DIVERSITY AND DISTRIBUTION OF MUSSELS (BIVALVIA: UNIONACEA) IN A EUTROPHIC RESERVOIR, LAKE ASHTABULA, NORTH DAKOTA

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ABSTRACT

Lake Ashtabula, a 28-year-old eutrophic reservoir on the Sheyenne River in southeastern North Dakota, was surveyed for mussels by scuba diving during the summer of 1974. Belt transects, 20 m by 1.75 m and paralleling depth contours, were run at six stations at each meter depth, usually to 6 m. Four species, in order of decreasing abundance, were found in the lake: Anodonta grandis *Say,* Lampsilis radiata *(Gmelin),* Amblema plicata *(Say), and* Lasmigona complanata *(Barnes). Eight species are known in the river above the lake and 11 species below the lake. Lake individuals of* A. grandis *were conspicuously smaller than those in the river; most (82.7%) had about two or three winter rings, and the largest had about five. Individuals of* L. radiata, *however, were of a size about normal for those in the river; the largest individual had about seven winter rings. Most mussel individuals occurred at 3 m (46.9%) and 2 m (25.0%), fewest (3.1%) occurred at 6 m, and none was found at 5 m. The maximum density was 0.43 individuals/m² for* A. grandis *at 3 m. Individuals of* A. grandis *(collectively from all depths) decreased in numbers down the reservoir toward the dam. The average density (from 2 and 3 m) of* A. grandis *in the lake (0.27 individuals/m²) was significantly (P=0.10) greater than that in the river below the lake (0.05 individuals/m²) and about the same as that above the lake (0.32 individuals/m²). The average density of* L. radiata *in the lake (0.05 individuals/m²) was significantly (P=0.10) less than that above the lake (0.24 individuals/m²) and about the same as that below the lake (0.07 individuals/m²). Possible causes for fewer mussel species in Lake Ashtabula are alteration of normal mussel reproductive processes and periodic low levels of oxygen content.*

INTRODUCTION

It is well-known that the impounding of rivers generally has adverse effects on the mussel (Bivalvia: Unionacea) fauna of a natural drainage, but the reasons are not always clear (for summary of effects, see Fuller, 1974: 247-250). This paper reports the results of a study of mussels in a 28-year-old eutrophic reservoir on the Sheyenne River in southeastern North Dakota.

Cvancara *et al.* (1976) have recently summarized the mollusks in the Sheyenne River and Lake Ashtabula and reported only two mussels, from one station (fig. 1, station 6), in the lake. Peterka (1972) analyzed the concentrations and depth-occurrences of four snail and two pill clam (Sphaeriidae) genera in Lake Ashtabula and said (written communication, May 2, 1974) that five young "Anodontidae" were collected (by Ekman dredge) from 2-4 m at the mouth of Baldhill Creek (station 4, fig. 1) and at 2.1 km above the dam in July and August, 1966.

