

REPRODUCTION AND EARLY LIFE HISTORY OF A LANDLOCKED

POPULATION OF ALEWIFE (ALOSA PSEUDOHARENGUS)

IN CLAYTOR LAKE, VIRGINIA

by

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INTRODUCTION

The alewife (Alosa pseudoharengus) is one of several species of anadromous fish that have developed freshwater, landlocked populations. Landlocked alewife populations have existed for sometime in the Great Lakes and other inland waters throughout the northern United States.

Management implications of alewife introductions into freshwater systems center around their utilization as a forage species. Odell (1934) found that in Seneca Lake, New York, alewife populations provided forage for a variety of sportfish including lake trout, small-mouth bass, pickerel, and yellow perch. Gross (1959) reported similar results in Lake Hopatcong, New Jersey. Wagner (1972) showed that alewives in Lake Michigan were utilized by a number of inshore piscivorous fish. Other investigators (Dymond 1928; Eaton 1928; Royce 1951; Havey 1952; Graham 1954; Spiers 1974) have demonstrated the importance of alewives in the diet of certain salmonids in Lake Ontario and inland waters of New York and Maine.

There is substantial evidence, however, that alewife introductions may exert deleterious effects on resident fish species. In the Great Lakes, dominance by alewives resulted in a severe reduction of overall fishery productivity and species diversity (Smith 1968, 1970). Extreme size selectivity by alewives may cause shifts in zooplankton species and size composition toward small forms (Brooks and Dodson 1965; Brooks 1968; Wells 1970; Hutchinson 1971; Warshaw 1972). Alewives may compete with other fish species in life stages which may be size-dependent and size-selective planktivores (Galbraith 1967; Siefert 1972; Wong and Ward 1972; Brynildson and Kempinger 1973). In addition, alewives may

directly affect populations of other fish species by predation on young (Smith 1970; Wells and McLain 1972; Kohler and Ney 1980).

Despite these apparent risks, potential benefits of alewives as forage for pelagic predators has prompted their widespread consideration for introduction into southeastern U.S. reservoirs. One of the earliest such systems to receive alewives was Claytor Lake, Pulaski County, Virginia. Alewives were introduced into Claytor Lake in 1968 and 1969 by the Virginia Commission of Game and Inland Fisheries in an effort to establish a planktivorous, pelagic forage fish in the reservoir. Alewives were observed to reproduce by 1970 (Boaze 1972) and have subsequently become a major component of the species complex of Claytor Lake. Boaze (1972) evaluated alewives as forage in Claytor Lake. Kohler (1980) further developed this evaluation and analyzed trophic interactions of alewives with resident sport fish. However, information on reproduction and early life history of landlocked alewives is only available for northern waters.

Biology of Landlocked Alewives in Northern Waters

Reproduction

Freshwater populations of alewives in northern waters spawn in streams, rivers, and inshore areas of lakes and reservoirs. In the Great Lakes, alewives spawn on shoals in bays and in major rivers (Norden 1967a; Edsall 1970). Alewife spawning occurs in numerous shallow areas (2-4 m) in the Finger Lakes, New York (Odell 1934; Rothschild 1966) and Lake Hopatcong, New Jersey (Gross 1959). Spawning grounds are characterized by sand or gravel bottoms with moderate vegetative growth (Gross 1959; Rothschild 1966).

Massive inshore movements of alewives into shallow water (<10 m) occur as water temperatures approach 10 C; in late April and early May in Lake Michigan (Edsall 1964; Norden 1967a) and Lake Hopatcong (Gross 1959) and in late May in the Finger Lakes (Odell 1934; Rothschild 1966). Spawning occurs at water temperatures of 13 to 27 C (Gross 1959; Rothschild 1966; Norden 1967a; Edsall 1970; Hardy 1978). The spawning period is variable, extending from late May to late August in Lake Ontario (Pritchard 1929; Graham 1956), Lake Michigan (Norden 1967a), and Lake Erie (Comm. Fish. Rev. 1961); late May to late June in Lake Hopatcong (Gross 1959); and early June to late August in the Finger Lakes (Odell 1934; Rothschild 1966).

Spawning behavior of landlocked alewives has been observed both diurnally and nocturnally. Greatest activity reportedly occurs at night (Graham 1956; Gross 1959; Edsall 1964; Rothschild 1966). In Cayuga Lake, New York, males appear on the spawning grounds first and females shortly afterward (Rothschild 1966). The spawning act involves two or more individuals which swim rapidly toward the water surface in a spiraling motion, break the surface, then descend rapidly towards the bottom while releasing sex products into the water column (Edsall 1964; Rothschild 1966).

Landlocked alewives of both sexes in Lake Hopatcong and Cayuga Lake mature in their third year of life at 102 to 142 mm TL (Gross 1959; Rothschild 1966). In Lake Ontario, males mature at age I at a mean of 127 mm TL and females at age II at a mean of 145 mm TL (Pritchard 1929).

The number of eggs per spawning female in landlocked alewife populations has been variously estimated to range from 10,000 in the Finger

Lakes (Odell 1934; Rothschild 1966) to 22,000 in Lake Michigan (Norden 1967a). Alewife eggs are broadcast at random, are essentially non-adhesive, and are demersal (Scott and Crossman 1973; Hardy 1978). Time from fertilization to hatching varies inversely with water temperature, ranging from two days at 28.9 C to 15 days at 7.2 C (Belding 1921; Bigelow and Welsh 1925; Mansueti and Hardy 1967; Cianci 1969; Edsall 1970).

Early Life History

At hatching, alewife larvae average 3.5 to 5.0 mm TL in Chesapeake Bay (Mansueti and Hardy 1967), 3.8 mm TL in Lake Michigan (Norden 1967b), and 4.1 mm TL in Bride Lake, Connecticut (Cianci 1969). The transition from prolarvae to postlarvae usually occurs the fourth day after hatching at 5.0 to 7.0 mm TL (Norden 1967b; Cianci 1969). Landlocked alewife larvae in Lake Michigan (Norden 1967a) and Cayuga Lake (Rothschild 1965) reach 15 mm TL by the end of their first month. Alewives hatched in mid-June in Lake Hopatcong (Gross 1959) and the Finger Lakes (Odell 1934; Rothschild 1965) average 40 to 60 mm TL by August and 90 to 120 mm TL by mid-October.

Abundance of larval (<30 mm TL) alewives in Lake Michigan (Wagner 1971) and Lake Huron (O'Gorman 1977) is closely related to shoreline topography with the highest densities of larvae in embayments and coves and the lowest densities off sections of featureless shoreline. In Lake Huron, the greatest concentrations of larvae are usually 1 to 3 m beneath the water surface (O'Gorman 1977). Larvae remain on spawning grounds until they reach 20 mm TL at which time they move to deeper (>10 m) water (Wagner 1971; O'Gorman 1977).

In Lake Michigan, copepods are the most common food item in the diet of larval alewives, especially those under 25 mm TL (Norden 1968; Wagner 1971). Diet composition of larval alewives in the Cape Fear River system in North Carolina is similar, but also includes crustacean eggs and dipteran parts (Davis and Cheek 1966). Larval alewives in Lake Michigan positively select for copepods and cladocerans although the relative abundance of these zooplankters in the diet is directly proportional to their abundance in the water column (Norden 1968).

Goals and Objectives

Latitudinal trends in life history strategies have been demonstrated in fish (Stearns 1976, 1977; Leggett and Carscadden 1978). As latitude decreases and food availability and/or quality increases, fish populations often exhibit faster growth, higher relative fecundity, and earlier age at maturity (Svardson 1949; Scott 1962; Nikolsky 1963; Bagenal 1969). Boaze (1972) found that alewives in Claytor Lake grow faster than their counterparts in more northerly waters (Odell 1934; Graham 1956; Gross 1959; Rothschild 1965; Norden 1967a). Correspondingly, warmer climate and more favorable growth conditions in Claytor Lake may allow increased fecundity, egg and larval survival, and recruitment to the alewife population.

Considering the negative effects that alewife populations may have on populations of other fish species and the lack of description of alewife biology in southeastern reservoirs, this investigation was initiated to describe and compare reproductive life history characteristics of the alewife in Claytor Lake. Specifically, objectives were:

- 1) to describe alewife reproduction in Claytor Lake

- a) to characterize age and size at maturity and estimate fecundity
- b) to identify spawning locations, describe spawning behavior, and delineate spawning period
- 2) to determine distribution and growth of young-of-the-year alewives
- 3) to examine food habits of young-of-the-year alewives
 - a) to determine diet composition
 - b) to describe the relationship between diet and food resource
 - c) to document changes in size of food items with changes in larval alewife size
- 4) to assess the manner in which these characteristics affect the benefits and risks of alewife introductions into southeastern reservoirs.

METHODS AND MATERIALS

Study Area

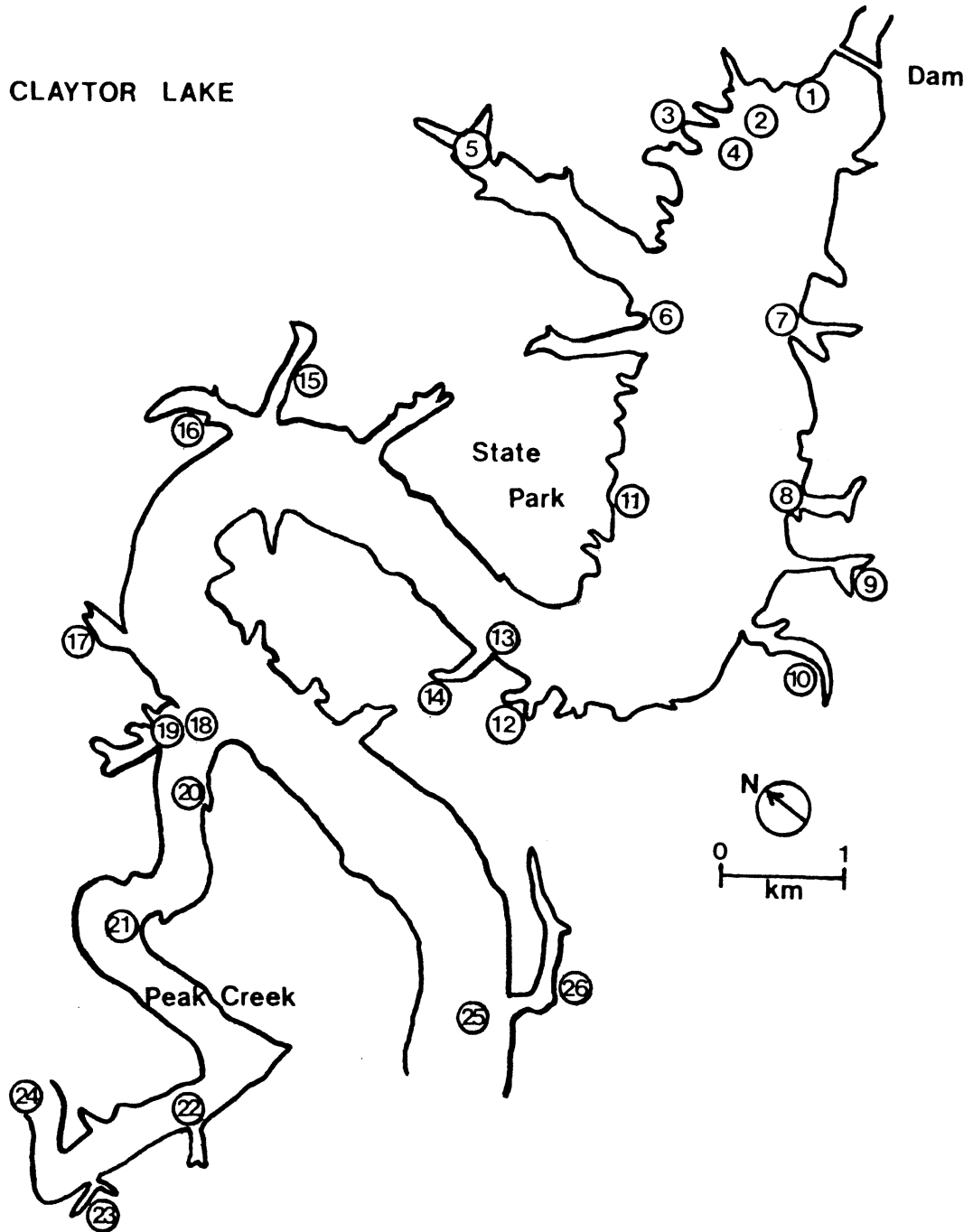
Claytor Lake is a mainstream hydroelectric impoundment of the New River formed in 1939 in Pulaski County, Virginia (Fig. 1). The reservoir has a drainage area of 6.14×10^5 ha with an average total inflow of 97.8 cms and a retention time of 63 days (U.S.E.P.A. 1978). At normal pool elevation of 663 m above mean sea level, the reservoir has a surface area of 1820 ha and a mean depth of 29 m. Claytor Lake includes approximately 161 km of shoreline containing several shallow coves which have little rooted aquatic vegetation. Major littoral regions (<5 m) are restricted to the northwestern section of the reservoir near the dam and grade steeply into the profundal zone.

Claytor Lake is dimictic, exhibiting characteristic spring and fall turnovers. Anoxic conditions occur in summer in the hypolimnion (Boaze 1972). Ice-cover commonly occurs from mid-January to March. Turbidity varies with inflow; a typical summer Secchi reading is 1.5 m (U.S.E.P.A. 1978). Median alkalinity is 32 mg/l CaCO_3 and median conductivity is 9 mhos (U.S.E.P.A. 1978). The reservoir is considered moderately eutrophic.

Field Collections

Study of reproductive and early life history characteristics of the alewife in Claytor Lake involved collection of adults, eggs, larvae, and juveniles. Adult alewives were caught to characterize age and size at maturity, estimate fecundity, and examine temporal changes in gonadal condition. Alewife eggs were sampled to identify spawning areas and delineate spawning period. Larval and juvenile alewives were collected

Fig. 1. Location of sampling sites for alewife adults, eggs, larvae, and juveniles, June through December 1978 and March through December 1979, Claytor Lake, Virginia.



to determine distribution, calculate first year growth, and examine food habits.

Samples were collected during ice-free months from April 1978 through December 1979. Sampling season and gear type varied for each life stage collected (Fig. 2). Water temperatures were recorded coincident with larval and adult sampling at 1-m intervals from the surface to 6 m depth with a Yellow Springs Instrument Model 54 thermister calibrated in the laboratory against a mercury thermometer.

