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THE ODONATA OF A NEW RESERVOIR IN THE SOUTHEASTERN UNITED STATES

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Lake Anna is a recent impoundment of the North Anna River in Virginia, USA. As part of a comprehensive ecological assessment the odonates were studied for 2 years prior to impoundment and 3 years following impoundment. Lake Anna was colonized immediately by odonates during the first summer after the river was impounded. After impoundment there was an initial reduction in the number of species present, but the diversity of odonates increased in subsequent years. The species composition of odonates in the reservoir was also quite different from that of the previous riverine ecosystem. Several obligate rheophilic species disappeared the first year after impoundment, but the reservoir was colonized by an early facultative or "pioneer" species. In succeeding years several additional or late facultative species became abundant, and several limnophilic species colonized the reservoir in significant numbers. From a review of the autecology of the species involved it appears that several physical factors determine the success of odonates during transition from a lotic to a lentic ecosystem: rate of flow, vegetation, and bottom composition.

INTRODUCTION

The few studies of new reservoirs in North America (most notably O'CONNELL & CAMPBELL, 1953; PATERSON & FERNANDO, 1969a, 1969b, 1970; AGGUS, 1971) have not included a detailed investigation of Odonata. The recent construction of a reservoir in the southeastern United States provided us with an opportunity to examine the faunas of a river and its subsequent impoundment. While our study included all macroinvertebrates, we placed special emphasis on Odonata for the following reasons: (1) in a given system it is possible to make species determinations of larvae; (2) many species have well-defined habitat requirements; and (3) their carnivorous habit makes them ecologically significant.

DESCRIPTION OF STUDY AREA

Lake Anna is a mainstream impoundment of the North Anna River, located in the Piedmont physiographic province of Virginia, USA (Fig. 1). The reservoir was built by Virginia Electric and Power Company to provide cooling water for a 4 million kilowatt nuclear-powered electricity generating facility. Several tributaries on the south side of the river were impounded separately from the main reservoir by earthen dikes to act as waste-heat treatment facilities or cooling lagoons. However, the power plant did not operate during this study. Lake Anna began filling in January 1972 and reached normal pool level by November 1972 – much sooner than expected because of heavy floods during the summer. Lake Anna is approximately 24 km long with a maximum depth at the dam of 24 m

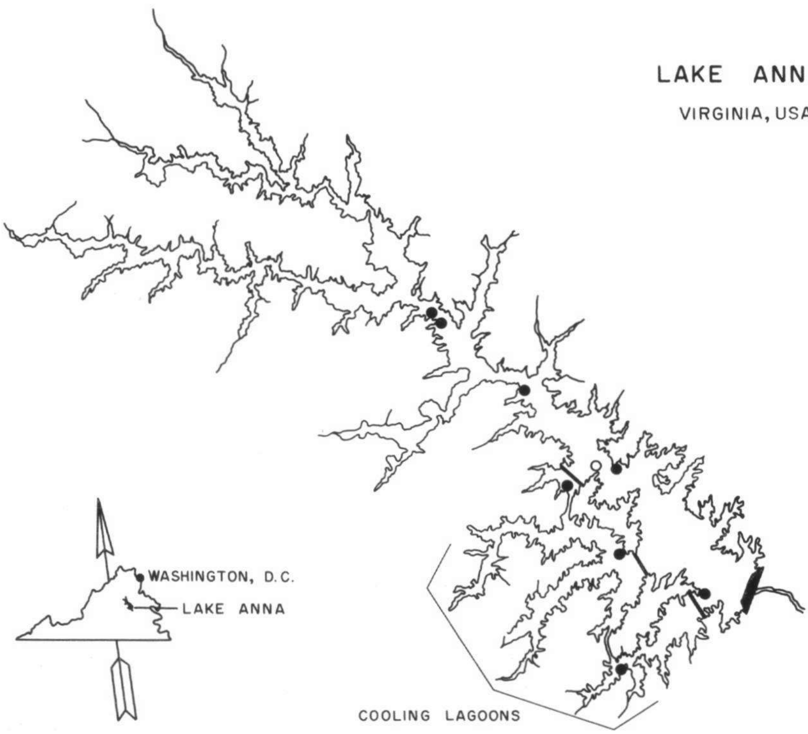

Fig. 1. Map of study area. Circles indicate post-impoundment sampling stations: open circle 1972-3; – dark circles 1973-4 and 1974-5. Inset, the state of Virginia showing the location of Lake Anna.

