland and 14 were in the Precambrian Shield. The five original ponds (C-1, C-3, PC-1, PC-2 and PC-3) studied in 1966 and 1967 were chosen on the basis of their geological location. Data from these ponds provided an insight into the relationships of geology and water chemistry within the study area. In order to broaden the scope of the study a series of ponds with a wide range of chemical conditions was selected in 1969 and 1970 on the basis of local geological variations within each of the Precambrian and sedimentary areas. There were 11 and 21 study ponds in 1969 and 1970 respectively.

During 1966, 1967 and 1969 similar ecological factors and conditions were confined to five core ponds: C-2, C-3, PC-1, PC-2 and PC-3, which represented a range of water chemical conditions found in the study area. In the remaining 16 ponds only sufficient environmental data were collected to allow comparison with the five core ponds, and provide a basis for the evaluation of the duck-habitat relationships.

Apart from the geological conditions, all study ponds had to have: (1) relatively open water, (2) a well defined edge, (3) contain water for the complete season, and (4) be relatively free of human disturbance.

A summary of the morphometric characteristics of the 21 ponds as measured in May 1970 is presented in Table 1.

TABLE 1

Summary of the morphometric characteristics of the study ponds.

Pond	Area(A) (Acres)	Shoreline Length(L) (Feet)	Shore Development(DL)
			$\frac{L}{2\sqrt{\pi A}}$
C-1	4.7	4,100	2.54
C-2	6.4	3,446	1.85
C-3	3.1	3,577	2.75
C-4	7.3	4,520	2.26
C-5	4.8	3,821	2.36
C-6	11.1	5,113	2.07
C-7	16.2	4,899	1.65
PC-1	6.2	7,256	3.92
PC-2	15.5	14,433	4.95
PC-3	3.3	4,253	3.17
PC-4	4.2	4,651	3.08
PC-5	2.5	4,219	3.63
PC-6	1.8	1,724	1.72
PC-7	5.5	9,906	5.71
PC-8	3.4	3,018	2.20
PC-9	7.0	4,764	2.44
PC-10	5.4	5,261	3.05
PC-11	4.7	5,108	3.19
PC-12	7.1	4,812	2.44
PC-13	9.7	8,639	3.75
PC-14	13.9	13,453	4.87

MATERIALS AND METHODS

Water Chemistry

There were several objectives in the water chemistry analysis: (1) to evaluate the importance of the geological substrate on the chemical composition of the ponds, (2) to determine the spatial and temporal variability of component ions under different biotic and abiotic conditions, (3) to provide a quantitative index of habitat quality to be used as a basis for the evaluation of the environmental regulation of duck populations.

In 1969, ten surface water samples were collected at monthly intervals in May, June, July and August in each of the 11 study ponds. A sample was collected by filling a one liter and a four ounce polyethelyne bottle just below the surface. In 1970, the five core ponds (PC-1, PC-2, PC-3, C-2 and C-3) were studied in more detail. The ponds were sampled eight times in the four-month period from early May to early September. In each collection, ten surface and ten bottom samples were taken in PC-2, and five surface and five bottom samples from the other four ponds. The surface samples were collected as in 1969. For bottom samples, a sampler with a horizontal brass collecting chamber was constructed. With it water could be collected from approximately 2 to 3 inches above the sediments.

In order to characterize the chemical composition of all ponds, two surface samples were collected from each of the 21 study ponds on July 10, 1970. The analyses of the total composition of the pond waters, and the

relationships between geology and water chemistry are based on the seasonal means of the surface samples from the five core ponds and the means of the two samples of July 10, 1970, in the remaining ponds.

All of the water samples were analysed by the Water Quality Division Laboratory, Inland Waters Branch, of the Department of Energy, Mines and Resources in Ottawa. The methods of analysis are as follows.

Specific conductance was determined in accordance with A.P.H.A. (1965).

pH was determined with a Corning Model 10 pH meter in accordance with the American Public Health Association (1965).

Alkalinity (as CaCO_3) concentrations were found by potentiometric titration as described by Thomas and Lynch (1960).

Calcium (as Ca) and magnesium (as Mg) were determined by atomic absorption spectrophotometry as described by Perkin-Elmer Corp. (1966).

Sodium (as Na) and potassium (as K) were determined by AutoAnalyser flame emission photometry in accordance with Technicon Instruments Corp. (1962).

Total iron concentrations were found colorimetrically by means of an AutoAnalyser with 2,4,6-Tripyridyl-s-triazine indicator. The method follows that of Collins, Deihl and Smith (1959).

Total manganese was determined colorimetrically by means of a Perkin-Elmer Model 303 atomic absorption spectrophotometer as described by Perkin-Elmer Corp. (1966).

Sulphate (as SO_4) concentrations were calculated by direct titration with barium perchlorate using Thorin indicator as described by Fritz and Yamamura (1955).

Chloride concentrations were determined colorimetrically using an AutoAnalyser with mercuric thiocyanate indicator as described by Iwasaki, Utsumi and Ozawan (1952).

Silica (as SiO_2) was determined with an AutoAnalyser following American Public Health Association (1965).

Nitrate nitrogen was determined by means of an AutoAnalyser in accordance with Brewer and Riley (1965) and Bendschneider and Robinson (1952).

With the exception of pH and specific conductance, all chemical concentrations are expressed as milligrams per liter (Mg/l).

The water chemical samples were analyzed within one to two weeks of the collection date. Since the samples were unfiltered, they would contain plankton and bacteria, and some chemical change would be expected. This change would especially affect such unstable substances as phosphorous and nitrogen, so that the analytical results must be regarded as approximate.

Submerged Macrophytes

The results of the field investigations prior to 1970 suggested that in mid, and late summer, ducks selected the more chemically concentrated ponds in the study area. The implication was that the birds were congregating on ponds which provided the most food. Therefore, in order

to explain the relationship between ducks and water chemistry, the seasonal production of submerged macrophytes was estimated in selected ponds of different water quality.

The production of submerged aquatic macrophytes was estimated in four core ponds in 1970. Originally ponds C-1, C-3, PC-1, PC-2 and PC-3 were selected, both to represent a wide range of chemical conditions, and because background data were available for the five ponds since 1966. Field work was initiated in C-1, but had to be terminated when the pond was drained in early June.

Estimates of macrophyte production were made from seasonal changes in plant biomass, essentially following the procedures of Westlake (1969). The locations of permanent sampling stations were determined by the use of random numbers to select points on grids overlaying detailed maps of the ponds. There were 15 stations in all ponds, except PC-2 in which there were 20. Collections were made on six occasions between mid May and mid August. On each of the collecting dates, sample points were randomly chosen from within a circular area of two meters in radius around the permanent station.

The macrophyte samples were acquired by pushing an eight-inch diameter cylinder into the substrate and removing all the enclosed plant material, including roots. The samples were then sorted from the debris and placed in appropriately labelled plastic bags for storage in a freezer.

In the laboratory, the samples were thawed, separated into species, and placed into 250 ml. Erlenmyer flasks. They were then dried in a constant temperature oven at 105°C for 24 hours. After drying, the flasks were stoppered and cooled to room temperature, and then weighed on an analytical balance without the stoppers. In order to remove encrusted carbonates, the plant material in each flask was covered with 0.02N HCl. Wetzel (1960) found that this concentration of acid was adequate for dissolving carbonate deposits, and caused minimal, if any, damage to the plant tissue. When the carbonates were removed, the acid was decanted and the plant material rinsed with glass distilled water. The plant samples, without encrusted carbonates, were dried and weighed as before. Finally, the samples were removed from the flasks, and the flasks were cleaned, dried and weighed. The results are expressed as grams of dry plant material per square meter.

All macrophytes were separated into species with the exception of Potamogeton pusillus and P. foliosus. While these two species were easily differentiated in their natural habitat, it proved to be extremely difficult to do so in the laboratory samples. As a result the two species were treated collectively, and the dominant species in each pond was used to describe the samples.

It should be noted that the macrophyte samples include attached epiphytic algae. Losses due to herbivore consumption have not been taken into account.

Duck Populations

Ducks were censused at weekly intervals from early May through to early September in each of the four years. Counts were usually made in early morning, but sightings made during the course of other work were used to supplement the censuses.

The methods of counting the duck populations depended on the season and the nature of the ponds. The usual technique was to travel around the pond periphery in a canoe with two retrievers working the edge. In counting broods it was found that a man walking on the shoreline, with the dogs between him and the canoe, proved to be the best method. The locations of all duck sightings were recorded on copies of base maps of the ponds. From these data, estimates were made of the total populations of breeding pairs, broods and fledged ducks on the study ponds.

Duck species observed on the ponds were as follows:

<u>Anas platyrhynchos</u>	- Mallard
<u>Anas rubripes</u>	- Black
<u>Anas discors</u>	- Blue-winged Teal
<u>Anas carolinensis</u>	- Green-winged Teal
<u>Aix sponsa</u>	- Wood Duck
<u>Aythya collaris</u>	- Ringneck
<u>Lophodytes cucullatus</u>	- Hooded Merganser

WATER CHEMISTRY

Water Chemical Composition

Results and Discussion

The water chemical composition of ponds in the Precambrian and carbonate study areas vary considerably in terms of absolute ionic concentrations, but all are of the bicarbonate type. The waters are dominated by calcium and bicarbonate. Cation composition is generally of the order $\text{Ca} > \text{Mg} > \text{Na} > \text{K}$, with the exceptions of ponds C-4, PC-8 and PC-14 where $\text{Na} > \text{Mg}$ (Table 2).

In relation to the modified standard Wisconsin categories of Brooks and Deevey (1963), ($\text{HCO}_3 < 10$ Mg/L, extremely soft; 10-27, soft; 28-84, medium hard; > 84 , hard) all carbonate ponds are far in excess of the lower limit for hard waters. The chemically rich Precambrian ponds, PC-2, PC-8 and PC-14, are near the upper limit of medium hard, and the remaining Precambrian ponds are in the low, medium hard and soft categories.

Moyle (1945, 1956) characterized Minnesota surface waters with a total alkalinity of less than 40 Mg/L as soft waters. With the exception of PC-2, PC-8 and PC-14, all Precambrian ponds would be included in Moyle's soft water category.

Considering the two systems of classification, and the discontinuous distribution of calcium and bicarbonate concentrations in the study ponds, all carbonate ponds are considered as hard; PC-2, PC-8 and PC-14 as medium

TABLE 2

Summary of mean 1970 surface water chemical concentrations in the study ponds.
(All values expressed as Mg/L with the exception of specific conductance
(microhmhos) and pH.)