Adult Alewives

In 1978, initial sampling for adult alewives was conducted from April through June at 25 locations between the dam and Peak Creek (Fig. 1 and Table 1). Each location had characteristics of alewife spawning grounds as described in the literature, i.e. mean depth less than 10 m, sparse to moderate vegetation, and sand, gravel or coarse-stone substrate. Five multifilament nylon horizontal gill nets were set for 12-hour periods overnight so that each location was sampled every two weeks. Three nets were 60 m long x 2 m deep with 25-mm bar mesh and two nets measured 30 m long x 2 m deep with 13-mm bar mesh. Sampling was modified in June when ripe adult alewives were located in an embayment on the western side of the reservoir immediately upstream from the dam (Fig. 1 and Table 1). The number of horizontal gill nets was reduced to two (one 25-mm and one 13-mm bar mesh) and efforts were confined to the embayment through December.

In 1979, an expanded total sampling regime required that gill netting be limited to three sites representing different potential spawning habitat (Fig. 1 and Table 1). The first (Site 1) was a large embayment

Fig. 2. Sampling season and gear type used to collect various life stages of alewives, 1978 and 1979, Claytor Lake, Virginia.

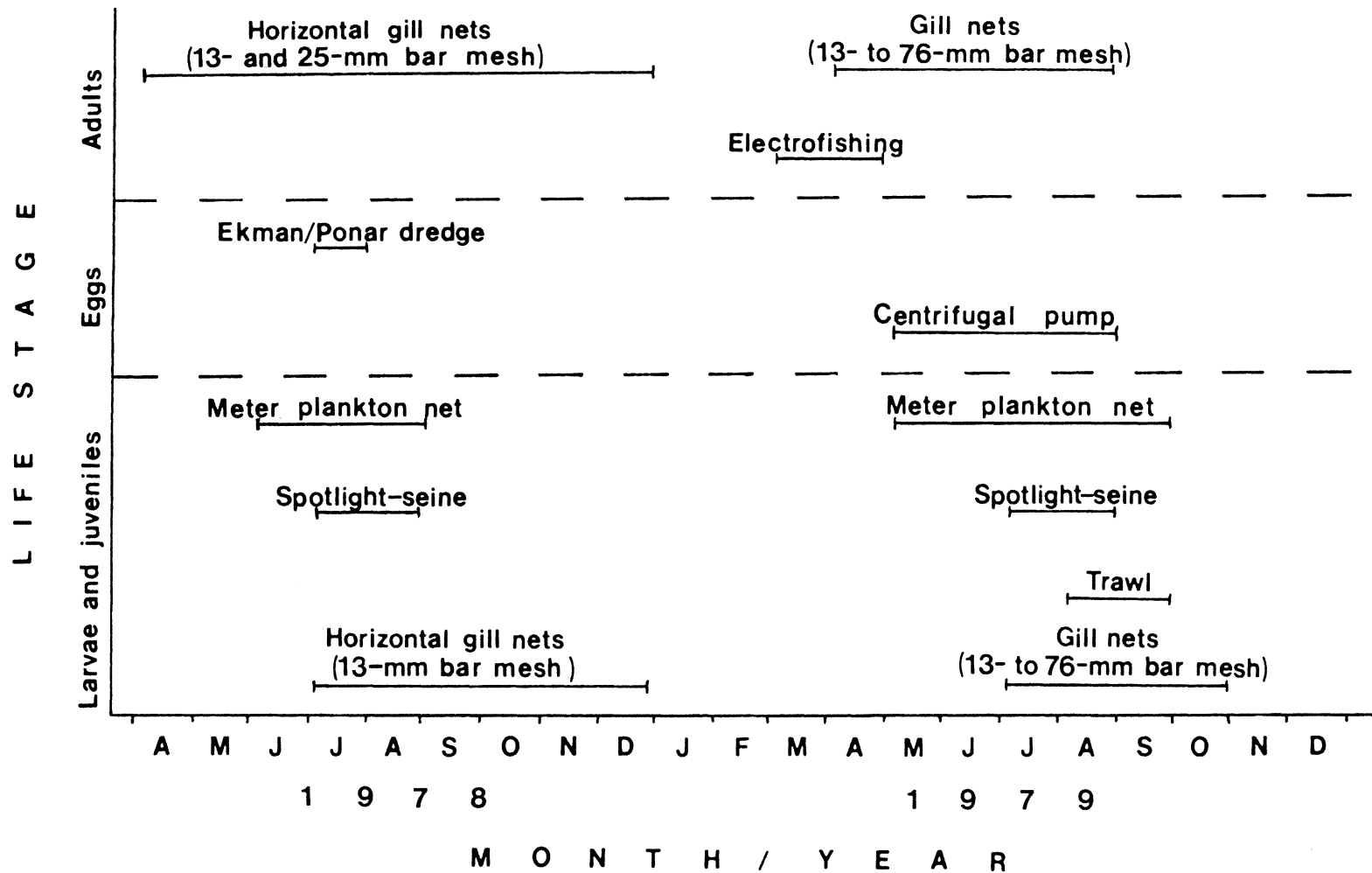


Table 1. Description of sampling sites and number of collections for alewife adults (A), fertilized eggs (E), larvae (L), and juveniles (J), June through December 1978 and March through August 1979, Claytor Lake, Virginia.

Site ^a	Location	Maximum depth (m) sampled	Upstream distance (km)	Collections							
				1978				1979			
				A	E	L	J	A	E	L	J
1	Embayment	8	0.40	26	4	8	11	15	18	15	8
2	Island shoal	10	0.83	7	-	-	-	-	-	-	8
3	Small cove	5	1.33	7	-	-	-	8	18	15	8
4	Mainstream shoal	15	1.03	7	-	-	-	-	-	-	8
5	Dublin Hollow	3	3.62	6	-	-	-	8	18	15	8
6	Chimney	6	2.38	7	-	-	-	-	-	15	8
7	Ridpath Hollow	12	2.38	4	-	-	-	-	-	-	-
8	Cook Hollow	12	3.71	4	-	-	-	-	-	-	-
9	Texas Hollow	12	4.21	4	-	-	-	-	-	-	-
10	Spooky Hollow	4	5.04	4	-	-	-	-	-	-	-
11	State Park	5	4.05	7	-	-	-	-	-	15	-
12	Spring Hollow	4	6.87	11	-	-	-	-	-	-	-
13	Mainstream shoal	15	7.37	7	-	-	-	-	-	15	-
14	Bighole Hollow	3	7.53	11	-	-	-	-	-	-	-
15	Smith Hollow	12	9.03	4	-	-	-	-	-	-	-
16	Felts Hollow	12	9.19	4	-	-	-	-	-	-	-
17	Newbern Hollow	4	12.19	11	-	-	-	-	-	-	-
18	Mouth Peak Creek	15	12.69	6	-	-	-	3	-	15	-
19	Baptist Camp	5	13.02	11	-	-	-	-	-	-	-
20	Cove Peak Creek	5	13.19	4	-	-	-	-	-	-	-
21	Mainstream Peak Creek	6	14.36	6	-	-	-	-	-	-	-
22	Cove Peak Creek	4	16.19	4	-	-	-	-	-	-	-
23	Cove Peak Creek	3	16.69	6	-	-	-	-	-	15	-
24	Rock House Marina	3	17.52	6	-	-	-	-	-	-	-
25	Mainstream Channel	40	15.69	-	-	-	-	-	-	15	-
26	Clapboard Hollow	4	15.85	4	-	-	-	-	-	15	-

^a Corresponds to Fig. 1.

immediately upstream from the dam; the second (Site 3) was a small exposed cove 1.1 km upstream from the dam; the third (Site 5) was Dublin Hollow, 1.5 km west at the main channel. An experimental gill net measuring 91.5 m long x 2 m deep and consisting of six 15.2-m panels of 13-, 19-, 25-, 38-, 51-, and 76-mm bar mesh was set overnight at each site once a week from April through August.

Additional adult alewives were collected from horizontal gill nets set from October through December, 1977 and 1978, by the Virginia Commission of Game and Inland Fisheries; vertical gill nets (Kohler et al. 1979) set from December 1977 through August 1979 for a concurrent study; and electrofishing during March and April 1979. Subsamples of female alewives collected prior to spawning in April 1979 were placed on ice, transported to the laboratory, and frozen for use in estimating fecundity. Other adult alewives collected were preserved in 10 percent formalin, transported to the laboratory, and transferred to 40 percent propanol to facilitate handling during later laboratory analyses.

Alewife Eggs

In 1978, attempts to collect demersal alewife eggs were made in July with Ekman and Ponar dredges. Efforts were concentrated in an embayment (Site 1) where concurrent gill netting operations collected ripe adult alewives (Fig. 1 and Table 1). Rocky substrate and an abundance of sunken debris prevented the dredges from properly closing, however, and samples could not be secured.

In 1979, benthic samples were collected from May through August with a portable centrifugal pump (8.8 l/s). Sampling sites were coincident with those of gill netting operations (Fig. 1 and Table 1). The

intake hose was weighted and towed along the bottom. Five-minute tows were made parallel to and approximately 10 m from shore. During each tow approximately 2650 l were filtered through a 1.0-m diameter plankton net (330 micron mesh). Samples were preserved in two percent formalin to prevent shrinkage of eggs (Bagenal 1978) and transported to the laboratory for further analyses.

Larval and Juvenile Alewives

Sampling for larval (<35 mm TL) alewives was conducted twice each week from June through August 1978 and May through September 1979 using a 1.0-m diameter plankton net with 330 micron mesh towed at 100 m/min. In 1978, sampling was restricted to littoral (<5 m) regions in an embayment (Site 1) where ripe adult alewives were concurrently collected (Fig. 1 and Table 1). In 1979, in order to determine larval distribution within the reservoir, efforts were expanded to include 10 sites in littoral and limnetic (>20 m) regions from the dam to 15.0 km upstream (Fig. 1 and Table 1).

Duration of larval fish tows varied from three to five minutes depending upon zooplankton concentrations which, when heavy, clogged the net and overflowed the collection bucket. Volume of water filtered was calculated from readings of a digital flow meter suspended at the mouth of the net. Tows were conducted between 0600- and 1200-h in the upper 3 m of the water column. Other studies (Graham 1956; O'Gorman 1977) showed a significant drop in larval alewife concentrations below 3 m and found no difference between daytime and nighttime collections.

Sampling for juvenile (35 to 160 mm TL) alewives was conducted to determine growth rate and food habits and was thus concentrated in the

lower reservoir where the highest concentrations of spawning adult and larval alewives were found (Fig. 1 and Table 1). Juvenile alewives 35 to 80 mm TL were collected with a midwater trawl and spotlight-seine apparatus (G. Martel and J. Jesse, personal communication) whereas juveniles greater than 80 mm TL were captured with horizontal (13-mm bar mesh) and experimental gill nets.

The spotlight-seine apparatus consisted of a 12-volt, single-beam spotlight, a rheostat to adjust beam intensity, and a 2.5 m long x 1.0 m wide seine with 6-mm bar mesh (Fig. 3). The seine was suspended vertically by pulleys from the front of the boat. Juveniles were attracted to the spotlight and concentrated just below the water surface by decreasing beam intensity. Fish were captured by raising the seine from below. Samples were collected after dark once a week from July through August 1978 and 1979. The trawl measured 4 m wide x 2 m deep x 8 m long with cod-end mesh of 6 mm. Tows at 83 m/min were made just below the water surface in depths of 10 to 30 m. Samples were collected after dark twice weekly in August and September 1979.

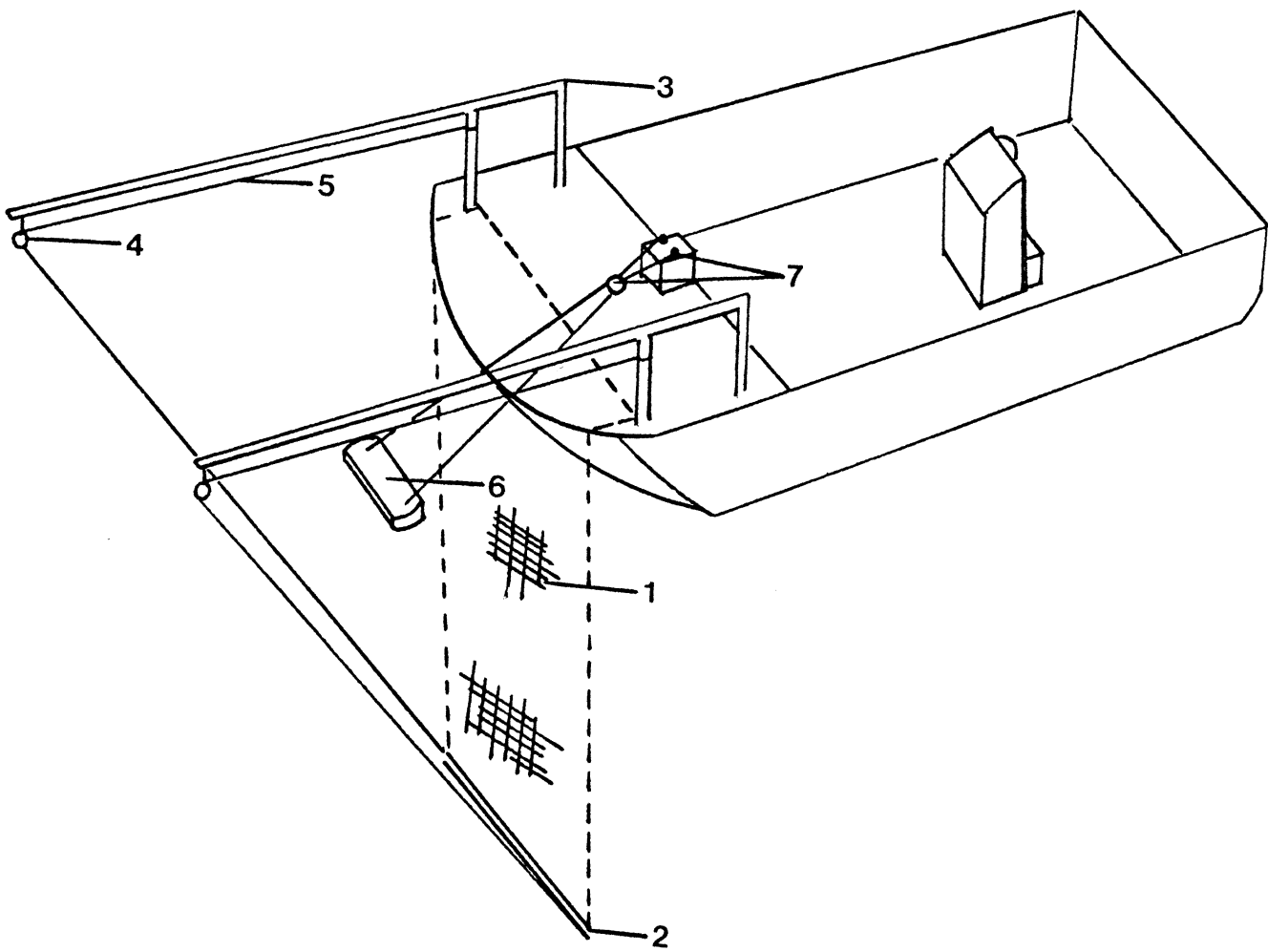
Gill nets were set once a week for 12-hour periods overnight. Two horizontal gill nets were used from July through December 1978 and two experimental gill nets from July through October 1979. Additional juvenile alewives were collected from concurrent sampling for other studies.

