

EFFECT OF RATE OF WATER DISCHARGE ON PHYTOPLANKTON IN CLAYTOR LAKE, VIRGINIA

*Thomas L. Schulte¹ and Robert T. Lackey
Department of Fisheries and Wildlife Sciences
Virginia Polytechnic Institute and State University
Blacksburg, Virginia 24061*

ABSTRACT

Claytor Lake, Virginia, an 1820 ha main stem hydroelectric reservoir, was studied for one year to determine the effect of water discharge on reservoir phytoplankton. Number/liter, areal units/liter, average cell size, and chlorophyll *a* content were used as measures of phytoplankton abundance. Rate of water discharge had an adverse effect on reservoir phytoplankton during spring and summer. Although increased rate of water discharge caused increased phytoplankton loss, the adverse effect of rate of water discharge on reservoir phytoplankton populations was probably at least partially due to additional discharge of nutrients. The inverse relationship between rate of water discharge and reservoir phytoplankton populations decreased in the uplake direction.

INTRODUCTION

Man-made impoundments provide a major opportunity to increase the amount of quality angling. Reservoirs often support standing crops of 80 kg of fish per ha and provided a sport catch of 55,000,000 kg in 1960 (Stanberry, 1967). Reservoirs supported about 160,000,000 angling days during 1970 and this pressure will increase in the future (Bureau of Sport Fisheries and Wildlife, 1971). As important as reservoirs are now in providing angling opportunity, their full potential has not been realized.

One common management practice utilized to improve reservoir fishing is the introduction of various forage fishes, usually clupeids. Introductions of this nature are often able to strengthen the trophic link between planktonic and piscivorous fishes. However, in reservoirs where plankton is relatively limited, planktivorous fishes may be adversely affected by reduction of food supply, ultimately having a detrimental influence on piscivorous game fishes.

One detrimental influence on phytoplankton in reservoirs may be the discharge of large volumes of water during certain periods of the year. Ruttner (1963) stated that water outflow is an important depletion factor as it removes part of the plankton from a lake. Van Landingham (1964) listed water discharge as one of the factors influencing phytoplankton standing crop and production. Usually there is a flow of water through a lake and consequently some phytoplankton loss, but a sudden flood may wash a plankton bloom out of a lake (Fogg, 1965).

The usual downstream increase of zooplankton in reservoirs is influenced by reservoir length, volume, and water exchange rate. In two Missouri River main stem reservoirs, zooplankton abundance in the downstream reservoir was most influenced by zooplankton discharge from the upstream reservoir, which had a fairly rapid exchange rate (Cowell, 1967). Low zooplankton standing crop has also been attributed to water exchange rates by Brook and Woodward (1956), Tonalli (1961), Axelson (1961), Johnson (1964), and Rodhe (1964).

¹Present address: Department of Natural Resources, San Juan, Puerto Rico 00906.

Short water retention time may affect reservoir productivity by limiting the time available for phytoplankton growth. Differential phytoplankton growth response has been attributed to a greater proportion of dissolved or particulate nutrient forms in "old water" (Findenegg, 1965). Funk and Gaufin (1971) found that low reservoir outflow appeared to have a positive effect on all algal forms. However, high reservoir outflow during midsummer months gave a negative correlation with growth of *Aphanizomenon flos-aquae*.

The relationship between phytoplankton standing crop and discharge has not been clearly defined. Benson and Cowell (1967) found that as phytoplankton standing crop increased or decreased, so did the amount in the discharge water, but it was not a proportional relationship. Differences in phytoplankton discharge were attributed to variations in water discharge rates; summer rates were approximately 3-fold greater than winter rates.

As part of an effort to improve the forage fish base in Claytor Lake, Virginia, a planktivorous pelagic species, the landlocked alewife (*Alosa pseudoharengus*), was introduced in 1968 and 1969. Alewives are now abundant in Claytor Lake and appear to be an important forage species. Because of the importance of plankton in the alewife diet and the rapid water exchange rate (9-50 days), the lake provided an ideal environment to study the effect of water discharge on reservoir phytoplankton.

STUDY AREA

Claytor Lake, a main stem hydroelectric reservoir on the New River, Pulaski County, Virginia, covers 1820 surface ha, has 161 km of shoreline, and a normal pool elevation of 663 m above sea level. Claytor Lake is relatively deep (mean depth = 15.8 m), narrow, and steep-sided. The epilimnion of this dimictic lake supports warmwater fishes, while the hypolimnion usually contains insufficient oxygen to support coldwater fishes.