Pond	pH	Total Alk.	Sp. Cond.	Ca	Mg	Na	K	Total Fe	Total Mn	Cl	NO3	SiO2
C-1	7.25	97.1	379	40.8	14.0	12.2	4.5	0.16	0.08	32.5	0.155	9.7
C-2	7.26	83.4	233	32.9	6.2	5.7	2.3	0.11	0.04	12.2	0.180	3.7
C-3	7.39	153.3	365	47.7	14.9	7.5	2.4	0.29	0.18	18.2	0.531	3.1
C-4	7.30	85.8	267	33.2	6.3	9.5	2.4	0.11	0.19	18.0	0.155	17.2
C-5	7.95	69.2	186	27.4	6.0	3.7	0.5	0.21	0.10	6.2	0.060	3.0
C-6	7.30	119.0	250	43.1	8.8	0.7	1.0	1.03	0.12	1.9	0.150	9.2
C-7	7.25	119.5	242	43.1	8.9	0.5	0.1	0.48	0.15	0.9	0.021	3.9
PC-1	6.67	31.9	94	15.9	1.9	0.9	0.5	0.61	0.09	0.6	0.178	0.6
PC-2	6.99	66.1	147	28.2	2.7	1.0	0.4	0.62	0.09	0.6	0.172	1.9
PC-3	6.58	26.4	76	12.7	0.8	0.8	0.5	0.77	0.05	0.5	0.210	0.4
PC-4	6.60	34.3	84	14.1	1.5	0.8	0.0	1.30	0.09	0.2	0.080	0.5
PC-5	6.45	22.0	66	10.7	1.2	0.9	0.1	0.88	0.04	0.1	0.170	0.2
PC-6	6.40	18.7	58	9.3	1.1	0.7	0.2	0.95	0.14	0.1	0.360	0.7
PC-7	6.30	15.4	50	7.6	0.7	0.4	0.5	0.92	0.03	0.1	0.570	0.3
PC-8	7.20	74.3	155	24.7	3.2	3.3	0.8	0.46	0.08	0.5	0.110	1.0
PC-9	6.60	27.9	66	10.3	2.3	0.8	0.4	0.73	0.35	0.4	0.150	0.4
PC-10	6.60	21.5	56	8.4	0.8	1.2	0.3	0.85	0.02	0.7	0.005	0.5
PC-11	6.45	19.7	56	8.6	0.8	0.7	0.1	1.20	0.05	0.3	0.015	0.5
PC-12	6.55	26.4	70	11.0	1.3	1.2	0.0	0.29	0.01	0.5	0.005	0.4
PC-13	6.35	18.4	54	8.6	0.8	0.5	0.1	0.96	0.09	0.5	0.000	0.4
PC-14	7.25	68.6	153	27.1	2.7	0.8	0.0	0.57	0.02	0.6	0.025	1.2

hard; PC-1, PC-3, PC-4, PC-9 and PC-12 as medium soft; and the remaining Precambrian ponds as soft.

The work of Rodhe (1949) indicates that in fresh waters of the bicarbonate type there are linear relationships between the total electrolyte composition and the major constituent ions. Rodhe attributes these relationships to a physico-chemical state of balance resulting from ionic exchanges between dissolved ions and the colloidal systems of the soils and lake muds. In order to investigate some of the ionic interrelationships of the study ponds, regression equations have been computed between the total electrolyte content (as measured by specific conductance (micromhos at 25°C)) and principal ions and combinations of ions.

In the Swedish Uppland Lakes data analysed by Rodhe, specific conductance had linear relationships to both calcium and magnesium. In this study, however, the regressions are both curvilinear. The plot of specific conductance on calcium (Figure 3) resembles an exponential curve which is asymptotic in the vicinity of 50 Mg/L of calcium. This apparent upper limit of dissolved calcium is not due to calcium availability because higher individual readings were found in the hard water ponds. The major limitation to mean concentrations of calcium can be attributed to the pond carbon dioxide budgets which regulate the solubility of calcium bicarbonate.

In the Precambrian ponds where the calcium concentrations are low, so that solubility problems are not as pronounced, the slope of the linear regression reflects

FIGURE 3

Relation between calcium concentration (mg/liter) and specific conductance (micromhos at 25°C). Open circles denote Precambrian ponds and closed circles denote carbonate ponds.

the variation in the availability of calcium to the pond drainage waters. The tight fit about the line further indicates the strong influence of calcium on the total ionic composition.

The relationship of specific conductance to magnesium is the inverse of that for calcium and resembles a logarithmic curve (Figure 4). Since MgCO_3 does not precipitate at low carbon dioxide tensions in the manner of CaCO_3 , the curve does not have an upper limit. Thus, both the carbonate and Precambrian linear regressions should reflect the availability of magnesium to the pond waters. The steeper slope of the Precambrian regression illustrates the minor role of magnesium in these waters in comparison to its importance to the total content of the hard water carbonate ponds.

If specific conductance is plotted on the sum of calcium and magnesium (Figure 5) the curves for the individual ions tend to cancel out resulting in a linear cluster. The total ionic content of the Precambrian ponds is almost completely dominated by calcium and magnesium.

As shown in Figures 6 and 7, only in carbonate ponds 1 to 5, do sodium, potassium and chloride significantly contribute to the total ionic content. Of the remaining ponds, only sodium and potassium in PC-8 depart from a vertically oriented cluster.

Only one surface sample per collection from the five core ponds was analysed for sulfate in 1970. The small number of samples does not allow a statistical evaluation of the contribution of sulfate to the total

FIGURE 4

Relation between magnesium concentration (mg/liter) and specific conductance (micromhos at 25°C). Open circles denote Precambrian ponds and closed circles denote carbonate ponds.

FIGURE 5

Relation between calcium and magnesium concentration (mg/liter) and specific conductance (micromhos at 25°C). Open circles denote Precambrian ponds and closed circles denote carbonate ponds.

FIGURE 6

Relation between the sum of sodium and potassium (mg/liter) and specific conductance (micromhos at 25°C). Open circles denote Precambrian ponds and closed circles denote carbonate ponds.

FIGURE 7

Relation between the chloride concentration (mg/liter) and specific conductance (micromhos at 25°C). Open circles denote Precambrian ponds and closed circles denote carbonate ponds.

ionic content, but as will be discussed later, sulfate appears to be influenced more by pond metabolism than by physico-chemical phenomena.

When the regression of specific conductance on the sum of calcium and magnesium is compared to that of specific conductance on total cations (Figure 8), the basic difference between the composition of the Precambrian and carbonate waters is evident. Since the water chemistry of the Precambrian ponds is almost completely dominated by calcium and magnesium, the addition of monovalent cations imparts very little change to the original regression. In the carbonate ponds, however, where the ionic composition is more diverse, the addition of sodium and potassium considerably tightens the cluster of points in the regression.

Regression of specific conductance on the minor constituents, iron, manganese and nitrate illustrate not only their very low concentrations but also their different behavior from the major ions. Figure 9 illustrates the loose negative correlation between specific conductance and total iron, while in Figures 10 and 11 specific conductance shows virtually no relationships with total manganese and nitrate respectively.

Rodhe (1946) states that one would not expect to find any close relationships between these minor constituents and the total ionic composition. They are present in low concentrations, and have low degrees of ionization. Furthermore, nitrogen is highly involved in biological

FIGURE 8

Relation between total major cation concentration (mg/liter) and specific conductance (micromhos at 25°C). Open circles denote Precambrian ponds and closed circles denote carbonate ponds.

FIGURE 9

Relation between total iron concentration (mg/liter) and specific conductance (micromhos at 25°C). Open circles denote Precambrian ponds and closed circles denote carbonate ponds.

FIGURE 10

Relation between total manganese concentration (mg/liter) and specific conductance (micromhos at 25°C). Open circles denote Precambrian ponds and closed circles denote carbonate ponds.

FIGURE 11

Relation between nitrate concentration (mg/liter)
and specific conductance (micromhos at 25°C).
Open circles denote Precambrian ponds and closed
circles denote carbonate ponds.

activity, and iron and manganese have the tendency to form complexes with organic compounds.

The slight negative relationships between specific conductance and total iron is to be expected since high pH and oxygen levels result in the precipitation of iron. Below neutrality the precipitation is much slower (Ruttner, 1963). Rodhe (1946) interpreted a similar correlation as probably being a positive correlation between iron and humic substances.

Manganese is hydrochemically similar to iron, but it is more easily reduced, and thus can exist in ionic form at high pH and oxygen levels. Since manganese can also form complexes, it is most likely its ability to be ionized at higher pH and oxygen levels that shifts the cluster of points away from the negative slope of iron.

The plot of specific conductance with nitrate (Figure 11) is similar to that of manganese. Whereas manganese levels are more a result of the products of pond metabolism (organic matter, carbon dioxide, pH), nitrate is actively involved in the metabolism. This fact coupled with the various possible sources of nitrogen combine to make the nitrate dynamics of each pond unique, with no apparent relationships with total ionic content.

The plot of specific conductance on SiO_2 appears to be intermediate between those of the major and minor constituents (Figure 12). Concentrations are relatively constant in the Precambrian ponds but are highly variable in the carbonate waters. Mortimer (1941/42) has shown the importance of reducing conditions in facilitating the

FIGURE 12

Relation between silica concentration (mg/liter) and specific conductance (micromhos at 25°C). Open circles denote Precambrian ponds and closed circles denote carbonate ponds.

dissolution of silica from mud to water. Since all ponds should have adequate amounts of silica in the bottom sediments, the relationship of specific conductance to SiO_2 can be attributed to lower redox potentials in the sediments of the hard water carbonate ponds.

Although all study ponds are of the bicarbonate type, the Precambrian waters are more strongly so. Absolute ionic concentrations are low, but the hydrochemistry is almost completely dominated by the bicarbonates of Ca and Mg. In contrast, the chemistry of the carbonate waters is more diverse. These ponds are also dominated by Ca and Mg bicarbonates, but with the exception of C-6 and C-7, other major ions make important contributions to the total content.

It is apparent that the separation of water chemicals into major and minor constituents is not just an arbitrary division based on concentrations. To a greater degree, the division is a functional one based on the behaviour of the ions within aquatic ecosystems. The minor constituent ions do not bear any close relationships with the over-all chemical composition. Their concentrations in any given pond do not appear to be a result of availability to the waters, but a response to the chemical and biological environment within the system.

In contrast, the major ionic constituents, though subject to variation due to climate and ecosystem metabolism (the net effects of photosynthesis and respiration), are present within recognisable ranges which are controlled by physico-chemical phenomena. The chemical composition

of the pond waters does not necessarily conform to Rodhe's concepts of 'standard composition,' but within each of the Precambrian and carbonate study areas there are recognisable ionic interrelationships. This suggests that within each of the geological study areas there are separate states of ionic balance, which should be related to the substrate characteristics.

Relationships Between Major Ions and Geology

Results and Discussion

Relationships between pond water chemistry and bedrock are straightforward in the carbonate study area. Each sedimentary rock formation occupies a large aerial expanse and is relatively homogeneous in composition. Relief is not pronounced, so that drainage patterns are simple and well defined.

Mean calcium concentrations in the carbonate ponds appear related to the amount of calcium carbonate in the local bedrock. Ponds C-1 and C-3 on the Oxford domomite, and C-6 and C-7 on the Ottawa limestone have calcium concentrations greater than 40 Mg/l, reflecting the high carbonate content and solubility of both formations (Table 2).

Ponds C-2, C-4 and C-5 receive drainage primarily from the March sandstone and sandy dolomite, and the associated sandy Nepean soil series. Calcium concentrations of around 30 Mg/l in the three ponds reflect the decreased carbonate content of the bedrock and the soils. The

slightly lower concentration in C-5 (27.4 Mg/l) is associated with the drainage into the pond from the alluvial sandy ridge.

Because of the increased heterogeneity of the bedrock, and the irregular topography, the relationships between water chemistry and geology are more complicated in the Precambrian study area. The location of the Precambrian ponds, their geology and approximate drainage patterns are shown in Figure 2.

The lowest calcium concentrations are in soft water ponds PC-6, PC-7, PC-10 and PC-11 situated within the southern portion of the monzonite stock (5), and in PC-13 on the quartz-rich feldspathic subunit of the granitic gneiss. The central portion of the monzonite stock is quartz poor and sphene rich, but towards the margin the rock is generally quartz rich and sphene deficient. The low calcium content of PC-6, PC-7, PC-10 and PC-11 appears to be a result of the drainage waters flowing over the quartz rich rocks of the stock margin. The higher calcium content in the centrally located PC-9 (10.3 Mg/l) corresponds with the decreased quartz content of the core of the stock.