All larval and juvenile alewives were preserved in 10 percent buffered formalin (Bagenal 1978), transported to the laboratory, and transferred to 40 percent propanol for further laboratory analyses.

Laboratory Analyses

Various laboratory analyses were performed on field collections.

Fig. 3. Spotlight-seine apparatus: (1) seine, (2) weighted spreader bar, (3) outrigger supports, (4) pulley, (5) retrieval line, (6) 12-volt single-beam spotlight with styrofoam float collar, (7) 12-volt battery and rheostat.



Scales of gonads of adult alewives were examined to determine age and size at maturity, estimate fecundity, and describe temporal changes in condition of gonads. Alewife eggs and larvae were identified, sorted, and enumerated by date and location. Total lengths of larval and juvenile alewives were recorded for growth determinations and digestive tracts removed for analyses of food habits.

Adult Alewives

Total length, wet body weight, sex, and state of maturity were determined for each of 1088 adult alewives collected. Ovaries were removed from 785 mature females to estimate fecundity and calculate gonosomatic indices (gonad:body weight ratios) (LeCren 1951; Vladykov 1956). Alewives were considered: 1) immature when sexual organs were ribbon-like and minute, located close under the vertebral column, and transparent with no visible sexual products; 2) gravid when sexual organs filled the ventral cavity, but sexual products were not extruded with slight abdominal pressure; 3) ripe when milt and roe were easily extruded; and 4) spent when sexual organs were small, bloodshot, and translucent with some residual sexual products.

Fecundity, the number of ripening eggs in females prior to next spawning, was estimated for 50 gravid females collected in April 1979. Ovaries were removed and preserved for one month in modified Gilson's fluid (Simpson 1951; Bagenal 1978). Preservation by this method not only hardened the eggs, but helped separate them by breaking down ovarian tissue. Hardened eggs were washed, placed in a 50-ml graduated cylinder with a stirring bar, and then water was added to achieve a total volume of 40 ml. The mixture was stirred to evenly distribute

eggs in the cylinder while four 1-ml subsamples were taken. Mean number of eggs in subsamples was calculated and fecundity estimated by direct proportion.

A homogenous distribution of eggs within the graduated cylinder was assumed because the median numbers of eggs in subsamples taken from upper, middle, and lower strata were not significantly different ($p=0.316$, Friedman test) based upon eggs from 10 fish. Comparisons of actual direct count and estimated fecundity of three alewives, one from each age class present in samples, showed no significant differences ($p=0.250$, Wilcoxon signed-rank test).

Temporal changes in condition of ovaries of 735 female alewives collected from June 1978 through August 1979 were examined by calculating gonosomatic indices (GSI). Although some individual variation exists, GSI tend to remain constant at any one season for all sizes of fish of the same sex and state of maturity and correlate well with ovum diameters and diameter frequencies (LeCren 1951; Vladykov 1956; Shelton 1964; Behmer 1965; Johnson 1971). Ovaries were removed from mature female alewives, weighed wet (g), and GSI calculated by the modified formula of Vladykov (1956) as:

$$GSI = \frac{\text{combined ovary wt}}{\text{total body wt} - \text{combined ovary wt}} \times 100$$

Alewife Eggs

Alewife eggs were identified based upon measurements of diameter, physical descriptions, and applied knowledge of spawning period, locations, and habits of adult alewives as reported in the literature (Norden 1967b; Boreman 1976; Hardy 1978). Eggs were sorted by date of capture, enumerated, and density (number eggs/m³ water sampled) was

determined.

Larval and Juvenile Alewives

Alewives are described in this thesis as larvae when less than 35 mm TL and as juveniles when total length exceeds 35 mm. This distinction is based upon morphological development of the digestive tract and certain meristic characteristics (e.g. scales, gill rakers) which are incomplete in alewives less than 35 mm TL. In addition, alewife larvae are described as prolarval when yolk-sac is still evident and postlarval (≤ 10 mm TL) immediately after yolk-sac absorption.

Larval alewives were identified according to key characteristics described by previous investigators (Norden 1967b; Cianci 1969; Boreman 1976; Hardy 1978). Because alewife larvae are extremely small at hatching, are distinctively elongate with a preanal to postanal length ratio of 4:1, and characteristically exhibit a unique ventro-posterior flexing of the head over the yolk sac as prolarvae, identification was simplified. Furthermore, Claytor Lake contains no other clupeid species with which alewives may be confused. Larvae were sorted by date and location of capture, enumerated, and density (number larvae/m³ water sampled) was determined.

Distribution of total lengths of larval and juvenile alewives grouped by date of capture was determined. When sample size was less than 100, total lengths of all fish in the sample were determined. When sample size exceeded 100, length distribution was estimated from the median for each 1-mm length class of three subsamples. Subsamples were obtained using a sorting tray, 150 mm long x 150 mm wide, superimposed with a grid system which divided the surface of the tray into 25 equal

sized squares, each of which was systematically assigned a number. Samples were diluted to a volume of 250 ml, poured into the tray, and a random number generator used to designate five squares from which larvae were removed and total lengths determined. This process was repeated three times with replacement and total length distribution estimated by direct proportion. There was no significant difference ($p=0.500$, Wilcoxon signed-rank test) between actual and estimated length distributions from ten samples.

Larval and juvenile alewives 5 to 70 mm TL were grouped by date of capture into 5-mm length intervals. For each interval and date, digestive tracts containing food were removed from 10 fish (when available) and examined. Phytoplankton, rotifers, zooplankton, and insects were identified using appropriate keys (Edmondson 1959; Pennak 1978). For larval alewives below 20 mm TL, all food items in the digestive tract were used in analyses because no clear demarcation existed between stomach and intestine, and few food items were present. In larvae greater than 20 mm TL and juveniles, analysis included only food items present in the stomach.

Permanent slides of all food items, stained to facilitate identification, were made for each fish. Food items were identified using a phase microscope at 100 X, enumerated by species, and body dimensions (exclusive of terminal spines and setae) were measured to the nearest 0.01 mm using an ocular micrometer. Volume of each food item was determined indirectly by assigning each a geometric figure approximating its shape and computing volume from respective geometric formulae (Kutkuhn 1958; McComish 1967; Kohler 1980).

Relative abundance (percent total number) of major zooplankters in the water column (upper 6 m) during months in which larval and juvenile alewives were collected was calculated from estimates of monthly standing crop (Kohler 1980). Failure of these estimates to correspond to specific collection dates of larval and juvenile alewives and restriction of available data concerning these estimates to monthly medians precluded electivity analyses.

Data Analyses

Data concerning reproductive characteristics of adult alewives (age and size at maturity, fecundity, and spawning period) and aspects of early life history (growth, distribution, and food habits) were analyzed statistically. Non-parametric statistical procedures (Table 2) were used because they require fewer assumptions (normality, variance) about underlying populations from which data were obtained and are only slightly less efficient under conditions of normality than their parametric counterparts (Hollander and Wolfe 1973; Pirie and Hubert 1977). Probability of committing a Type I error was controlled at $p=0.05$.

Reproductive Characteristics

Age composition and size ranges of immature and mature alewives of both sexes were determined and median lengths of each compared (Table 2). Tests of ordered alternatives (Table 2) were used to define the relationship of age versus total length and fecundity and thus permit inference concerning the relationship of fecundity versus total length. This approach was used because total length was discontinuous between age classes and standard regression analysis was inappropriate. Comparisons were made among age classes of the median number of eggs per gram ovary

Table 2. Statistical procedures applied to analyze various data sets, 1978 and 1979, Claytor Lake, Virginia.

Data set	Statistical procedure
Lengths of immature vs. mature alewives	Wilcoxon rank-sum
Lengths vs. age of mature alewives	Jonckheere ordered-alternatives
Fecundities vs. age of mature alewives	Jonckheere ordered-alternatives
Eggs per gram ovary weight vs. age of mature alewives	Kruskal-Wallis oneway analysis
Fecundity vs. length within age classes of mature alewives	Spearman rank correlation
Fecundity vs. somatic body weight within age classes of mature alewives	Spearman rank correlation
Estimation of daily growth increment of young-of-the-year alewives, 1978 and 1979	Theil test for slope coefficient
Estimated daily growth increment, 1978 vs. 1979, of young-of-the-year alewives	Modified Sen procedure (W.R. Pirie, personal communication)
Percent prey in water column vs. percent prey in Y-O-Y alewife stomachs	Spearman rank correlation
Lengths of food items vs. lengths of larval alewives	Spearman rank correlation
Lengths of cyclopoid copepods in diet vs. lengths of larval alewives	Spearman rank correlation
Lengths of cyclopoid copepods in diet of Y-O-Y alewives vs. lengths of cyclopoid copepods in water column	Wilcoxon rank-sum
Lengths of cyclopoid copepods in diet of Y-O-Y vs. adult alewives	Wilcoxon rank-sum

weight (Table 2) to determine whether age-specific differences in development of maturing ova were present. The relationship of fecundity versus total length and somatic weight (body weight minus ovary weight) was defined within age classes (Table 2).

Mature female alewives were grouped by date of capture and median gonosomatic indices (GSI) were calculated to examine temporal changes in gonadal condition and to delineate spawning period. Spawning period was further defined by following changes over time in density of alewife eggs in benthic samples. Gonosomatic indices were also used to determine whether spawning was prolonged for individual female alewives by defining the relationship between GSI and reproductive stages and examining changes in GSI frequency distributions by month.

Early Life History

Analyses of first year growth were complicated by the disproportionately high number of small larvae in samples due to higher and more frequent success of 1.0-m diameter plankton net tows relative to other gear used to collect young-of-the-year. With the assumption that maximum lengths of larvae in samples represented the earliest cohort, i.e. those first spawned, regression analyses were applied to maximum rather than median total lengths (Table 2) in estimating daily growth increments during linear phase of growth. Comparisons were made of estimated daily growth increments of young-of-the-year alewives collected in 1978 and 1979 (Table 2).

Larval distribution within the reservoir was examined by calculating density (number per m^3) of larvae at each of 10 sampling sites. Distribution within the water column was inferred from catches with the

1.0-m diameter plankton net and from vertical gill net catches.

Food habits of young-of-the-year alewives were analyzed using frequency of occurrence, numerical, and volumetric methodology (Lagler 1956; Bagenal 1978). The relative importance of principal food items in the diet was examined by calculating their percent composition by number and volume. Frequency of occurrence of a particular food item was used to estimate the proportion of the population which utilized the item.

The relative abundance (percent total number) of major zooplankters in the water column (upper 6 m) was compared to their relative abundance in diets of young-of-the-year alewives (Table 2) grouped by total length and month of capture.

Median total lengths of all food items, and specifically of cyclopoid copepods, were determined and their relationship to total lengths of young-of-the-year alewives defined (Table 2). Comparisons of size-selective predation by young-of-the-year and adult alewives on cyclopoid copepods were made statistically (Table 2) and by examining percent deviations in size of copepods in diets versus water column.

RESULTS AND DISCUSSION

Analyses of data concerning reproduction and early life history of the alewife in Claytor Lake are described. Reproductive characteristics of adult alewives examined include age and size at maturity, fecundity, spawning behavior, spawning sites, and spawning period. Morphological development, first year growth, distribution, and food habits of larval and juvenile alewives were investigated as principal elements of early life history.

Reproduction

Age and Size at Maturity

The age composition of mature alewives in Claytor Lake was similar for 1978 and 1979 (Table 3). Eighty-six percent of all age I alewives of both sexes combined ($n=94$), ranging from 153 to 172 mm TL ($M=161$ mm TL), were sexually mature. Sexes were combined because of difficulty in determining sex of immature fish. Comparisons showed no statistically significant ($p=0.337$) difference in total lengths of sexually mature and immature individuals. All alewives examined above age I were sexually mature.

Information on age and size at maturity of landlocked alewife populations in other lacustrine systems is limited (Table 4). However, results of the present study indicate that landlocked alewives in Claytor Lake mature at an earlier age, although at approximately the same size, as landlocked populations in the Great Lakes (Pritchard 1929; Graham 1956; Norden 1967a) and other northern inland waters (Gross 1959; Rothschild 1966).

Earlier maturity may be a result of accelerated growth rates of

Table 3. Percent age composition of sexually mature alewives of both sexes, June through August 1978 and April through August 1979, Claytor Lake, Virginia. Median total lengths (mm) in parentheses.

Year	Male				Female			
	N	I	II	III	N	I	II	III
1978	345	40.2 (154)	54.0 (200)	5.8 (214)	255	42.8 (158)	50.0 (198)	7.2 (216)
1979	515	45.3 (160)	46.8 (210)	7.9 (218)	294	34.9 (161)	54.3 (216)	10.8 (225)

Table 4. Total lengths (mm) of mature fish, earliest age at maturity, and percent mature at earliest age of both sexes combined for various landlocked alewife populations in the United States.

Location	Sex	Total lengths	Age at maturity	Percent mature
Claytor Lake, VA (present study)	M, F	153-172	I	86
Lake Hopatcong, NJ (Gross 1959)	M, F	102-142	II	83
Cayuga Lake, NY (Rothschild 1966)	M, F	122	II	--
Lake Ontario (Pritchard 1929)	M F	127 145	I II	-- --
Lake Michigan (Norden 1967a)	M, F	130-189	II	54

alewives in Claytor Lake relative to populations in these northern systems (Boaze 1972; Kohler 1980) since in many fishes the onset of maturity is often related to the attainment of a certain size, and is often earlier in faster growing individuals (Nikolsky 1963). Tyus (1974) observed this in anadromous alewife populations; faster growing individuals in North Carolina mature one year younger than their counterparts in Maine (Havey 1961) or Connecticut (Marcy 1969).

Size of age I alewives in Claytor Lake did not appear to be a factor in determining maturity. However, the narrow range of total lengths of age I alewives in samples may indicate that smaller fish were not present in littoral areas or were not vulnerable to sampling gear.

Alewives of both sexes in Claytor Lake mature at the same age and approximately the same size. This is consistent with findings for alewife populations in Lake Hopatcong, New Jersey (Gross 1959), Cayuga Lake, New York (Rothschild 1966), and Lake Michigan (Norden 1967a), but conflicts with that in Lake Ontario (Pritchard 1929) where males mature one year earlier than females. Quality and quantity of available food, adult survivorship, and genetic adaptations to the reproductive environment have been cited as possible factors which influence age at maturity (Nikolsky 1963; Williams 1966; Bagenal 1969; Mathur and Ramsey 1974; Leggett and Carscadden 1978). Varying effects of interactions of these factors on different populations and on each sex within a population may be responsible for observed differences in the onset of maturity.

Fecundity

Median individual fecundity of gravid female alewives in Claytor Lake ranged from 17307 eggs at age I to 37147 eggs at age III (Table 5).