During the study year (August, 1971-July, 1972), Claytor Lake had a storage ratio (ratio of reservoir volume to the average annual discharge) of 0.068 with 14.75 complete water turnovers. In comparison, approximately 84% of the 207 reservoirs reported by Jenkins (1967) had a greater storage ratio. Sixty-eight of these reservoirs were classified by use as hydroelectric, with an average storage ratio of 0.33 (62% had a larger storage ratio than Claytor Lake). Although the Claytor Lake storage ratio is lower than most reservoirs, it is not unlike that for most hydroelectric reservoirs.

METHODS

Sampling Stations

Phytoplankton sampling stations were numbered 1 through 16; the immediate area in front of the dam being station 1, and Lowman's Ferry (Bridge 672), station 16 (Fig. 1). Remaining stations were located equidistantly between stations 1 and 16 and numbered accordingly. The distance from station 1 to station 16 was 16 km, resulting in approximately 1 km distances between stations. The tailrace was treated as a separate sampling station. Each station, except the tailrace, was divided into four substations (A, B, C, and D). Substation A was one-fifth the distance from one shore to the other shore, and B, C, and D were each an additional one-fifth distance across the lake. For some analyses, the lake was also considered in quadrants. Station 1 through 4 (and respective substations) comprised sampling areas in quadrant I; station 5 through 8, quadrant II; stations 9-12, quadrant III; and stations 13-16, quadrant IV.

Experimental Design

A systematic sampling procedure was utilized to ensure sampling all 16 lake stations on an approximately monthly basis during spring, summer, and autumn. For the first week of a month, station 1, 2, 3, or 4 was randomly selected. Selection of station 3, for example, resulted in the sampling of stations 3, 7, 11, and 15 and respective substations. For the second week, station 1, 2, or 4 was randomly selected. If number 2 was chosen, stations 2, 6, 10, and 14 and respective substations were sampled. This method continued until all 16 stations (64 substations) were sampled and the procedure was then again initiated for the next month. The tailrace station was sampled during every sampling routine. Sampling during winter was performed at about three week intervals.

Phytoplankton Collection

At each sampling substation, except the tailrace, a vertical column of water was obtained from the euphotic zone (depth where light intensity is 1% of surface light intensity). The water column was obtained by lowering weighted transparent polyethylene tubing (2.5 cm, inside diameter) to the bottom of the euphotic zone. The upper end of the tubing was then stoppered and the submerged end pulled to the surface by an attached rope. At all lake substations, a double tube was utilized to provide replicates for determination of sampling error. At the tailrace station, two containers were lowered to obtain individual 4 liter samples.

Phytoplankton Enumeration

Water samples were preserved in a solution of 4% neutralized formalin and centrifuged with a continuous flow centrifuge at a rate of one liter per eight minutes. Enumeration consisted of measurement of number and surface area of all phytoplankters viewed through an inverted microscope. For each water sample, ten microscope fields in each of two Sedgewick-Rafter counting cells were viewed. Individual phytoplankters and colonies were included in the count if they crossed the top or left-hand edges of a Whippel eyepiece grid; those crossing the bottom or right-hand edges were excluded. Concentration of organisms in the Sedgewick-Rafter cells was adjusted to levels suggested by McAlice (1971) to increase statistical reliability of enumeration.

Chlorophyll a Analysis

A half liter of water was immediately removed from each sample and placed on ice. The method of chlorophyll *a* analysis was that used by Strickland and Parsons (1968).

Interpretation of Phytoplankton Measurements

Phytoplankton enumeration and chlorophyll *a* analysis yielded several estimates of phytoplankton in the euphotic zone and discharge water: (1) number of phytoplankters per liter; (2) areal units of phytoplankters per liter; (3) average cell size (surface area) of phytoplankters in each sample; and (4) chlorophyll *a* concentration in mg/m³.