As illustrated in Figure 2, PC-5, PC-6 and PC-7 straddle the contact of the monzonite and the granitic gneiss (3a). PC-7 receives all its drainage from the monzonite wall rock and has a calcium concentration of 7.6 Mg/l. PC-6, located on the contact, receives drainage from both the stock and the granitic gneiss and has a slightly higher calcium level (9.3 Mg/l). Influent

drainage for PC-5 is primarily from the gneiss and the pond has yet a higher calcium content of 10.7 Mg/l. PC-12 which receives drainage waters solely from the granitic gneiss has a mean calcium concentration of 11 Mg/l indicating its similarity to PC-5. Although the differences in concentrations are not great, there does seem to be a definite trend of increased calcium away from the monzonite wall rock into the granitic gneiss. While one would not normally associate an increase in calcium with a granitic gneiss, it can be accounted for by the presence of the intercalated mafic gneisses and schists (quartz-feldspar gneiss, hornblende, pyroxene and biotite) (Livingstone et al., 1969).

The medium soft ponds PC-1, PC-3 and PC-4 lie on a contact of the granitic gneiss and the red syenite stock (4). Their respective calcium concentrations of 15.9, 12.7 and 14.1 Mg/l differentiate them from the ponds on the granitic gneiss. Although the syenite lacks the mafic component of the gneiss, its plagioclase content indicates the presence of the calcium rich and more easily weathered lime feldspar, anorthite.

The medium hard ponds PC-2, PC-8 and PC-14 are quite distinct from the other Precambrian ponds, in that they have calcium concentrations of 28, 25 and 27 Mg/l respectively. In Nesbitt's (1968) petrographic analysis of the monzonite stock he found that in an area located within the drainage basin of PC-8 the bedrock contained intergrown scapolite and epidote. The scapolite was high in calcium and carbonate, and associated with the rock was considerable interstitial calcite. Although PC-2 and

PC-14 overly the granitic gneiss (3a), influent drainage comes from calcium carbonate bearing rocks to the west and south west. Influent is received from the mafic gneiss and schist, and the marble unit (2) to the west, and the marble calcic subunit (3b) of the gneiss to the south west.

The discontinuous distribution of calcium concentrations in the Precambrian pond waters seems to be caused by widely different geological sources. Calcium variations found between the soft and medium soft ponds can be explained by the distribution of the various types of feldspar and calc-silicate rocks within the pond drainage basins. The higher calcium concentrations in the medium hard ponds are related to sources of non-silicate, calcium carbonate rocks.

Magnesium concentrations in the carbonate study area reflect the dolomitic content of the surrounding bedrock. Ponds C-1 and C-3, on the magnesium rich Oxford dolomite are highest, in the 14 Mg/l range. Concentrations approaching 9 Mg/l in C-6 and C-7 are higher than expected in areas underlain by limestone. Perhaps the bedrock in this western portion of the Ottawa formation is a lower part of the strata. Wilson (1946) describes such a lower phase as being an impure limestone with some dolomite. The three ponds receiving drainage from the March sandstone and sandy dolomite have magnesium concentrations of 6 Mg/l, the lowest in the carbonate study area. This reflects the lower magnesium and carbonate content of the bedrock, and perhaps the decreased solubility of the sandstones.

The relationships between calcium and magnesium are plotted separately for the Precambrian and carbonate ponds (Figure 13). The slope of the carbonate curve illustrates the greater relative variability of magnesium in the waters overlying sedimentary rocks. In the Precambrian waters, on the other hand, the uniform rise in magnesium levels contrasts with the discontinuous distribution of calcium concentrations. Previously it was suggested that the discontinuity of calcium concentrations in the Precambrian ponds was a result of sources of calcium carbonate in the drainage basins of the three medium hard ponds. Stumm and Morgan (1970) note that calcite has a tendency to accommodate magnesium in its structure. Thus, it is probable that the high magnesium levels in the three medium hard ponds are partially a result of magnesium carbonates. Variation in the magnesium content of the other Precambrian ponds, though not clearly accounted for, is most likely a result of the distribution of pyroxenes and amphiboles of calc-alkalic rocks.

Concentrations of the alkali earth metals, sodium and potassium, have quite different relationships with the geological substrate than do calcium and magnesium. The calcium and magnesium content of the waters not only reflects the composition of the bedrock, but also its solubility. In the Precambrian ponds the uniform concentrations of sodium and potassium can be explained by their source in sodium and potassium alumino-silicate rocks of low solubility. The one unexplained exception to this generalization is found in PC-8 which has a higher sodium concentration of 3.3 Mg/l.

FIGURE 13

Relation between calcium concentration (mg/liter) and magnesium concentration (mg/liter). Open circles denote Precambrian ponds and closed circles denote carbonate ponds.

In the carbonate study area, only ponds C-1 to C-5 have high sodium and potassium concentrations. Although little is known about the role of sedimentary rocks in providing these ions to waters, it is obvious that waters from dolomite and dolomitic sandstones are enriched with them. The Ottawa limestone, though magnesium bearing, appears to be free of alkalies.

Silica levels are higher in the carbonate ponds than in the Precambrian ponds. Hutchinson (1957) notes that the silica content of water draining igneous rocks, as with most other constituents, is likely to be less than that draining sedimentary rock. This points out the fact that the solubility of the bedrock is often of more importance to water composition than the bedrock composition.

Spatial and Temporal Chemical Variation

Results and Discussion

Fluctuations in specific conductance as shown in Figure 14 illustrate the major pattern of seasonal water chemical variation in the study ponds. The seasonal dynamics of pH are shown in Figure 15.

The similarity between specific conductance and calcium (Figure 16) further indicates the importance of calcium salts to the total composition of the pond waters. One of the most striking features of calcium dynamics is the relationship between temporal variation and mean calcium concentration. In the soft water Precambrian ponds calcium concentrations do not appreciably

FIGURE 14

Seasonal fluctuations of specific conductance (micromhos at 25°C) in the study ponds. In 1970, heavy lines represent bottom water and light lines represent surface water. In 1969, heavy lines represent carbonate ponds, broken lines represent medium hard Precambrian ponds and light lines represent the medium soft and soft water Precambrian ponds.

FIGURE 15

Seasonal fluctuations of pH in the study ponds. In 1970, heavy lines represent bottom water and light lines represent surface water. In 1969, heavy lines represent carbonate ponds, broken lines represent medium hard Precambrian ponds and light lines represent the medium soft and soft water Precambrian ponds.

FIGURE 16

Seasonal fluctuations in calcium concentrations (mg/liter) in the study ponds. In 1970, heavy lines represent bottom water and light lines represent surface water. In 1969, heavy lines represent carbonate ponds, broken lines represent medium hard Precambrian ponds and light lines represent the medium soft and soft water Precambrian ponds.

change from the seasonal mean, but as the waters increase in hardness, the seasonal fluctuations and stratifications become more pronounced.

In the hard water ponds calcium levels tend to be high in the spring, then drop in early summer and rise again in mid or late summer. Although the exact pattern varies from year to year, similar seasonal fluctuations were observed in 1966 and 1967 (Patterson, 1969), and thus appear to be characteristic of hard water ponds in the study area. Hutchinson (1957) notes that small productive lakes are often characterised by a striking increase in bicarbonates and associated calcium and magnesium at the height of the summer stagnation. However, he makes no mention of a spring maxima. In contrast to the carbonate ponds, calcium levels in the Precambrian ponds are lowest in the spring, but for the remainder of the summer the fluctuations follow a similar, though much less pronounced pattern.

An obvious exception to the above generalisation is the 1969 late summer calcium decline in C-1. The landowner destroyed the beaver dam in June so that much of the pond water was lost. He repaired the dam in mid July, and the pond partially refilled with drainage water. Obviously this influent was dilute in comparison with the water normally present in the pond basin.

The disproportionately high calcium peaks in PC-1 and PC-6 during the late summer of 1969 coincide with extremely low water levels in the two ponds. This

suggests that the high levels are related to the effects of concentration.

The pronounced differences in spring calcium levels between the Precambrian and carbonate ponds provides a good functional comparison of the calcium hydrochemistry in the two study areas. At this time of year most influent drainage originates as surface, snow-melt runoff. As shown by Pitty (1968), surface runoff, because of its brief contact with rocks, is often low in dissolved solids. He states that in this respect snow-melt is a particularly well documented factor, causing substantial dilutions in the solute concentrations of streams. Most likely then, the high spring calcium levels observed in the hard water ponds were derived from calcium sources within the ponds and not from influent drainage.

In the shallow, biologically rich carbonate ponds one would expect high carbon dioxide and calcium bicarbonate concentrations under the winter ice cover. Mortimer (1941/42) has shown that on freezing there is practically complete removal of dissolved salts from ice, so that the upper waters would be concentrated. At the same time ice formation decreases the water volume, further concentrating the solutes.

At the surface of the sediments in the hard water ponds, calcium carbonate would be present as a result of both winter and the previous summers pond metabolism. Ahl (1966b) found that in hard water Swedish lakes such carbonates were largely composed of material from submerged macrophytes. Thus, during winter stagnation, reduced

surface sediments and sources of carbonates would result in the enrichment of the bottom water with calcium bicarbonate. Mortimer (1941/42) found that under reducing conditions the rates of dissolution of bicarbonates and related cations across the mud-water interface are higher than those for other ions.

At spring breakup, a carbonate pond would be expected to contain calcium, in one form or another, in excess of that which can be maintained in aqueous solution. Thus, in the spring, when pond volumes are greatest, and the influent is dilute, calcium may be present in very high concentrations.

The contrasting low spring calcium concentrations in the Precambrian ponds indicate that these soft water systems are calcium deficient, and that concentrations are more directly related to the immediate rate of supply via influent waters. Hutchinson (1957) states that hard water sediments would be expected to contain calcium carbonate, but in the sediments of soft water or even moderately hard water there is no reason to expect the presence of calcium carbonate.

The early summer decline in calcium levels which appears to be characteristic of the hard water study ponds, bears an interesting relationship with the aquatic macrophytes. As will be shown in a later section, the calcium decrease coincides with the period of greatest productivity of the submerged vegetation. During the early summer rapid growth phase of the macrophytes, pond metabolism should be characterised by P/R ratios in excess

of 1. As a result, the total carbon dioxide budgets would drop, calcium carbonate would be precipitated, and calcium bicarbonate concentrations would decline. However, once maximum macrophyte production is reached, and higher summer water temperatures prevail, the pond respiratory activity would increase and the over-all metabolism would be expected to shift so that P/R ratios would be less than unity. Under such conditions the pond waters would be progressively enriched with carbon dioxide and show maximum concentrations in the bottom waters.

The occurrence of such a shift in the metabolism of the ponds in 1970 is reflected by the general summer decline in pH, especially in the bottom waters. Further evidence that only the hard water ponds contain calcium carbonate in the surface sediments is provided by the fact that significant calcium enrichment of the bottom waters only occurs in ponds C-2 and C-3.

The smaller degree of calcium stratification in C-3 in comparison to C-2 can be explained by the presence of a floating mat of Wolffia columbiana in parts of C-3. Carbon dioxide levels have been found to be higher under the mat than in open water (author's unpublished data).

Thus, with higher carbon dioxide tensions, the surface water in C-3 can accommodate more dissolved calcium bicarbonate.

The decrease in the stratification of calcium in late summer coincides with dropping water levels. It appears that the reduced water depth and decreased rates of photosynthesis at this time of year produces more

constant carbon dioxide tensions throughout the water column, resulting in less differentiation between calcium concentrations in the surface and bottom water.