Table 5. Fecundity estimates, gonad weights (g), and number of eggs per gram ovary weight of gravid females by age for various landlocked alewife populations in the United States. Median total lengths (mm) and range of fecundity in parentheses.

Location	Age	Fecundity	Gonad weight	Eggs per gram ovary weight
Claytor Lake, VA (present study)	I (161)	17307 (13266-24026)	4.1 (3.6-5.8)	4221 (3904-4418)
	II (216)	35400 (27307-49200)	7.9 (6.7-8.4)	4481 (4179-4708)
	III (225)	39147 (31700-49022)	8.9 (7.6-10.1)	4398 (4012-4536)
Seneca Lake (Odell 1934)	III+(179)	--- (10000-12000)	---	--
Cayuga Lake, NY (Rothschild 1966)	II (120)	8750 (7771-9040)	---	--
	III (127)	7790 (5796-10011)	---	--
Lake Michigan (Norden 1967a)	II (160)	11147	3.3	3378
	III (176)	16138	4.4	3668
	IV (192)	22407	6.6	3395

There was a significant ($p < 0.002$) increase in total length and fecundity with age. In contrast, number of eggs per gram ovary weight did not differ significantly ($p = 0.291$) among age classes (Table 5). No significant ($p > 0.250$) correlation within age classes existed between fecundity and total length or somatic weight.

Fecundity of alewives in Claytor Lake is greater than that of corresponding age classes in landlocked populations in Lake Michigan (Norden 1967a), Seneca Lake, New York (Odell 1934), or Cayuga Lake, New York (Rothschild 1966) (Table 5). Factors that may influence egg production in fish are size of females and nutritional and environmental conditions prior to reproduction (Scott 1962; Nikolsky 1963; Bagenal 1969; Leggett and Carscadden 1978). Size of females is important because egg number is proportional to surface area of the ovary which, in turn, increases exponentially with fish length (Bagenal 1967). Nutritional and environmental conditions during pre-reproductive period can ultimately determine egg number by affecting development of maturing ova (Nikolsky 1963; Bagenal 1969).

Potential influence of these factors on fecundity of landlocked alewife populations can be examined for Claytor Lake and Lake Michigan (Norden 1967a). Comparisons are limited to Lake Michigan because only Norden (1967a) presents essential data. Fecundity of alewives in Claytor Lake increased with age and length, a relationship similar to that found for alewives in Lake Michigan. However, total length and ovary weight of Claytor Lake alewives exceeds that of corresponding age classes in Lake Michigan (Table 5). In addition, the number of eggs per gram ovary weight is greater for alewives in Claytor Lake despite the fact that

diameter of fertilized eggs is similar (1.02 mm Claytor Lake vs. 1.00 mm Lake Michigan).

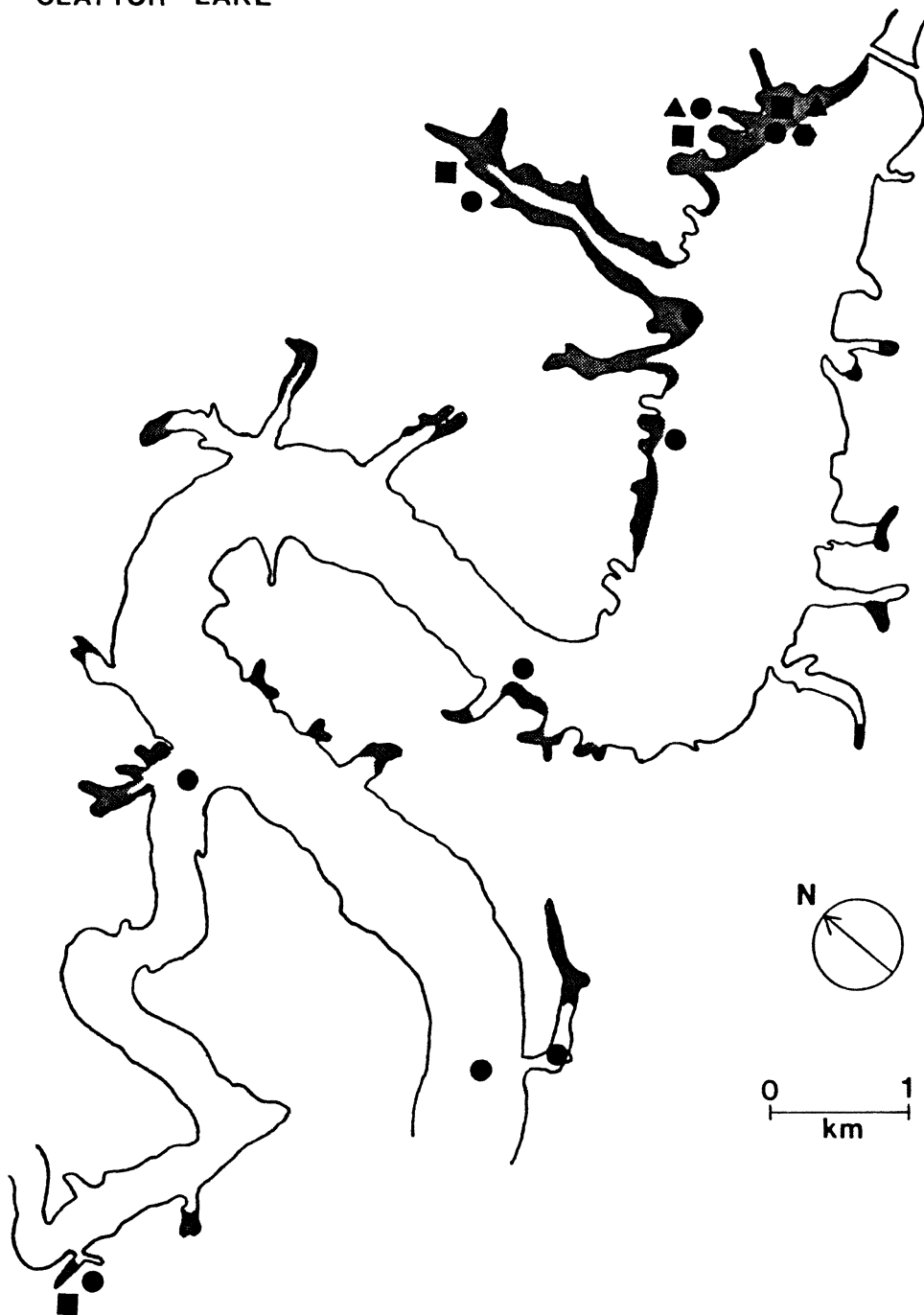
Possible causes for these differences may be environmental conditions confronting each population. Previous investigations (Boaze 1972; Kohler 1980) indicate that alewives in Claytor Lake may experience an extended period of optimal growth conditions relative to Lake Michigan as reflected by accelerated growth rates. Consequently, individuals in Claytor Lake attain larger sizes and probably experience more favorable conditions for the development of a new generation of oogonia and oocytes than their counterparts in Lake Michigan. This may allow a larger capacity for egg production (greater ovary weights) and increased egg density within ovaries due to greater numbers of maturing ova in alewives in Claytor Lake which is ultimately manifested as higher fecundity.

Spawning Behavior

Alewife spawning activity was observed at night (2100-0100 hr) in July 1978 and during May through July 1979 in littoral (<5 m) areas at Site 1, an embayment on the western side of the reservoir immediately upstream of the dam (Fig. 4). The spawning act was similar to that described by Edsall (1964) and Rothschild (1966). Two or more individuals swam rapidly toward the surface with sides touching in a tight spiral approximately 0.5 m in diameter. At the surface, fish broke water and then swam rapidly downward and out of sight. Total duration of the spawning act varied from 15 to 30 seconds. Males seemed aggressive and often struck at 9 cm silver balsa lures slowly retrieved through spawning aggregations. Examination of alewives of both sexes revealed gonads in spawning condition with mature sex products.

Fig. 4. Sampling sites where ripe adults (■), fertilized eggs (▲), prolarvae (●), and postlarvae (●) of alewives were collected, May through August 1979, Claytor Lake, Virginia. Shaded areas represent littoral (<5 m) areas within the reservoir.

CLAYTOR LAKE



Spawning Sites

Spawning sites of alewives in Claytor Lake in 1979 were identified by the presence of ripe adults, spawning activity, and fertilized eggs which are present at sites during and immediately after spawning, and prolarvae and postlarvae which are present within one week after spawning (Norden 1967b; Edsall 1970) and characteristically remain in areas of and adjacent to sites of egg deposition (Scott and Crossman 1973).

Alewife spawning activity and prolarval alewives were present in an embayment immediately upstream from the dam (Site 1); fertilized alewife eggs at Site 1 and in a small cove (Site 3); ripe adult alewives at Sites 1 and 3, in Dublin Hollow (Site 5), and in Peak Creek (Site 19); and postlarval alewives at 10 sampling sites throughout the reservoir (Fig. 4).

Investigations of landlocked alewife populations in northern waters (Gross 1959; Edsall 1964; Rothschild 1966; Norden 1967a) indicate that alewives will indiscriminately spawn in littoral (<5 m) areas with relatively little attached vegetation and a sand and/or gravel bottom. In Claytor Lake, the presence of postlarval alewives in 1979 at sites throughout the reservoir (Fig. 4) indicates that some alewife spawning probably occurs wherever proper spawning habitat is present.

Littoral (<5 m) areas in Claytor Lake are not extensive and potential spawning sites are limited. Based upon direct observations of spawning activity and the relative abundance of spawning adults, fertilized eggs, prolarvae, and postlarvae, it appears that Site 1, the largest expanse of suitable alewife spawning habitat, is the primary spawning site in Claytor Lake. It may be the only site capable of accomodat-

ing the massive inshore spawning concentration of alewives.

Spawning Period

Observations of spawning activity, gonosomatic indices of mature females, and egg densities were used to delineate spawning season of alewives in Claytor Lake. Efforts were concentrated in the embayment (Site 1) since observations of spawning activity and collections of eggs were inconsistent elsewhere. Detailed observations of spawning activity and sampling for alewife eggs were conducted only in 1979.

Spawning activity. Concentrations of alewives were first observed in littoral (<5 m) areas during the week of April 15 at water temperatures of 12 to 13 C. No spawning activity was observed, although examinations in the field showed that ripe alewives of both sexes were present. Sex composition of catches (n=57) showed 82 percent males.

Limited spawning activity (occurring along approximately 50 m of shoreline) was first observed during the week of May 6 at water temperatures of 16 to 18 C. Correspondingly, the percentage of females in the total catch (n=42) increased from 18 to 38 percent.

Observations made twice weekly from May 14 through July 3 showed a dramatic increase in amount of spawning activity (occurring along approximately 600 m of shoreline). Percentage of females in the catches during this period varied from 38 to 42 percent; water temperatures varied from 21 to 26 C.

Observations during the week of July 9 indicated a marked decrease in amount of spawning activity (occurring along approximately 30 m of shoreline) which remained low but consistent through July. By August 3, spawning activity was no longer evident, and the concentrations of

alewives were dispersed. Water temperatures in July and August ranged from 24 to 27 C.

Gonosomatic indices. Examination of 72 gravid female alewives in Claytor Lake showed 88 percent with mature ova when GSI exceeded 10 percent. In contrast, 97 percent of 108 spent females had GSI below two percent. Therefore, females with GSI greater than ten percent were assumed ready to spawn whereas individuals with GSI less than two percent were considered spent.

Median GSI of female alewives collected in 1978 declined gradually from a high of 7.3 percent on June 14 to a low of 0.5 percent on September 20 (Fig. 5). No GSI greater than 10 percent were evident past June 30, and by September 3 over 90 percent of GSI were less than two percent of somatic weight (Fig. 6). Median GSI increased during the last three months of 1978, however, reaching 3.5 percent by December 19.

In March 1979, median GSI of female alewives was 6.3 percent (Fig. 5). No females collected in March and April had GSI less than 5.0 percent (Fig. 6). When spawning activity was first observed on May 6, median GSI had reached 10.1 percent. This trend continued until May 16 when median GSI peaked at 13.5 percent. Sixty percent of females collected on that date had GSI greater than 10 percent (Fig. 6).

By June 4 median GSI had declined to 8.5 percent (Fig. 5) and only 13 percent of females collected had GSI greater than 10 percent (Fig. 6). In addition, two percent of females collected had GSI less than 2.0 percent. This trend continued until August 6 at which time 95 percent of females collected had GSI less than 2.0 percent and none had GSI greater than 5.0 percent (Fig. 6).

Fig. 5. Spawning period of alewives as indicated by gonosomatic indices of females and egg densities, June through December 1978 and March through August 1979, Claytor Lake, Virginia. Medians are represented by circles and ranges by horizontal lines.