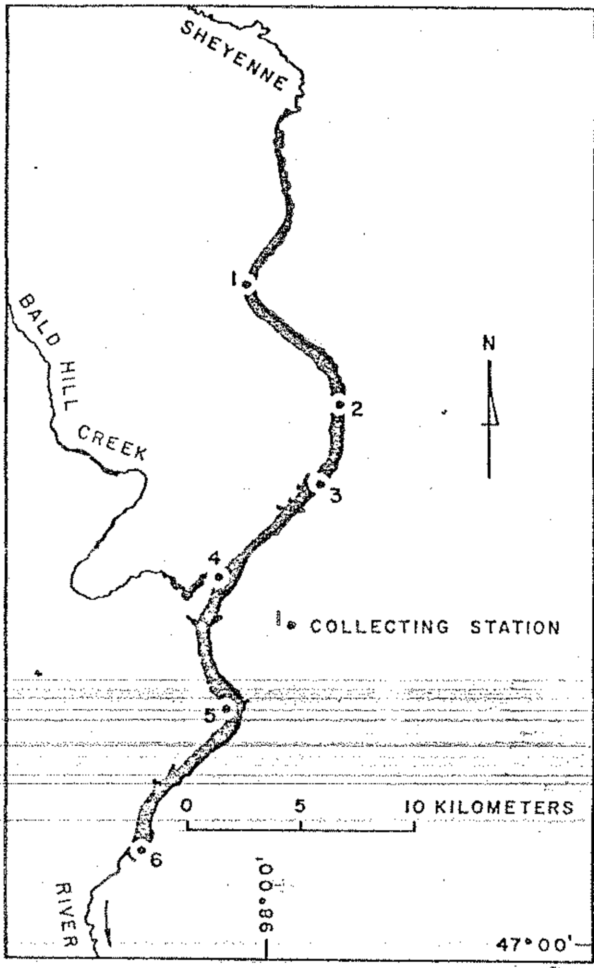

FIG. 1. *Map of Lake Ashtabula and vicinity showing mussel collecting stations.*

The generally north-trending Lake Ashtabula (fig. 1) is backed up by Baldhill Dam (NW 1/4 sec. 18, T. 141 N., R. 58 W. 47° 02′ N., 98°05′ W.), 8.4 km northwest of Valley City in Barnes County, North Dakota. The reservoir occupies the Sheyenne River Valley, whose floor is about 656 m below the surrounding terrain at the dam. Occupying a glacial meltwater trench (Aronow, 1963), the valley is cut into late Quaternary bouldery sand, silt, and clay (glacial till), sand and gravel (glacial meltwater deposits), and silty clay (glacial lake sediment) and Late Cretaceous shales (Kelly and Block, 1967; Merritt, 1966). The major tributary of the valley at the reservoir is Baldhill Creek (fig. 1). The bottom sediment of the reservoir is generally soft, organic mud beyond a depth of 1-3 m (Table 1).

Peterka (1972), Peterka and Knutson (1970), and Peterka and Reid (1969) have described the physical, chemical, and biological characteristics of Lake Ashtabula. The reservoir began storage in July, 1949; it is 43.5 km long at normal full pool and up to 0.97 km wide. The maximum depth, in the old river channel, is slightly over 15 m, and the mean depth is 4.0 m. At normal full-pool elevation the surface area is 2197.5 ha and the storage capacity is 8720.7 ha-m.

The water generally did not stratify (physical and chemical measurements from April 1966 to April 1967 unless otherwise stated (during ice-free periods. Dissolved oxygen concentration was 6.4-13.9 mg/1 during ice-free periods (at a single station) and nearly uniform throughout the water column. Supersaturated oxygen levels occurred often during April through September, 1966. During ice cover, oxygen concentrations dropped to lows of 8.2 mg/1 at the surface and 0.4 mg/1 at the bottom. Secchi disc transparency (at a single station) was 0.5-3.8 m, affected by both suspended sediment and phytoplankton. Transparency increased down-reservoir, was generally less than 1 m near station 2 (fig. 1), and averaged 2 m near the dam; this generally agrees with the results of Johnson *et al.* (1974: 16-17), obtained in July and August, 1974.

Total dissolved solids (at a single station) have varied from a little more than 200 mg/1 (April) to more than 600 mg/1 (February) (Peterka and Reid, 1969: fig. 5). Total alkalinity ranged from 140-160 mg/1 (April-May 1966) at all depths to 330 and 440 mg/1 (April 1967) at the surface and bottom. The pH values were 7.5-8.3 in April-May 1966, 8.8-9.2 in June 1966—January 1967, and decreased to about 8.0 in March-April 1967. Generally, fluctuations of sulfate, ammonia, nitrite, nitrate and total phosphate were similar to those of dissolved solids and alkalinity; low concentrations followed spring run-off and higher concentrations were reached just before ice break-up. The mean concentrations of total iron, total and ortho phosphate, and bicarbonate alkalinity (June 1967 to July 1968) were significantly less in the lower and middle reaches of the reservoir than in the upper part (Peterka and Knutson, 1970: 19). Conversely, the mean

TABLE 1. Estimated predominant bottom sediment and percentage of rooted aquatic plant cover for six stations in Lake Ashtabula in 1974 (stations are shown in fig. 1).