Because only one surface sample per collection in 1970 was analysed for magnesium, only the 1969 data are presented in Figure 17. From these results it appears that in the Precambrian ponds, magnesium concentrations follow similar seasonal patterns as calcium. Ahl (1966b) mentions that in Lohammar's (1938) investigation of north and central Swedish lakes, the magnesium concentrations varied generally in parallel with the calcium concentrations. In the hard water ponds this relationship does not hold. In contrast to calcium, magnesium levels are lowest in the spring. Since $MgCO_3$ is soluble the sediments should not be enriched as in the manner of $CaCO_3$, and the spring concentrations would be expected to reflect the dilution of magnesium by snow-melt influent. As mentioned in the previous section, the high magnesium values in PC-8 are due to carbonate sources.

As shown in Figure 18, sodium concentrations remained virtually constant in the Precambrian ponds during 1969, but with the lower water conditions of 1970 they were somewhat more variable. There is a progressive increase in Na concentration in the hard water ponds throughout the summer, but there is very little enrichment of the bottom waters. Hutchinson (1941) found no clear stratification of sodium in Linsley Pond during the period of stratification, and Ahl (1966b) found that sodium ions had an obvious tendency to be lower in the bottom water.

FIGURE 17

Seasonal fluctuations in magnesium concentrations (mg/liter) in the study ponds. Heavy lines represent carbonate ponds, broken lines represent medium hard Precambrian ponds, and light lines represent the medium soft and soft water Precambrian ponds.

FIGURE 18

Seasonal fluctuations in sodium concentrations (mg/liter) in the study ponds. In 1970, heavy lines represent bottom water and light lines represent surface water. In 1969, heavy lines represent carbonate ponds, broken lines represent medium hard Precambrian ponds and light lines represent the medium soft and soft water Precambrian ponds.

Chloride (Figure 19) behaves in a manner similar to sodium but the seasonal fluctuations are more pronounced. Concentrations of both sodium and chloride, which are not assimilated to a great degree by plants, appear to vary primarily in response to water level regimes.

Potassium, on the other hand, (Figure 20) is much more variable than sodium and chloride. Its seasonal dynamics somewhat parallels calcium. Concentrations decrease in early summer and then increase and exhibit bottom water enrichment in later summer. Apparently potassium is assimilated during the growth of the macrophytes. Ahl (1966b) notes that potassium decreases during the summer are partly due to uptake by vegetation, but also as a consequence of precipitation by clay colloids. The build up of potassium in late summer is likely a result of dissolution from the sediments under reducing conditions.

As shown in Figure 21, silica concentrations reached highest levels in the late summer of 1970. Similar silica peaks were found in the dry summer of 1966 (Patterson, 1969) suggesting that in the relatively small, shallow study ponds silica is concentrated by evaporation.

According to Hutchinson (1957) much of the silica flux in lakes is due to exchanges between the water and sediments. This exchange can be especially apparent in waters having no blooms of diatoms. Mortimer (1941/42) has shown that although exchange can occur in the presence of oxygen, the dissolution of silica from the sediments to the water is greatly facilitated by reducing conditions.

FIGURE 19

Seasonal fluctuations in chloride concentrations (mg/liter) in the study ponds. In 1970, heavy lines represent bottom water and light lines represent surface water. In 1969, heavy lines represent carbonate ponds, broken lines represent medium hard Precambrian ponds and light lines represent the medium soft and soft water Precambrian ponds.

FIGURE 20

Seasonal fluctuations in potassium concentrations (mg/liter) in the study ponds. In 1970, heavy lines represent bottom water and light lines represent surface water. In 1969, heavy lines represent carbonate ponds, broken lines represent medium hard Precambrian ponds and light lines represent the medium soft and soft water Precambrian ponds.

POTASSIUM mg/l

FIGURE 21

Seasonal fluctuations in silica concentrations (mg/liter) in the study ponds. In 1970, heavy lines represent bottom water and light lines represent surface water. In 1969, heavy lines represent carbonate ponds, broken lines represent medium hard Precambrian ponds and light lines represent the medium soft and soft water Precambrian ponds.

- As a result, in productive lakes there is commonly a silica enrichment of the hypolimnion, which in general parallels that of calcium.

In the five core ponds the later summer silica peaks coincide with those of calcium, but the difference between surface and bottom waters is much less pronounced. In the case of calcium bicarbonate, the stratification is primarily due to its solubility dependence on carbon dioxide. Within the pH ranges of the study ponds silica would be almost exclusively in the form of undissociated silicic acid (Stumm and Morgan, 1970). Once in solution the silica should be relatively independent of carbon dioxide fluxes and not subject to chemically induced stratification.

Hutchinson (1957) has postulated that appreciable quantities of silica can diffuse from shallow water sediments into oxygenated waters. He suggests that the rate of this exchange is controlled by temperature. If such a phenomenon was important in the study ponds one would expect that it would operate in all ponds having adequate supplies of silica in the sediments. In fact, high silica concentrations are only found in the harder water ponds, indicating that the major factor regulating silica transport from the sediments in the study ponds is a reducing environment in the bottom waters.

By the end of the 1970 collecting period all ponds, with the exception of C-3 showed a marked decline in silica concentrations. Hutchinson (1957) suggests that silica can become associated with colloidal ferric and

aluminum hydroxides, and also, in neutral or acidic waters form a neutral silica sol. As shown in Figure 23 total iron concentrations decline at the same time, so that it is quite likely that silica is precipitating with the ferric iron.

The one exception to this generalization is found in C-3 where silica is still rising at the end of the sampling period. With its abundance of floating vegetation there would be reducing conditions in the bottom water so that there is still a net movement of silica from the sediments to the water.

Only one surface sample per collection was analysed for sulfate in 1970. Although the small amount of data precludes reliable interpretation of the results (Figure 22) it appears that there is a general trend of decreasing sulfate concentrations throughout the summer. Since the uptake of sulfate by aquatic plants is small (Ruttner, 1963) such a decline would result from a reduction of SO_4^{4-} to H_2S . The loss of sulfate from all pond waters suggests that there were reducing conditions to some degree in the sediments of all five ponds.

A comparison of Figures 23 and 24 shows that concentrations of total iron are much higher than those of total manganese. As Ruttner (1963) notes, surface waters with high O_2 contents and an alkaline pH cannot theoretically contain any detectable amounts of iron. In the presence of oxygen, ferrous iron is rapidly oxidized to insoluble ferric hydroxide. If any iron is

FIGURE 22

Seasonal fluctuations in sulfate concentrations (mg/liter) in the study ponds in 1970. Heavy lines represent carbonate ponds, broken lines represent medium hard Precambrian ponds and light lines represent the medium soft and soft water Precambrian ponds.

FIGURE 23

Seasonal fluctuations in total iron concentrations (mg/liter) in the study ponds. In 1970, heavy lines represent bottom water and light lines represent surface water. In 1969, heavy lines represent carbonate ponds, broken lines represent medium hard Precambrian ponds and light lines represent the medium soft and soft water Precambrian ponds.

FIGURE 24

Seasonal fluctuations in total manganese concentrations (mg/liter) in the study ponds. In 1970, heavy lines represent bottom water and light lines represent surface water. In 1969, heavy lines represent carbonate ponds, broken lines represent medium hard Precambrian ponds and light lines represent the medium soft and soft water Precambrian ponds.

detected it must be present as colloidal iron or as a supersaturated solution.

Manganese, on the other hand, reduces more easily than iron and is more difficult to oxidize, thus manganous ions can be expected at redox potentials too high to permit the presence of ferrous iron. Although manganese can exist in ionic form over a wider range of conditions than iron, ferric ions generally have a much stronger tendency to form complexes than manganous ions. Strum and Wagner (1970) state that ferric complex formation with orthophosphate and many organic bases is well established. Within neutral or slightly alkaline pH ranges, however, hydroxide ions often have stronger affinity for Fe^{3+} than do inorganic or organic bases. The incorporation of coordinating anions into basic ferric precipitates alters the solubility relations and also strongly affects the colloidal chemical properties of the dispersed phase. An enhancement of the colloidal stability of these suspensions frequently results. In natural waters then, high concentrations of organic material are frequently associated with high concentrations of operationally "soluble" iron(III). Within the pH ranges of natural waters the affinity of Mn^{4+} for OH^- is much greater than that of Fe^{3+} , so that it is more difficult for other potential organic or inorganic ligands to compete successfully with OH^- . As a result, in natural waters complex formation is much more common with Fe^{3+} than with Mn^{4+} .

In the early summer of 1970 both Fe and Mn concentrations decline to minimum levels, coincident with the period of greatest productivity of the aquatic macrophytes. The drop in iron is very pronounced and occurs simultaneously in all five ponds. Apparently the photosynthetic production of oxygen, which at this time of year would be at or near the mud-water interface, results in the oxidation and subsequent precipitation to the sediments of most of the iron in the waters.

In contrast, the decline in Mn lags behind that of iron by about two weeks, and is not nearly as well defined. This difference in behaviour illustrates how, at the low Mn concentrations and the ambient pH ranges, the oxygenation of Mn occurs much less readily than that of Fe.

During mid summer, concentrations of both Mn and Fe are greatly increased and there is substantial enrichment of the bottom waters. The one exception to this generalization is in PC-3 where there is more Fe in the surface water. In ponds having anaerobic bottom water, enrichment would follow from the reduction of ferric oxide to Fe(II). Even if some oxygen remains, however, reduction of ferric iron can still be expected in the surface sediments. As a result there would be a flux of reduced iron to the bottom waters which may remain in solution or be oxidized. The fact that the surface waters of all five ponds have substantial quantities of total iron suggests that much of the iron coming from the sediments is oxidized, but subsequently remains in the

water in such forms as ferric complexes and stabilised ferric oxides.

Although some manganese complexes might be expected, much of the total Mn content of the ponds during the 1970 mid summer peaks is probably in the form of Mn(II). Delfino and Lee (1968) have shown that Mn(II) can be present even if dissolved oxygen is not fully depleted. Strum and Morgan (1970) note that Mn(II) can be absorbed by ferric oxide. Thus, one could expect the distribution of Mn(II) to somewhat parallel that of iron complexes. The Mn enrichment of the bottom waters is most likely a result of a combination of the following processes: (a) the decrease in pH shifts the exchange-adsorption equilibrium in such a way as to desorb Mn(II) from the higher valent Mn oxides and ferric hydroxide; (b) reduction of ferric oxide releases sorbed Mn(II). Thus, manganese oxides can be reduced and made soluble by ferrous iron and other organic reductants.

SUBMERGED MACROPHYTES

Results and Discussion

As shown in Figure 25, values for maximum mean biomass in four core ponds ranged from 44 g/M² in PC-1 to 61 g/M² in PC-2. Although the sampling period does not include the point of inflection of the biomass curve in PC-2, it is doubtful if the standing crop would have increased appreciably beyond that of the last sample date.

The production of submerged macrophytes in the study ponds is intermediate in the range of values found in the literature. Wilson (1937) found that in soft water Sweeney Lake, in northeastern Wisconsin, the average yield of dry plant tissue in the plant zone was 1.73 g/M². In southeastern Wisconsin, in a calcareous area of hard water lakes, Rickett (1924) found the standing crop of macrophytes in Green Lake to be 178 g/M², and 202 g/M² in Lake Mendota. One of the highest values for submerged macrophyte biomass recorded in the literature is 680 g/M² for Ceratophyllum demersum in the fertile hard water Lake Osbysjon in Sweden (Forsberg, 1960). In the same lake, Forsberg (1959) recorded seasonal maxima of 240 g/M² for Myriophyllum verticillatum and 310 g/M² for Nitella mucronata. It should be noted that in Forsberg's studies, sampling was confined to homogeneous macrophyte communities. His results then, would approach the actual maximum biomass attained by a given species. In the present study, and those reported from Wisconsin, the results represent the means of samples randomly selected from the heterogeneously distributed vegetation. As a

FIGURE 25

Seasonal production of total submerged macrophyte biomass (grams of dry weight/m²) in the four core study ponds.

result, the data cannot be expected to represent the maximum biomass attained for any component species.