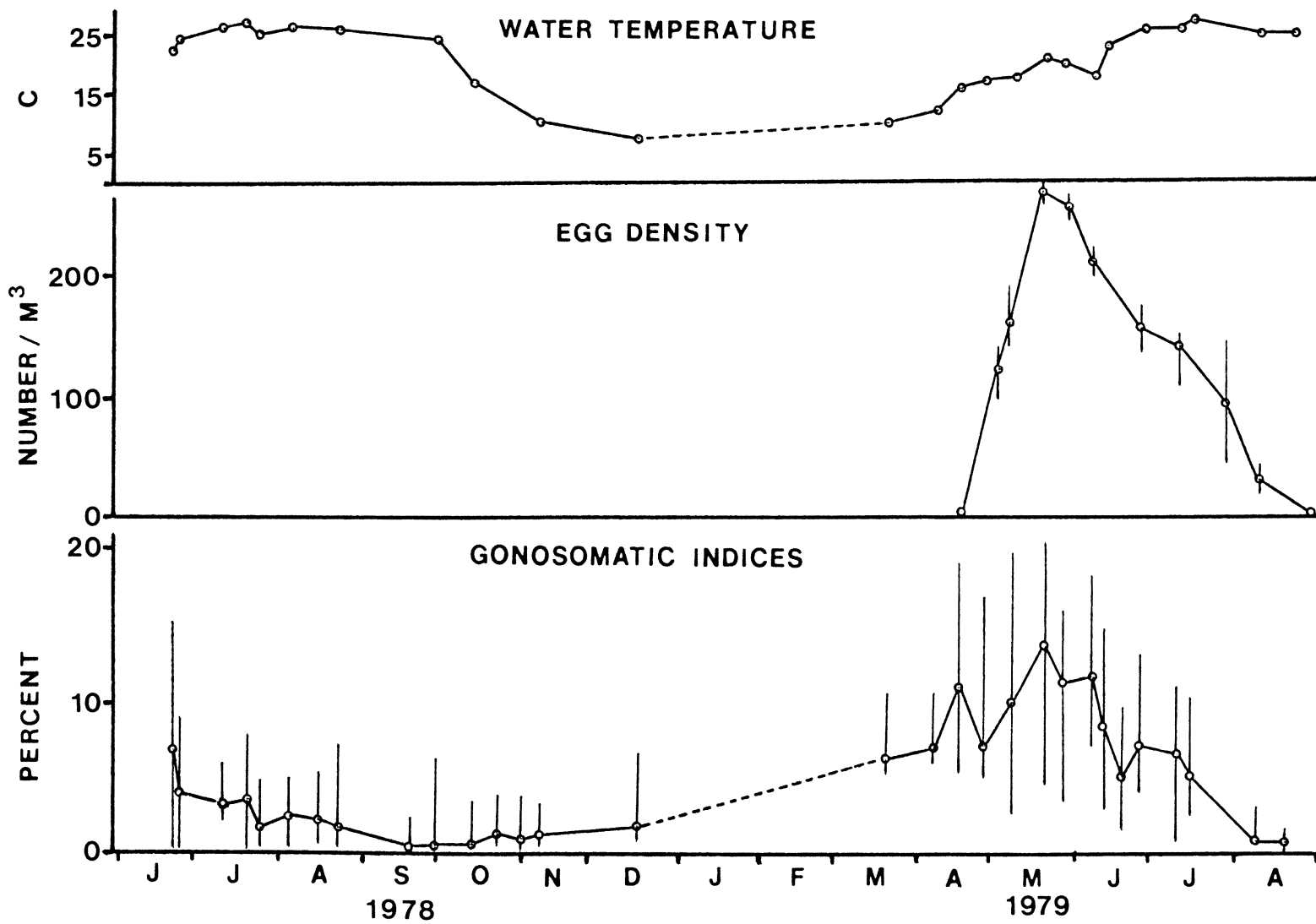
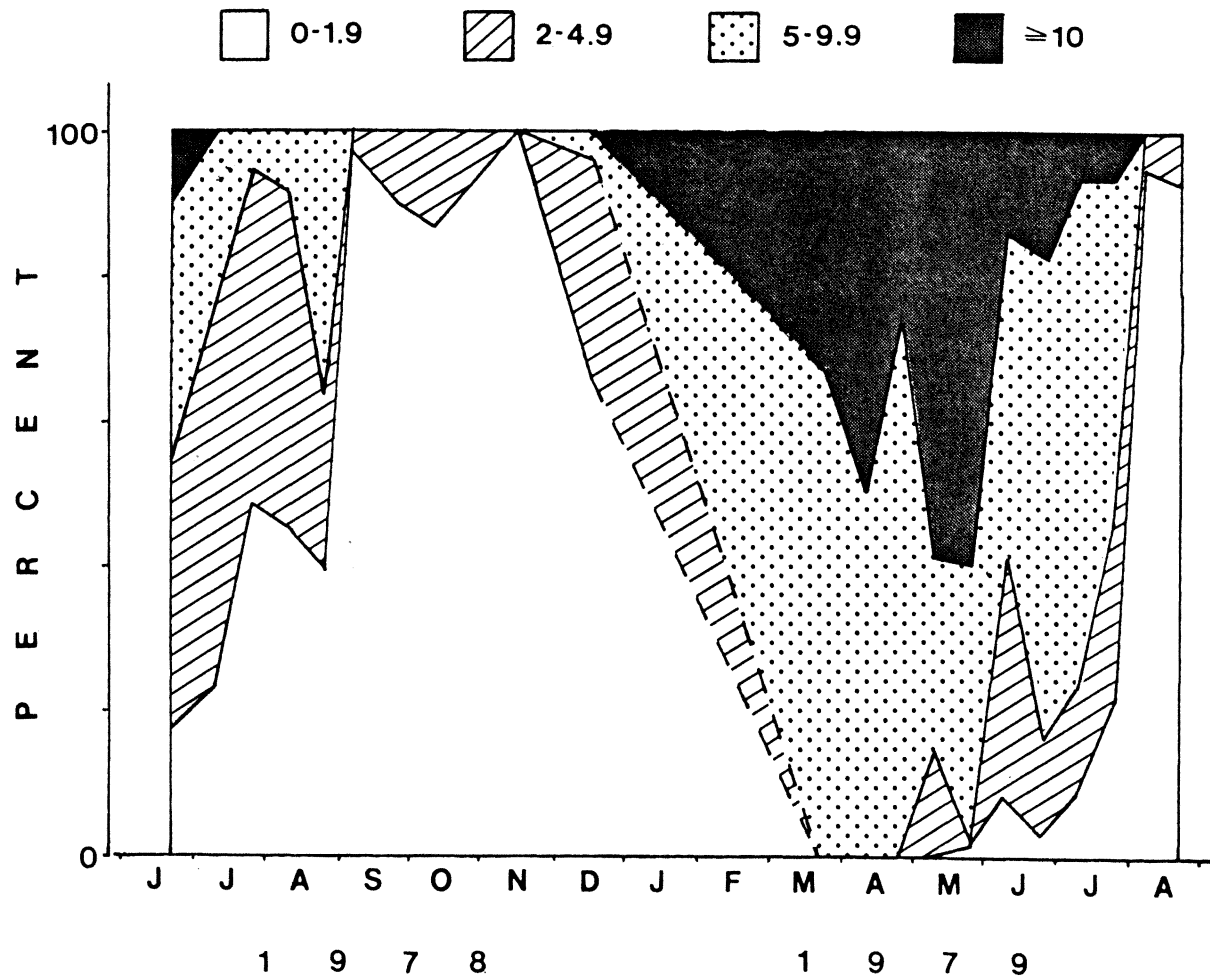


Fig. 6. Percentage fistribution of gonosomatic index values of female alewives indicative of various stages of reproductive condition, June through December 1978 and March through August 1979, Claytor Lake, Virginia.



Alewife egg density. Alewife eggs were first evident in benthic samples on May 8 (Fig. 5). Egg density increased dramatically during the next two weeks, peaking on May 17 at 262 eggs per m^3 . In early June densities remained high, but fell by approximately 25 percent by the end of the month (Fig. 5). This trend continued through July; last eggs were collected on August 8.

Evaluation of spawning period indicators. Observations of spawning activity, GSI of mature females, and densities of alewife eggs indicate that alewives in Claytor Lake have a protracted spawning season beginning in early May and lasting until early August (Fig. 5). Gonosomatic indices of females collected from September 1978 through April 1979 indicate that elaboration of gonadal tissue begins immediately following spawning and is accelerated in late winter and early spring.

Concentrations of alewives, predominantly males, entered littoral (<5 m) areas in mid-April at water temperatures of 12 to 13 C. As water temperatures increased females moved inshore and comprised approximately 40 percent of aggregations by the time spawning began. Spawning activity became evident in the first week of May and was accompanied by a corresponding increase in percentage of ripe females (GSI $\geq$ 10 percent) and the appearance of alewife eggs in benthic samples (Figs. 5 and 6).

Increases in spawning activity, median GSI and egg densities in May followed by sharp declines in each in June and July indicate that peak spawning occurred in the third week of May at water temperatures of 21 to 23 C (Fig. 5). The absence of alewife eggs in benthic samples and the high percentage of spent females indicates that spawning was essentially complete by early August.

Potter (1978) noted that in 1976 larval alewives from Claytor Lake were entrained from May 20 through August 6 by Glen Lyn power plant on the New River approximately 80 km downriver of Claytor Lake. He subsequently concluded that in 1976 alewives either had two separate spawns in late spring and mid-summer or one sustained spawn from May to August. Gross (1959) observed that in Lake Hopatcong, New Jersey, alewives first appear inshore (<5 m) in late April at water temperatures of 10 to 13 C. Spawning subsequently begins in late May at water temperatures of 17 to 18 C. Norden (1967a) reported that alewives move inshore in Milwaukee Harbor, Lake Michigan, toward the end of April and first part of May and that spawning occurs from late June through early August, peaking in July at water temperatures of 17 to 21 C. Edsall (1970) noted that alewives in the Kalamazoo River, Michigan, enter shallow areas as water temperatures approach 10 C, but do not spawn until late May or early June when water temperatures reach 16 C. Rothschild (1966) observed that alewives first enter littoral areas of Cayuga Lake, New York, in late May as water temperatures approach 12 C. However, the onset of courtship and spawning does not occur until mid-June when water temperatures reach approximately 17 C.

Water temperature has often been cited as an important factor in regulating gonadal maturation and initiating spawning activity in fish (LeCren 1951; Nikolsky 1963; Mathur and Ramsey 1974; Muth and Tarter 1975). Inshore movements of alewives and subsequent spawning occurs at approximately the same water temperature in Claytor Lake as in northern lacustrine systems. However, temporal differences are evident. Alewives in Claytor Lake move inshore and begin spawning approximately one month

earlier than those in Lake Hopatcong (Gross 1959) or the Kalamazoo River (Edsall 1970), and two months earlier than observed in Cayuga Lake (Rothschild 1966) or Milwaukee Harbor (Norden 1967a). Increases in water temperature vary between systems primarily due to differences in latitudinal, climatological, and limnological characteristics. Consequently, water temperatures reach levels necessary to elicit physiological and behavioral responses associated with spawning at different times in the season and ultimately may cause variation in onset of spawning.

Alewives in Claytor Lake were observed spawning until the first week of August at water temperatures of 24 to 27 C. At no time in 1979 did water temperatures exceed 27 C. Gross (1959) observed that in Lake Hopatcong alewife spawning was complete by the time water temperatures were 19 C. Rothschild (1966) noted that in Cayuga Lake spawning ceased at water temperatures of 21 C. Only Edsall (1970) discussed possible upper temperature limits for alewife spawning. He found that in the Kalamazoo River, Lake Michigan, alewife spawning was interrupted when water temperatures rose above 28 C. All mature unspawned female alewives collected in the river at this time contained slightly opaque eggs that could not be fertilized. Ripe males concurrently collected contained highly viscous sperm masses that would not readily mix with water. Although an upper temperature limit for successful alewife spawning exists, that temperature is rarely reached in lacustrine systems where alewives occur and thus may not be a primary determinant of spawning period in those systems. However, in reservoirs more southerly and/or at lower elevations than Claytor Lake, water temperatures may exceed the upper temperature limit and alewife spawning may be interrupted and

spawning period significantly curtailed.

Spawning period of alewives in Claytor Lake is 13 weeks, compared to nine weeks in Cayuga Lake (Rothschild 1966) or Lake Michigan (Norden 1967a) and four weeks in Lake Hopatcong (Gross 1959). Time and place of spawning are adaptations which ensure optimum conditions for growth and survival of young (Nikolsky 1963). As latitude decreases, conditions favorable for spawning may occur earlier and persist longer if the upper temperature limit is not reached, thus allowing for more individual variation in timing of gonadal maturation and subsequent spawning. The wide range of gonosomatic indices of female alewives and longer spawning season in Claytor Lake may be evidence of a more lenient environment.

Egg deposition. In 1978 and 1979 over 70 percent of females collected during the last two weeks of July had intermediate GSI values between ripe and spent conditions (GSI: 2 to 10 percent) (Fig. 6). However, neither ripe fish nor spawning activity was noted in August, indicating that ovaries were at least partially spent rather than developing.

Examination of ovaries of ripe females showed mature eggs, free of stroma posteriorly, with immature eggs increasing in abundance anteriorly. In contrast, examination of females with intermediate GSI in June and July showed ovaries with mature eggs, free of stroma, throughout. If female alewives with intermediate GSI were resorbing eggs, ovaries would contain immature ova with extensive stroma (Bagenal 1978). However, the prominence of mature ova in these female alewives indicates that in Claytor Lake, eggs may not be extruded at one time, but may be spawned over several days, possibly weeks, as ova develop.

Rothschild (1966) noted that in Cayuga Lake, New York, most female

alewives reach an advanced state of maturity at approximately the same time and that the majority of spawning occurs within two weeks. Since there is little variation in the time that females become ripe, individual females may spawn over a substantial part of the two week period. In Claytor Lake, dramatic increases in median GSI and percentage of ripe females during the third week in May followed by decreases in both of similar magnitude in the first week of June indicate that the majority of spawning may have occurred over two to three weeks. Minimum duration of spawning by individual females, estimated from when spawning began to when spent individuals appeared in the catch, was approximately two weeks. The high proportion of partially spent female alewives to ripe or spent fish in June and July, however, indicates that the median duration of individual spawning may have been longer.

Observations on spawning behavior of several species of fish (Fabricus and Gustafson 1954; Jones and Ball 1954) indicate that repeated spawning acts, with the extrusion of small numbers of eggs each time, together with wide distribution of eggs and a protracted spawning period increases the likelihood that some of the eggs will survive unfavorable periods during development.

Early Life History

Morphological Development

Alewife eggs in Claytor Lake were found in various stages of development from ripe unfertilized to embryonic. Egg characteristics are consistent with those of alewife populations in other systems (Norden 1967b; Cianci 1969). Median diameter of fertilized eggs was 1.01 mm (0.96 to 1.07 mm) and is well within the range reported in the literature (Table

6).

Median total lengths of prolarval and postlarval alewives in Claytor Lake were 4.0 mm (3.1 to 5.4 mm TL) and 6.4 mm (4.8 to 7.1 mm TL), respectively, and concur with reports on alewife populations in other systems (Table 6). Changes in body shape and pigmentation, ossification of bony parts, and development of digestive tract of larval alewives in Claytor Lake are consistent with literature reports (Norden 1967b; Cianci 1969; Dorr et al. 1976; Hardy 1978). The only disparity is in length at scale formation. In Claytor Lake, scales first become evident on alewife larvae at 22 to 24 mm TL. Other investigators (Hildebrand 1963; Norden 1967b) first noticed scales on alewife larvae at 28 and 29 mm TL.

Morphology of juvenile alewives parallels that of adults at total lengths equal to and greater than 35 mm. Ratio of body depth to total length is 0.20, well within the 0.18 to 0.22 range reported for adults (Hardy 1978). Gill rakers are elongate and number 34 to 41 on the first arch compared to 38 to 46 in adults (Hardy 1978). Stomach conforms to adult morphology and is an enlarged V-shaped organ with numerous caeca, some of which extend the entire length of the stomach.

