Effects of Seasonal Habitat Limitations on the Distribution and Energetics of Stocked Salmonids in Lake Moomaw, Virginia

by

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ABSTRACT

Lake Moomaw, a 1024 ha flood control reservoir in western Virginia, retains sufficient cold, oxygenated water (< 21°C, ≥ 5.0 mg/L) to allow trout survival throughout most of the summer. However, trout habitat declines to an annual minimum in September. Vertical gillnets and ultrasonic telemetry were used to determine the horizontal and vertical distribution of two cohorts of brown trout, Salmo trutta, and rainbow trout, Oncorhynchus mykiss, relative to ambient temperature and dissolved oxygen. Capture of trout in gillnets afforded the assessment of condition (K), relative liver weight (HSI), and daily consumption (C_D) of age 1+ brown and rainbow trout in relation to habitat dynamics.

Most age 1+ brown and rainbow trout were distributed in the metalimnion (12 - 21°C) from July to October, even when dissolved oxygen declined below 5.0 mg/L. Location in the metalimnion placed young trout near optimum temperatures and maximum prey abundance. The growth, condition, relative liver weight, and daily consumption of age 1+ brown and rainbow trout were apparently unaffected by habitat limitations. Age 1+ brown trout preyed almost exclusively on alewives, Alosa pseudoharengus, whereas aquatic and terrestrial insects constituted a substantial portion of young rainbow trout diet.

Age 2+ rainbow trout were distributed in the metalimnion from July to September, but were located in the hypolimnion (< 12°C) in October. Adult brown trout were located in the metalimnion during July, but were distributed in the hypolimnion from August to October. Adult trout in the hypolimnion were at low temperature (10°C) and diminished dissolved oxygen concentrations (< 5.0 mg/L). Distribution in the hypolimnion also resulted in isolation from primary forage, alewives. Age 2+ brown trout effectively were not feeding, as only one of 16 adult brown trout collected in two years of sampling contained food. Adult rainbow trout consumed primarily alewives in August and aquatic insects in September, but were apparently not feeding in October. Small sample size precluded the direct measurement of the effects of this isolation on the growth of age 2+ trout in Lake Moomaw. A bioenergetics model predicted that even brief durations of isolation from prey could severely limit the growth of age 2+ brown and rainbow trout.

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INTRODUCTION

Reservoir Habitat Dynamics

Warmwater reservoirs sometimes contain sufficient cold, oxygenated water to support productive salmonid fisheries in the relatively unoccupied pelagic zone. These reservoirs are often referred to as "two-story fisheries" (Kirkland and Bowling 1966). Two-story fisheries provide the opportunity to efficiently utilize reservoir resources, while establishing trout fisheries in regions where natural coldwater habitat is limited. Fisheries managers in the Southeast have capitalized on this opportunity for more than three decades (Stevenson and Hulsey 1961; Kirkland and Bowling 1966; Axon 1971; Jones 1982).

Conditions favoring the establishment of two-story fisheries can usually be attributed to one of two limnological situations: (1) lakes with warmwater inflow that are able to store enough winter-cooled water in the hypolimnion to provide sufficient summer habitat for trout; and (2) lakes that receive cold water from tributary streams (Wilkins et al. 1967). The discharge from these streams travels through the reservoir via density currents, providing a stable source of cold water (Cole 1983). The latter limnological situation can also result when a reservoir receives hypolimnetic discharge from an upstream reservoir (Austin et al 1978).

Because natural reproduction is seldom sufficient to sustain reservoir trout fisheries, most are managed on a put-grow-and-take basis. Trout stocked as sub-catchables grow and become naturalized in the reservoir, before attaining harvestable size. When a suitable forage species is present, growth of stocked trout in two-story reservoirs can be exceptional. First-year growth rates of 30 mm per month have been reported (Wilkins et al. 1967; Axon 1971). When longevity is coupled with excellent growth, the potential to produce trophy fish is maximized. One requisite of growth and survival is the presence and accessibility of suitable habitat.