Number of phytoplankters per liter is often considered one of the best estimates of phytoplankton standing crop (Findenegg, 1969; Welch, 1948), but overall estimates of mixed populations in such units as individuals/liter may be misleading if the nature of the individuals is not explained (cells, filaments, or colonies) (Lund and Talling, 1957). To partially alleviate this problem, surface area measurements were made of all phytoplankters. Total cell surface has been shown to be highly correlated with photosynthetic rate ($r = 0.74$ as compared to $r = 0.45$ for number and $r = 0.62$ for cell volume) (Paasche, 1960).

The third measurement, cell size, may reflect stage of growth in phytoplankton. Since surface development controls absorption phenomena, estimates of population in terms of cell surface relate to production rate (Paasche, 1960). Fogg (1965) found, as one might expect from surface/volume ratio, small phytoplankters are more active per unit mass of cell material than larger ones.

The common chemical method for estimating living plant matter in the particulate organic part of water is to determine characteristic plant pigments. Unfortunately the amount of organic substance associated with a given quantity of plant pigment is variable, depending on the particular phytoplankter and its condition. Total plant carbon is from 25 to 100 times the chlorophyll *a* estimate (Strickland and Parsons, 1968). Chlorophyll *a* is at least a gross indicator of quantity and quality of biomass and is used in this regard in this paper.

RESULTS

Rate of Water Discharge vs. Reservoir Phytoplankton

Simple linear regression was utilized to evaluate correlation between rate of water discharge and each of the following four phytoplankton population measurements: (1) number/liter; (2) areal units/liter; (3) average cell size; and (4) chlorophyll *a*. Number/liter and areal units/liter data were transformed to common logarithms.

Demarcation of the lake into four quadrants required a standard format for estimating the influence of water discharge on each quadrant. Phytoplankton in quadrant IV, 12 to 16 km uplake from the dam, had not been in the lake as long as those in quadrant I. To account for the difference of in-lake residence time, the time required to complete one lake turnover (water in the euphotic zone was assumed to move through the quadrants at a constant rate) prior to noon of the sampling date was determined from discharge records. For example, for a 28 day turnover period, average rate of water discharge of the 7 days (28/4) prior to noon of the sampling date was determined and used in the simple linear regression for quadrant IV. The average rate of water discharge of 14 days (2 X 28/4) was used for quadrant III. In a similar manner, average rate of water discharge to use for quadrants I and II were determined.

The most striking relationship between rate of water discharge and phytoplankton number/liter occurred during summer (Table 1). An inverse relationship exists and, with the exception of quadrant IV, is significant at all locations. With the influence of quadrants removed (total lake), a significant inverse relationship still exists for summer. No relationship between rate of water discharge and phytoplankton number/liter was detected during autumn. Regression analysis shows that about 11% of the spring variation in number/liter for the total lake can be accounted for by the rate of water discharge. During winter, a positive correlation between rate of water discharge and number/liter for the entire lake was indicated. Smaller sample size during winter required the correlation coefficients to be larger than during other seasons to reach significance. Inverse correlations were greatest between rate of water discharge and phytoplankton areal units/liter during summer (Table 2). Starting with the highly significant inverse correlation in quadrant I ($r^2 = .64$), the inverse relationship generally decreases in uplake direction.

Correlations between rate of water discharge and average phytoplankton cell size show no relationship in spring and autumn (Table 3). Cell size had a relatively high negative correlation with rate of water discharge in quadrants I and II during winter, different from the relationship between rate of water discharge and number/liter and areal units/liter. This difference is also reflected by the correlation coefficient of -.38 obtained when the quadrant factor was excluded by using data from the entire lake.

Correlations between rate of water discharge and chlorophyll *a* are not significant during spring and autumn, nor does it appear that the inverse relationship increases as the location uplake increases (Table 4). While summer data show a significant relationship at all quadrants and the entire lake, no significant relationship exists in winter.

Rate of Water Discharge vs. Rate of Phytoplankton Discharge

Multiple regression analysis was used to clarify results from simple regression analysis. Simple linear regression would only indicate if rate of water discharge had an effect on reservoir phytoplankton populations. Multiple regression could indicate if the effect was due to increased physical removal of phytoplankton from the reservoir by increased rates of water discharge, or perhaps to some indirect effect. Number/liter, areal units/liter, and average cell size of phytoplankton in the tail-race (discharge) water were used as dependent variables in multiple regression analyses (Table 5). Independent variables were rate of water discharge and selected reservoir phytoplankton population measurements.