As noted by Westlake (1963), the production of submerged macrophytes is very poor in comparison with other types of communities. Sculthorpe (1967) states, that although macrophyte communities may look luxurious, they are, in fact, not. Characteristically, many of the species have high volume to dry weight ratios, lack substantial underground parts, and commonly grow in shallow waters where the ratio of occupied volume of water to occupied surface area is small. Although the percentage aerial cover of submerged communities may be high, their dry weight biomass per unit area is often small.

Only Potamogeton pusillus L. and Chara sp. make significant contributions to the total macrophyte biomass in C-3 (Figure 26). Both species exhibit rapid growth rates during May but Chara subsequently declines for the remainder of the season. By midsummer the submerged vegetation is almost exclusively dominated by Potamogeton. The growth curve for Potamogeton levels off by the end of May when the foliage reaches the surface and spreads out. A second period of growth occurs in late June with the development of the reproductive structures. However, once the seeds reach maturity in mid-July Potamogeton deteriorates rapidly.

Chara does not form homogeneous communities in C-3 but is dispersed amongst the Potamogeton. Unlike Potamogeton, which grows to the surface, Chara remains submerged throughout the growing season. The decline in

FIGURE 26

Seasonal production of submerged macrophytes
(grams of dry weight/m²) in pond C-3.

its biomass after May appears to be the result of shading from both the surface foliage of Potamogeton and the floating mat of Wolffia columbiana.

As shown in Figure 27 total macrophyte production is more complex in PC-2. There are more species present and each has a unique seasonal growth curve. Chara sp. is a perennial, so that spring growth begins from overwintering foliage. The drop in biomass in early June appears to represent a loss of older tissue. After the initial spring growth Chara biomass remains constant until late July when it increases again. Since Chara grows in relatively homogeneous stands in PC-2, this late growth would not be due to decreased competition from the other macrophytes, but appears to result from the development of reproductive structures. Potamogeton zosteriformis, P. foliosus and Ceratophyllum demersum all have seasonal growth curves with mid summer maxima. The moss Drepanocladus fluitans is a minor component throughout most of the summer but increases in biomass in August. Najas flexilis on the other hand is absent from the May samples, but appears in the second collection and steadily increases in biomass for the remainder of the season. Most of the aquatic macrophytes can reproduce by vegetative structures, and consequently they have a high potential for rapid spring growth. N. flexilis, on the other hand, reproduces only by seed, which may explain the slower rate of development.

The summation of the individual growth curves for the component species in PC-2 illustrates the relatively

FIGURE 27

Seasonal production of submerged macrophytes (grams of dry weight/m²) in pond PC-2.

wide plateau of high levels of plant biomass. Although spring growth is slower than in C-3, the late season development of Chara and Najas extends high biomass levels into the late summer.

In PC-1, only Potamogeton foliosus and Chara sp. are important in terms of total macrophyte biomass (Figure 28). Potamogeton peaks in late June and the maximum for Chara is in mid July. As a result of the two separate peaks, there is a short plateau in total biomass from the end of June to mid July. In comparison with C-3 and PC-2 the rates of growth of macrophytes in PC-1 are much slower, and high levels of plant biomass are present for only a short time.

As in PC-1, PC-3 is dominated by Potamogeton foliosus (Figure 29). However, in this softer water pond, maximum biomass is lower, and occurs later in the season. Chara sp., Utricularia vulgaris and Ceratophyllum demersum are individually present in small amounts, but collectively raise the total production to levels which are comparable to the other ponds.

According to Westlake (1969), "... If, apart from respiration, there are no losses of plant material between two sampling times the net production, by definition, is equal to the observed change in biomass." Wetzel (1965), however, has shown that estimates of net productivity of macrophytes determined from biomass measurements often bear little relationship to growth rates measured by C^{14} techniques. He states that "... while estimates of the total seasonal productivity of macrophytes can be

FIGURE 28

Seasonal production of submerged macrophytes (grams of dry weight/m²) in pond PC-1.

FIGURE 29

Seasonal production of submerged macrophytes (grams of dry weight/m²) in pond PC-3.

DRY WEIGHT MACROPHYTE BIOMASS

approximated from biomass measurements, static appraisal of growth by biomass can be erroneous in intraseasonal comparisons of the productivities of several producer components.

Since pond to pond differences in the maximum seasonal biomass are small, estimates of annual net productivity of the macrophytes from the biomass data would result in similar values for all four ponds. Although such estimates would be valid by both Westlake's and Wetzel's criteria, they would, by themselves, give misleading information about the functional role of submerged vegetation in the pond ecosystems. When the temporal distribution of macrophyte biomass is taken into account, the ponds are obviously very different. In the hard water C-3 the rate of total macrophyte growth is very rapid so that maximum biomass levels exist for a considerable portion of the season. In the other three ponds growth rates decrease with decreasing water hardness. In PC-3 which has the softest water, maximum production is not realised until mid July, and there is no plateau. Thus, in the four ponds studied, the growth rates of total pond macrophytes from spring minima appears to be a function of water hardness. Although the species composition does not appear to be as important as water quality in affecting the rates of spring growth of total macrophytes, component species are important in terms of the duration of production. For example, the biomass of all species of Potamogeton decreases by early August in all water conditions. However, plants

such as Chara sp. and Najas flexilis in PC-2 reach peak biomass levels in late summer, thus extending the high levels of total biomass beyond those of the other ponds.

Pond to pond differences in the temporal distribution of macrophyte biomass are of great importance to the functioning of the pond ecosystems. One aspect to be considered is that of nutrient cycling. As Buscemi (1958) has shown, the presence of submerged macrophytes can greatly affect the metabolism of the water column. In dense communities of submerged macrophytes high rates of photosynthesis occur at the surface, but because of shading, photosynthesis is limited in the underlying vegetation. In the surface photosynthetic zone P/R ratios are greater than 1, while the underlying water becomes a zone of respiration. Thus, the direct action of the macrophytes can result in the development of anaerobic conditions in the lower portions of the water column. As discussed in the water chemistry section, reducing conditions at the mud-water interface can greatly affect the release of ions from the sediments. Thus, the interaction of the plants and chemicals can be thought of as autocatalytic. A given chemical regime allows a given rate of macrophyte production. The degree of plant metabolism then influences the rate of nutrient release from the sediments which, in turn, can be assimilated by the plants. Both the degree of productivity and the seasonal longevity of the plant communities would be important in this respect.

The differences in the temporal distribution of macrophyte biomass can also be of direct importance to other biotic components of the ecosystem. Many studies (Klugh, 1926; McGaha, 1952; Surber, 1930; Andrews and Hasler, 1944 and Krull, 1970) have stressed the relationships of invertebrate production and macrophyte production. The plants provide a substratum and, along with attached epiphytes, a food source for invertebrates. In terms of a resource base for consumers the temporal dimension of primary production may be as important as the degree of production. For example, in a pond such as C-3 the macrophytes would provide a stable resource base for much of the summer. However, in a soft water pond such as PC-3, the short duration of maximum macrophyte biomass would result in a more unstable environment for consumers and, in effect, provide a smaller resource base.

DUCK-HABITAT RELATIONSHIPS

Results and Discussion

The results of the 1966 and 1967 censuses of breeding pairs, broods and fledged ducks are shown in Tables 3 to 8. Although the data were collected from a small number (5) of ponds, the patterns of pond use by ducks did not appear to be constant throughout the breeding season. The population distributions suggested that breeding pairs, broods and fledged ducks did not have the same environmental requirements.

In order to more critically investigate the environmental factors important in the regulation of duck populations in the study area, and to determine if the regulating mechanisms changed seasonally, a larger number of study ponds was selected for the 1969 field season. To represent a wide range of water conditions, twelve ponds were chosen from a variety of geological areas, but two were drained and one replacement pond, C-2, was selected in June, 1969. The five study ponds from 1966 and 1967 were included.

The 1969 results supported the previous observation that the value of particular ponds as duck habitat was not constant throughout the breeding season. As shown in Table 9, all ponds were utilised by breeding pairs, with densities ranging from a low of 0.48 in PC-4 to a high of 2.00 pairs per acre in PC-5. During the brood season, however, the pattern of pond use changed (Table 10). Brood densities were nil or low on the soft

TABLE 3

Number of breeding pairs of ducks observed on the study ponds in 1966.

	C-1	C-3	PC-1	PC-2	PC-3	Total
Blue-winged Teal			2	3	1	6
Green-winged Teal			1			1
Mallard			1	1		2
Black			1	2		3
Wood Duck			2	1		3
Hooded Merganser			1	1		2
Ringneck			1		1	2
Total Pairs			9	8	2	19
Pairs per Acre			1.45	0.52	0.61	

TABLE 4

Number of duck broods observed on the study ponds in 1966.

	C-1	C-3	PC-1	PC-2	PC-3	Total
Blue-winged Teal	6	4	4	3	2	19
Mallard		1				1
Black	1					1
Total Broods	7	5	4	3	2	21
Broods per Acre	1.49	2.17	0.83	0.25	0.87	

TABLE 5

Number of fledged ducks observed on the study ponds in 1966.

	C-1	C-3	PC-1	PC-2	PC-3	Total
Blue-winged Teal	80	7	20	100	11	218
Green-winged Teal	2			50		52
Mallard	7			30		37
Black	6		12	30		48
Wood Duck						
Hooded Merganser			3		2	5
Total Ducks	95	7	35	210	13	360
Ducks per Acre	29.7	4.7	10.9	23.3	6.8	

TABLE 6

Number of breeding pairs of ducks observed on the study ponds in 1967.

	C-1	C-3	PC-1	PC-2	PC-3	Total
Blue-winged Teal	2	2	1	2	1	8
Green-winged Teal				1	1	2
Mallard		1	1			2
Black	1		1	1		3
Wood Duck				1		1
Hooded Merganser			1	1		2
Ringneck					1	1
Total Pairs	3	3	4	6	3	19
Pairs per Acre	0.38	0.97	0.65	0.39	0.91	

TABLE 7
Number of duck broods observed on the study ponds in 1967.

	C-1	C-3	PC-1	PC-2	PC-3	Total
Blue-winged Teal		2	2	2		6
Mallard		1		1		2
Black						
Wood Duck			1	1		2
Total Broods	0	3	3	4	0	10
Broods per Acre	0.0	0.97	0.48	0.26	0.0	

TABLE 8

Number of fledged ducks observed on the study ponds in 1967.

	C-1	C-3	PC-1	PC-2	PC-3	Total
Blue-winged Teal	4	38	5	50		97
Green-winged Teal				75		75
Mallard	18		7	100		125
Black	18		2	100		120
Wood Duck			2			2
Hooded Merganser			4		2	6
Ringneck				11		11
Total Ducks	40	38	20	336	2	436
Ducks per Acre	6.8	16.5	4.2	27.5	0.9	

TABLE 9

Number of breeding pairs of ducks observed on the study ponds in 1969.

	C-1	C-2	C-3	PC-1	PC-2	PC-3	PC-4	PC-5	PC-6	PC-7	PC-8	Total
Blue-winged Teal	2		2	1	1	1	1	2	1	2	1	14
Green-winged Teal				1	1	1	1	1		1	1	7
Mallard	1		1	1	1			1		2	1	8
Black	1		1	1	2	1		1		2	1	10
Wood Duck					2					1		3
Hooded Merganser				1	1							2
Ringneck					1					1		2
Total Pairs	4		4	5	9	3	2	5	1	9	4	46
Pairs per Acre	0.51		1.29	0.81	0.58	0.91	0.48	2.00	0.56	1.64	1.18	

TABLE 10

Number of duck broods observed on the study ponds in 1969.