Depth (m)	Stations and dates of observations					
	(6/26) 1	(8/21-22) 2	(6/25-26) 3	(6/25) 4	(8/20) 5	(5/27) 6
1	Muddy sand[a]	Muddy sand	Sand	Gravelly sand	Sandy mud	Muddy gravelly sand
	85	20	80	90	90	2
2	Mud	Mud	Muddy sand	Gravelly Muddy sand	Mud	Muddy sand
	15	0	1	60	0	17
3	Mud	Mud	Muddy gravelly sand	Sandy mud	Mud	Sandy mud
	0	0	0	20	0	8
4	Mud	Mud	Mud	Mud	Mud	Mud
	0	0	0	0	0	2
5	--	Mud	Mud	Mud	Mud	Mud
		0	0	1	0	0
6	--	Mud	Mud	Mud	Mud	Mud
		0	0	1	0	0

[a]Estimate of bottom sediment made by generally following percentage limits of Shepard (1954).

concentrations of nitrate nitrogen and carbonate alkalinity were higher in the middle and upper reaches of the reservoir.

Lake Ashtabula is highly productive with an average annual gross primary productivity of 4.1 and 6.8 g O_2/m²/day for 1967 and 1968. Heavy algal blooms occurred during the summer and autumn of 1967 and 1968 when *Aphanizomenon holsaticum* comprised about 90% of the blooms in numbers and volume (Peterka and Knutson, 1970: 59, 62-63). A band of submergent vegetation, largely of species of *Potamogeton*, occurred along the shores of the reservoir in water 0.6-2.5 m deep (Peterka and Knutson, 1970: 67). The existence of this vegetation band is partly reflected in Table 1. The total zooplankton dry weight standing crop was dominated by *Daphnia*, comprising 84% of the standing crop in 1967 and 81% in 1968; the average dry weight standing crop for *D. pulex* was 1110 mg/m² in 1967 and 2851 mg/m² in 1968 (Peterka and Knutson, 1970: 25, 28). The average standing crop of benthic invertebrates (spring and summer of 1967; single station 3.2 km north of the dam, fig. 1) was 7.2 g/m² and 2126 individuals. The total biomass consisted of mollusks (snails and pill clams), dipterans, annelids, ephemeropterans, and others (e.g., amphipods), in order of relative abundance. Most (90% by weight) of the invertebrates occurred at depths of 0-8 m (Peterka, 1972).

MATERIALS AND METHODS

During the summer of 1974, mussels were surveyed at six stations in Lake Ashtabula by scuba diving. The stations (fig. 1) were chosen so as to be distributed over most of the lake, be about equally spaced, and be in relatively undisturbed areas. No sampling was done above station 1 because Lake Ashtabula above this point is very shallow and largely a marsh. Belt transects, 20 m by 1.75 m and paralleling depth contours, were run at each meter depth to 6 m, except at station 1 where the maximum depth was less than 5 m. The transects were limited to 6 m because of extremely low lateral visibility; estimated values of visibility at 6 m for four stations were 0-0.4 m. (At 3 m, the estimated values at four stations were 0.6-1 m). To gain access to the 6-m depth, it was usually necessary to locate the former river channel; this was accomplished by use of a Lowrance Electronics Mfg. Corp. Fish-Lo-K-Tor. Each transect line was begun from a bearing normal to shore, established with an underwater compass. The transect line, a nylon cord 5 mm in diameter with lead weights, was held by a diver at one end while the other diver extended it along the desired depth contour by means of an underwater depth gauge. All mussels (alive and empty shells) that could be reached on either side of the transect line (a 1.75-m-wide belt or band) were placed in a numbered bag. Collecting was commonly done strictly by feel because of the generally low visibility. Observations on the estimated predominant bottom sediment and percentage of aquatic plant cover were made for each transect. More than 20 underwater manhours were devoted to this survey.

Shells were measured (to the nearest millimeter) for length (greatest distance parallel to the hinge line), height (greatest dorsoventral distance normal to the hinge line), width (greatest distance across both valves normal to a plane passing between them), and posterior length (greatest distance parallel to the hinge line from the beak to the posterior margin) in the field by use of a specially contructed measuring box with a sliding guide and by vernier calipers. The total weight (body and shell) and shell weight were measured to the nearest tenth of a gram. All excess moisture was removed before weighing live individuals, and shells were dried before weighing. Specimens used are encompassed within accession numbers A1203-1222 of the Department of Geology, University of North Dakota.