When reservoir phytoplankton data from only station I was used in multiple regression, the coefficient of determination, R^2 , for each discharge phytoplankton estimate was higher than R^2 values resulting from the use of reservoir phytoplankton data of all four stations in quadrant I. An additional 18-29% of the variation in the dependent variable was explained when reservoir phytoplankton measurements were those from only station I.

A comparison of standard partial regression coefficients indicates the relative importance of the independent variables since each standard partial regression coefficient is independent of the original units of measurement (Steel and Torrie, 1960). Standard regression coefficients show that the importance of rate of water discharge was considerably reduced when reservoir phytoplankton measurements of all stations in quadrant I were used. The rate of water discharge was generally as important as the remaining variable when station I phytoplankton measurements were used in the regression.

Effect of Lake Location on Phytoplankton

A 4 X 4 factorial analysis, with sampling days treated as blocks to remove the influence of time, was used to evaluate effect of lake location on phytoplankton populations. One factor was substation (shoreline to shoreline location); the other was quadrant. Analysis of variance F values for differences in quadrant measurements were: (1) number/liter ($P < 0.02$); (2) areal units/liter ($P < 0.01$); (3) average cell size ($P < 0.01$); and (4) chlorophyll *a* measurements ($P < 0.07$). Only chlorophyll *a* measurements showed significant ($P < 0.02$) differences due to substation location. None of the interactions were significant. Duncan's new multiple-range test was used to determine which quadrants and substations were significantly different (Table 6).

DISCUSSION

The following results should be considered in interpreting the total impact of reservoir discharge on phytoplankton: (1) increased rate of discharge did increase the amount of phytoplankton removed from the reservoir; (2) rate of water discharge had less effect on removal of reservoir phytoplankton from locations further uplake; and (3) increase in rate of water discharge had an adverse effect on reservoir phytoplankton populations during spring and summer.

If the adverse effect of discharge was only due to removal of phytoplankton, the expected result, based on average seasonal rate of discharge (summer -

80,000 cubic feet per second/hour (CFSH); autumn - 86,000 CFSH; winter - 110,000 CFSH; and spring - 123,000 CFSH), would be most adverse in the spring, lowest in summer, and intermediate in autumn and winter. Since this relationship did not occur, the adverse effect of rate of water discharge on phytoplankton populations must be partially due to another factor.

During summer, the metalimnion prevents movement of nutrients from the hypolimnion to the epilimnion, which possibly caused the Claytor Lake phytoplankton populations to be limited by nutrient levels. This is indicated by a reduction in phytoplankton populations, primarily *Asterionella*, *Tabellaria*, and *Melosira*, following a spring pulse. Fogg (1965) reported that final phytoplankton standing crop is sometimes roughly proportional to the initial amount of a limiting nutrient and a deficiency of a mineral nutrient may be one of the most important factors causing cessation of spring growth. Clear instances of this are few, but Lund (1950) did show this to be the case for *Asterionella*. Autumn and winter phytoplankton populations are usually not limited by nutrient levels (Fogg, 1965; Findenegg, 1965).

If nutrients were limiting spring and summer phytoplankton abundances, the inverse relationship of rate of water discharge and reservoir phytoplankton population levels during spring and summer may have been partially due to the effect of rate of water discharge on nutrient levels. Increased rate of water discharge would perhaps cause greater removal and dilution of reservoir nutrients. Large amounts of phytoplankton in the increased water discharge also results in loss of nutrients available to normal lake recycling mechanisms. Removal of additional nutrients due to increased rate of water discharge would have a deleterious effect on phytoplankton populations limited by nutrient supply. Phytoplankton populations, probably not limited by nutrient levels (autumn and winter), generally showed no inverse relationship even though influenced by higher discharge rates.

Results of the analysis of variance indicate that all phytoplankton measurements except chlorophyll *a* had highest average values in quadrant I. Simple linear regression showed that rate of water discharge generally had the greatest adverse effect on phytoplankton populations in quadrant I. Higher standing crops would more likely be limited by nutrient supply and increased removal of phytoplankton and nutrients would be deleterious. Highest standing crop values in quadrant I were probably due to decreasing turbidity (resulting in greater euphotic zone depth) and increasing availability of dissolved or particulate nutrient forms in the downlake direction.