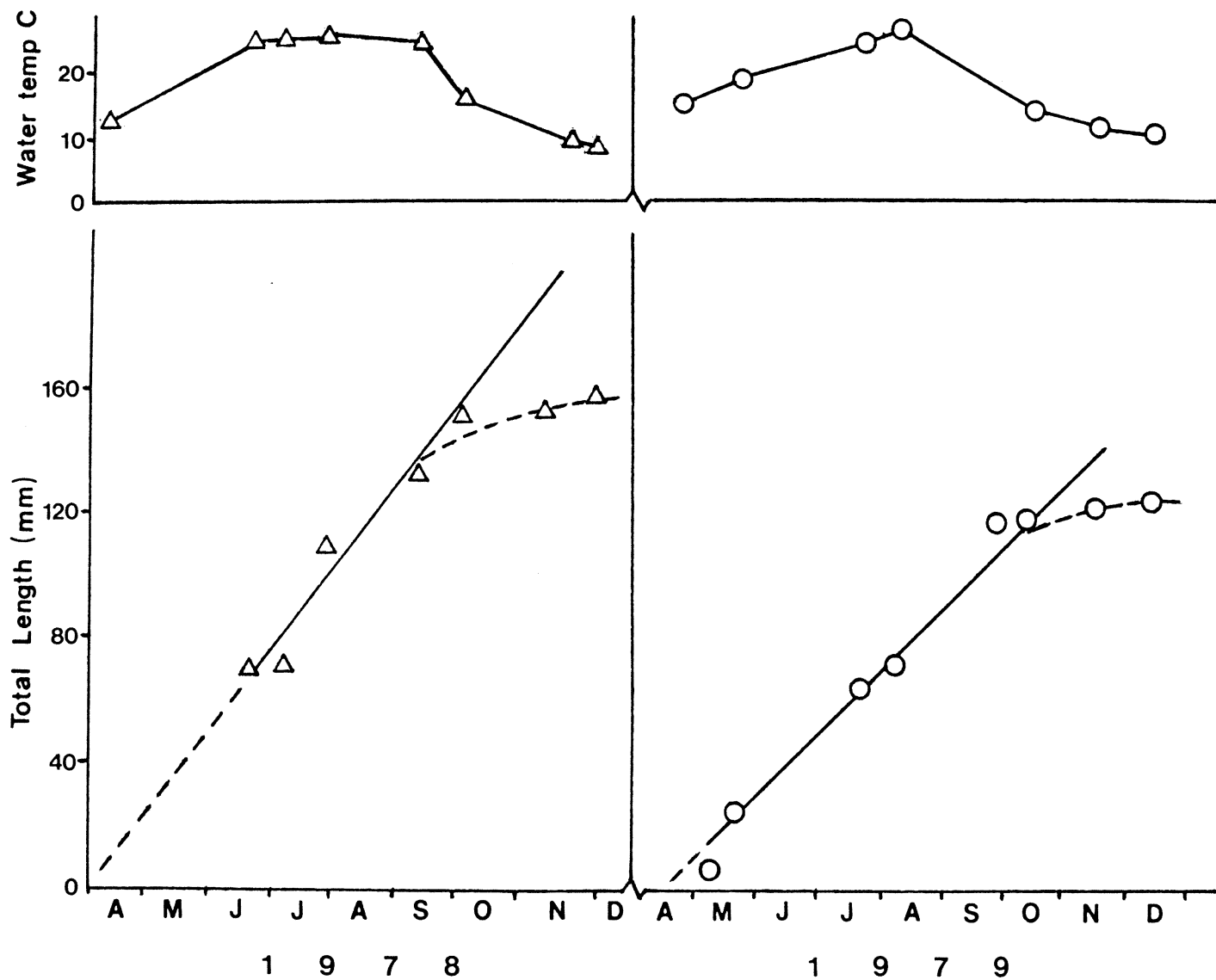
First Year Growth

A significant linear relationship existed ($p=0.042$ and $p=0.001$) when maximum total lengths of young-of-the-year alewives collected in 1978 and 1979, respectively, were regressed over time (Fig. 7). Least squares regression fitted for the linear phase of each year explained 96.5 percent in 1978 and 95.5 percent in 1979 of the variation about overall total lengths. Growth beyond October in both years appeared

Table 6. Size range (mm) of fertilized eggs and prolarvae of alewife populations at various locations in the United States. Median size in parentheses.

Location	Life stage	
	Egg	Prolarvae
Claytor Lake, VA (present study)	0.96-1.07 (1.01)	3.1-5.4 (4.0)
Lake Michigan (Dorr et al. 1976)	0.90-1.40	2.5-3.5 (at hatching)
Bride Lake, CT (Cianci 1969)	---	4.1-6.4
Lake Michigan (Norden 1967b)	0.80-1.06 (1.00)	3.3-5.0 (3.8)

Fig. 7. First year growth of young-of-the-year alewives, June through December 1978 and May through December 1979, Claytor Lake, Virginia.



asymptotic, gradually declining from the linear.

Estimated daily growth increments were 0.84 mm per day in 1978 and 0.68 mm per day in 1979 and were significantly ($p=0.003$) different between years. Back extrapolation of linear plots (Fig. 7) showed larvae first hatching (4.0 mm TL) on April 13, 1978 and April 25, 1979 indicating that initial growth may not be linear since spawning was not observed to begin until May.

Estimates of daily growth increments and examinations of first year growth of young-of-the-year alewives in other lacustrine systems are lacking. However, data presented by investigators concerned with other aspects of alewife life history (Gross 1959; Rothschild 1966; Norden 1967a) allow estimation of growth rates of young-of-the-year alewives in these systems. Linear growth of young-of-the-year alewives in Claytor Lake is similar to that in Lake Hopatcong, New Jersey (0.77 mm per day: Gross 1959), Cayuga Lake, New York (0.82 mm per day: Rothschild 1966), and Lake Michigan (0.86 mm per day: Norden 1967a) even though Claytor Lake alewives attain a larger maximum size at the end of their first year of life (Boaze 1972; Kohler 1980). Early spawned alewives in Claytor Lake have higher first year growth due to a longer growing season rather than to any variation in physiology or genetics.

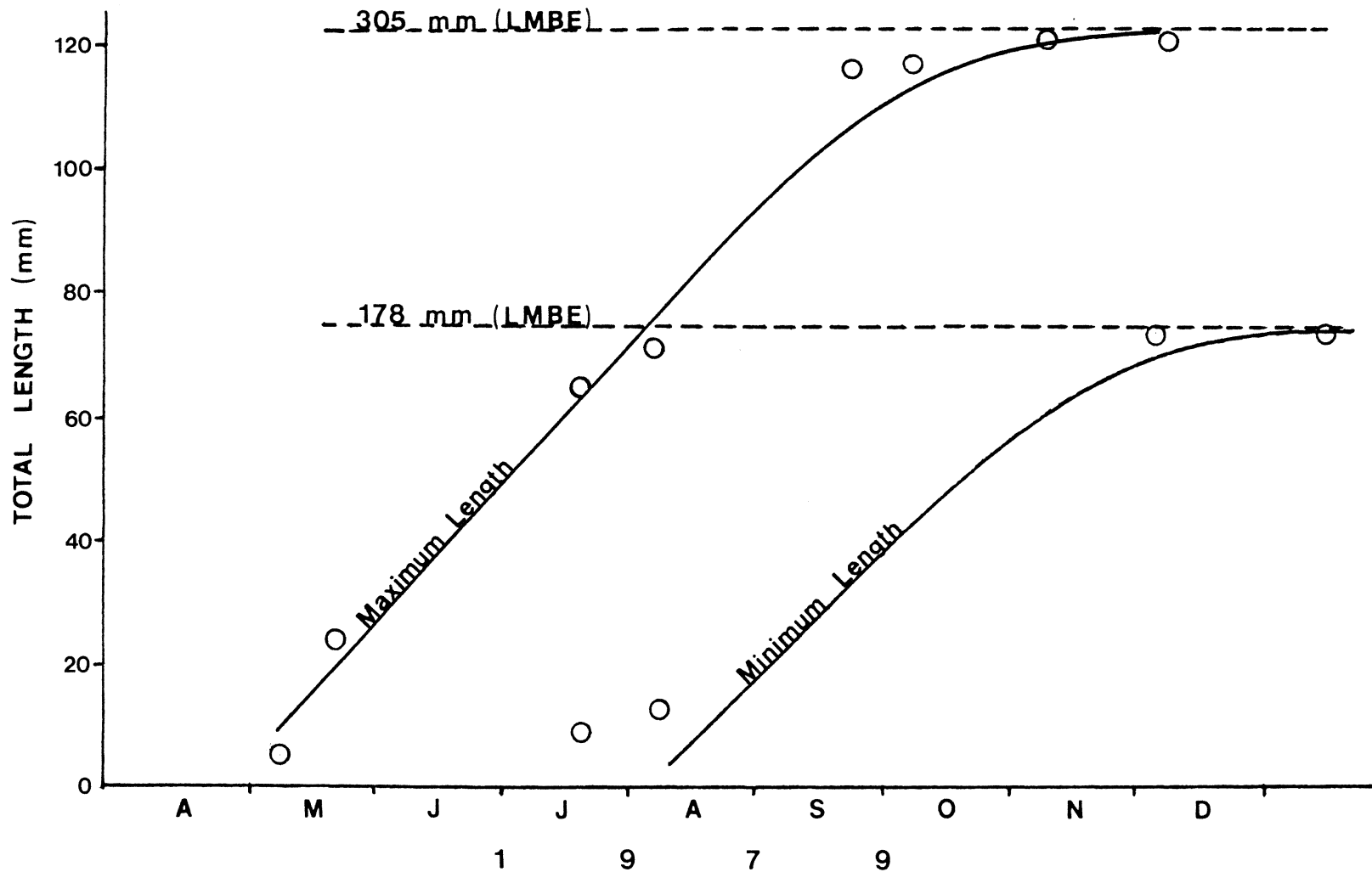
First year growth of fish is determined by the integration of climatological and biological conditions that may influence food availability, competition for food and space, and predation (Ney and Smith 1975). In Claytor Lake, a massive alewife die-off during the exceptionally cold winter of 1977-1978 and the resultant effect of the die-off on species composition and size distribution of the zooplankton community may have

caused the disparity in first year alewife growth between 1978 and 1979. Growth of young-of-the-year alewives in Claytor Lake in 1978 immediately following the die-off was significantly greater than growth the following year when population levels again expanded. This was consistent with changes in growth rates observed for adult alewives over the same period (Kohler 1980). Decreased abundance of adults in 1978 may have resulted in reduced intraspecific competition for food and space and allowed increased availability of larger, more energetically profitable (net energy/food item) zooplankters. Brown (1972) noted that reduction in population density of alewives in Lake Michigan following a massive die-off in 1967 was most likely responsible for the corresponding increase in growth rate. Other investigators (Brooks 1968; Wells 1970) have described a direct relation between changes in growth of alewives and their selective depletion of larger zooplankton species.

Effect of Growth on Availability as Prey

Size ranges of young-of-the-year alewives in samples collected in Claytor Lake in 1979 were only considered representative of the population in July and August, when larval and juvenile alewives were concurrently collected with the 1.0-m diameter plankton net and two experimental gill nets, respectively; and in December, when all sizes of young-of-the-year alewives were assumed vulnerable to the experimental gill nets. Differences between maximum and minimum total lengths of young-of-the-year alewives collected in those three months were similar. Size ranges of young-of-the-year alewives in remaining months, for which maximum total lengths were available, were subsequently estimated (Fig. 8).

Fig. 8. Size ranges of young-of-the-year alewives, April through December 1979, Claytor Lake, Virginia. Estimates were obtained from relation of maximum and minimum total lengths as defined by size ranges on July 18, August 8, and December 10. Horizontal lines represent minimum sizes of predators (large-mouth bass equivalents: LMBE) that can feed on all young-of-the-year alewives and on minimum sized young-of-the-year alewives year round.



The effect of growth on morphological availability of young-of-the-year alewives in Claytor Lake as prey was examined by the technique of Jenkins and Morais (1978). Based upon the relation of mouth size of largemouth bass to maximum body depth of various clupeids, they derived a regression:

$$y = 0.0141x^2 + 0.1668x + 1.0972$$

that estimated sizes of clupeids (y) in inches that were morphologically available to largemouth bass of a given size (x) in inches. Factors were then calculated to convert other predators to largemouth bass total length equivalents (LMBE) including flathead catfish, 1.0; other catfish and crappies, 1.5; white and striped bass, 1.3; and walleye, 1.7.

The minimum-sized predator that could feed on all young-of-the-year alewives in Claytor Lake year round in 1979 was 305 mm TL (LMBE; Fig. 8). This size corresponds to white bass at age IV, striped bass at age II, and walleye at age III (Kohler 1980). Minimum sized young-of-the-year alewives in Claytor Lake were morphologically available year round to age II white bass and walleye, and age I striped bass (178 mm TL; LMBE). Young-of-the-year alewives between 5 and 70 mm TL were morphologically available to predator sizes (152 mm TL; LMBE) equivalent to age I white bass, age I walleye, and age 0 striped bass for 12 to 16 weeks; whereas availability of alewives 70 to 125 mm TL was restricted to older age classes. The extended spawning season of alewives in Claytor Lake appears to mitigate availability of young-of-the-year as prey, despite rapid growth by providing a large range of sizes over a protracted period of time.

Distribution

Larval alewives were collected at ten sites in Claytor Lake from May through August 1979 (Fig. 4). Median density of larval alewives at all sites was 0.037 larvae per m^3 . Greatest density of larvae was found in littoral (<5 m) areas in an embayment (Site 1) (Table 7). Median larval density at sampling sites within 4.0 km of the dam was approximately four times that at remaining sites (Table 7). Of those sites located more than 4.0 km from the dam, a cove in Peak Creek (Site 22) had the highest larval density (Table 7). Mainstream sites (Sites 11, 13, and 25) had a median larval density of 0.031.

Abundance of larval alewives in Lake Michigan (Wagner 1971) and Lake Huron (O'Gorman 1977) is closely related to shoreline topography. Larvae are most abundant in littoral (<10 m) areas in coves and bays with infrequent or no upwellings. In Claytor Lake, greatest larval densities occur along shoreline of similar topography in littoral (<5 m) areas in the lower reservoir (4.0 km from the dam) and in coves. Collection of larval alewives up to 31 mm TL in areas identified as spawning sites suggests that these areas may also serve as nursery grounds until young migrate to deeper water later in the season. Alewife larvae were collected at mainstream sites in Claytor Lake. Once in the main channel, larvae may eventually be lost from the reservoir through escape-ment. Larval alewives entrained by the Glen Lyn power plant on the New River approximately 80 km downstream of Claytor Lake have been attributed to such losses (Potter 1978).

In Lake Huron (O'Gorman 1977) the greatest concentrations of larval alewives occur in the upper 3 m of the water column. Correspondingly,

Table 7. Density of alewife larvae (number/m³), May through July 1979, Claytor Lake, Virginia.

Site ^a	m ³ water filtered	Larval density
1	2556.9	0.670
3	2274.7	0.071
5	2106.8	0.203
6	1486.3	0.040
11	1515.7	0.031
13	1114.3	0.034
18	1471.8	0.032
22	1622.3	0.091
25	1584.3	0.011
26	1589.3	0.024

^a Corresponds to Figs. 1 and 4 and Table 1

alewife larvae in Claytor Lake were abundant in samples collected 1 to 3 m below the water surface with the 1.0-m diameter plankton net (330 micron mesh). Juvenile alewives (35 to 100 mm TL) were caught exclusively in the upper 4 m of the water column using vertical gill nets 3 m wide x 20 m deep set adjacent to littoral areas where larvae were collected. Vertical distribution of young-of-the-year alewives in Claytor Lake was confined to depths where temperature and dissolved oxygen levels were highest. However, depth distribution of young-of-the-year alewives may not solely be a function of these parameters. Distribution of young-of-the-year alewives at greater water depths may be limited by impairment of visual feeding behavior.