and mean depth of 7 m. The impounded section of the North Anna River was characteristic of the Piedmont physiographic province, having long stretches of slow-moving water with shifting sand bottom interspersed with riffles, logs, and accompanying leaf debris. The tributaries of the river were small woodland streams with a dense forest canopy. There was a history of acid-mine drainage in the pre-impoundment basin, but SIMMONS (1972a, 1972b) and SIMMONS & REED (1973) found that the insect fauna recovered very quickly below the source of pollution and was generally indicative of a "healthy" stream. Detailed morphometric data for the reservoir and a complete description of the pre-impoundment basin can be found in SIMMONS (1972a).

METHODS

From 1969 to 1971 we took bottom samples quarterly at several stations in the pre-impoundment basin, including both the North Anna River and its tributaries. Samples were taken with D-frame dip nets and equal effort was expended at each collection site. Post-impoundment sampling began in October 1972 when the reservoir was still approximately 3 m below normal pool level. In the reservoir we sampled macrobenthos by means of artificial substrates placed on the bottom and retrieved with SCUBA. In an evaluation of this method (VOSHELL & SIMMONS, 1977) we found that certain artificial substrate samplers placed on the bottom were preferable over traditional grab samplers for investigating changes in the shallow-water macrobenthos of a new reservoir. These artificial substrate samplers collected both sediment-inhabiting organisms and organisms requiring a firm substrate (herpobenthos and haptobenthos, respectively, of HUTCHINSON, 1967), thus, we felt they gave the most accurate representation of all organisms actually present in the reservoir. In the present study we used two different artificial substrate materials (3M Corporation's # 200 conservation web and leaves collected near the reservoir) placed separately in plastic baskets. A complete description of these materials and containers can be found in VOSHELL & SIMMONS (1977). For the first three years after impoundment we collected monthly replicates of each type of sampler from depths of 2 m, 4 m, and 7 m at several stations (Fig. 1). In addition we collected with D-frame dip nets from various habitats in shallow water (< 0.5 m) at each station. Species determinations of larvae were facilitated by collecting adults at each sampling site and by rearing larvae from artificial substrate samplers brought back to the laboratory.

RESULTS AND DISCUSSION

Before impoundment at least 16 species were present in the North Anna River and its tributaries (Tab. I). During the pre-impoundment study it was possible to identify some larvae only to the generic level. Based on recent surveys of adult odonates in other parts of the North Anna River, there could have been as

Table I

List of species collected

Species	Pre-impoundment 1969-1970		Post-impoundment		
	1969-1970		*1972-3*	*1973-4*	*1974-5*
	River	Tributaries			
Argia spp.	+	+			
A. apicalis (Say)				+	+
Enallagma spp.	+				
E. basidens Calvert				+	+
E. civile (Hagen)			+		
Ischnura sp.				+	+
Nehalennia sp.	+				
Calopteryx maculata (P. de Beauvois)		+			
Dromogomphus spinosus Selys	+	+			+
Hagenius brevistylus Selys	+			+	
Progomphus obscurus (Rambur)	+				
Aeshna sp.	+	+			
Anax sp.		+			
Boyeria vinosa (Say)	+	+			+
Cordulegaster maculatus Selys		+			
Macromia georgina (Selys)	+	+		+	+
Epitheca cynosura (Say)			+	+	+
E. princeps Hagen			+	+	+
Neurocordulia sp.		+			
Erythemis simplicicollis (Say)			+		
Ladona sp.		+			
Leucorrhinia frigida Hagen	+				
Pachydiplax longipennis (Burmeister)			+	+	
Perithemis tenera (Say)	+	+	+	+'	+
Totals	11	11	6	9	9
Number of species	*16*			*13*	

many as 24 species present before impoundment. Transition from a lotic to a lentic ecosystem caused a reduction in the number of species. In the first year after impoundment, 1972-3 (sampling years ran from one autumn to the next), only 6 species were collected. In the second and third years after impoundment, 9 species were collected each year, bringing the total number of species encountered after impoundment up to 13.

