# Ecological Changes Following an Alewife Introduction in an Oligotrophic Reservoir: A Case History

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*Abstract:* Alewife *(Alosa pseudoharengus)* was introduced into oligotrophic Mayo Reservoir, North Carolina, during 1992 or 1993. The species established a self-sustaining population and increased from <1% of total fish biomass in 1993 to 31% in 2000. Size-selective planktivory by the species, a well-documented phenomenon in other alewife introductions, was implicated in observed changes in the reservoir zooplankton community. Large- and mid-sized zooplankton (> 0.7 mm) *(Onchyodiaptomus birgei*, calanoid copepodites, *Daphnia* spp., *Diaphanosoma brachyurum*, and *Holopedium gibberum)* decreased in density and biomass within a year after the alewife introduction. Total cladoceran densities and biomass and total copepod biomass also exhibited the same pattern. Conversely, smaller or more evasive zooplankton (e.g., *Bosmina longirostris, Mesocyclops edax, Tropocyclops prasinus*, cyclopoid copepodites, and rotifers) either increased or did not change in abundance following introduction. Subsequent linkages between changes in zooplankton composition and key water quality variables were not apparent in this study. Chlorophyll *a* concentrations remained low, indicative of oligotrophy, and there were no apparent long-term blooms or detectable changes in water clarity after the alewife introduction. Total nitrogen and phosphorus concentrations were highly variable; only total nitrogen exhibited an increasing trend after the alewife introduction. Changes in the fish community were minimal, which likely reflected the slow buildup of the alewife population during the study period. Alewife supplanted gizzard shad as the dominant clupeid within four to seven years after introduction. Chain pickerel and redear sunfish abundance increased after alewife introduction, which corresponded with increased aquatic vegetation in the reservoir littoral zone. Decreases in green sunfish and pumpkinseed were noted, but most likely were related to littoral zone competitive interactions with bluegill, warmouth, and redear sunfish populations or predation from increased chain pickerel abundance. Early life stages of the dominant centrarchids—bluegill, warmouth, largemouth bass, and crappie—may have spatially segregated zooplankton and other invertebrate prey resources and utilized those resources within nearshore, vegetated zones to minimize interspecific competition with alewife.

*Key Words:* alewife, planktivore, non-native, prey species, size-selective planktivory

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Alewife *(Alosa pseudoharengus)* has been introduced throughout North America as an additional prey species for predatory sport fishes (Christie 1974, Ney 1981, Noble 1981, Stewart et al. 1981, Tisa and Ney 1991). Various investigators have documented significant restructuring of zooplankton communities following alewife introductions due to the species' size-selective planktivory (Wells 1970, Hutchinson 1971, Hewett and Stewart 1989, Johannsson et al. 1991). Alewife planktivory has usually resulted in a shift from larger-bodied taxa (e.g., *Daphnia* spp.) to smaller-bodied taxa (e.g., *Bosmina longirostris*) in zooplankton communities (Almond et al. 1996). Alewives have also been implicated in negatively impacting native fish populations through competitive interactions for available zooplankton food resources or direct predation on larval fish (Crowder 1980, Kohler and Ney 1980, 1981, Brandt et al. 1987). Additionally, limnological research has demonstrated linkages between planktivore abundance and predation pressure, the resultant abundance of zooplankton and phytoplankton, and, subsequently, the overall water quality of lentic systems (i.e., trophic cascade or top-down control hypothesis) (Lynch and Shapiro 1981, Carpenter and Kitchell 1984, Mills and Forney 1988).

The degree of alewife impact on the zooplankton and fish communities in lentic systems can depend on overwintering mortality rates of alewife, seasonality and alewife recruitment dynamics, productivity of the water body, and the predator-prey complex present in the system (Eck and Wells 1987, Hewett and Stewart 1989, O'Gorman et. al 1991, Tisa and Ney 1991). In southeastern reservoirs, alewife have been introduced to augment the pelagic prey base for striped bass *(Morone saxatilis)*, white bass *(Morone chrysops)*, and walleye *(Stizostedion vitreum)* (Kohler and Ney 1982). Competitive interactions between alewife and the native gizzard shad, and other facultative planktivores such as bluegill *(Lepomis macrochirus)*, may be more pronounced in nutrient-limited reservoirs where primary and secondary food production is low. Furthermore, alewives may switch to larval predation in reservoirs with low zooplankton food resources which could further impact native fish populations. Tisa and Ney (1991) indicated that alewife appeared trophically compatible with gizzard shad in Smith Mountain Lake, a mesotrophic to eutrophic hydroelectric impoundment located in south-central Virginia. However, the authors speculated that reservoirs having horizontally homogeneous temperature and fertility conditions would not likely support abundant populations of both alewife and gizzard shad. Such homogeneous conditions would not spatially segregate the reproduction of both species nor the subsequent larval distribution and feeding patterns.

The objectives of this paper are to: (1) present a case history of an alewife introduction in an oligotrophic North Carolina reservoir and (2) evaluate the impacts of this non-native planktivore introduction on the water quality, zooplankton, and fish populations of Mayo Reservoir.

