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LONG-TERM CHANGES IN ZOOPLANKTON SPECIES COMPOSITION AND SELECTED PHYSICOCHEMICAL PARAMETERS IN WOODS RESERVOIR, TENNESSEE

James L. Elmore
University of South Florida
Tampa, Florida 33620
and
Dewey L. Bunting
University of Tennessee
Knoxville, Tennessee 37916

Abstract

In 1972-73 zooplankton and physicochemical data were collected from Woods Reservoir, a 20 year-old impoundment on the Elk River, Franklin County, Tennessee. These data were compared with Yeatman's (1956) on the same reservoir shortly after impoundment in 1953-54.

Over the 19-year period transparency and dissolved oxygen of surface water increased, whereas total alkalinity and hardness declined. This was attributed to decomposition and leaching being more prevalent in the newly formed reservoir.

Several changes were noted in the zooplankton composition of the impoundment. All genera of rotifers present in Yeatman's study also were found in 1972-73, plus five additional limnetic genera were encountered. Four new species of limnetic Cladocera were identified, but *Daphnia pulex* apparently disappeared. This disappearance was attributed either to taxonomic problems or size selective predation. With the exception of *Mesocyclops leuckarti*, all limnetic copepods found in the 1953-54 study were found in 1972-73. This apparent extinction may have been due to competition with the closely related *Mesocyclops edax* now prevalent in the reservoir.

The majority of the changes in the zooplankton community seemed to be caused simply by introduction of new species, in most cases without exclusion of species already present. The speed of colonization was rapid with 73% of the taxa occurring in both studies. The structure of the copepod assemblage seemed to stabilize quickly, whereas the cladocerans and rotifers showed continued additions. It was proposed that this lag may have been due to the distance of dispersal from source populations.

Introduction

Temporal changes in the species composition of the limnetic zooplankton community of natural lakes have been the interest of many publications (e.g., Brooks and Dodson, 1965; Smyly, 1972; Edmondson, 1969; Zyblut, 1970; McNaught and Buzzard, 1973; and Richards, Goldman, Frantz and Wickwire, 1975). However, relatively little information is available on long-term changes in this community in man-made lakes (Murphy, 1962 and Luferova and Monakov, 1966). This is unfortunate since reservoirs are becoming increasingly prevalent structures in many areas (Jenkins, 1964). Moreover, it is often possible to study these bodies of water from their construction, which is usually not the case with natural lakes.

From June, 1953, to November, 1954, the plankton development in Woods Reservoir, Franklin County, Tennessee, was studied by Yeatman (1956). His paper presented an excellent opportunity to study the physicochemical and zooplankton composition changes in a reservoir. Since the original study was performed only on the part of the reservoir below Morris Ferry Bridge, our investigation was restricted to that area.

Woods Reservoir was constructed on the Elk River by Arnold Engineering Development Center as a source of water to cool wind tunnels. It first reached full-pool level in the winter of 1952-53 (Benson, 1959). It has a maximum depth of about 20 m at full-pool and an area of 1620 ha. Most of the reservoir above Morris Ferry Bridge is less than 1.5 m deep except for the area of the old river channel. The center-line of the penstock is located at an elevation of 275 m, creating a hypolimnetic discharge during stratification. This impoundment is different from most others in Tennessee in that it was not built for flood control, navigation or power.

Materials and Methods

Several physical and chemical aspects of the water were determined monthly in July and August, 1972, and January through May, 1973. The transparency of the water was measured with a 62 cm, all-white Secchi Disc. Temperature profiles were established with a thermistor. A Van-Dorn Bottle was used to collect water from various depths and a Hach Kit (Hach Chemical Company, Ames, Iowa) was utilized for chemical determinations, i.e., dissolved oxygen, pH, alkalinity and hardness.

Eight plankton sampling stations were chosen in the reservoir and monthly samples were taken from June, 1972, to May, 1973 (exclusive of December). A centrifugal plankton pump was used from June through August and a Clark-Bumpus Plankton Sampler was utilized from September through May. Details of sampling procedures may be found in Elmore (1973).

Quantitative plankton samples were preserved in a 10% formalin solution and a live sample was taken on each sampling date in case there were soft-bodied forms present which could not be identified after fixation. An extensive qualitative survey was carried out for each sampling date before quantification was attempted. Estimations of population densities were determined either by making total counts of the organisms in a sample or by counting all of the animals in two to five 1-ml subsamples.

Rotifer genera were identified with Edmondson (1959) and most rotifer species were determined using Voigt (1956, 1957).