Since different sampling methods were used in the study, the abundance of each species is presented as a percentage of total odonates (Fig. 2). In the North Anna River the dominant odonates were *Progomphus obscurus* (56%) and *Macromia georgina* (19%). In the tributaries of the river, *Calopteryx maculata* (41%) and *Argia* spp. (37%) were most common. In the first year after impound-

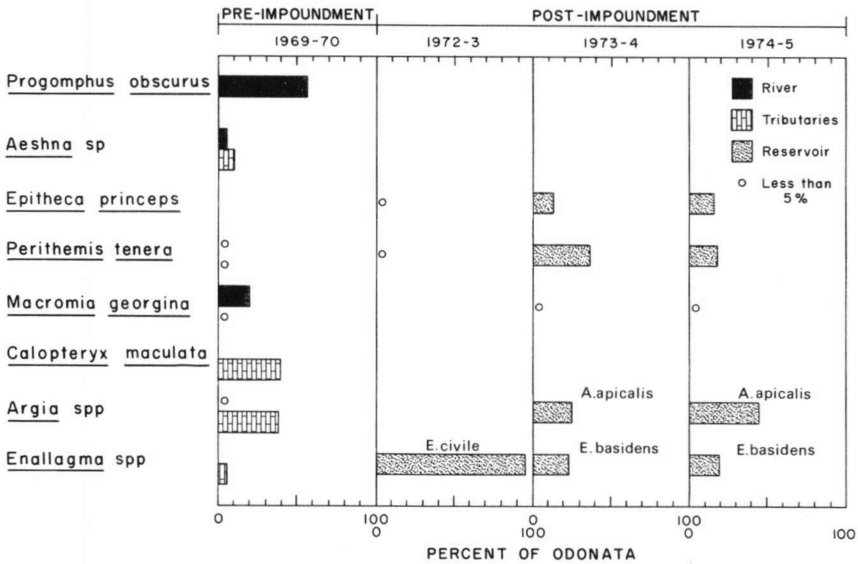

Fig. 2. Percent composition of dominant Odonata. The numbers are percent of total dragonflies, not total fauna.

ment a single species, *Enallagma civile*, accounted for 95% of all odonates collected in the reservoir. *E. civile* disappeared and other odonates became abundant in the second year after impoundment. *Perithemis tenera* was the most common (36%), but *Argia apicalis, Enallagma basidens*, and *Epitheca princeps* were also abundant (24%, 23%, and 12%, respectively). In the third year after impoundment, the same four species were most abundant, but the relative composition of the species changed considerably. *Argia apicalis* became the most common species, accounting for 45% of all odonates, while the other three species were 15% to 19% each.

PATERSON & FERNANDO (1969b) proposed a model for the colonization of a new reservoir which included three groups of aquatic insects: obligate rheophilic species, which never successfully colonized the reservoir; facultative species, which were the first colonizers; and limnophilic species, which appeared later. Our studies of the colonization of Lake Anna indicate that the species of odonates involved can also be placed in these same groups. However, our data indicate that the facultative group consists of distinct early and late species. Table II lists the species in each of these four groups. Those species for which only 1 or 2 specimens were collected are not included in Table II.

Since the autecology of many odonates is fairly well known, we can offer some explanation for the trends in colonization. WRIGHT (1943) listed ten physical parameters of aquatic habitats which affect the distribution of odonates:

Table II

Classification of species according to trends in colonization

Obligate rheophilic	Early facultative	Late facultative	Limnophilic
Calopteryx maculata	*Enallagma civile*	*Argia apicalis*	*Epitheca cynosura*
Cordulegaster maculatus		*Enallagma basidens*	*E. princeps*
Progomphus obscurus		*Dromogomphus spinosus*	
		Macromia georgina	
		Perithemis tenera	