## Methods

### Study Area

Mayo Reservoir is an 1135-ha impoundment located in the north-central Piedmont of North Carolina (Fig. 1). Progress Energy impounded the reservoir in 1983 to provide condenser cooling water and receiving waters for coal-ash pond effluent for the Mayo Steam Electric Plant. The power plant began commercial electrical generation during 1983. The power plant has 745 MW of generating capacity and operates year-round with cooling towers.

The reservoir is oligotrophic, narrow, with three major tributaries: Mayo Creek, Mill Creek, and Crutchfield Branch (Fig. 1). The power plant intake structure and ash pond discharge are located in the lower reservoir, and the ash pond discharges into the reservoir via Crutchfield Branch. Mayo Reservoir has a drainage area of 135 $km^2$, a mean depth of 9 m, a mean inflow of 1.42 $m^{-3}$ $sec^{-1}$, and a mean hydraulic residence time of 3 yr.

The reservoir has relatively clear waters with submerged and emergent aquatic macrophytes. The reservoir fishery developed from existing populations present in tributaries prior to impoundment. No additional prey or predator fish have been introduced into the reservoir. Two non-native macrophytes, *Egeria densa* and *Hydrillia verticillata*, were inadvertently introduced into the reservoir during the mid 1980s. The non-native Asiatic clam *Corbicula fluminea* is also present in the reservoir.

Three transects were sampled for water quality, zooplankton, and fish during the pre-alewife introduction (1985–1992) and alewife introduction (1993–2000) periods: Transect 1 (lower reservoir near power plant), Transect 2 (mid-reservoir), and Transect 3 (upper reservoir headwaters) (Fig. 1).

### Water Quality

Total nitrogen (TN) and total phosphorus (TP) surface water samples (0.5 m depth) were collected bimonthly (February, April, June, August, October, and December) with a 6.2 L alpha bottle at mid-reservoir from each transect during 1985–2000. Samples were transferred to labeled polyethylene containers and kept on ice in the dark until returned to the laboratory for analysis. Laboratory detection levels were 0.003 mg/L for TP and 0.10 mg/L for TN. Water clarity was measured with a Secchi disk. Phytoplankton samples were collected with a Van Dorn sampler for chlorophyll *a* analysis, with equal volumes of water composited from the surface, Secchi disk transparency depth, and twice the Secchi disk depth. The sample volumes were mixed in a plastic container with a one liter subsample collected in a dark bottle. The TN, TP, and chlorophyll *a* samples were analyzed with standard methods (EPA 1979, American Public Health Association 1995).

### Zooplankton Community

Zooplankton samples were also collected bimonthly from the limnetic zone during 1985–2000. Samples were obtained by taking vertical hauls from either the bottom or 13 m to the surface with 156 μm and 760 μm mesh size plankton nets. Samples were preserved with 3% formalin.

In the laboratory, samples were poured into a plastic graduated cylinder, mixed thoroughly, and an aliquot was withdrawn with a pipette and placed in a circular plankton counting wheel. The aliquot volume was determined by estimating the volume that would contain at least 100 organisms. Zooplankton counts were made with a dissecting scope at appropriate magnification. Smaller zooplankters were identified

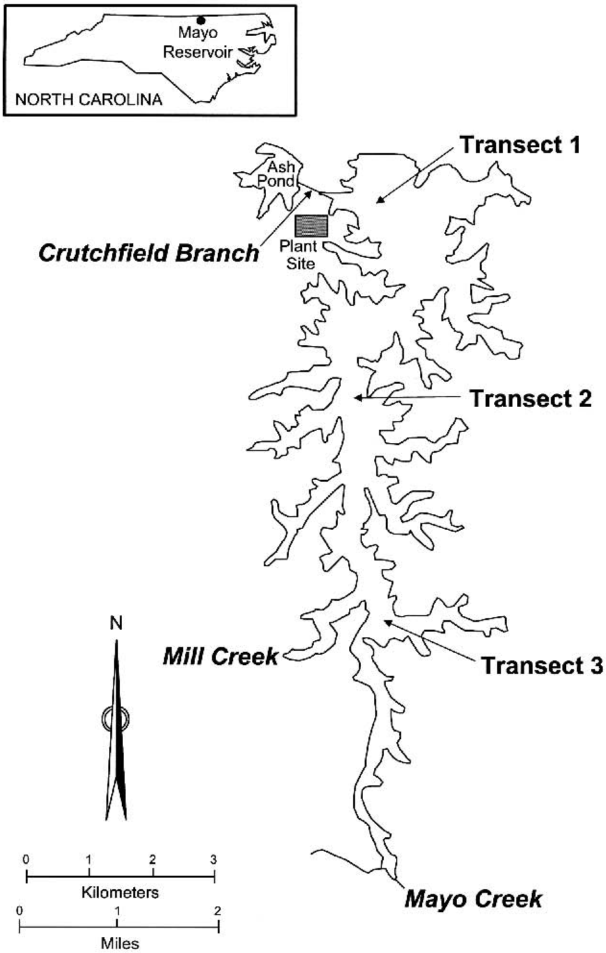


**Figure 1.** Map of Mayo Reservoir, North Carolina, showing sampling locations for water quality, zooplankton, and fish.