	C-1	C-2	C-3	PC-1	PC-2	PC-3	PC-4	PC-5	PC-6	PC-7	PC-8	Total
Blue-winged Teal	3	3	3		1			1		1	1	13
Green-winged Teal					1		1				1	3
Mallard	1		1		1						1	4
Black	1	1		1				1		1		5
Wood Duck					1						1	2
Ringneck					1							1
Total Broods	5	4	4	1	5	0	1	2	0	2	4	28
Broods per Acre	0.85	0.63	1.29	0.16	0.32	0.0	0.24	0.80	0.0	0.36	1.48	

water Precambrian ponds, but relatively high (up to 1.29 broods per acre on C-3) on the harder water ponds. By late summer, there was a complete shift in the distribution of fledged ducks (Table 11) so that high densities were found only on the harder water ponds.

The results of the analytical field studies of 1966, 1967 and 1969 provided a basis for an hypothesis to describe the environmental regulation of duck populations in the study area. The hypothesis advanced was that densities of breeding pairs were primarily related to the physical attributes of a pond, while densities of fledged ducks were a function of pond fertility. The habitat requirements of broods were intermediate between those of breeding pairs and fledged ducks. Brood densities were a function of both the physical characteristics of a pond and its fertility. Breeding pairs were dispersed over all available ponds in response to behavioural spacing mechanisms while fledged ducks, and to a lesser degree broods, selected more fertile ponds on the basis of food availability. Habitat selection by both broods and fledged ducks could be accomplished by movement from their natal ponds.

To test this hypothesis, an experiment utilising a large number of ponds was designed for the 1970 field season. Twenty-one ponds, including all those previously studied, were selected to represent the range of chemical conditions found in the study area. Using existing geological information an attempt was made to choose equal numbers of soft, medium-hard and hard water ponds.

TABLE 11

Number of fledged ducks observed on the study ponds in 1969.

	C-1	C-2	C-3	PC-1	PC-2	PC-3	PC-4	PC-5	PC-6	PC-7	PC-8	Total
Blue-winged Teal	48	47	18	6	85		5	9		3	3	224
Green-winged Teal		4		7	30	2	10				10	63
Mallard	10	13		7	90		1	1		6	9	137
Black	8	37		9	90				1	7		152
Wood Duck					8			3			7	18
Hooded Merganser	1				1							2
Ringneck				2	122							14
Total Ducks	67	101	18	31	316	2	16	13	1	16	29	610
Ducks per Acre	11.36	25.90	7.83	6.46	25.90	0.87	6.96	6.84	2.38	3.56	18.13	

In order to compare the importance of physical and chemical factors, ponds of various sizes were chosen from within each of the chemical ranges.

The results of the 1970 breeding pair, brood and fledged duck censuses are shown in Tables 12, 13 and 14, respectively.

In order to evaluate the environmental regulation of duck populations in the study area, analyses of variance were used to relate duck numbers (transformed by $\log_{10}+1$) to physical and chemical pond characteristics. To determine if there was a temporal shift in the regulation, the three stages of the breeding cycle were analysed separately. In each of the three analyses data from all four years were included, so that a pond which was studied for more than one year was treated as a separate pond for each year.

Since it had been established that pond use by ducks did vary throughout the breeding season, pond morphometric parameters were determined separately for each stage of the breeding cycle. It was assumed that the morphometric measurements should reflect conditions when the ducks were selecting the ponds. Therefore, the area and shore length were estimated for each pond in all years in early May, late June and mid August to represent conditions during the peak periods of habitat selection by breeding pairs, broods and fledged ducks, respectively. On the other hand, it did not appear necessary to separately establish water chemical concentrations for the three periods. It was assumed that the

TABLE 12

Number of breeding pairs of ducks observed on the study ponds in 1970.

	C-1	C-2	C-3	C-4	C-5	C-6	C-7	PC-1	PC-2	PC-3	PC-4	PC-5
Blue-winged Teal		3	1	1	1	1	4	2	2	2		1
Green-winged Teal				1		1	2	1	1	1		
Mallard	1	1				2	1	2	2			1
Black	1			1	1	1	1	1	1		1	
Wood Duck				1			1		1			
Hooded Merganser					1				2	1		
Ringneck						1	1	2	1			
Total Pairs	2	4	1	4	3	6	10	8	10	4	1	2
Pairs per Acre	0.43	0.63	0.32	0.55	0.63	0.54	0.62	1.29	0.64	1.21	0.24	0.80

TABLE 12 (cont'd.)

PC-6	PC-7	PC-8	PC-9	PC-10	PC-11	PC-12	PC-13	PC-14	Total
	2	2	3	1	1	1	1	3	32
	1		1		1	1		3	14
		1	1	1	1			1	15
				1	2	1	1	3	16
									3
1	1		1	1		1			9
	1								6
1	5	3	6	4	5	4	2	10	95
0.56	0.91	0.88	0.86	0.74	1.06	0.56	0.21	0.72	

TABLE 13

Number of duck broods observed on the study ponds in 1970.

	C-1	C-2	C-3	C-4	C-6	C-7	PC-1	PC-2	PC-3	PC-4	PC-5	PC-6
Blue-winged Teal		3	3	2	2	2			1			
Green-winged Teal	1	1	1			1		1				
Mallard					2	2						
Black		1		1	1	3						
Wood Duck						1						
Ringneck					1	1						
Total Broods	1	5	4	3	6	10	0	1	1	0	0	0
Broods per Acre	0.71	1.03	2.17	0.60	0.54	0.99	0.0	0.08	0.44	0.0	0.0	0.0

TABLE 13 (cont'd.)

PC-7	PC-8	PC-9	PC-10	PC-11	PC-12	PC-13	PC-14	Total
	1	2			2	1	1	20
		1		1				5
								6
1	1	1		1		1	4	15
								1
		1						3
1	2	5	0	2	2	2	5	50
0.22	0.74	0.71	0.0	0.43	0.43	0.22	0.55	

TABLE 14

Number of fledged ducks observed on the study ponds in 1970.

	C-1	C-2	C-3	C-4	C-6	C-7	PC-1	PC-2	PC-3	PC-4	PC-5	PC-6
Blue-winged Teal	4	50	26	30	50	59	12	50	2		1	
Green-winged Teal	35	65		45	80	100		100				
Mallard		3	10	11	28	12		72				
Black	5	3	15	13	40	32	8	125			2	
Wood Duck						7		1				
Hooded Merganser												
Ringneck					6			1				
Total Ducks	44	121	51	99	204	210	20	349	2	0	3	0
Fledged per Acre	88.0	50.4	34.0	27.5	27.9	31.8	6.3	38.8	1.1	0.0	3.0	0.0

TABLE 14 (cont'd.)

PC-7	PC-8	PC-9	PC-10	PC-11	PC-12	PC-13	PC-14	Total
1	18	24	6	1	6	10	13	363
6		10	1					442
	3	4	1	1	7	2	9	163
12	4		7	7	13	8	25	319
			1					9
				2				2
				5				12
19	25	38	16	16	26	20	47	1310
4.9	15.6	5.6	3.3	3.8	5.1	2.4	6.9	

biological characteristics of the ponds which would be important to ducks would integrate the water chemical conditions over the season. Thus, in the 1966, 1967 and 1969 ponds, and the five 1970 core ponds, the water chemical concentrations used in the analyses are the seasonal means of surface samples. The values for the remaining 1970 ponds are the means of the two surface samples from each pond collected on July 10, 1970. The chemical characteristics employed in the analyses are: 1-Calcium, 2-Magnesium, 3-Sodium, 4-Potassium, 5-Total Iron, 6-Total manganese, 7-Chloride, 8-Nitrate, and 9-Silica, all expressed as Mg/l.

The analysis of variance for breeding pairs is shown in Table 15. The high F value for pond area indicates the strong relationship between pair numbers and pond size. Associated with this response, however, are significant negative relationships with concentrations of calcium and chloride. Since both of these ions are lower in the soft water ponds, the negative relationships indicate a trend towards selection of more sterile waters by breeding pairs.

The analysis of variance for broods (Table 16) shows that their environmental requirements are different from those of pairs. Brood numbers are positively related to concentrations of calcium and silica, and negatively related to total manganese. These associations indicate that the broods are selecting for the harder water ponds. As shown in the water chemistry section, chloride concentrations are uniformly low in all non-

TABLE 15

Analysis of variance table for breeding pairs.

Source of Variation	D.F.	Sums of Squares	Mean Square	F Value	Treatment Effects
Area	1	2.72992	2.72992	117.163***	+0.023670
Shore Length	1	0.02242	0.02242	0.961	-0.000002
Calcium	1	0.18830	0.18830	8.082**	-0.010168
Magnesium	1	0.06168	0.06168	2.648	+0.020279
Sodium	1	0.03314	0.03314	1.421	-0.052213
Potassium	1	0.03887	0.03887	1.669	+0.095959
Iron	1	0.07251	0.07251	3.112	-0.249703
Manganese	1	0.00370	0.00370	0.155	+0.020872
Chloride	1	0.20820	0.20820	8.93**	-0.010601
Nitrate	1	0.00000	0.00000		-0.037301
Silica	1	0.06038	0.06038	2.592	+0.026361
Year	3	0.21563	0.07188	3.086	
Season	2	7.22140	3.61070	154.966***	
Year x Season	6	0.14487	0.02415	1.034	
Pond	20	0.59459	0.02973	1.275	
Residual	78	1.81930	0.02332		
Total	120	13.41491	0.11180		

Total reduction in sum of squares is 86.44 per cent.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

TABLE 16

Analysis of variance table for broods.

Source of Variation	D.F.	Sums of Squares	Mean Square	F Value	Treatment Effects
Area	1	0.09233	0.09233	2.622	-0.02931
Shore Length	1	0.14482	0.14482	4.114*	+0.00010
Calcium	1	0.58956	0.58956	16.750***	+0.02387
Magnesium	1	0.02539	0.02539	0.722	+0.00456
Sodium	1	0.00799	0.00799	0.227	-0.00848
Potassium	1	0.12719	0.12719	3.614	+0.1064
Iron	1	0.09409	0.09409	2.673	-0.01723
Manganese	1	0.24496	0.24496	6.960*	-2.191
Chloride	1	0.27229	0.27229	7.736**	-0.05263
Nitrate	1	0.10165	0.10165	2.889	+0.4968
Silica	1	0.24368	0.24368	6.923	+0.08364
Year	3	0.12432	0.04144	1.176	
Season	2	4.31159	2.15580	61.244***	
Year x Season	6	0.07228	0.01205	0.341	
Pond	20	1.18753	0.05938	1.688	
Residual	78	2.74897	0.03524		
Total	120	10.38864	0.08657		

Total reduction in sum of squares is 73.54 per cent.
 * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

dolomitic ponds. Since brood numbers are high in some of these ponds (especially C-6 and C-7) there is a negative relationship between brood numbers and chloride. Although broods do select more fertile ponds, they are still associated with pond morphometry. Brood numbers also are positively related to shoreline length.

In the analysis of variance for fledged ducks (Table 17), population size is seen to be independent of the morphometric characteristics of the ponds. All significant relationships are with chemical parameters. The positive associations with calcium and silica and the negative relationship with iron, reflect the selection of harder water ponds. There are also negative relationships with magnesium and chloride, both of which have low concentrations in the Precambrian ponds. The significant year effect in this analysis indicates that there is some annual variation in the fledged duck populations. However, the relatively high total reduction in sums of squares for the three analyses indicates that the selected environmental characteristics account for a large proportion of the variability in the distributions of duck populations.