Other taxonomic references for the rotifer species were: Ahlstrom (1940) for *Brachionus* and *Platyias*, Ahlstrom (1943) for *Keratella* and Bartos (1948) for *Hexarthra*. Other taxonomic references used were: Brunson (1959) for the Gastrotrich, Brooks (1957) for *Daphnia*, Deevey and Deevey (1971) for *Eubosmina*, Brooks (1959) for all other cladoceran species, Wilson (1959) for calanoid copepods, Yeatman (1959) for cyclopoid copepods, Wilson and Yeatman (1959) for the harpacticoid copepod and Cook (1956) for *Chaoborus*.

Results

Physicochemical Data

The physicochemical data collected in 1972 are compared to the 1954 data in Table 1. Water transparency was greater in 1972 than in 1954. The differences in the values may have been due to differences in acuity of vision and/or technique of the researchers. However, a reading of 3.4 m recorded by Yeatman (unpublished data) in August, 1969, was found to be considerably greater than any recorded in his original study.

The values for dissolved oxygen in surface water were low in 1954 compared to 1972. Surface water pH was slightly higher in 1972 but this factor can vary greatly over a short period of time. Temperature, total alkalinity and total hardness of surface water were greater in 1954. Phenopthalein alkalinity was detected twice in 1954, whereas none was found in 1972. Magnesium hardness was greater in 1972. Additional physical and chemical data for 1972-73 may be found in Elmore (1973).

Zooplankton Data

Since taxonomy tends to change with time, revisions must be made before comparisons can be attempted in a study of this type. The *Daphnia* reported as *Daphnia longispina galeata* in Yeatman's study is now called *Daphnia ambigua* (Brooks, 1957 and Yeatman, personal communication). *Diaphanosoma brachyurum* was reported in the 1953-54 study, but *Diaphanosoma leuchtenbergianum* is a more recent name for the limnetic species of the genus. Since the genus *Bosmina* was reworked by Deevey and Deevey (1971), little can be said about species changes in this taxon and it is assumed that the species present is the same as in the original study. *Pedalia* reported in the 1953-54 investigation is now referred to as *Hexarthra* (Hemming, 1955 in Edmondson, 1959).

Yeatman (1956) used Pennak (1953) for determination of the rotifers and *Chaoborus*. Since the keys in this reference result in generic determinations, only genera could be compared in these taxa. In all other groups, comparisons are made at the species level.

Seasonal quantitative zooplankton data for the 1972-73 study may be found in Elmore (1973). Taxa collected during both studies are compared in Table 2.

Forty-five species of rotifers were collected during the 1972-73 study. Of this number, 32 have been reported to be limnetic. All of the genera of rotifers collected in 1953-54 were found in 1972-73. In addition, seven new genera were encountered, of which all but two have been reported to be primarily limnetic.

Seventeen species of cladocerans (eight limnetic) were found during this study, whereas only six species (five limnetic) were reported in 1953-54. *Daphnia pulex* disappeared by 1972, and *Daphnia parvula*, *Daphnia retrocurva*, *Daphnia galeata mendotae* and *Leptodora kindtii* found their way into the impoundment and established populations.

Twelve species of copepods (six limnetic) were encountered during the recent study, whereas nine species (seven limnetic) were found in the 1953-54 investigation. All limnetic species present in 1953-54 were collected in this study, except *Mesocyclops leuckarti*.

Chaoborus was collected in both studies. *Neogossea*, a gastrotrich, was found only in 1972.

Many more species of benthic Crustacea were collected in 1972-73 than in 1953-54. This may have been due to differences in sampling techniques, as the 1972-73 samples were collected using an oblique tow which often started near the bottom at the shallower stations.

Discussion

Physicochemical changes similar to those which occurred in Woods Reservoir have been noted in other reservoirs which were studied for several years after impoundment. The Dnieper Reservoir, Russia, was constructed in 1934 and low oxygen conditions were present for its first two years of existence due to decompo-

TABLE 1. *Summer physical and chemical parameters of Woods Reservoir limnetic surface water, 1954 and 1972.*

Parameter	31 July 1954[a]	4 Aug 1954	21 Aug 1954	8 July 1972	5 Aug 1972
Secchi Disc					
Transparency (m)	2.7	2.4	2.4	—	3.2
Oxygen (mg/1)	5.5	5.3	3.5	7.0	7.0
pH	8.4	8.2	8.0	8.6	8.4
Temperature (°C)	31.8	30.5	30.5	27.5	28.0
Phenopthalein					
Alkalinity (mg/1 $CaCO_3$)	0.0	—	8.0	0.0	0.0
Total Alkalinity					
(mg/1 $CaCO_3$)	96.0	—	85.8	70.0	75.0
Calcium (mg/1 $CaCO_3$)	—	—	265.0		—
				75.0[b]	
Magnesium (mg/1 $CaCO_3$)	—	—	4.9		