with a compound microscope. Copepodites, adult copepods, and adult cladocerans were counted from the 156 μm samples, while copepod nauplii, rotifers, and protozoans were counted from the 760 μm samples. Extrapolations to determine densities were then made on a volumetric basis. Biomass estimates of copepods and cladocerans were determined with logarithmic length-weight regression equations published for Piedmont reservoir zooplankton and expressed on a dry-weight basis (Horton and Carter 1980). Copepods were measured from the anterior end to the end of the caudal rami, while nauplii were measured from the anterior to posterior end. Cladocerans were measured from top of the head to the base of the spine. Rotifer biomass estimates were based on biovolumes derived from geometric formula for taxa.

**Table 1.** Mean density (number/ha) and biomass (kg/ha) of fishes collected by cove rotenone sampling at Mayo Reservoir, 1985–2000.

| | Year | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1985 | | 1986 | | 1988 | | 1989 | | 1991 | |
| Taxa | Density | Biomass | Density | Biomass | Density | Biomass | Density | Biomass | Density | Biomass |
| Alewife | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gizzard shad | 640 | 48.3 | 1,221 | 94.3 | 625 | 52.8 | 489 | 50.2 | 103 | 12.7 |
| Chain pickerel | 11 | 3.7 | 21 | 4.5 | 15 | 0.9 | 23 | 2.6 | 146 | 4.2 |
| Common carp | 9 | 12.8 | 6 | 7.5 | 6 | 8.7 | 11 | 23.1 | 4 | 5.6 |
| Creek chubsucker | 27 | 2.5 | 12 | 2.0 | 1 | 0.3 | 1 | 0.4 | 0 | 0 |
| *Moxostoma* spp. | 4 | 2.4 | 8 | 4.4 | 1 | 0.5 | 2 | 0.7 | 1 | 1.6 |
| Bullhead catfishes | 91 | 0.1 | 73 | 0.1 | 96 | 0.5 | 96 | 0.4 | 75 | 0.1 |
| White catfish | 26 | 1.7 | 32 | 2.7 | 36 | 0.1 | 14 | 0.9 | 47 | 0.9 |
| Yellow bullhead | 37 | 1.3 | 39 | 2.9 | 37 | 1.4 | 34 | 2.8 | 53 | 4.9 |
| Brown bullhead | 45 | 5.8 | 41 | 3.2 | 19 | 2.5 | 15 | 1.9 | 34 | 3.2 |
| Eastern mosquitofish | 300 | 0.1 | 216 | 0.1 | 79 | <0.1 | 40 | <0.1 | 208 | 0.1 |
| *Lepomis* spp. | 568 | 0.3 | 23 | 0.8 | 7 | 0.3 | 9 | 0.3 | 4 | 0.1 |
| Redbreast sunfish | 49 | 0.9 | 228 | 2.5 | 261 | 2.3 | 286 | 1.8 | 200 | 1.4 |
| Green sunfish | 470 | 1.8 | 519 | 2.8 | 619 | 2.6 | 643 | 3.1 | 352 | 2.1 |
| Pumpkinseed | 1,311 | 5.0 | 861 | 4.3 | 368 | 2.7 | 208 | 1.8 | 78 | 1.0 |
| Warmouth | 255 | 2.7 | 632 | 10.4 | 356 | 6.0 | 552 | 5.6 | 656 | 8.4 |
| Bluegill | 6,828 | 20.1 | 23,025 | 57.4 | 19,779 | 43.0 | 24,661 | 55.7 | 26,896 | 55.5 |
| Redear sunfish | 6 | 0.2 | 14 | 0.2 | 4 | 0.5 | 39 | 0.8 | 78 | 1.6 |
| Largemouth bass | 216 | 4.5 | 475 | 9.4 | 928 | 13.1 | 758 | 19.2 | 895 | 7.5 |
| *Pomoxis* spp. | 55 | 1.1 | 266 | 5.4 | 369 | 9.4 | 326 | 7.0 | 159 | 6.7 |
| Other taxa[a] | 214 | 3.0 | 117 | 10.1 | 108 | 4.8 | 94 | 7.5 | 121 | 5.4 |
| Total | 11,162 | 118.3 | 27,829 | 225.0 | 23,714 | 152.5 | 28,301 | 185.9 | 30,110 | 123.0 |
| Number of taxa | 31 | | 30 | | 26 | | 26 | | 25 | |

a. Other taxa include redfin pickerel, comely shiner, satinfin shiner, golden shiner, flat bullhead, snail bullhead, channel catfish, and *Etheostoma* spp.