During spring, the inverse relationship between rate of water discharge and three of the phytoplankton measurements appeared to increase in the uplake direction. This is in opposition to the relationships of other seasons when either no relationship was evident or the inverse relationship decreased with uplake location. The latter relationship might be expected since effect of rate of water discharge on the amount of phytoplankton discharged decreased in the uplake direction. One possible explanation of increasing inverse relationships in the uplake direction during spring is that the rate of water discharge in Claytor Lake is not only dependent upon hydroelectric needs, but also on rate of water inflow. Infusion of relatively cold river water from increased inflow would be reflected in discharge rate and have a negative effect on the developing spring phytoplankton population. The negative effect would decrease rapidly as inflow water was mixed with warmer downlake water or dropped below the euphotic zone.

In conclusion, results from the various analyses indicate that the adverse effect of rate of water discharge on reservoir phytoplankton populations is due to direct and indirect causes. Rate of water discharge has a direct effect because, as it increases, larger amounts of phytoplankton are removed from the reservoir.

Rate of water discharge may also have an indirect effect because it could affect some other factor, such as nutrient levels, which may limit reservoir phytoplankton populations.

ACKNOWLEDGMENTS

This project was funded by the Virginia Commission of Game and Inland Fisheries. Raymond V. Corning and Kenneth B. Cumming assisted with project planning and design.

Table 1. Correlation coefficients between rate of water discharge and phytoplankton (number/liter) as influenced by season and location in Claytor Lake.

Time Period	Location				
	Quadrant I	Quadrant II	Quadrant III	Quadrant IV	Entire Lake
Spring	.19	-.34	-.49	-.51	-.34*
Summer	-.76***	-.55*	-.64**	-.39	-.46***
Autumn	-.24	.07	.01	-.13	-.06
Winter	.61	.48	-.23	.78	.45*
Year	-.26	-.22	-.22	-.06	-.16*

*Significant at $\alpha = 0.10$

**Significant at $\alpha = 0.05$

***Significant at $\alpha = 0.01$

Table 2. Correlation coefficients between rate of water discharge and phytoplankton (areal units/liter) as influenced by season and location in Claytor Lake.

Time Period	Location				
	Quadrant I	Quadrant II	Quadrant III	Quadrant IV	Entire Lake
Spring	.30	-.26	-.58	-.45	-.29*
Summer	-.80***	-.69**	-.69**	-.50	-.55**
Autumn	-.19	-.05	.05	-.06	-.05
Winter	.32	.02	-.29	.70	.22
Year	-.32*	-.35*	-.38*	-.17	-.27***

*Significant at $\alpha = 0.10$

**Significant at $\alpha = 0.05$

***Significant at $\alpha = 0.01$

Table 3. Correlation coefficients between rate of water discharge and phytoplankton (average cell size) as influenced by season and location in Claytor Lake.

Time Period	Location				
	Quadrant I	Quadrant II	Quadrant III	Quadrant IV	Entire Lake
Spring	.39	.09	-.39	.33	.09
Summer	-.64*	-.64*	-.57	-.42	-.46**
Autumn	-.22	-.29	.01	-.05	-.12
Winter	-.85*	-.77	-.07	-.15	-.38*
Year	-.35*	-.34	-.37**	-.21	-.28***

*Significant at $\alpha = 0.10$
 **Significant at $\alpha = 0.05$
 ***Significant at $\alpha = 0.01$

Table 4. Correlation coefficients between rate of water discharge and phytoplankton (chlorophyll *a*) as influenced by season and location in Claytor Lake.

Time Period	Location				
	Quadrant I	Quadrant II	Quadrant III	Quadrant IV	Entire Lake
Spring	.34	.10	-.41	-.51	-.06
Summer	-.73**	-.65**	-.64*	-.68**	-.62***
Autumn	-.45	.02	.28	-.11	-.03
Winter	-.50	-.49	.13	.28	-.23
Year	-.34*	-.17	-.31*	-.34*	-.28***

*Significant at $\alpha = 0.10$
 **Significant at $\alpha = 0.05$
 ***Significant at $\alpha = 0.01$

Table 5. Multiple regression analysis relating discharge phytoplankton measurements to rate of water discharge and selected reservoir phytoplankton measurements. Lake location was included as an independent variable by using reservoir phytoplankton measurements from station I and quadrant I (stations 1-4) in two multiple regression analyses.