Reservoir trout habitat is defined and determined by two parameters--temperature and dissolved oxygen (D.O.). Habitat criteria should provide ample protection from lethal concentrations, minimize physiological stress, and provide conditions that promote growth.

Most of the published literature lists 21°C as the maximum temperature for suitable reservoir trout habitat

(Stevenson and Hulsey 1961; Kirkland and Bowling 1966; Baker and Mathis 1967; Axon 1971; Oliver et al. 1977; Love 1979; Jones 1982). The 21°C consensus is higher than the preferred temperatures (14 - 18° C) of brown trout (Salmo trutta), and rainbow trout (Oncorhynchus mykiss) (Coutant 1977). The temperature does not necessarily depict the lethal threshold, but represents the conservative end of the range of accepted upper avoidance temperatures.

Cherry et al. (1977) reported upper avoidance temperatures ranging from 21-24°C for brown and rainbow trout acclimated at 18°C. These avoidance temperatures were determined during rising temperature conditions. Because the laboratory acclimation temperature falls within the expected temperature preferenda of trout, and rising temperature conditions are typical in reservoirs during the summer, the results should be relevant to reservoir habitat delineation. Temperature can be a controlling factor of both the consumption and metabolism of fish, consequently affecting fish growth (Wooton 1990). Growth of brown trout fed on maximum rations decreases to zero as the temperature approaches 20°C (Elliott 1975). Thus, the 21°C maximum temperature criterion is also indicative of habitat conditions that are conducive to growth of trout.

A single dissolved oxygen (D.O.) criterion has proven more difficult to establish. Low solubility of oxygen in water creates inherent limitations to fish physiology and behavior (Wooton 1990). In the early days of two-story reservoir management, researchers used oxygen consumption requirements based on the work of Burdick et al. (1954). These data corresponded to lethal D.O. limits, determined in the laboratory. Concentrations were determined at different temperatures; by depleting available dissolved oxygen rapidly, the trout were not allowed to acclimate. Critical concentrations for rainbow and brown trout at 21°C were listed as 2.47 mg/L and 2.82 mg/L respectively. Fry (1951) had already noted that given time to acclimate, a fish's lethal oxygen minimum could be reduced by as much as 50 percent. Seeking a level of protection that would avoid the lethal threshold, early managers supported the 3.0 mg/L criterion (Stevenson and Hulsey 1961; Kirkland and Bowling 1966; Baker and Mathis 1967). A criterion based solely on the lethal threshold neglects to address the effect of oxygen on other aspects of fish physiology and behavior.

When Davis (1975) reviewed the literature on the oxygen requirements of fish, he defined the threshold oxygen concentration as the level at or below which exposure resulted in physiological stress (e.g., increased metabolism, decreased activity, reduced growth, poor condition). A minimum of 4.67 mg/L was reported to provide protection for the average member of a population of brown or rainbow trout. Davis also addressed the question of fish acclimation to low oxygen, determining that there was not enough evidence from laboratory or field studies to warrant altering an oxygen criterion based on the potential for fish to acclimate to low oxygen conditions.

Oxygen can act as a limiting factor to the growth of fish (Kramer 1987; Weatherley and Gill 1987; Wooton 1990). Below a critical oxygen threshold (5.0 mg/L), growth rate of salmonids can decline even when food is available in excess (Brett 1979; Brett and Blackburn 1981). Growth rate declines because metabolic costs increase in low oxygen conditions, and foraging success is reduced due to the additional energy and time required to ventilate.

The preceding discussion of temperature and oxygen criteria provides the derivation of trout habitat parameters to be used in this study. Reservoir trout habitat will be defined as waters where temperatures are below 21°C, and D.O. concentrations are at or above 5.0 mg/L. These criteria describe conditions that provide protection from lethal concentrations, as well as promote the productivity of a fishery.

The critical time period for trout habitat in Southeastern two-story reservoirs begins in mid to late August and continues until the lake becomes destratified (Kirkland and Bowling 1966; Baker and Mathis 1967; Jones 1982).