### Fish Population Assessment

The relative abundance of fishes was determined with cove rotenone sampling during August or September. Sampling was conducted at one cove each from Transects 1, 2, and 3 during the "pre-alewife" years 1985, 1986, 1988, 1989, and 1991 and the "alewife" years 1993, 1995, 1997, and 2000. Surface area of the sampled coves ranged from 0.3 to 0.6 ha, and maximum depths ranged from 3.7 to 5.5 m. Cove rotenone sampling procedures followed those outlined by Grinstead et al. (1978) with fish collected for 3 days after treatment. The block nets employed in sampling had 5-mm square mesh. All fish were identified, measured to the nearest millimeter (total length), and weighed to the nearest gram. The most abundant fish taxa were subsampled for length and weight measurements. The data were not adjusted for nonrecovery of fish.

### Data Analysis

Water quality, zooplankton, and cove rotenone fish data were analyzed with split-plot repeated measures ANOVA (Maceina et al. 1994, Littell et al. 2002). The main plot tested treatment period (i.e., pre-alewife *vs.* alewife years), and treatment nested within sample location while the subplot included time (time 1 defined as first year of each treatment period, time 2 defined as second year of each treatment peri-

**Table 1. (Continued)**

| | Year | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1993 | | 1995 | | 1997 | | 2000 | |
| Taxa | Density | Biomass | Density | Biomass | Density | Biomass | Density | Biomas |
| Alewife | 8 | <0.1 | 310 | 0.8 | 218 | 0.3 | 39,027 | 71.7 |
| Gizzard shad | 189 | 21.3 | 256 | 40.9 | 218 | 23.8 | 123 | 21.5 |
| Chain pickerel | 259 | 14.3 | 235 | 15.2 | 358 | 12.5 | 169 | 11.5 |
| Common carp | 1 | 3.2 | 1 | 2.6 | 4 | 11.9 | 3 | 7.7 |
| Creek chubsucker | 2 | 0.5 | 10 | 2.4 | 0 | 0 | 2 | <0.1 |
| *Moxostoma* spp. | 0 | 0 | 0 | 0 | 1 | < 0.1 | 0 | 0 |
| Bullhead catfishes | 0 | 0 | 91 | 0.1 | 173 | 0.4 | 78 | 0.2 |
| White catfish | 57 | 1.6 | 64 | 1.5 | 70 | 5.2 | 28 | 0.8 |
| Yellow bullhead | 88 | 4.4 | 176 | 4.6 | 81 | 6.4 | 27 | 1.4 |
| Brown bullhead | 5 | 0.1 | 8 | 1.0 | 8 | 0.5 | 4 | <0.1 |
| Eastern mosquitofish | 359 | 0.2 | 136 | <0.1 | 166 | <0.1 | 147 | <0.1 |
| *Lepomis* spp. | 2 | <0.1 | 12 | 0.3 | 3 | <0.1 | 4 | <0.1 |
| Redbreast sunfish | 181 | 2.3 | 198 | 1.5 | 57 | 0.5 | 32 | 0.4 |
| Green sunfish | 205 | 1.7 | 109 | 0.8 | 205 | 1.2 | 31 | 0.2 |
| Pumpkinseed | 86 | 1.0 | 40 | 0.3 | 36 | 0.5 | 0 | 0 |
| Warmouth | 1,958 | 14.7 | 1,274 | 12.2 | 1,256 | 13.4 | 1,111 | 5.8 |
| Bluegill | 27,379 | 79.5 | 47,017 | 102.3 | 36,133 | 103.4 | 20,859 | 77.1 |
| Redear sunfish | 327 | 7.8 | 242 | 7.0 | 281 | 9.1 | 151 | 10.1 |
| Largemouth bass | 539 | 8.9 | 390 | 6.9 | 719 | 10.9 | 241 | 8.0 |
| *Pomoxis* spp. | 136 | 2.1 | 56 | 3.3 | 206 | 3.1 | 82 | 3.7 |
| Other taxa[a] | 280 | 3.0 | 304 | 8.3 | 241 | 9.3 | 201 | 8.6 |
| Total | 32,061 | 166.8 | 50,929 | 212.1 | 40,434 | 212.7 | 62,320 | 229.1 |
| Number of taxa | 23 | | 23 | | 24 | | 21 | |

od, etc.), and a treatment×time interaction term. Treatment period (i.e., pre-alewife *vs.* alewife years) nested within the sample location (i.e., transect or station) was used as the error term for testing treatment effects. For cove rotenone data, 1991 was dropped from the pre-alewife years to balance the data set for statistical analysis (i.e., n = 8 for pre-alewife and alewife years). Zooplankton and cove rotenone data were normalized with a $\log_e$ transformation prior to statistical analyses with the General Linear Models Procedure of the Statistical Analysis System (SAS 1990). A Type I error rate of 5% ($\alpha = 0.05$) was used to judge the significance of the tests.

## Results

### Fish Community

Alewives were initially discovered in the reservoir during 1993 and constituted <1% of the total fish mean density and biomass (Table 1). The suspected source of the alewife introduction was either through accidental release from an angler's bait tank or an intentional release by anglers. No shad species were stocked in the reservoir by the North Carolina Wildlife Resources Commission that could have served as an introduction source for alewife (S. L. Van Horn, North Carolina Wildlife Resources Commission, pers. commun.). The closest known population of alewife existed in the Dan River and Kerr Reservoir, approximately 20 km from Mayo Reservoir. The exact year of alewife introduction could not be determined but probably occurred sometime during 1992 or 1993. Alewife were absent in cove rotenone samples obtained from 1985 to 1991. Additionally, alewife did not appear in electrofishing samples collected by Progress Energy until 1993 (Carolina Power and Light 1994).