Dependent variable	Constant for model	Independent variables	Regression coefficients	Standard partial regression coefficients	R ²
Number/liter in discharge	0.5869	Number/liter at station I	0.7545	.780	.75
		Rate of water discharge	0.00000304	.629	0.06
Number/liter in discharge	1.2480	Number/liter at quadrant I stations	0.7078	.743	.50
		Rate of water discharge	0.00000102	.158	0.01
Areal units/liter in discharge	0.9916	Areal units/liter at station I	0.7171	.676	.78
		Rate of water discharge	0.00000251	.667	0.05
Areal units/liter in discharge	1.4632	Areal units/liter at quadrant I stations	0.6722	.850	.64
		Rate of water discharge	0.00000135	.273	0.01

Average cell size in discharge	-0.3955	Average cell size at station 1	.980	.78	0.05
		Rate of water discharge	.404	---	---
			0.00000228		
Average cell size in discharge	0.0798	Average cell size at quadrant 1 stations	.703	.49	0.01
		Rate of water discharge	.009	---	---
			0.00000007		

Table 6. Multiple-range test of effect of lake location on phytoplankton measurements in Claytor Lake. Underlined values are not significantly different at $\alpha = 0.05$.

Phytoplankton measurement	Factor (Location)	Level (Mean)
Number/liter	Quadrant	I(5.78) IV(5.73) II(5.71) III(5.71)
Areal units/liter	Quadrant	I(5.55) II(5.47) IV(5.46) III(5.44)
Average cell size	Quadrant	I(.72) II(.69) III(.62) IV(.60)
Chlorophyll a	Quadrant	IV(12.96) I(11.55) III(11.40) II(11.33)
Chlorophyll a	Substation	D(12.92) C(11.75) B(11.47) A(11.09)

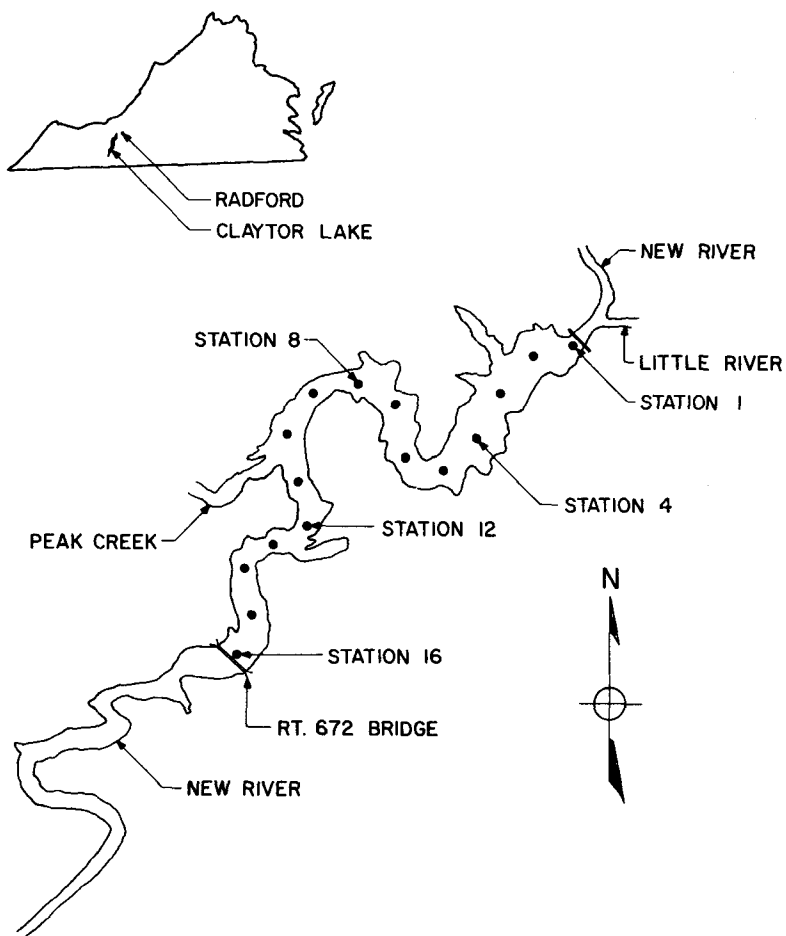


Figure 1. Claytor Lake, Virginia, showing location of sampling stations.