RESULTS

Four mussel species, in order of decreasing abundance, were found living in Lake Ashtabula (Table 2): *Anodonta grandis* Say, *Lampsilis radiata* (Gmelin), *Amblema plicata* (Say), and *Lasmigona complanata* (Barnes). Individuals of *A. grandis* were conspicuously small (Table 3); most (82.7%) had about two or three winter rings and the largest had about five. The ratios of posterior length/length, total weight/length, and shell weight/length of lake individuals of this species were less than those of Sheyenne River individuals. Individuals of *L. radiata* were of a size about normal for those in the river, and the largest had about seven winter rings. The male/female ratio of this species was 2. Too few

TABLE 2. Individuals of four species of mussels recovered from six stations in Lake Ashtabula.

Depth (m)	*Anodonta grandis* Stations 1	2	3	4	5	6	Total	*Lampsilis radiata* Stations 1	2	3	4	5	6	Total
1	0[a] (0)	1 (5)	1 (1)	5 (0)	0 (0)	0 (0)	7 (6)	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	0 (0)	1 (0)
2	4 (5)	10 (17)	4 (0)	3 (0)	1 (0)	0 (1)	22 (23)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	0 (1)	1 (1)
3	15 (11)	8 (7)	8 (16)	4 (4)	0 (0)	0 (1)	35 (39)	1 (0)	0 (0)	2 (1)	0 (0)	0 (0)	6 (0)	9 (1)
4	14 (5)	2 (0)	0 (0)	0 (0)	0 (0)	0 (0)	16 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (1)	0 (1)
5	NS (NS)	0 (0)	0 (3)	0 (0)	0 (0)	0 (0)	0 (3)	NS (NS)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
6	NS (NS)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	NS (NS)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	1 (0)
Total individuals	33 (21)	22 (29)	13 (20)	12 (4)	1 (0)	0 (2)	81 (76)	1 (0)	0 (0)	2 (1)	1 (0)	1 (0)	7 (2)	12 (3)

Depth (m)	*Amblema plicata* Stations 1	2	3	4	5	6	Total	*Lasmigona complanata* Stations 1	2	3	4	5	6	Total
1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (2)	0 (0)	1 (2)
3	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
4	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
5	NS (NS)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	NS (NS)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
6	NS (NS)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	NS (NS)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Total individuals	0 (0)	2 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (2)	0 (0)	1 (2)

[a]Each entry represents the individuals (empty shells indicated by parentheses) collected from a 20-m by 1.75-m transect. NS = not sampled because the maximum depth was less than 5 m.

TABLE 3. Statistical data of shell measurements, shell measurement ratios, weights, and weight/length ratios for *Anodonta grandis* Say and *Lampsilis radiata* (Gmelin) from six stations in Lake Ashtabula and 21 stations from the Sheyenne River above and below the lake.

	Lake			River[a]		
	Mean ±S.E.	N.	Range	Mean ±S.E.	N.	Range
Anodonta grandis Say						
Length	55±1.0	81	38-84	93±1.2	259	60-156
Height	33±0.6	81	23-50	53±0.7	259	37-87
Width	21±0.5	81	12-36	33±0.5	259	19-60
Height/length	0.60±0.003	81	0.55-0.67	0.57±0.002	259	0.51-0.74
Width/height	0.62±0.005	81	0.52-0.74	0.62±0.002	259	0.49-0.74
Posterior length	35±0.6	80	24-52	54±1.0	35	45-70
Posterior length/length	0.64±0.002	80	0.58-0.70	0.70±0.003	35	0.67-0.74
Total weight	18.4±1.1	78	5.2-69	98.3±6.5	157	17.4-355.3
Shell weight	3.3±0.2	80	1.1-11.5	20.6±1.3	130	7.6-146.9
Total weight/length	0.32±0.013	78	0.14-0.82	0.95±0.04	157	0.29-2.50
Shell weight/length	0.06±0.002	80	0.03-0.14	0.22±0.009	130	0.10-0.94
Lampsilis radiata (Gmelin)[b]						
Length	90±8.4	8	37-112	91±0.7	252	68-122
Height	53±5.1	8	23-71	53±0.4	252	40-85
Width	31±3.5	8	10-40	31±0.3	252	21-46
Height/length	0.60±0.014	8	0.52-0.65	0.59±0.002	252	0.48-0.79
Width/height	0.58±0.026	8	0.44-0.69	0.59±0.002	252	0.40-0.76
Posterior length	64±8.0	8	25-87	69±1.1	60	55-88
Posterior length/length	0.73±0.011	8	0.58-0.78	0.76±0.002	60	0.72-0.80
Total weight	95.6±22.0	8	4.3-168.7	92.9±2.8	168	29.6-233.2
Shell weight	43.7±8.1	8	1.3-75.6	45.3±1.9	144	10.5-123.1
Total weight/length	0.95±0.19	8	0.12-1.51	1.00±0.022	168	0.42-1.91
Shell weight/length	0.43±0.071	8	0.04-0.68	0.47±0.016	144	0.15-1.05