Alewife established a self-sustaining population and expanded over a 7-year period (Table 1). The largest increase in alewife abundance in cove rotenone samples occurred from 1997 to 2000. By 2000, the species comprised 63% and 31% of the total fish mean density and biomass, respectively. Alewife was the numerically dominant species in cove rotenone samples during 2000 and was the second to bluegill as the most abundant species by biomass. Actual abundance of limnetic alewives in Mayo Reservoir was likely underestimated by the cove rotenone sampling, which typically provides more representative samples of shallow water, littoral-dwelling species (Bettoli and Maceina 1996). Thus, alewife may have constituted an even greater proportion of the Mayo Reservoir fish community than estimated with cove rotenone.

Changes in the native fish community following the alewife introduction were minimal (Table 1). The number of collected taxa was greater in the period prior to alewife introduction (25–31), although taxa richness during 1985 and 1986 may have reflected early impoundment conditions. Some species (e.g., redfin pickerel [*Esox americanus americanus*] and comely shiner [*Notropis amoenus*]) declined in abundance with reservoir stabilization and establishment of lentic species. Generally, fish taxa richness in cove rotenone samples was similar immediately before and after the alewife introduction.

No significant differences in density or biomass ($P > 0.05$) were observed for gizzard shad, brown bullhead, yellow bullhead, white catfish, bluegill, redbreast sunfish, warmouth, crappie spp., or largemouth bass between the pre-alewife and alewife periods (Table 1). However, the mean weight per gizzard shad increased after the alewife introduction, which indicated a shift in the population to larger, older individuals (i.e., 93 g/fish for 1985–1991 and 139 g/fish for 1993–2000). Prior to the alewife introduction, gizzard shad ranked as the first or second most abundant species by biomass. Alewife surpassed gizzard shad as the dominant clupeid during 2000, the last year of the study.

Chain pickerel density ($F_{1,22} = 19.4$, $P = 0.01$) and redear sunfish density ($F_{1,22} = 34.3$, $P = 0.004$) and biomass ($F_{1,22} = 20.6$, $P = 0.01$) significantly increased during the alewife period and reflected the increased aquatic vegetation in the reservoir during the mid 1980s, which these species favor (Table 1). Conversely, green sunfish density ($F_{1,22} = 7.3$, $P = 0.05$) and pumpkinseed density ($F_{1,22} = 12.1$, $P = 0.03$) and biomass ($F_{1,22} = 13.5$, $P = 0.02$) significantly declined between the pre-alewife and alewife periods. Decreased abundance of these lepomid species may have been related to predation from the increased chain pickerel population or competitive interactions with other lepomids (e.g., redear sunfish, bluegill, and warmouth).

### Water Quality

Total nitrogen (TN) and total phosphorus (TP) concentrations were low, and the TP concentrations were indicative of oligotrophic conditions. TN:TP ratios indicated