LITERATURE CITED

- Axelson, J. 1961. Zooplankton and impoundment of two lakes in Northern Sweden (Ransaren and Kuttsson). Rept. Inst. Freshwater Res. Drottningholm. 42:84-168.
- Benson, N. G., and B. C. Cowell. 1967. The environment and plankton density in Missouri River reservoirs. p. 358-373. In: Reservoir Fishery Resources Symposium. Reservoir Committee of the Southern Division, Amer. Fish. Soc., University of Georgia, Athens.
- Brook, A. J., and W. B. Woodward. 1956. Some observations of the effect of water inflow and outflow on the plankton of small lakes. *J. Animal Ecol.* 25:22-35.

- Bureau of Sport Fisheries and Wildlife. 1971. 1970 national survey of fishing and hunting. Resource Publication No. 95. 108 p.
- Cowell, B. C. 1967. The Copepoda and Cladocera of a Missouri River reservoir: a comparison of sampling in the reservoir and the discharge. *Limnol. Oceanogr.* 12:125-136.
- Findenegg, I. 1965. Factors controlling primary productivity, especially with regard to water replenishment, stratification, and mixing. p. 105-119. In: C. R. Goldman (ed.), Primary productivity in aquatic environments. Mem. Ist. Ital. Idrobiol., 18 Suppl., University of California Press, Berkeley.
- Findenegg, I. 1969. Expressions of populations. p. 16-17. In: R. A. Vollenweider (ed.), A manual on methods for measuring primary productivity in aquatic environments. IPB Handbook No. 12. Blackwell Scientific Publications, Oxford and Edinburgh.
- Fogg, G. E. 1965. Algal cultures and phytoplankton ecology. University of Wisconsin Press, Madison. 126 p.
- Funk, W. H., and A. R. Gaufin. 1971. Phytoplankton productivity in a Wyoming cooling-water reservoir. p. 167-178. In: G. E. Hall (ed.), Reservoir fisheries and limnology. Spec. Publ. No. 5, Amer. Fish. Soc., Washington, D.C.
- Jenkins, R. M. 1967. The influence of some environmental factors on standing crop of fishes in U.S. reservoirs. p. 298-321. In: Reservoir Fishery Resources Symposium. Reservoir Committee of the Southern Division. Amer. Fish. Soc., University of Georgia, Athens.
- Johnson, W. E. 1964. Quantitative aspects of the pelagic, entomostracan zooplankton of a multibasin lake system over a 6-year period. *Verhandl. Intern. Ver. Limnol.* 15:727-734.
- Lund, J. W. G. 1950. Studies on *Asterionella formosa* Hass. II. Nutrient depletion and the spring maximum. *J. Ecol.* 38:1-14, 15-35.
- Lund, J. W. G., and J. F. Talling. 1957. Botanical limnological methods with special reference to the algae. *Bot. Rev.* 23:1-12.
- McAlice, B. J. 1971. Phytoplankton sampling with the Sedgewick-Rafter cell. *Limnol. Oceanogr.* 16:19-28.
- Paasche, E. 1960. On the relationship between primary production and standing stock of phytoplankton. *J. Cons. Int. Explor. Mer.* 26:33-48.
- Rodhe, W. 1964. Effects of impoundment on water chemistry and plankton in Lake Ransaren (Swedish Lapland). *Verhandl. Intern. Ver. Limnol.* 15:437-443.
- Ruttner, F. 1963. Fundamentals of limnology. 3rd ed. University of Toronto Press, Toronto. 295 p.
- Stanberry, F. W. 1967. Future role of reservoirs in state fisheries management programs. p. 21-25. In: Reservoir Fishery Resources Symposium. Reservoir Committee of the Southern Division, Amer. Fish. Soc. University of Georgia, Athens.
- Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, N. Y. 481 p.
- Strickland, J. D. H., and T. R. Parsons. 1968. A practical handbook of seawater analysis. *Bull. 167 Fish. Res. Bd. Canada*, 1961. 311 p.
- Tonolli, V. 1961. The migration currents of zooplankton organisms of small lakes. *Verhandl. Intern. Ver. Limnol.* 12:412-420.
- Van Landingham, S. L. 1964. Some physical and generic aspects of fluctuations in non-marine plankton diatom populations. *Bot. Rev.* 30:437-478.
- Welch, P. S. 1948. Limnology. McGraw-Hill, N. Y. 381 p.