[a] = all 1954 data from Yeatman (1956)
[b] = total hardness

TABLE 2. *Zooplankton of Woods Reservoir in 1953-54 and 1972-73.*

Zooplankter	1953-54	1972-73 (yearly mean, no./m^3)
Rotifera:		
Brachionus Pallas	X	70
Euchlanis Ehrenberg*	X	2
Kellicottia Ahlstrom	X	15
Keratella Bory de St. Vincent	X	22908
Platyias Harring	X	9
Trichotria Bory de St. Vincent*	O	16
Lecane Nitzsch	X	14
Monostyla Ehrenberg*	O	7
Trichocerca Lamarck	X	93
Gastropus Imhof	O	80
Asplanchna Gosse	X	717
Ploesoma Herrick	O	543
Polyarthra Ehrenberg	X	8540
Synchaeta Ehrenberg	O	10690
Filinia Bory de St. Vincent	X	30
Hexarthra Schmarda	X	13
Sinantherina Bory de St. Vincent	O	36
Conochiloides Hlava	X	209
Conochilus Hlava	X	458
Collotheca Harring	O	8
Cladocera:		
Leptodora kindtii (Focke)	O	53
Sida crystallina (O. F. Müller)*	O	T
Latona setifer (O. F. Müller)*	O	T
Diaphanosoma leuchtenbergianum Fischer	X	302
Daphnia ambigua Scourfield	X	T
Daphnia pulex Leydig emend. Richard	X	0
Daphnia parvula Fordyce	O	878
Daphnia retrocurva Forbes	O	543
Daphnia galeata Sars *mendotae* Birge	O	1091
Simocephalus serrulatus (Koch)*	O	T
Ceriodaphnia quadrangula (O. F. Müller)	X	67
Bosmina Baird or *Eubosmina* Seligo	X	1318
Eurycercus lamellatus (O. F. Müller)*	O	T
Camptocercus rectirostris Schødler*	O	T
Alona guttata Sars*	O	T
Alona rectangula Sars*	O	5
Leydigia quadrangularis (Leydig)*	O	2
Pleuroxus denticulatus Birge*	X	0
Chydorus sphaericus (O. F. Müller)*	X	13
Copepoda:		
Onychodiaptomus sanguineus (*S. A. Forbes*)	X	18
Skistodiaptomus pallidus (Herrick)	X	450
Skistodiaptomus reighardi (Marsh)	X	557
Mesocyclops edax (S. A. Forbes)	X	548
Mesocyclops leuckarti (Claus)	X	0
Cyclops vernalis Fischer	X	T
Cyclops thomasi (S. A. Forbes)	X	232
Paracyclops fimbriatus poppei (Rehberg)*	O	T
Tropocyclops prasinus (Fischer)	X	11
Eucyclops prionophorus Kiefer*	O	T
Eucyclops speratus (Lilljeborg)*	O	T
Eucyclops agilis (Koch)*	O	T
Canthocamptus vagus Coker and Morgan*	O	T
Miscellaneous:		
Neogossea Remane	O	31
Chaoborus Lichtenstein	X	T

* = not limnetic species
X = present
O = absent
T = less than one organism per cubic meter

sition of flooded organic matter (Frey, 1968). Two years after Garrison Reservoir was constructed on the Missouri River, bed-element solutes added 10 ppm to the annual average alkalinity and 14 ppm to annual average hardness (Neel, 1966). These two parameters then declined below inflow levels three years later.

The above explanations are probably applicable to Woods Reservoir. Since the reservoir reached full-pool level for the first time in the winter of 1952-53 (Benson, 1959), the 1954 data were taken approximately 1.5 years after impoundment. Microbial activity could have still been dominant, thus producing a low oxygen condition in conjunction with possibly a slightly higher temperature and lower transparency. Bedrock would probably have still been exposed at this time, resulting in leaching of ions into the water and increased alkalinity and hardness. As the years went by, the organic material was broken down and carried downstream. The exposed bedrock was covered by sediment and the leached ions carried away. These actions would result in a decrease in alkalinity and hardness, and increases in transparency and dissolved oxygen.

The changes in zooplankton species composition are

not as easy to explain as the physicochemical data because of changes in taxonomy and unequal degrees of thoroughness of different investigators. Even considering these problems, there seemed to be some real changes which could be discerned. Of the five genera of limnetic rotifers found only in the 1972-73 study, three were in the reservoir for more than one sampling period. Of these three, *Synchaeta* and *Ploesoma* were found in considerable densities. Thus, it is probably reasonable to say that several genera of rotifers have become established in Woods Reservoir in addition to the ones originally found. Murphy's (1962) data on the plankton development in the newly formed Lake Meredith seem to corroborate these findings. Thus, for rotifers, the new environment of a reservoir contains many microhabitats. Some are filled immediately with persistent genera, whereas others are gradually filled over the years with little loss of the original genera.