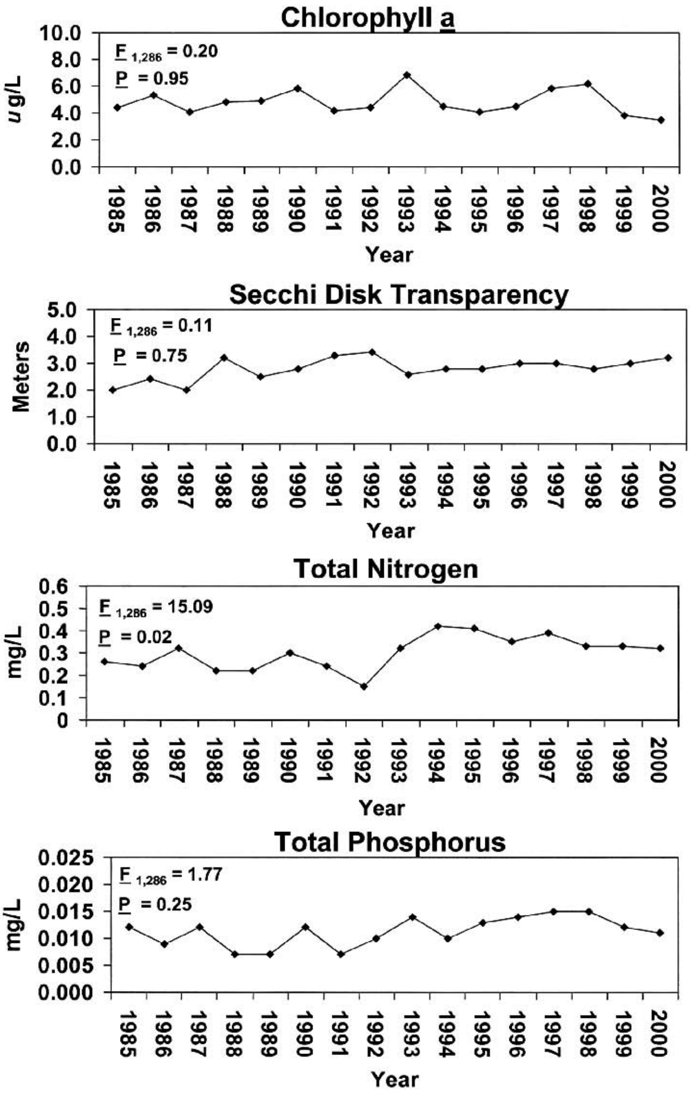


**Figure 2.** Temporal trends of chlorophyll *a*, Secchi disk transparency depth, total nitrogen, and total phosphorus in Mayo Reservoir, 1985–2000. Note that results of split-plot repeated measures ANOVA are shown in each graph.

phosphorus-limiting trophic conditions prior to and after the alewife introduction (i.e., 21–34 for 1985–1992 and 14–43 for 1993–2000). Total nitrogen concentrations significantly increased after the alewife introduction; however, total phosphorus concentrations did not show the same pattern (Fig. 2). Chlorophyll *a* concentrations were low and did not significantly differ between the pre-alewife and alewife periods (Fig. 2). Correspondingly, Secchi disk transparencies did not significantly differ between the two periods.

### Zooplankton Community

Significant changes occurred in the zooplankton community composition following the alewife introduction (Table 2). *Onchyodiaptomus birgei*, a dominant large-bodied calanoid copepod, and calanoid copepodites significantly decreased in density and biomass between the pre-alewife and alewife periods. Prior to the alewife introduction (1985–1992), the mean density of *Onchyodiaptomus birgei* was 2,080 organisms/$m^3$, but declined to 64 organisms/$m^3$ during the 1993–2000 period when alewives were present. Biomass of *Onchyodiaptomus birgei* also showed a marked decline, which resulted in a concomitant significant decrease in total copepod biomass. Similarly, most larger to mid-sized cladocerans (0.8–1.5 mm) (i.e., *Daphnia* spp., *Diaphnanosoma brachyurum*, *Holopedium gibberum*, and total cladocerans) significantly declined in density and biomass following the alewife introduction (Table 2). Overall mean densities and biomass of these taxa declined by 76%–89% after the alewife introduction. Marked declines in the abundance of *Onchyodiaptomus birgei*, *Daphnia* spp., *Diaphanosoma brachyurum*, and *Holopedium gibberum* occurred in 1994, one year after alewife were detected in the reservoir. *Ceriodaphnia* spp. was the only larger cladoceran that did not significantly differ in density or biomass between the two periods.

Smaller-bodied zooplankton (< 0.5 to 0.7 mm) either did not show any significant differences or significantly increased between the pre-alewife and alewife periods (Table 2). The cyclopoid *Tropocyclops prasinus*, cyclopoid copepodites, the rotifers *Keratella cochlearis* and *Polyarthra* spp., and total rotifers significantly increased between treatment periods. The mean density of *Tropocyclops prasinus* for the 1993–2000 period (1,000 organisms/$m^3$) increased by a factor of 7.9 when compared to the mean density for the 1985–1992 period (126 organisms/$m^3$). The mean density of total rotifers approximately doubled between the two periods (i.e., 22,170 organisms/$m^3$ for 1985–1992 *vs.* 45,498 organisms/$m^3$ for 1993–2000). *Bosmina longirostris* abundance did not significantly differ between treatment periods. *Bosmina longirostris* remained the dominant cladoceran before and after the alewife introduction. Copepod nauplii and *Mesocyclops edax* also did not show any significant temporal trends. *Mesocyclops edax* was a minor copepod taxa before and after the alewife introduction.

## Discussion

Introduction of alewife into Mayo Reservoir resulted in a self-sustaining population. The actual initial size of the introduced alewife population was unknown; however, the species did not become a dominant component of the fish community until four to seven years after detection. The buildup of the alewife population, as determined with cove rotenone samples, appeared slower in Mayo Reservoir as compared to other documented introductions from nearby lakes. Kohler and Ney (1981) reported that alewife became the dominant species in Claytor Lake, Virginia, within two years after introductions in 1968 and 1969. Differences in the expansion rates of introduced populations were likely related to initial stocking size, which suggested

**Table 2.** Results of split-plot repeated measures ANOVA of zooplankton taxa densities ($N/m^3$) and biomass ($mg/m^3$) from Mayo Reservoir, 1985–2000[a].