Table III

Basic physical-chemical parameters after impoundment

Parameter	Depth (m)	1972-3	1973-4	1974-5
Temperature	2	3-28	6-27	3-29
(°C)	4	3-27	6-25	1-29
	7	3-20	6-21	1-21
Oxygen	2	6.3-12.5	6.0-13.0	5.9-14.4
(mg/l)	4	3.0-12.5	7.0-11.8	5.2-13.1
	7	0.2-12.6	0.0-11.3	0.4-12.8

(1) permanency, (2) size, (3) vegetation, (4) depth, (5) bottom composition, (6) rate of flow, (7) temperature, (8) pollution, (9) salinity, and (10) turbidity. Temperature and oxygen data for the post-impoundment years are presented in Table III, and similar data for the pre-impoundment period can be found in SIMMONS (1972a). At the depths where most odonate larvae were collected in the reservoir (2 m - 4 m), there was little difference between any of the pre- or post-impoundment years. Therefore, of the ten factors listed by Wright, 3, 5, and 6 appear to be the most significant with regard to the changes in the odonate fauna which occurred the first three years after impoundment.

Of the species we have included in the obligate rheophilic group, *Calopteryx maculata* and *Cordulegaster maculatus* are well known to occur only in lotic habitats. During our studies, *C. maculata* and *C. maculatus* were collected only in the tributaries of the North Anna River before impoundment. These small woodland streams fit the description of the preferred habitats given by NEEDHAM (1903) and WALKER (1953) for *C. maculata* – and by BYERS (1930) for *C. maculatus*. KENNEDY (1922) and WRIGHT (1943) suggested that the larvae restricted to streams are those odonates with a primitive respiratory apparatus able to survive only under the best aerated conditions. The shade which usually accompanies small streams is also an important factor not found in man-made lakes. The third species which we have listed as obligate rheophilic, *Progomphus obscurus*, was the most common odonate in the North Anna River. Its abundance there was understandable, because the larva is adapted to rapid burrowing in streams with beds of flowing sand (KENNEDY, 1917). However, other workers (BYERS, 1939; NEEDHAM & WESTFALL, 1955) have indicated that this species also occurs in sandy areas of lakes. Since dip net samples in suitable areas of Lake Anna did not yield any larvae of this species for three years after impoundment, we have included *P. obscurus* in the obligate rheophilic group.

One of the most distinct changes that occurred during the entire study was the complete dominance of the odonate fauna by one species, *Enallagma civile*, the first year after impoundment and its sudden disappearance the second year. Although the larvae of enallagmas were not identified to species before impoundment, our recent collections in other areas of the river indicate that *E. civile* was probably present in the basin. For this reason we have placed *E. civile* in the early facultative groups of organisms which immediately colonized the reservoir. *E. civile* was reported as a "pioneer" species of new ponds by PERRY (1975), and WILSON (1920) also listed this species as one which would do well in a new pond. Before impoundment much of the basin was rich pasture land with a luxuriant growth of tall grass, and, therefore, we speculate that the early success of *E. civile* in Lake Anna was due to the abundance of inundated living terrestrial vegetation. NEEDHAM (1903) reported that enallagmas in general live in tangled, submerged vegetation and that eggs are deposited in punctures in the tissue of green plants just beneath the surface. Apparently, while the terrestrial vegetation was first being flooded, *E. civile* was the only odonate that found this to be a suitable breeding site and quickly colonized the new habitat. This hypothesis is supported by the fact that the disappearance of *E. civile* coincided with the decay of the terrestrial vegetation between the first and second years.