[a]River data were generated during the study of Cvancara *et al* (1977).
[b]Only data for males are given.

lake individuals make comparisons with river individuals uncertain. The two individuals of *A. plicata* were 81 and 100 mm, 62 and 78 mm, and 29 and 39 mm in length, height, and width, and had about 4 and 7 winter rings. The single live *L. complanata* was 80 mm, 65 mm, and 28 mm long, high, and wide and had five winter rings. Oviferous individuals were found of *A. grandis* (stations 2 and 5 at 2-4 m; 20-21 August), *L. radiata* (station 5 at 2 m; 20 August), and *L. complanata* (station 5 at 2 m; 20 August).

Most (71.9%) mussel individuals occurred at 3 m (46.9%) and 2 m (25.0%), fewest (3.1%) at 6 m, and none was found alive at 5 m. Empty shells commonly occurred in numbers comparable to those for live individuals (Table 2). The maximum density was 0.43 individuals/m² for *A. grandis* at 3 m. The average densities (individuals/m²) for *A. grandis* and *L. radiata* at combined 2- and 3-m depths were 0.27 and 0.05. Total *A. grandis* decreased significantly ($P<0.01$) and linearly down the reservoir toward the dam ($r=-0.96$).

Densities of *A. grandis* and *L. radiata* in the lake did not show a consistent pattern as compared with densities in the river (Table 4). The average density of *A. grandis* in the lake was significantly greater than that in the river below the lake, but about the same as that above the lake. The average density of *L. radiata* was significantly less than that above the lake, but about the same as that below the lake. The relative abundances of the two species were about the same above and below the lake, but decidedly different in the lake.

TABLE 4. Density of *Anodonta grandis* Say and *Lampsilis radiata* (Gmelin) in Lake Ashtabula (from 2- and 3-m depths) and Sheyenne River above (three stations) and below (four stations) the lake.

Km above or below lake dam	*A. grandis* density (individuals/m^2)	*A. grandis* group mean	*L. radiata* density (individuals/m^2)	*L. radiata* group mean
250.0	0.14[a]	Mean =0.32	0.04	Mean =0.24
150.6	0.21		0.23	
58.2	0.60		0.46	
30.6	0.54	Mean =0.27	0.03	Mean =0.05
23.6	0.51		0.00	
20.1	0.34		0.06	
14.2	0.20		0.00	
8.0	0.03		0.03	
0.5	0.00		0.17	
3.0	0.01	Mean =0.05	0.09	Mean =0.07
111.3	0.14		0.16	
274.8	0.00		0.01	
399.4	0.05		0.02	

A. grandis: Mean =0.32 vs. Mean =0.27: NS; Mean =0.27 vs. Mean =0.05: S; Mean =0.32 vs. Mean =0.05: S[b]

L. radiata: Mean =0.24 vs. Mean =0.05: S; Mean =0.05 vs. Mean =0.07: NS; Mean =0.24 vs. Mean =0.07: NS

[a] Values are listed in downstream and downlake order. Lake values are underlined.
[b] S= compared means are significantly different (t-test; P=0.10). NS=compared means are not significantly different (t-test; P=0.10).

TABLE 5. Comparison of mussel species in Lake Ashtabula with those in the Sheyenne River above and below the lake.