| Taxa | 1985–1992 Mean | 1993–2000 Mean | *F* | *P* |
|---|---|---|---|---|
| | Density ($N/m^3$) | | | |
| Copepods | | | | |
| *Mesocyclops edax* | 372 | 510 | 2.28 | 0.21 |
| *Tropocyclops prasinus* | 126 | 1,000 | 87.99 | <0.001 |
| Cyclopoid copepodites | 732 | 3,006 | 111.99 | <0.001 |
| *Onchyodiaptomus birgei* | 2,080 | 64 | 722.05 | <0.001 |
| Calanoid copepodites | 1,076 | 127 | 34.14 | 0.004 |
| Copepod nauplii | 6,676 | 5,684 | 2.05 | 0.22 |
| Total copepods | 11,933 | 10,587 | 1.03 | 0.37 |
| Cladocerans | | | | |
| *Bosmina longirostris* | 3,505 | 5,307 | 0.04 | 0.85 |
| *Ceriodaphnia* spp. | 2,045 | 946 | 2.20 | 0.21 |
| *Daphnia* spp. | 1,813 | 433 | 70.87 | 0.001 |
| *Diaphanosoma brachyurum* | 845 | 166 | 577.94 | <0.001 |
| *Holopedium gibberum* | 655 | 74 | 2005.34 | <0.001 |
| Total cladocerans | 9,013 | 7,071 | 22.42 | 0.009 |
| Rotifers | | | | |
| *Keratella cochlearis* | 6,215 | 19,997 | 7.88 | 0.05 |
| *Polyarthra* spp. | 4,544 | 5,518 | 537.36 | <0.001 |
| Total rotifers | 22,170 | 45,498 | 14.60 | 0.002 |
| | Biomass ($mg/m^3$) | | | |
| Copepods | | | | |
| *Mesocyclops edax* | 2.6 | 3.6 | 1.95 | 0.23 |
| *Tropocyclops prasinus* | 0.1 | 1.0 | 88.10 | <0.001 |
| Cyclopoid copepodites | 1.0 | 4.2 | 119.77 | <0.001 |
| *Onchyodiaptomus birgei* | 28.5 | 0.9 | 694.29 | <0.001 |
| Calanoid copepodites | 2.2 | 0.3 | 30.81 | 0.005 |
| *Copepod nauplii* | 1.1 | 0.9 | 1.87 | 0.24 |
| Total copepods | 37.2 | 12.0 | 17.12 | 0.014 |
| Cladocerans | | | | |
| *Bosmina longirostris* | 1.7 | 2.6 | 0.02 | 0.88 |
| *Ceriodaphnia* spp. | 6.9 | 3.4 | 1.20 | 0.33 |
| *Daphnia* spp. | 7.4 | 1.4 | 68.93 | 0.001 |
| *Diaphanosoma brachyurum* | 1.4 | 0.2 | 581.43 | <0.001 |
| *Holopedium gibberum* | 2.0 | 0.3 | 1296.03 | <0.001 |
| Total cladocerans | 19.4 | 7.9 | 153.68 | <0.001 |
| Rotifers | | | | |
| *Keratella cochlearis* | <0.1 | 0.2 | 6.19 | 0.07 |
| *Polyarthra* spp. | 0.8 | 1.0 | 262.14 | <0.001 |
| Total rotifers | 1.2 | 2.4 | 17.26 | 0.008 |

a. Degrees of freedom for *F* tests were 1,286.

the Mayo Reservoir population originated from a small number of introduced individuals.

Introductions of the selective-feeding planktivore in other lentic systems have resulted in restructuring of zooplankton community composition and a shift in dominance from larger-bodied to smaller-bodied taxa (Wells 1970, Hutchinson 1971, Kohler and Ney 1981, Hewett and Stewart 1989). In Mayo Reservoir, the zooplankton community showed similar shifts that coincided with the appearance of alewife and subsequent population expansion. Changes in the zooplankton community were evident within a year after alewife was detected, and smaller-bodied zooplankton taxa have dominated the community since 1993. Rapid shifts in zooplankton composition have been documented in other lentic systems where alewife abundance fluctuated through time with either die-offs or changes in the seasonal distribution of the population (Kohler and Ney 1981, Hewett and Stewart 1989, Evans 1990). No food habit studies were conducted during this study to confirm actual predation or selection of larger-bodied zooplankton taxa. However, the marked decline of mid- to larger-sized taxa following the alewife introduction, coupled with evidence from previous studies, implicated alewife in the changes of the Mayo Reservoir zooplankton community. Kohler and Ney (1981) reported that alewife diet was seasonally dominated by *Cyclops* sp., *Diaptomus reighardi, Daphnia retrocurva*, and *Diaphanosoma leuchtenbergianum* in the limnetic zone of Claytor Lake, Virginia. Hutchinson (1971) found alewives initially preyed upon larger copepods and cladocerans *(Diaptomus, Epischura, Mesocyclops*, and *Daphnia)* in Black Pond, Connecticut, but shifted their diet to small to mid-sized zooplankton and other larger invertebrates (*Bosmina, Holopedium, Cyclops, Macrocyclops, Tropocyclops*, and chironomid pupae) after larger-bodied taxa were eliminated from the zooplankton community.