Food Habits

Stomach analyses were performed on young-of-the-year alewives 6 to 70 mm TL. Diet composition, relation of diet to food resource, and relation of size of food items to size of young-of-the-year alewives were investigated.

Diet composition. Cyclopoid copepods were the principal food items in diets of alewives 6 to 35 mm TL, with Bosmina longirostris dominating diets of alewives 36 to 70 mm TL (Table 8). Other food items included phytoplankton, copepod nauplii, ostracods, adult terrestrial dipterans, and cladocerans (principally Alona quadrangularis, Daphnia sp., Diaphanosoma brachyurum, and Leptodora kindtii).

Chlorophytes and diatoms were only present in diets of larvae 6 to 15 mm TL. Copepod nauplii were confined to diets of larvae 6 to 45 mm TL. Cyclopoid copepods and Diaphanosoma were present in diets of larvae as small as 6 mm TL, whereas Bosmina, Daphnia, rotifers, and ostracods

Table 8. Percent frequency of occurrence and percent total volume of food items in stomachs of young-of-the-year alewives 6 to 70 mm TL, May through July 1979, Claytor Lake, Virginia. Numbers of stomachs examined in parentheses.

Food items	Length class									
	6-10 mm (10)		11-15 mm (10)		16-20 mm (12)		21-25 mm (10)		26-30 mm (2)	
	% freq	% vol	% freq	% vol	% freq	% vol	% freq	% vol	% freq	% vol
Algae										
Chlorophyta/	20.0	T ^a	10.0	T	--	--	--	--	--	--
Chrysophyta										
Rotifera										
<u>Keratella</u>	--	--	--	--	17.0	1.0	50.0	1.0	100.0	2.0
<u>Branchionus</u>	--	--	--	--	--	--	10.0	T	--	--
Microcrustacea										
Copepoda										
Cyclopoid	90.0	65.0	90.0	96.0	100.0	53.0	100.0	41.0	100.0	43.0
Nauplii	80.0	32.0	40.0	3.0	8.0	T	20.0	T	--	--
Cladocera										
<u>Alona</u>	--	--	--	--	--	--	--	--	--	--
<u>Bosmina</u>	--	--	--	--	17.0	4.0	60.0	7.0	100.0	21.0
<u>Daphnia</u>	--	--	--	--	8.0	1.0	50.0	16.0	--	--
<u>Diaphanosoma</u>	20.0	3.0	10.0	1.0	67.0	22.0	90.0	33.0	100.0	T
<u>Leptodora</u>	--	--	--	--	--	--	--	--	--	--
Ostracoda	--	--	--	--	8.0	T	30.0	2.0	50.0	34.0
Insecta										
Adult terres-	--	--	--	--	--	--	--	--	--	--
trial dipteran										

^a T ≤ 1%

Table 8. Percent frequency of occurrence and percent total volume of food items in stomachs of young-of-the-year alewives 6 to 70 mm TL, May through July 1979, Claytor Lake, Virginia (continued).

Food items	Length class							
	31-35 mm (6)		36-40 mm (10)		41-45 mm (10)		46-50 mm (4)	
	% freq	% vol	% freq	% vol	% freq	% vol	% freq	% vol
Algae								
Chlorophyta/	--	--	--	--	--	--	--	--
Chrysophyta								
Rotifera								
<u>Keratella</u>	83.0	T ^a	50.0	T	30.0	T	50.0	T
<u>Branchionus</u>	--	--	--	--	--	--	--	--
Microcrustacea								
Copepoda								
Cyclopoid	100.0	79.0	100.0	76.0	100.0	62.0	100.0	13.0
Nauplii	--	--	--	--	10.0	T	--	--
Cladocera								
<u>Alona</u>	17.0	T	30.0	1.0	20.0	1.0	50.0	1.0
<u>Bosmina</u>	100.0	3.0	100.0	2.0	90.0	10.0	100.0	77.0
<u>Daphnia</u>	17.0	T	--	--	40.0	8.0	--	--
<u>Diaphanosoma</u>	33.0	1.0	--	--	60.0	3.0	--	--
<u>Leptodora</u>	50.0	T	30.0	T	30.0	6.0	50.0	T
Ostracoda	100.0	17.0	90.0	21.0	90.0	10.0	100.0	6.0
Insecta								
Adult terres- trial dipteran	--	--	--	--	--	--	50.0	2.0

^a T ≤ 1%

Table 8. Percent frequency of occurrence and percent total volume of food items in stomachs of young-of-the-year alewives 6 to 70 mm TL, May through July 1979, Claytor Lake, Virginia (continued).

Food items	Length class							
	51-55 mm (2)		56-60 mm (4)		61-65 mm (3)		66-70 mm (3)	
	% freq	% vol	% freq	% vol	% freq	% vol	% freq	% vol
Algae								
Chlorophyta/	--	--	--	--	--	--	--	--
Chrysophyta								
Rotifera								
<u>Keratella</u>	50.0	T	100.0	T	--	--	33.0	T
<u>Branchionus</u>	--	--	--	--	--	--	--	--
Microcrustacea								
Copepoda								
Cyclopoid	100.0	31.0	100.0	8.0	67.0	66.0	100.0	7.0
Nauplii	--	--	--	--	--	--	--	--
Cladocera								
<u>Alona</u>	--	--	50.0	3.0	67.0	21.0	--	--
<u>Bosmina</u>	100.0	46.0	100.0	8.0	67.0	1.0	100.0	77.0
<u>Daphnia</u>	--	--	--	--	--	--	--	--
<u>Diaphanosoma</u>	50.0	T	--	--	--	--	--	--
<u>Leptodora</u>	50.0	T	100.0	T	67.0	T	67.0	T
Ostracoda	100.0	19.0	100.0	2.0	33.0	3.0	--	--
Insecta								
Adult terres- trial dipteran	50.0	3.0	50.0	79.0	100.0	10.0	33.0	16.0

^a T ≤ 1%

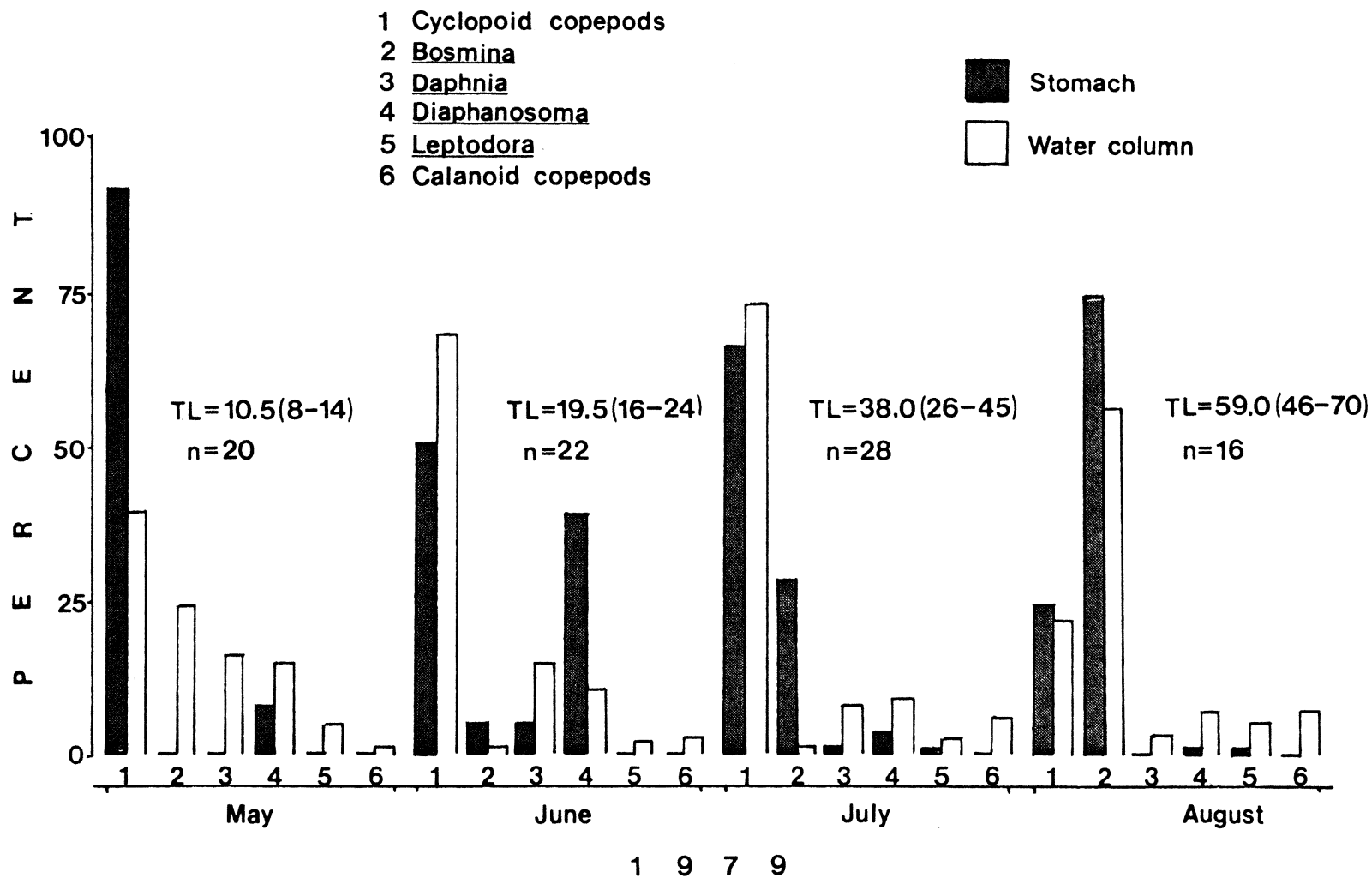
were not incorporated into diets until larvae reached 16 mm TL. Cladocerans such as Alona and Leptodora were first evident in stomach samples at 30 mm TL while adult terrestrial dipterans occurred exclusively in diets of alewives greater than 45 mm TL.

Diet composition of young-of-the-year alewives in Claytor Lake is similar to that of corresponding length classes in Lake Michigan (Norden 1968; Wagner 1971). Norden (1968) observed that in alewives 6 to 25 mm TL, diets consist primarily of cyclopoid copepods (42 percent by number), followed by cladocerans, mainly Bosmina (23 percent), and copepod nauplii (17 percent). Wagner (1971), on the other hand, found that larvae 7 to 22 mm TL feed heavily on cyclopoid copepods (62 percent by number) and a rotifer, Polyyarthra sp. (37 percent). In diets of alewife larvae greater than 25 mm TL, Norden (1968) found that Bosmina become the principal food item (43 percent) with a corresponding decrease in cyclopoid copepods (15 percent).

Relation of diet to food resource. There was a significant positive correlation ($r=0.796$, $p=0.010$) between the relative abundance of major zooplankters in the water column and in the diets of young-of-the-year alewives. Cyclopoid copepods were the dominant zooplankton in diets of alewife larvae and water column samples collected coincidentally from May through July (Fig. 9). In August, a large increase in number of Bosmina in the water column was reflected by a correspondingly significant increase of Bosmina in diets of concurrently collected young-of-the-year alewives (Fig. 9). Calanoid copepods, despite their presence in the water column, were not found in diets of young-of-the-year alewives (Fig. 9).

Relative abundance of major zooplankters in diets of young-of-the-

Fig. 9. Percent total number of major zooplankters in the upper 6 m of the water column versus diet of larval and juvenile alewives, May through August 1979, Claytor Lake, Virginia. Median total lengths and range of fish examined (TL) and sample size (n) are given.



year alewives in Claytor Lake appears to be related to relative abundance of these zooplankters in the water column, as evidenced by the continual predominance of cyclopoid copepods in diets and the water column, and the dramatic increase of Bosmina in diets after a similar increase in the water column. Diets of adult alewives concurrently collected in littoral areas of Claytor Lake (Kohler 1980) similarly included cyclopoid copepods as a principal food item throughout the summer and reflected significant increases in utilization of Bosmina during increases in population levels of this cladoceran. Failure of larval and juvenile alewives to utilize calanoid copepods correspond with apparent lack of active selection by adult alewives (Kohler 1980) and may be due to the considerable evasion skills of these large, agile zooplankters (O'Brien 1979).

In the Milwaukee Harbor, Norden (1968) observed that young-of-the-year (5.3 to 67.1 mm TL) alewives positively select for cladocerans and copepods and that these zooplankters correspondingly comprise the greatest percentage of zooplankters in the water column. Wagner (1971) reported similar results concerning cyclopoid copepods in diets of alewife larvae (7 to 22 mm TL) in Little Bay de Noc, Lake Michigan, but found that cladocerans, despite their abundance in the water column, did not appear to be utilized.

Changes in size of food items. A positive correlation ($r=0.719$, $p=0.006$) existed between total lengths of young-of-the-year alewives and total lengths of food items in their diets (Table 9). When comparisons were restricted to total lengths of cyclopoid copepods, chosen as an index of size selectivity because of their broad length distribution and abundance

Table 9. Median length (mm) and range of lengths of food items of young-of-the-year alewives (YOY), May through August 1979, Claytor Lake, Virginia. Number of stomach examined in parentheses.