Most species were considered to be late facultative, because they were present before impoundment but apparently could not become successful until the lentic ecosystem had matured. For several of these species, it is possible that the elimination of the terrestrial components of the bottom during maturation of the reservoir was important. Immediately after inundation the bottom consisted of living terrestrial vegetation, coarse organic litter, topsoil, or clay which had been excavated and baked hard by the sun. During the first year after impoundment we observed that the vegetation and organic matter decomposed, leaving the bottom clear but covered with a layer of fine sediment from the establishment of planktonic communities and the input of the river. Of the late facultative species, *Argia apicalis* has become the most abundant odonate in Lake Anna. GARMAN (1917) reported that the larvae live in mud at the bottom of large-sized streams. In addition, JOHNSON (1972) mentioned that *A. apicalis* occurs in greatest abundance in association with large, muddy rivers and that man-made lakes derive their colonies from the original river fauna. This species was probably present among the argias of the pre-impoundment basin (Tab. I) and maintained small populations as the bottom of the reservoir became suitable for its later success. Other members of the late facultative group, which probably did not reappear until the second or third year for similar reasons, include *Dromogomphus spinosus* and *Macromia georgina*. However, the success of two other abundant members of the late facultative group, *Enallagma basidens* and *Perithemis tenera*, cannot be explained by an increase in the mud bottom. In addition to the information previously cited from NEEDHAM (1903) concerning enallagmas in general, BIRD (1931) reported that the larvae of *E. basidens* crawl about watercress or other plants where there is a gentle current. Likewise, *P. tenera* is more commonly encountered on vegetation than on a mud bottom. We speculate that the success of these latter species may have been dependent on the development of true aquatic plants in the reservoir. The abundance of both species coincided with the appearance of extensive beds of *Potomogeton crispus; E. basidens* and *P. tenera* were common in dip net samples from the macrophytes as well as on the artificial substrates.

The species from Lake Anna, which we have included in the limnophilic group, *Epitheca cynosura* and *E. princeps*, are both well documented as typically lentic species. WALKER & CORBET (1975) listed marsh-bordered lakes, bays, and mouths of slow streams with submerged and emergent vegetation as the preferred habitat for *E. cynosura*, while KORMONDY (1959) stated that it is primarily an inhabitant of marl lakes with eutrophic tendencies. Inasmuch as *E. cynosura* has consistently occurred in Lake Anna every year since impoundment, but never comprised more the 4% of the odonates, we feel that a reservoir does not completely meet the habitat requirements of this species. However, the closely related species, *E. princeps*, has been quite successful in the mud cenosis of the reservoir. WRIGHT (1943) reported that he found *E. princeps* only in areas of a reservoir with rich mucky bottoms having but scanty vegetation. Therefore, the colonization of limnophilic species such as *E. princeps* in a new reservoir might also be directly dependent on the development of a suitable mud bottom, as previously mentioned for several species in the late facultative group.

The species which colonize a new habitat can also be classified as either "r strategists" or "K strategists". The "r strategists" are those species with a high value for the Malthusian parameter (r) in the logistic growth equation. They are successful in short-lived habitats because they reproduce rapidly and exploit the resources before other species move in. The "r strategists" cannot permanently occupy a niche because they lack competitive ability, and thus disperse in search of new habitats when the present one becomes unsuitable. *E. civile*, which was included in the early facultative group in Table II, appears to exemplify all of the previously mentioned characteristics of an "r strategist". All of the species included in the late facultative and limnophilic groups in Table II appear to be good examples of "K strategists". The "K strategists" are those organisms which have the ability to compete when the number of organisms approaches the carrying capacity of the environment (K) in the logistic growth equation. They are characteristic of long-lived habitats and demonstrate increased specialization which enables them to permanently occupy a given niche. Analysis of the depth distribution of odonates during the first three years after impoundment illustrates this point. In the first year the "r strategist" *E. civile* was evenly distributed down to 4 m and was even collected as deep as 7 m. This would be expected of an "r strategist" since it has no competition and its success depends upon rapid exploitation of resources. In succeeding years the "K strategists" tended to segregate themselves according to depth. *E. basidens* and *A. apicalis* were almost entirely restricted to depths of 2 m or less, while *P. tenera* was consistently most abundant at 4 m. This would appear to be a specialization to avoid competition brought about by niche overlap, and thus assure success for each species as the number of organisms approaches the carrying capacity.

From our study of odonates during the transformation of a free-flowing river into a man-made reservoir, it was possible to discern distinct trends in colonization. As expected, those species requiring flowing water for proper physiological function disappeared immediately. The sudden transformation of a river into a unique lentic ecosystem dominated by the components of a terrestrial ecosystem set the stage for a facultative species with the correct adaptations to exploit the situation ("r strategist"). As the lentic ecosystem matured, the bottom developed more fine sediment and aquatic macrophytes began to grow. Thus, with more niches available to the odonates, some facultative species from the river reappeared and other new limnophilic species became established in the reservoir ("K strategists").

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