Reductions in *Onchyodiaptomus birgei* and the larger cladoceran taxa likely resulted in reduced predation or competitive interactions with *Tropocyclops prasinus* and rotifers (mainly *Keratella cochlearis*), as abundance of these organisms increased after the alewife introduction. *Onchyodiaptomus birgei* was the dominant copepod in the reservoir prior to alewife introduction, whereas the dominance shifted to *Tropocyclops prasinus* after the *Onchyodiaptomus birgei* declined in abundance. In this study, abundance of the mid-sized cladoceran *Diaphanosoma* spp. was also reduced which may have reflected the efficient predation of alewife in the clear waters of the reservoir.

Although changes in the zooplankton community were evident, we were unable to detect consistent, concomitant changes in water quality following the alewife introduction. As predicted by the top-down control hypothesis, selective planktivorous fish predation on larger-bodied zooplankton and the resultant shifts to smaller taxa would reduce grazing pressure on the phytoplankton community, thereby reducing water clarity. Chlorophyll *a* concentrations did not significantly increase nor did water clarity decrease in Mayo Reservoir after removal of larger zooplankton by alewife. The lack of response in chlorophyll *a* may have been related to several factors: (1) the phosphorus-limiting conditions of the reservoir may have been more influential in controlling phytoplankton abundance than zooplankton filtering rates, (2) the increased abundance of smaller zooplankton and their subsequent phytoplankton filtering rates may have compensated for the loss of the larger filter-feeding taxa, or (3) that our bimonthly sampling time scale could not detect short-term water quality changes that occurred with the shift in the zooplankton community. The reservoir has a long hydraulic residence time (3 yr), so the loss of nutrients, zooplankton, or phytoplankton from the system was likely minimal. Other studies have also failed to detect strong long-term, annual linkages among trophic levels in larger, complex multi-species lentic systems (Lehman 1988, Evans 1992, McQueen et al. 1992). Evans (1992) evaluated long-term, historic data for Lake Michigan and determined that top-down effects attributed to alewife predation on zooplankton and subsequent phytoplankton abundance were inconclusive. The lack of top-down effects was attributed to interannual variability of zooplankton and alewife abundances, spatial sampling differences in phytoplankton and zooplankton, estimates of *Daphnia* grazing pressure, and historical water clarity data.

Resulting changes to the fish community, based on cove rotenone data, were variable, but minimal. Young-of-year recruitment and the subsequent abundance of gizzard shad, chain pickerel, bullhead catfishes, and the dominant centrarchids—bluegill, warmouth, redbreast sunfish, redear sunfish, largemouth bass, and crappie spp.—appeared unaffected following the alewife introduction. These populations either did not change or increased after 1993. Young-of-year of these species may have been able to spatially partition zooplankton food resources and utilize both zooplankton and benthic invertebrate prey in nearshore vegetated areas to minimize competitive interactions with alewife (Kelso and Ney 1985). *Egeria densa* and *Hydrilla verticillata* increased in littoral zone areas after the introductions in the mid 1980s, and these macrophytes provided additional cover and associated invertebrate food sources for fish species. Largemouth bass, the major piscivorous predator in the reservoir, apparently exerted minimal predation effect on alewife as the population continued to expand during the study.

The longer-term consequences of the alewife introduction on the native fish population in Mayo Reservoir remains unclear. The lag effect of the alewife expansion on native fish recruitment may not yet be fully realized as alewife did not become a dominant species in the fish community until the last year of this study. Alewife also supplanted gizzard shad as the dominant clupeid during the last study year that possibly was related to lower gizzard shad young-of-year recruitment from competitive interactions for food resources in the limnetic zone.

The zooplankton community structure will likely remain altered with the presence of alewife; however, the nutrient-limited conditions of the reservoir will also likely limit the production of alewife in the reservoir. There is the potential for alewife predation on larval fishes that may affect future young-of-year recruitment of native fishes, particularly in low flow years, when nutrient inputs into the reservoir may further limit primary and secondary production of food resources.

## Lessons Learned

Fishery managers are sometimes confronted with the consequences of introduction of non-native aquatic organisms into non-targeted waters through intentional or unintentional means. Water bodies that have not been stocked with non-native species in the same watershed or nearby watersheds of stocked water bodies may have a higher degree of risk from this type of introduction. Fishery managers need to determine the degree of risk of such introductions to a water body and weigh these consequences in making management decisions when stocking non-natives in nearby waters. Educational outreach programs may help to inform anglers on why certain water bodies are stocked with non-native species while others are not, due to differences in fish assemblages, water quality characteristics, the potential for escapement from the system, etc. Outreach programs can also inform the public of the benefits and consequences of non-native introductions on aquatic communities.

The Mayo Reservoir case history provided further evidence on how rapidly alewives can restructure limnetic zooplankton communities, even at low population levels. Even with the restructuring of the zooplankton community, the expected ecological effects of this introduction into Mayo Reservoir were not clearly evident compared to results from previous studies. The slow buildup of the alewife population, coupled with the reservoir's phosphorus-limiting conditions, may have accounted for the lack of a consistent trophic level response. Alewife may not yet have exerted its full influence on the fish community given that the population did not begin rapidly expanding until four to seven years after introduction. This study also suggested that largemouth bass, in oligotrophic reservoirs, might not exert a high degree of predation pressure on alewife populations.

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