Species	Lake Ashtabula	River[b] above lake	River[b] below lake
1. *Amblema plicata* (Say)	1[a]	3	9
2. *Fusconaia flava* (Rafinesque)		2	7
3. *Quadrula quadrula* (Rafinesque)[c]			
4. *Anodonta grandis* (Say)	5	10	11
5. *Anodontoides ferussacianus* (Lea)		3	6
6. *Lasmigona complanata* (Barnes)	1	5	10
7. *L. compressa* (Lea)		3	1
8. *Strophitus undulatus* (Say)		1	4
9. *Lampsilis ovata* (Say)			6
10. *L. radiata* (Gmelin)	5	8	9
11. *Ligumia recta* (Lamarck)			2
12. *Proptera alata* (Say)			1

[a] Number of stations at which a species was found among totals of 6, 16, and 11 in the lake, above the lake, and below the lake.
[b] Data for the Sheyenne River are from Cvancara *et. al.* (1976).
[c] Only empty shells of this species were found, in the river below the lake.

DISCUSSION

Considerably fewer mussel species were found in Lake Ashtabula than are known to exist in the Sheyenne River above and below the lake (Table 5). Those found in the lake are the same species as those found at most stations in the river. The chances of finding additional species in the lake can be estimated from the Poisson distribution, which fits the observed species distribution remarkably well. The Poisson probability of finding more than four species is 0.003 based on an extension of the observed data (Darnell, 1971: 189-193). One might ask, what would the mussel fauna be like if Lake Ashtabula were elsewhere on the Sheyenne River? If farther downstream, more species might occur since diversity is greater in the lower reaches of the river (Table 5). Other studies (summarized by Fuller, 1974: 247-250) have demonstrated the smaller number of mussel species in reservoirs as compared to those in the nonimpounded river. Shifts in the species composition may also occur, with commonly increased prominence of members of the Anodontinae. This was documented for reservoirs on the Tennessee River (Bates, 1962; Isom, 1969, 1971). Baker (1928), in a dammed-up creek system in Wisconsin, found that only two mussels out of eight remained in the man-made lakes—*Anodonta grandis* (including *"Anodonta marginata"*) and *Lampsilis radiata*. *A. grandis*, an anodotine, was the dominant mussel found in Lake Ashtabula, followed by *L. radiata* (Table 2).

Possible causes for fewer mussel species in Lake Ashtabula are 1) alteration of reproductive processes and 2) periodic low levels of oxygen content. Since most mussels are dependent on a fish host for dispersal and development of the glochidial larva, fish species in Lake Ashtabula were checked (from Farmer, 1974 and from a list compiled by Dr. John B. Owen, Department of Biology, University of North Dakota and his students). Fuller (1974: 228-237) has compiled a list of host fishes for many mussel species from the literature. With the exception of *Anodontoides ferussacianus* (Lea), all mussels in the Sheyenne River with known fish hosts have one or more host fishes present in Lake Ashtabula. Therefore, there seems to be no problem with glochidial host availability. However, even though a suitable host is present, the level of infection by glochidia in reservoirs may be very low. Also, the reproductive process may be altered by loss of glochidia in the soft substrate or by increased attacks upon larvae by microorganisms, especially under conditions of high siltation and organic enrichment (summarized by Fuller, 1974: 222, 247, 252), as are present in Lake Ashtabula.

Periodic low levels of oxygen also may be responsible for low mussel diversity in the lake. Peterka and Reid (1969: 145) recorded a low of 0.4 mg/1 on the bottom (8 m) between stations 5 and 6 on 27 February 1967; Mr. James Ragan, of the North Dakota Game and Fish Department, reported (letter dated 4 August 1975) 0.5 mg/1 at 4.5 m depth at station 2 on 18 February 1970. The preponderance of *Anodonta grandis* in the lake suggests that this species is physiologically more adaptable to conditions of marginal oxygen. Isom (1971) attributed the sparse mussel fauna in Fort Loudon Reservoir on the Tennessee River to periodic insufficient oxygen resulting from organic enrichment entering the upper reservoir.