Reservoir habitat is depleted as strata temperatures exceed 21°C, or dissolved oxygen concentrations fall below 5.0 mg/L. Timing and intensity of habitat reduction vary depending on climatic conditions, reservoir function, and dam operation.

Epilimnetic habitat is depleted in early summer, when temperatures exceed 21°C. Oxygen-related habitat depletion develops in three distinct zones (Figure 1). These zones, in order of descending depth, are the metalimnetic, the middle, and the benthic zones (Gordon and Skeleton 1977).

Oxygen depletion in the metalimnetic zone is primarily the result of a density gradient that creates a "fall-out zone" first described by Hutchinson (1957). This zone was later described as an area of "hindered settling", where seston and other sinking organics pour into a stratum faster than the matter can exit (Gordon and Skelton 1977). Decomposition of these organics creates a reducing environment and rapidly leads to hypoxic conditions.

Organic material travels through the middle zone of oxygen demand at a more uniform rate. Thus the conditions that enhanced oxygen depletion in the metalimnic zone do not exist in this stratum. Depletion occurs at a diminished rate.

The benthic zone is an area of intense oxygen demand. Oxygen depletion in this zone can be attributed to benthic respiration, and the mechanisms of biochemical oxygen demand (BOD) (Gordon and Nicholas 1977). Because detritus and other organic matter will eventually settle in the benthic zone, severe oxygen depletion can be expected.

As the summer progresses, the two oxygen depletion zones begin to expand. With the metalimnic demand extending downward and the benthic demand enlarging upward, the middle zone of oxygenated water is squeezed into a successively smaller stratum. Sometimes the layer of suitable habitat may remain as thick as 21 m (Axon 1971). Usually the remaining habitat is much reduced (1-2 m; Bivens and Strange 1987).

Horizontal depletion of suitable reservoir trout habitat is also prevalent (Kirkland and Bowling 1966; Wilkins et al. 1967; Baker and Mathis 1967; Axon 1971; Love 1979). As the summer progresses, two mechanisms of oxygen depletion reduce the oxygen and consequently the trout habitat from all but the deepest areas of the reservoir, usually near the dam. These mechanisms are: (1) the oxygen consumption associated with the biochemical oxygen demand; and (2) the discharge of reservoir water exporting oxygen from the system. Habitat remains in the deepest area of the reservoir because the middle zone is thicker, and because fertility decreases downstream.

The combined effects of vertical and horizontal habitat limitations can result in severe reduction of trout distribution potential. In some instances, oxygen depletion is so intense that habitat is eliminated entirely. Jones (1982) reported complete loss of trout habitat and no