The limnetic cladocerans exhibited a pattern similar to the rotifers with the exception of the loss of *Daphnia pulex*. There are at least two possible explanations of this apparent extinction. It could have been misidentified, as our specimens determined with the use of Brooks (1957) to be *Daphnia parvula* keyed out to *D. pulex* in the reference used in the 1953-54 study, i.e., Pennak (1953). If *D. pulex* were actually present in the impoundment, it could have been eliminated by size selective predation. Galbraith (1966) found that *D. pulex* was replaced by *Daphnia galeata* and *Daphnia retrocurva* because of size selective predation by *Salmo gairdneri*. Hall (1964) observed that adult cisco (*Leucicythys atredi*) and black crappie (*Pomoxis nigromaculatus*) consumed the larger *D. pulex* but not the smaller *D. galeata mendotae*.

Until the threadfin shad (*Dorosoma petenense*) was introduced in 1955, there were no forage species that regularly inhabited the limnetic zone in Woods Reservoir (Benson, 1959). This species is known to be a voracious planktivore (Applegate and Mullan, 1969). White crappie (*Pomoxis annularis*) were also introduced in 1955. Black crappie were not present in either 1953 or 1956 (Benson, 1959), but they must have been introduced into the impoundment as a catch of fish was observed in the spring of 1973 composed of primarily black crappie.

The 1953-54 cladoceran species composition was comprised of species common to the area prior to impoundment. The species assemblage of Woods Reservoir in 1972-73 included both these species and others common to glaciated northern latitudes. This was essentially the same situation found in Bull Shoals Reservoir (Applegate and Mullan, 1969) and in many Tennessee Valley reservoirs (Bunting, 1970).

The copepods did not exhibit a colonization pattern similar to the rotifers and cladocerans. The same species present in the 1953-54 study were also present in 1972-73 with the exception of *Mesocyclops leuckarti*. Yeatman (1956) collected this species in the Elk River prior to completion of the Woods Reservoir dam. He also collected it in the reservoir during his 1953-54 study and in 1956 (Yeatman, personal communication). However, it was not found in several of his summer samples taken since 1956 and it probably no longer inhabits this impoundment. Perhaps this species was not able to compete with the closely related *Mesocyclops edax* which is now abundant in the reservoir.

One striking aspect of the data was the rapidity of colonization. A rough estimate of the speed of colonization was derived by comparing data collected from June to October in 1953, 1954 and 1972. Seventy-three percent of the total taxa found in 1972 was already present in 1954, including 75% of the rotifer genera, 67% of the cladoceran species and 125% of the copepod species. All of the species of copepods and cladocerans found in 1954 were present in 1953, whereas only 50% of the rotifer genera collected in 1954 were found in 1953. Therefore, the number of rotifer genera showed a relatively steady increase between 1953 and 1954 and between 1954 and 1972, whereas the number of cladoceran species showed no increase between 1953 and 1954 but did exhibit an increase between 1954 and 1972. The number of copepod species stabilized as the cladocerans did between 1953 and 1954, but a decrease occurred in 1972 due to the loss of *Mesocyclops leuckarti*.

The distance of dispersal has been suggested to be important in studies of island colonization (MacArthur and Wilson, 1967) and this factor appears to be significant in explaining the patterns of colonization in Woods Reservoir. The lag in species additions noted in the cladocerans may be explained by the long distances from source populations, since three of the new species found in 1972 are usually restricted to northern areas (Brooks 1957, 1959). These three species (*Leptodora kindtii, Daphnia retrocurva*, and *Daphnia galeata mendotae*) have been found in the southeastern United States only in recent years in man-made impoundments (Bunting, 1970). Since no reservoirs were in close proximity to Woods Reservoir during the period of colonization, it is reasonable to assume that introduction of these species would be slow. The same explanation may apply to some of the rotifers although it would be difficult to ascertain since only genera were compared in this group.

The persistence of the taxa once they had arrived was another outstanding feature of the data. Some studies have shown very little change in the species roster of the limetic zooplankton of lakes (Smyly, 1972; Edmondson, 1969 and Zyblut, 1970) and Murphy (1962) and Luferova and Monakov (1966) found that few species were lost during the colonization of two different reservoirs. Other investigations have shown large changes in species composition attributed either to predation, competition, eutrophication or a combination of these factors (Hrbácek, 1962; Brooks and Dodson, 1965; Wells, 1970; McNaught and Buzzard, 1973; Richards, Goldman, Frantz and Wickwire, 1975). Of the numerous taxa originally reported from Woods Reservoir, apparently only *Daphnia pulex* and *Mesocyclops leuckarti* were eliminated after 19 years. Indeed, this is a very slow rate of species turnover.

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