The results have clearly shown that, within the present study area, there is a temporal shift in the environmental regulation of breeding duck populations. The number of breeding pairs which a given pond can support is primarily a function of pond size. There is no selection of edaphically rich waters, in fact, the only relationships with chemical parameters indicate selection of sterile waters. The fact that more breeding pairs

TABLE 17
Analysis of variance table for fledged ducks.

Source of Variation	D.F.	Sums of Squares	Mean Square	F Value	Treatment Effects
Area	1	0.06021	0.06021	0.348	-0.11731
Shore Length	1	0.18255	0.18255	1.055	+0.00012
Calcium	1	3.65706	3.65706	21.139***	+0.03423
Magnesium	1	1.80173	1.80173	10.414**	-0.01017
Sodium	1	0.64362	0.64362	3.720	-0.10167
Potassium	1	0.03481	0.03481	0.201	+0.23584
Iron	1	1.29512	1.29512	7.486**	-0.57040
Manganese	1	0.11698	0.11698	0.676	-0.79566
Chloride	1	1.70035	1.70035	9.829**	-0.05109
Nitrate	1	0.32395	0.32395	1.873	-0.11602
Silica	1	1.16584	1.16584	6.739*	+0.15299
Year	3	3.23125	1.07708	6.225*	
Season	2	34.39180	17.19590	99.398***	
Year x Season	6	1.42721	0.23787	1.375	
Pond	20	4.76336	0.23817	1.377	
Residual	78	13.49537	0.17302		
Total	120	68.29122	0.56909		

Total reduction in sum of squares is 80.24 per cent.
* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

were found on the soft water ponds is possibly due to the fact that there are greater densities of ponds in the Precambrian study area, so that pair movement from pond to pond may inflate the counts to some degree.

Breeding pairs then, tend to be distributed over all ponds in the study area. The fact that pair densities are more or less equal in a spatially heterogeneous environment, points to dispersion of the population by behavioural spacing. Both Hochbaum (1944) and Sowls (1955) conclude that territoriality in breeding ducks is an important dispersal mechanism.

Although the phenomenon of territoriality and the resulting spacing of breeding ducks is generally acknowledged by most waterfowl biologists, there are various interpretations of its implications. A common conclusion is that ducks prefer fertile wetlands and only inhabit less fertile ones when they are forced into them by overcrowding. In Wisconsin, where breeding populations are low as a result of heavy hunting pressure, Jessen et al. (1964) concluded that breeding pairs did select more fertile habitats. In the Waubay region of South Dakota, Evans and Black (1956) found that breeding ducks were evenly dispersed over all available habitat. They further state that this occurs only after the population builds up and leads to dispersal of the birds into parts of the habitat which are not otherwise used.

Dzubin (1969) concludes that spacing mechanisms function to disperse pairs and nests, but usually result

in the utilization of poorer quality habitat with resulting decreased production.

No such implications can be made about the results of spacing mechanisms in this study. It can only be concluded that the breeding pair population in the study area is dispersed, primarily as a result of the availability of water. Ponds of all types of water quality are utilized.

The distribution of broods in the study area was strikingly different from that of breeding pairs. Whereas pairs were dispersed over all ponds and had no preference for fertile habitat, broods showed a definite selection for harder water ponds. As is shown in the previous section, the growth rates of submerged macrophytes are much higher in the hard water ponds. The pond to pond variation in macrophyte biomass is greatest in early summer, coinciding with the peak of the brood activity. Thus, brood distributions are related to the growth rates of submerged macrophytes.

Young ducks are known to eat very little vegetation. Since their protein requirement is high, and their digestive system is unable to break down fibrous plant material until they are several weeks old, broods feed primarily on invertebrates (Penney and Bailey, 1970). Johnson (1971) found that protein deficiency in young wood ducks considerably reduced growth and development. He suggested that in the wild, a lack of natural foods high in protein could be a significant mortality factor.

According to Moyle (1961) the "... protein content of the green parts of water plants appears to usually be

between 1 and 2 per cent of the wet weight, seeds and dry fruit average perhaps 10 per cent.... and aquatic invertebrates usually have between 10 and 20 per cent protein." If food is a limiting factor to the distribution of brood populations then, their distribution should be related to availability of aquatic invertebrates.

In a previous study (Patterson, 1969) densities of invertebrates were found to be much higher in ponds C-1 and C-3 than in PC-1, PC-2 and PC-3. Moyle (1961) summarised the literature on bottom fauna by stating that "production of bottom fauna differs greatly in waters of different quality, on different soil types and in different physical and chemical situations in the same body of water." He considered that hard carbonate waters were much more productive of bottom fauna than soft waters.

Krull (1970) investigated aquatic plant-macroinvertebrate relationships in northern New York. He found that invertebrate production was greater in vegetated than non-vegetated areas. In general, there was 1 gm. macroinvertebrates per 100 grams of plant material. An important finding of Krull's was that invertebrate abundance reached its peak soon after the plants appear.

Although the macrophytes in the study ponds may not be directly utilized as a food resource by duck broods, they are important as a resource base and substratum for invertebrate populations. Thus, rates of macrophyte production in ponds of different water quality would reflect the relative production of invertebrates.

Although the distribution of broods showed a movement to harder water ponds, the selection was not a complete one. There was an associated relationship with pond shoreline length, reflecting the requirement of broods for escape cover. Most brood sightings were near the shoreline, in, or close to, cover of some sort. Evans and Black (1956) conclude that the selection of brood rearing habitat depends on the availability of a means of escape from predators. In the case of dabbling ducks this was found to be furnished primarily by emergent vegetation.

Examples of the habitat requirements of broods are provided by a comparison of ponds with similar chemical regimes. PC-2 and PC-14 have essentially the same water chemical composition, but PC-14 has a more irregular shoreline and much more emergent vegetation. Brood densities in 1970 of 0.55 in PC-14 and only 0.08 per acre in PC-2 illustrate the importance of escape cover. The water chemistry of C-1 and C-3 is similar, but in 1970 there were 2.17 broods per acre in C-3 where there is abundant cover, and only 0.71 broods per acre in C-1 which has a more open shoreline.

Since there are both behavioural and nutritional environmental requirements, densities of broods are related to both physical and chemical parameters of the ponds.

By late summer, fledged ducks showed an even stronger selection of edaphically rich ponds than did

broods. Highest densities were consistently found on the hard and medium-hard water ponds, regardless of pond size or shoreline configuration.

Flying ducks have often been noted to congregate on larger bodies of water in late summer. Evans and Black (1956) found that fledged ducks made heaviest use of large open water areas. Although food availability was considered important they felt that habitat selection was extremely haphazard, and seemed to depend as much on a flocking tendency as on other factors. Moyle (1964) notes that by mid August, ducks in Minnesota congregate on larger waters, presumably those with a good source of food. In Backus Lake, Michigan, Kadlec (1962) found that by early August, duck aggregations became large and were concentrated on the better food areas. Although the occurrence of gregarious behavioural tendencies at this time of year is not discounted, the results of this study suggest that habitat fertility is the most important factor regulating fledged duck numbers.

Clear examples of food regulation of fledged duck populations are provided by pond utilization in the Pre-cambrian study area. In late summer, submerged macrophyte biomass levels are low in PC-1 and PC-3. Fledged ducks make little use of these and other soft water ponds. In PC-2, however, the maximum seasonal macrophyte biomass occurs in the late summer, primarily as a result of increases in Chara and Najas. In each of the four years of the study, large numbers of fledged ducks congregated

on this pond, in response to the abundance of food. Many of the birds were observed to feed heavily in the Najas communities. Martin, Zim and Nelson (1951) consider both Chara and Najas to be among the top ranking duck foods.

An interpretation of the environmental regulation of duck breeding populations as determined in this study is shown in the conceptual model in Figure 30. It indicates the environmental components and mechanisms involved in the temporal shift in population regulation. The major point is that the environmental requirements of each stage of the breeding cycle are different. As a result, overall population regulation could be a result of a combination of factors or any one of them. It is further suggested that the most healthy state is when duck populations are regulated at all stages, so that the population is in equilibrium with the ability of the environment to support it for an extended period of time.

Hochbaum (1944) and Sowl (1955) have documented the phenomenon of a homing instinct in ducks, whereby breeding birds return to the area in which they were fledged. As Smith (1969) has shown, the size of potential breeding pair populations in an area is related to the number of ducks produced in that area in the previous year. According to the findings of this study, if a duck population was food limited, this would not directly regulate the density of breeding pairs. Their regulation would be in the form of a negative feedback mechanism with a one-year lag relative to the number of produced

FIGURE 30

A conceptual model describing the environmental regulation of duck populations in the study area.

ENVIRONMENTAL FACTORS
REGULATING BREEDING
DUCK DENSITIES:

DEGREE OF EFFECT:

PHENOLOGY OF LIFE
HISTORY STAGES ON
BREEDING HABITAT:

MECHANISMS:

ducks that the habitat resources could support in the intervening year.

In the present study area, the temporal shift in regulatory mechanisms allows a much higher regional population size. If all stages of the breeding cycle were food limited to the degree that fledged ducks are, then pairs would be mainly confined to the edaphically rich ponds. As it is, the breeding pairs can make full use of even the most sterile ponds, where they can have isolation from other pairs. The broods and fledged ducks which are food regulated, can then be accommodated on the more fertile waters in the area. The high densities of breeding birds found on the study ponds (0.69 pairs per acre in 1970) indicates the high degree of utilization of the area as a whole.

In a uniformly sterile area such as much of the Precambrian Shield, it would seem that the major regulatory factor is the lack of food for broods and fledged ducks. The findings of this study suggest that there is under-utilization of the habitat by breeding pairs. Populations are low enough so that they do not approach the level where behavioural spacing mechanisms would influence population size. Produced ducks are limited to low densities resulting in relatively small numbers returning in the spring to breed. Thus, when food does become the sole limiting factor to duck populations, the populations are held at low levels.

In a uniformly rich area such as the prairie pothole region of North America where food is abundant, ducks are primarily regulated by the pair densities which can be accommodated behaviourally on the available water. If a static situation existed whereby the prairies had long term stable water conditions, then behaviourally regulated duck populations would be lower than that which could be supported by the available food. The prairie region, however, is subject to drought cycles in which the number of wetlands is drastically reduced. In such dry years, when water is limiting, the behavioural spacing mechanisms tend to keep the population low, more or less in equilibrium with the available water. The validity of this relationship is illustrated by the annual high correlation between available water and the size of the breeding population (Crissey, 1969). If the population was not behaviourally regulated, then in dry years when there are fewer wetlands, large breeding populations would be crowded into the remaining water areas, with resultant heavy mortality rates and possible damage to the environment.

The variety of ways in which duck populations can be regulated allows the population to be maintained in equilibrium with the environment. In the prairie pothole region where there is considerable temporal environmental heterogeneity, the populations are kept down, relative to habitat availability, and with a minimum of mortality. In a spatially heterogeneous environment, such as the present

study area, the opposite function is served. The populations can exist at high densities, making full use of both the available water area and food resources.

GENERAL DISCUSSION

The study has shown that in order to investigate the specific environmental requirements of duck populations it is essential to analyse not only the internal functions of the ecosystems in which the populations occur, but also recognise the relationships of those ecosystems with the over-all environment.