Individuals of *A. grandis* were conspicuously smaller in the lake than in the river (Table 3), not because of stunting, but because the lake forms were consistently younger, as mentioned under Results. It is possible that the preponderance of young individuals is due to significantly low water causing a dying off prior to their birth. The lowest levels (below normal reservoir level) during 1969-1974 were 8.22 feet (early April), 3.40 feet (early April), 4.34 feet (late March), 3.90 feet (early March), 2.79 feet (early March), and 8.49 feet (early April) (data from Mr. Melvin Rieman, Flood Control Dam Operator for the U.S. Army Corps of Engineers, 11 August 1975). The 8.22-foot drawdown in 1969 may be significant because most individuals of *A. grandis* were found at 2 and 3 m in 1974, and the time of the drawdown is close to the estimated time of birth of most of the individuals collected. Most of the adults may have died during the drawdown, and the shallow-water populations may have been dominated thereafter by juveniles developed after the water level rose. If reservoir level-lowering is significant, however, it is unclear why *Lampsilis* *radiata* was not represented primarily by young individuals. Also, the possible detrimental effects of the 8.49-foot drawdown in 1974 were not evident in either species.

The smaller posterior length/length ratio of lake individuals of *A. grandis* implies more centrally placed beaks, but may be the result of generally younger individuals in the lake than in the river. Clarke (1973: 69, 80) found high values of the anterior to beak length/length ratio (which correspond to low values of the posterior length/length ratio) in individuals of *A. grandis* from large lakes. He said such values imply a superior development of the foot for maintaining position better in lakes in exposed habitats and on shifting substrates (of sand). This explanation is questionable since one might expect currents in rivers, especially during flood stage, to affect a mussel's position on the bottom as drastically as does wave action.

The greatest concentration of individuals at 3 m differs notably from 1 m in Long Lake, a natural lake in northwestern Minnesota. However, the maximum density of 0.43 individuals/m^2 is similar to the 54 mussels/m^2 in Long Lake (Cvancara, 1972: 155). The scarcity of trees and long fetch at Lake Ashtabula are conducive to frequent, strong wave action that may result in more disturbance and fewer individuals at depths less than 3 m.

The fewer individuals with increasing depth in Lake Ashtabula also occurred in Long Lake. In both lakes, this may be because of decreased biological activity (slower metabolism, reproduction and growth) as related to lower temperatures (Cvancara, 1972: 157). In Lake Ashtabula, however, thermal stratification has generally not been observed (1966-1967) during ice-free periods, but does occur during such times in Long Lake. It may be, too, that periodic low levels of oxygen on the bottom result in fewer individuals with depth.

The decrease in numbers of individuals of *A. grandis* down the reservoir toward the dam may be due to a chemical factor. As mentioned under *Introduction*, total iron, total and orthophosphate, and bicarbonate alkalinity were less in the lower and middle reaches of the reservoir whereas nitrate nitrogen and carbonate alkalinity were higher in the middle and upper reaches. It is unclear, however, which chemical factor might be responsible and how it might relate to mussel density.

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REDESCRIPTION OF *BITTIUM PROTEUM* (JOUSSEAUME, 1930) WITH COMMENTS ON ITS GENERIC PLACEMENT

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While examining cerithiid-type-material from the Museum d'Histoire Naturelle, Paris, I came across five lots of specimens from Aden that were described by Jousseaume in 1930 as *Cerithium proteum.* All of the specimens are less than 5.2 mm in length and have extremely variable sculpture that consists of intersecting axial and sprial cords. Jousseaume (1930) noted the conchological polymorphism and remarked that each individual could be construed as a separate species were it not for the intergradation of forms within a population. The type-shells have wide, shallow, short anterior siphonal canals and very weak anal sinuses that are indicative of the genus *Bittium* Gray, 1847 rather than *Cerithium* Bruguière, 1789.

To my knowledge, *Cerithium proteum* was not mentioned again in the literature until 1971 when Biggs examined a series of small cerithiids collected in beach drift from the Dahlak Island, Ethiopia, by the Polish Expedition to the Red Sea ("Dar Opola"). Biggs (1971) was unable to identify the specimens or place them into any known genus; consequently, he proposed the genus *Dahlakia* which he suggested should be placed somewhere near the potamidid genera *Pirenella* Gray, 1847 and *Cerithidea* Swainson, 1840. He described four new species based on the material collected at the Dahlak Islands: *Dahlakia leilae* (type-species of the genus), *D. striata*, *D. jugosa* and *D. pirenelloides*. I believe these four species are conspecific with *Cerithium proteum* Jousseaume, 1930. Examination of Jousseaume's type-material, which consists about 100 specimens, shows that all of the characters used by Biggs (1971) to define his species