Length class (mm) of YOY	Length of food items	
	Median	Range
6-10 (10)	0.30	0.13-0.53
11-15 (10)	0.48	0.10-0.83
16-20 (12)	0.55	0.12-0.90
21-25 (10)	0.47	0.13-0.96
26-30 (2)	0.33	0.14-0.99
31-35 (6)	0.42	0.12-1.35
36-40 (10)	1.16	0.11-1.35
41-45 (10)	0.63	0.21-1.73
46-50 (4)	0.63	0.26-1.34
51-55 (2)	0.76	0.12-2.25
56-60 (4)	0.55	0.11-3.78
61-65 (3)	0.67	0.35-4.50
66-70 (3)	0.89	0.22-1.44

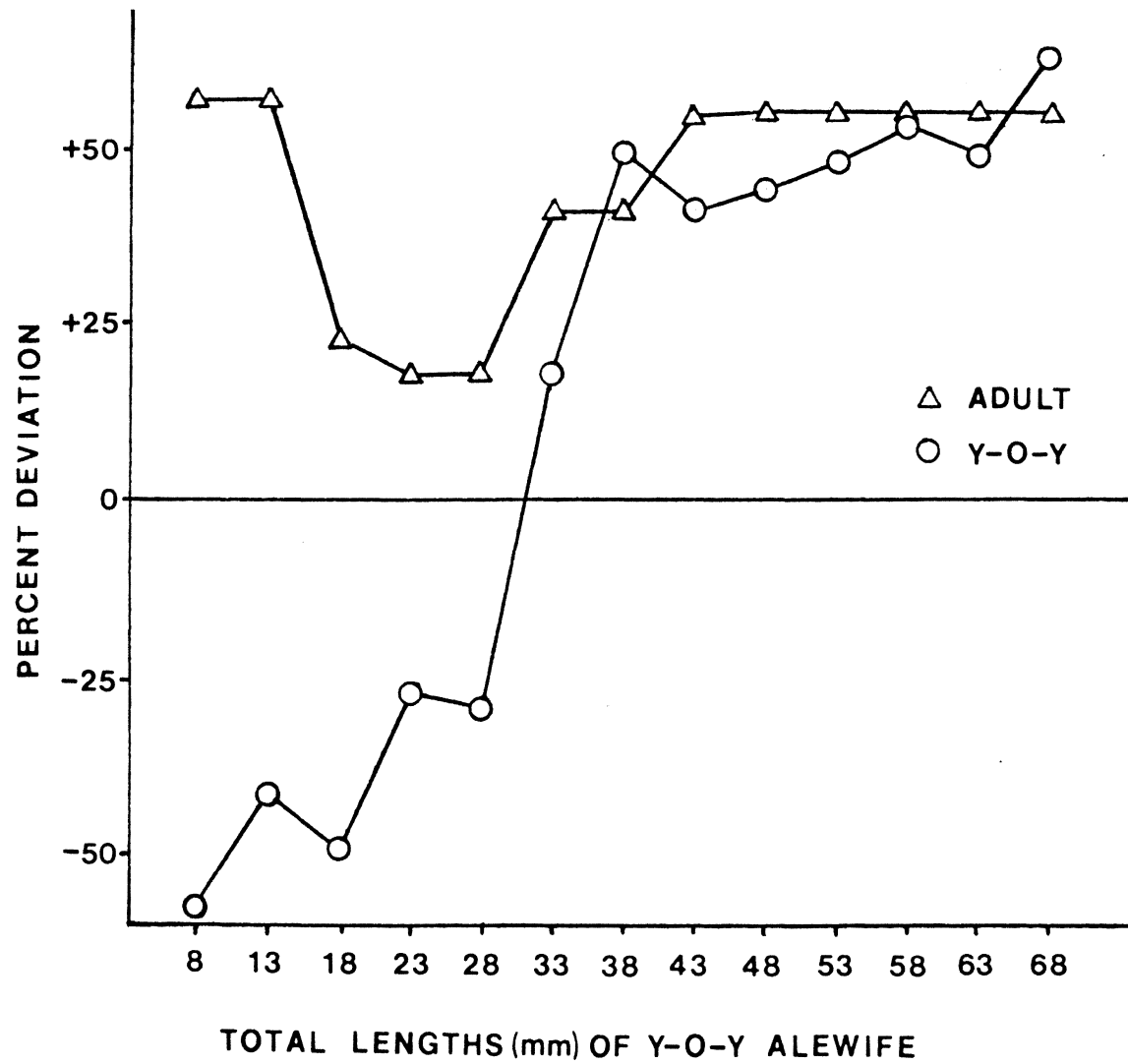
in alewife diets and the water column, a stronger positive correlation ($r=0.858$, $p=0.002$) with total lengths of young-of-the-year alewives was evident.

Total lengths of cyclopoid copepods in diets of young-of-the-year alewives less than or equal to 30 mm TL were significantly less than those in diets of adult alewives ($p=0.008$) or water column samples ($p=0.008$) concurrently collected (Fig. 10). In contrast, total lengths of cyclopoid copepods in diets of young-of-the-year alewives greater than 30 mm TL were significantly ($p=0.022$) greater than those in concurrently collected water column samples, but not significantly ($p=0.444$) different than those in diets of concurrently collected adult alewives (Fig. 10).

Alewives in Claytor Lake less than or equal to 30 mm TL select for cyclopoid copepods significantly smaller than those in the water column or those selected by adult alewives. Sizes of copepods available to alewife larvae in this size range may be dependent upon morphological and behavioral characteristics of larvae which restrict their ability to catch certain size prey (Allen 1941; Norden 1968), as well as the demonstrated ability of copepods to avoid predation (Drenner et al. 1978; O'Brien 1979).

Size selection of cyclopoid copepods by alewives greater than 30 mm TL corresponds directly to that of adult alewives and is positive for cyclopoid copepods significantly larger than those most abundant in the water column. Consequently, at sizes as small as 35 mm TL, young-of-the-year alewives may significantly contribute to the considerable influence that adult alewives exert on zooplankton community structure in Claytor

Fig. 10. Percent deviation of size of cyclopoid copepods in diets of young-of-the-year (YOY) and adult alewives versus cyclopoid copepod body sizes in the water column, May through August 1979, Claytor Lake, Virginia. Points are date specific for YOY, adults, and water column samples. Total lengths of YOY represent medians of 5-mm length intervals.



Lake, i.e. a shift in size distribution toward smaller microcrustaceans (Kohler 1980).

The potential magnitude of the added impact of young-of-the-year alewives on zooplankton populations becomes more substantial when the abundance of young-of-the-year alewives inshore (<10 m) is considered. Although no estimates of population size were made, catches in vertical gill nets indicate heavy concentrations of young alewives inshore until at least late fall when they begin movements to deeper water. This can only compound the potentially major negative impact of alewives on young-of-the-year sportfish which not only rely on littoral concentrations of zooplankton, but on pelagic zooplankton populations which immigrate inshore and renew their source of food (Noble 1975).

SUMMARY AND CONCLUSION

1. Alewives of both sexes in Claytor Lake matured in their second year of life at approximately 160 mm TL. Total lengths of sexually immature and mature alewives did not significantly differ. Over 90 percent of mature alewives in samples were age I and age II.
2. Median individual fecundity of gravid female alewives in Claytor Lake increased with age and length, ranging from 17307 eggs at age I to 37147 eggs at age III. Number of eggs per gram ovary weight did not significantly differ between age groups but was higher than elsewhere. No significant correlation within age class existed between fecundity and total length or somatic body weight.
3. Alewife spawning activity in Claytor Lake was observed at night (2100 to 0100 h) from May through July in littoral (<5 m) areas of an embayment immediately upstream of the dam. Duration of a spawning act varied from 15 to 30 seconds. Males seemed aggressive and often struck at artificial lures slowly retrieved through spawning aggregations.
4. The majority of alewife spawning in Claytor Lake appeared to be concentrated in littoral (<5 m) areas of an embayment immediately upstream of the dam. Some alewife spawning occurred in other littoral areas throughout the reservoir.
5. The spawning period of alewives in Claytor Lake was protracted (13 weeks), beginning in early May and lasting until early August. Inshore movements of alewives were observed at water temperatures of 12 to 13 C and subsequent spawning at 16 to 18 C. Peak spawning occurred at water temperatures of 21 to 23 C and was complete at 24 to 27 C.
6. Examination of ovaries of ripe female alewives showed mature eggs

posteriorly, with immature eggs increasing in abundance anteriorly. In contrast, ovaries of females with GSI between ripe and spent conditions collected after peak spawning contained only mature ova. Spawning female alewives, therefore, may not extrude eggs at one time, but spawn repeatedly with extrusion of small numbers of eggs each time.

7. Median diameter of fertilized eggs of alewives in Claytor Lake was 1.01 mm with a range of 0.96 to 1.07 mm. Median total lengths of prolarval and postlarval alewives was 4.0 mm (3.1 to 5.4 mm) and 6.4 mm (4.8 mm to 7.1 mm), respectively. Scales first became evident on alewife larvae at 22 to 24 mm TL. In juvenile alewives (>35 mm TL), ratio of body depth to total length, number and length of gill rakers, and morphology of digestive tract was comparable to adults.

8. Estimated daily growth increments of young-of-the-year alewives in Claytor Lake were significantly different in 1978 (0.84 mm/d) and 1979 (0.68 mm/d). Higher growth rates in 1978 may have been caused by reduced intraspecific competition for food and space and increased availability of larger zooplankton following a massive alewife die-off in winter 1977-1978.

9. Young-of-the-year alewives of the first cohort (those first spawned) in Claytor Lake were morphologically unavailable to predators less than 178 mm TL (largemouth bass equivalents: LMBE) by early August. Young-of-the-year alewives remained available to predators less than 178 mm TL (LMBE) beyond August because of later cohorts (those subsequently spawned). Extended spawning period of alewives in Claytor Lake appears to mitigate availability of young-of-the-year alewives despite rapid growth by providing a large range of sizes over a protracted period of time.

10. Greatest densities of larval alewives in Claytor Lake occurred in the upper 3 m of the water column in littoral (<5 m) areas of coves and embayments within 4.0 km of the dam. Abundance of planktonic larvae indicates that spawning areas may also serve as nursery areas until young-of-the-year alewives become more mobile. Larval alewives were present in the main channel where they may eventually be lost from the reservoir through escapement.

11. Cyclopoid copepods were the principal food item in diets of alewives 6 to 35 mm TL. Bosmina longirostris dominated diets of alewives 36 to 70 mm TL. Other food items included phytoplankton, copepod nauplii, ostracods, adult terrestrial dipterans, and cladocerans. Relative abundance of major zooplankters in diets was positively correlated to relative abundance of these zooplankters in the water column. Larval and juvenile alewives failed to utilize calanoid copepods whose size, agility, and considerable evasion skills may limit their availability.

12. Total lengths of young-of-the-year alewives in Claytor Lake were positively correlated to total lengths of food items, particularly cyclopoid copepods, in their diets. Size selection of cyclopoid copepods was positive by alewives as small as 31 mm TL and corresponded directly to adult size selection. Young-of-the-year alewives may significantly compound the potentially major negative impact that adult alewives, through modification of size distribution and species composition of zooplankton communities, may exert on young-of-the-year sportfish.

The self-sustaining alewife population in Claytor Lake demonstrates that introductions of alewives into southeastern reservoirs can be successful. Introductions of alewives would probably be most successful in

reservoirs with an abundant microcrustacean forage base to provide favorable trophic conditions, and large expanses of littoral (<5 m) areas that could accomodate massive inshore spawning concentrations, characteristic of alewives. Favorable growth conditions, as demonstrated by alewives in Claytor Lake versus their counterparts in northern lakes, may result in a more prolific alewife population that could better accomodate intensive predator pressure. Reproductive success would be further enhanced by abundant spawning habitat because intra-specific competition might be reduced allowing increased juvenile survival rates and ultimate recruitment to the adult population.

Although latitudinal trends in growth and reproduction of landlocked alewives are indicated, each system is unique. In Flannegan Reservoir, Virginia, alewives reach maximum total lengths of 80 mm, spawn once (semelparity), and die (G. Martel, personal communication). Also, in reservoirs more southerly and/or at lower elevations than Claytor Lake, water temperatures may reach levels that inhibit growth and spawning of the alewife. Alewife populations in these reservoirs may not be as prolific nor have as extended a spawning period as those in reservoirs with temperature regimes similar to Claytor Lake, and thus may be less able to accomodate intensive predator pressure. Attempts to establish alewife populations in warmer water reservoirs, therefore, may meet with limited success.

An evaluation of the utility of establishing alewife populations as pelagic forage fish in southeastern reservoirs was made as part of a concurrent study of the trophic ecology of alewives in Claytor Lake (Kohler 1980). This evaluation was based upon criteria thought to be

indicative of an ideal pelagic forage fish, including: (1) prolific, self-sustaining population, (2) extended spawning period and (3) devoid of adverse interspecific impact.

The alewife population in Claytor Lake has been self-sustaining since initial introduction in 1968-1969. Claytor Lake alewives mature in their second year of life and are highly fecund relative to their counterparts in northern lakes. Although winter mortality does occur, alewives apparently have acclimated to the winter temperature regime of Claytor Lake and may, in fact, be emigrating down river (Kohler 1980). Expansion of the Claytor Lake alewife population after a massive winter die-off in 1977-1978 indicates that the population, possibly because of early recruitment of highly fecund spawners, can withstand extreme fluctuations in abundance.

Alewives in Claytor Lake spawn from early May to early August. Young-of-the-year alewives that hatch in early May grow rapidly and become morphologically unavailable to age I white bass (148 mm TL) and walleye (253 mm TL) by mid-July and age I striped bass (214 mm TL) by early August (Jenkins and Morais 1978). However, rapid growth of young-of-the-year alewives is mitigated by the extended alewife spawning period which assures, through subsequently spawned cohorts, that young-of-the-year alewives remain available to age 0 and age I sportfish through the growing season.

Young-of-the-year alewives in Claytor Lake exhibit size-selective planktivory equivalent to that of adult alewives at sizes as small as 35 mm TL, and may significantly contribute to observed shifts in size and species composition of zooplankton communities toward smaller forms.

Heavy concentrations of young-of-the-year alewives in littoral areas may exert a significant negative impact on young-of-the-year sportfish which depend on littoral zooplankton populations as a food source.

Consequently, as with any introduction of an exotic forage species, potential benefits of alewives to targeted predator species should be weighed against their potential impacts on zooplankton populations and on planktivorous life stages of resident fish species. In addition, the potential of alewife populations to expand dramatically in the absence of sustained predator pressure, as demonstrated in the Great Lakes, should warrant careful consideration regarding alewife introductions in southeastern reservoirs without a well established pelagic predator population.

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REPRODUCTION AND EARLY LIFE HISTORY OF A LANDLOCKED
POPULATION OF ALEWIFE (ALOSA PSEUDOHARENGUS)

IN CLAYTOR LAKE, VIRGINIA

by

Anthony Albert Nigro

(ABSTRACT)

Alewives in Claytor Lake matured at age I at 160 mm TL. Fecundity of gravid females increased with age and length, ranging from 17307 eggs at age I to 37147 eggs at age III. The majority of alewife spawning was concentrated in littoral areas of a large embayment. Spawning period was protracted (13 weeks), beginning in May and lasting until August. Females apparently did not extrude eggs at one time, but spawned repeatedly.

Growth rates of young-of-the-year alewives were higher in 1978 than in 1979, possibly due to reduced intraspecific competition for food and space following an alewife die-off in winter 1977-1978. Rapid growth of young-of-the-year alewives allowed the earliest spawned cohorts to become morphologically unavailable as prey to age 0 and age I sportfish by mid-July. However, the extended alewife spawning season mitigated availability of alewives by assuring, through subsequently spawned cohorts, that they remain available as prey through the growing season.

Cyclopoid copepods were the principal food item in diets of alewives 6 to 35 mm TL. Bosmina longirostris dominated diets of alewives 36 to 70 mm TL. Size-selective planktivory of larval alewives was equivalent to that of adults at sizes as small as 31 mm TL, and may

have significantly contributed to observed changes of zooplankton communities toward smaller forms. Concentrations of young-of-the-year alewives in littoral areas may exert a negative impact on age 0 sportfish which depend on littoral zooplankton populations as a food source.