Conceptually, the ecosystem is viewed as a functional unit with recognisable boundaries and an internal homogeneity (Smith, 1970). Because of progressive successional changes, such ecosystem boundaries have to be in both spatial and temporal dimensions. For example, shallow, upland aquatic ecosystems which provide the breeding habitat for the majority of dabbling ducks, occupy a tenuous temporal position. In an edaphically rich environment, succession can rapidly alter both the physical and biological characteristics, so that there is a progression into a recognisably different system. The time period in which wetland ecosystems can provide an environment for breeding ducks can be very short. Examples of the time scale are provided by the fates of artificial impoundments created for waterfowl breeding habitat. Kadlec (1962) reports that in Michigan, artificial flowages are heavily utilised by ducks in the first few years of impoundment, but can begin to decline in usefulness after only 4 or 5 years. Since succession is primarily a result of biological development, the time scale is related to biological productivity. Succession occurs more rapidly

in fertile wetlands than in sterile ones. Therefore, there is a tendency towards an inverse relationship between productivity and the persistence of these ecosystems.

The importance of the time factor is stressed in the hypothesis advanced by Loucks (1970), that evolution in ecosystems has brought about an adaptation to both heterogeneous environments and to a repeating pattern of changing environments. He suggests that high levels of ecosystem diversity and productivity can be due to temporal environmental heterogeneity which triggers the recycling and rejuvenation of the biotic systems. Loucks concludes that the periodicity of such environmental changes can range from several centuries in the northern lake forest to periods of a few decades or even annually at the edge of the grasslands.

Wetland ecosystems in the prairie pothole region of North America provide a good example of Loucks' hypothesis. Wetlands in this fertile area are highly productive. Succession here should be rapid, and the wetlands short-lived. However, since temporal environmental heterogeneity in the form of drought cycles dries out many of the basins, the ecosystems are periodically rejuvenated. Thus, the wetlands are maintained at early successional stages, and provide suitable breeding habitat for ducks.

The necessity of this type of exogeneous influence in maintaining productive wetland ecosystems in a desired state of successional development has been empirically recognised by waterfowl managers. Periodic drainage is

used as a technique of restoring fertility and altering succession to stages most productive of breeding ducks (Cook and Powers, 1958; Kadlec, 1962; Harris and Marshall, 1963).

Slobodkin and Sanders (1969) characterise physically controlled and unpredictable ecosystems as being low in species diversity and unstable. Because of the changing environment, component species have broad, flexible niches. They state that "...for species in 'unpredictable' environments it is generally the case that different life history stages show different sensitivity to environmental changes."

In this discussion, the major point is that the persistence of upland wetland ecosystems, which provide most of the breeding habitat for dabbling ducks is in great part due to environmental heterogeneity. Such wetlands are dependent on periodic climatic changes, and as such are unstable ecosystems. Ducks, as component species in these ecosystems are adapted to environmental change. Although the variations in the environmental requirements of the different life history stages may be an evolutionary adaptation to temporal environmental heterogeneity, they allow duck populations a high degree of utilisation of a spatially heterogeneous environment.

In recent years there has been considerable discussion concerning the relationships between species diversity and stability. Margalef (1968) considers the ecosystem as a channel which projects information into the future. The distribution of individuals into species

affords a preliminary measure of the width of the channel of information. Two types of stability are recognised. In the first, stability is analogous to persistence, in that the system is achieving a steady state under constant conditions. In the second, stability refers to lability, or the system's resistance to changes that are external to the system in their origin (Margalef, 1968, 1969). Stability of a regional system of wetlands as considered in this study refers to lability.

While species diversity provides a numerical measure of certain properties of an ecosystem, it does not fully describe all the 'information' which may affect the future of the system. In terms of the lability of ecosystems, abiotic or functional biotic heterogeneity can be very important. For example, the flexibility of environmental requirements or niche breadth, which allows a species to adapt to unstable conditions, may be thought of as a potential form of information which allows the species to maintain stability in a changing environment.

Although the degrees of heterogeneity of abiotic components and functional processes are not readily quantifiable, as is species diversity, the recognition of such dimensions of environmental heterogeneity can be very important in understanding the functioning and predictability of ecosystems.

A means of looking at such regional system heterogeneity in the present study area is provided by the simple flow diagram shown in Figure 31. In this abstraction, different levels of heterogeneity have been isolated

FIGURE 31

A conceptual model identifying different levels of regional system heterogeneity and possible feedback loops which give rise to the over-all degree of system heterogeneity. (---->) Pathways of potential heterogeneity. (—>). Pathways of functionally derived heterogeneity.

in order to conceptualise the interactions of the biotic and abiotic components.

The first term in the flow diagram, abiotic heterogeneity, refers to all variations in the physical and chemical components of the system. Included are such factors as climate, geology, topography and the resultant morphometry and chemical composition of the ponds. In terms of its effect on the over-all system, abiotic heterogeneity is being considered in terms of a potential; that is, its effect in providing the spectrum of resources available for utilisation by the living components of the system.

A function of the degree of abiotic heterogeneity is the variability or diversity of the biotic components of the system. Collectively the biotic and abiotic components determine the potential level of system heterogeneity. In the context of the present study area this potential level of regional system heterogeneity is analogous to the situation recognised by Slobodkin and Sanders (1969) whereby "... diversity of animals can be related to diversity of plants, which in turn can be related to the geometric, mineralogical and chemical diversity of the substrate."

In the functioning of the system, the biota utilises resources and thereby imparts change. Thus, another dimension has been added to the abstract model, that of functional heterogeneity. As a result there is derived structural heterogeneity which can feed back to give greater structural and functional heterogeneity to the

over-all system. The stability or lability of the regional system is related to both species diversity and the over-all dimension of system heterogeneity.

In the present study area the variability of the composition and solubility of the substrate produces a regional system of chemically heterogeneous ponds. In response to the chemical variability there are pond to pond variations in the biota. Although there are some species of plants and animals which are common to all water chemical conditions in the area, there is a definite shift in the composition of the biota in response to the chemical environment. Thus, in the regional complex of ponds there is system heterogeneity as a result of both the biotic and abiotic components. At this point the diversity of the regional system could be quantitatively described by its biotic components, but it would not necessarily provide a basis for understanding the system, or allow much in the way of predictive powers as to the future of the system. Recognition of the functional heterogeneity provides a much stronger basis for understanding and prediction.

Examples of functional and derived heterogeneity are provided by the interactions between the submerged macrophytes and the water chemistry of the ponds. In the soft water ponds, where the concentrations of major ions are low and there are low growth rates of macrophytes, plant metabolism imparts little change to the chemistry. The slow macrophyte growth does not produce strongly

reduced bottom water, hence there is not much interchange of major ions between the water and sediments.

In the hard water ponds, not only are there higher concentrations of chemicals in the water which provide a resource base for primary producers, but there is greater mobility of chemicals within the pond ecosystems. The metabolism of the dense communities of submerged macrophytes produces a respiratory zone in the lower water column. As a result, oxygen in this zone is depleted, and the dissolution of chemicals from the sediments to the water is greatly facilitated. The effect of the rates of macrophyte production then, is to alter the role of the sediments in the chemical dynamics of the pond systems. High macrophyte productivity results in anaerobic sediments which release more nutrients which in turn can act as a feedback mechanism to promote more plant production.

Such forms of functional heterogeneity can result in derived structural heterogeneity. For example, the detritus-rich respiratory zone of the hard water ponds provides an environment for another assemblage of organisms. Apart from the anaerobic decomposers, macro-invertebrates such as Chironomidae and Sphaeriidae can reach very high densities (Patterson, 1969). These organisms can provide further functional change to the system by affecting nutrient release from the sediments. Tessenow (1964) has shown that the feeding activity of chironomids can have a marked effect on the dissolution of silica across the mud-water interface.

In the regional system of ponds then, there are many dimensions of system heterogeneity which result from functional interactions. Perhaps one of the most important forms of functional heterogeneity is that of time. One aspect of this is the pond to pond variations in the temporal distribution of macrophyte biomass. These variations have been shown to be important to the chemical dynamics of the ponds, but they are also important to the consumer organisms. The rich ponds which have high biomass levels for much of the summer can provide a stable resource base for consumers, in contrast to the soft water ponds in which high biomass levels are present for only a short time.

Another important consideration in the regional system is the longevity of the individual pond ecosystems. In the productive hard water ponds high rates of macrophyte production result in both large amounts of plant material, and anaerobic conditions in the bottom water. In such ecosystems there is a net imbalance between production and decomposition so that the pond basins fill up with organic sediments. In highly productive ponds there can be a rapid accumulation of organic matter so that there is a relatively fast development into another type of ecosystem such as a marsh.

Soft water ponds, on the other hand, have lower rates of macrophyte production and, as a result, have more aerobic bottom water conditions. In the ponds investigated in this study, decomposition appears to be more in tune

with production so that there is a slower accumulation of organic sediments, and the pond ecosystems have a longer life span. In the regional context then, there is heterogeneity in the longevity of the individual pond ecosystems.

The functional interactions between the biotic and abiotic components of the regional system produce structural changes which in turn can give further functional change. The whole process as shown in Figure 31 resembles an autocatalytic feedback system.

The long term lability of a regional system of wetland ecosystems is dependent on both spatial and temporal abiotic heterogeneity. As discussed previously, the creation and management of wetlands for duck production in an edaphically rich area requires considerable effort in artificially providing the temporal heterogeneity necessary to maintain the ecosystems at the desired state of development. The results of this study suggest two major reasons why the management of wetlands for duck production in an edaphically heterogeneous area could be more stable and efficient. First, the variations in the environmental requirements of the different life history stages of ducks allow a high degree of utilisation of such an area. Second, the edaphic heterogeneity can result in increased longevity of the more sterile wetlands. Duck habitat management in a spatially heterogeneous environment such as the present study area would require much less management effort, as one could take advantage of

the less productive ponds and apply intensive management only to the productive waters.

Although this study deals with a narrowly defined part of the environment, it does point to the fact that in natural and managed ecosystems there can be tangible value in the maintenance and utilisation of environmental heterogeneity. Much of man's management activities, whether in agriculture, forestry, wildlife management or urban planning and human ecology result in the simplification of ecosystems and potential loss of 'information' which can help provide stability. Perhaps duck populations are representative of many populations including man's which benefit from and, in fact, require environmental heterogeneity for their long term stability and welfare.

CONCLUSIONS

1. The water chemical composition of ponds in the study area was found to be mainly determined by the composition and solubility of the bedrock in the pond drainage basins. Ponds overlying sedimentary rock were characterised by hard water, with all major cations significantly contributing to the total ionic content. Individual ions showed considerable seasonal variation and stratification and the sediments were actively involved in this movement.

In the Precambrian study area ponds were of the soft to medium hard type dominated by calcium. Seasonal variations and stratification of ions were much less pronounced than in the sedimentary ponds, and the sediments played a minor role.

2. The maximum seasonal production of submerged macrophytes was found to be similar in all types of ponds. Rates of production from spring minima, however, increased from soft to hard waters. As a result, maximum levels of macrophyte biomass were present for much longer periods of the growing season in the harder water ponds. It was concluded that the differences in production rates were of major ecological importance in terms of pond mineral cycling and the provision of a resource base for consumer organisms.

3. The regulation of duck populations on the study area was found to be independent for the three life history stages considered. Breeding pairs were regulated

by behavioural spacing mechanisms, broods by the availability of escape cover and energy resources and fledged ducks by the availability of energy resources.

It was concluded that the variations in regulatory mechanisms are an evolutionary adaptation to a temporally heterogeneous environment. This adaptation to temporal heterogeneity allows high levels of utilisation of a spatially heterogeneous environment.

4. It was concluded that the management of wetlands for duck production could best be accomplished by taking advantage of natural environmental heterogeneity.

5. In conclusion, the findings of this study were used as a basis for the concept that not only biotic diversity, but all dimensions of system heterogeneity can have an effect on the stability of ecosystems.

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APPENDIX A

Structural map of the Ottawa-St.Lawrence Lowland in Canada, showing location of study area (from Wilson, 1946).