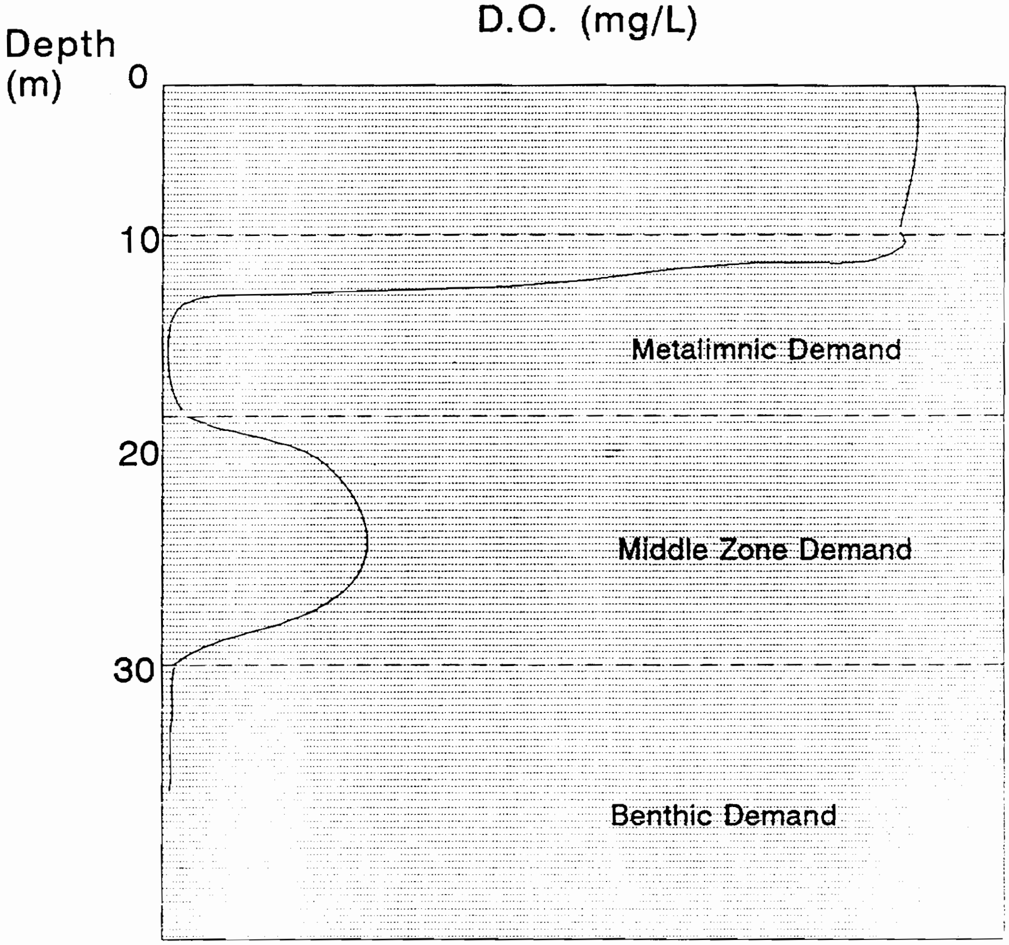


Figure 1. Zones of dissolved oxygen depletion in reservoirs. Adapted from Gordon and Skelton 1977.

over-summer survival of trout in Laurel River Lake, Kentucky. Complete habitat loss has also been noted in Lake McConaughy, Nebraska, but no mortality estimate was reported (Van Velson 1974). This suggested that either trout endured the brief habitat loss, or mortality was inconspicuous. Many lakes stocked with trout on a trial-and-error basis have failed to achieve trout survival over the summer. For example, Claytor Lake, Virginia, was stocked with trout for a decade without developing a holdover population before the practice was evaluated and abandoned (Kohler et al. 1986).

Duration and intensity of habitat reduction or loss dictates the potential effect on the fishery. The typical duration of severe habitat reduction in Southeastern reservoirs has been reported as two to three weeks (Wilkins et al 1967; Axon 1971; Love 1979). Cooling temperatures and increased wind will initially destratify the well-oxygenated epilimnion. Unfortunately, this is not always the endpoint of critical habitat stress and restricted distribution.

Love (1979) reported that trout in Bull Shoals Lake, Arkansas, remained isolated in the waning habitat of the hypolimnion two weeks after the epilimnetic habitat had been replenished. This occurred because an anoxic layer 15 m thick remained between subsistence habitat in the hypolimnion and ideal habitat in the epilimnion. Therefore, it cannot be assumed that habitat-related stress is immediately alleviated when the epilimnion of a two-story reservoir contains suitable trout habitat. Habitat limitations may continue until the reservoir is completely destratified (i.e., at fall turnover).

Habitat Dynamics at Lake Moomaw

Lake Moomaw, a 1024-ha flood-control reservoir in montane western Virginia, provides an ideal situation to examine the potential effects of habitat limitations on a reservoir trout population. Brown and rainbow trout are stocked annually as sub-catchables (150-200 mm TL). Trout habitat typically reaches a minimum in early September, before the epilimnion cools to 21°C. In addition to the common mechanisms of oxygen depletion, a recent alteration in the operation of the dam apparently magnifies habitat reduction.

The discharge tower at Gathright Dam was constructed to allow a variety of withdrawal depths (9 portals spanning 23 m). This structure provides the potential to achieve a given discharge temperature by two methods: releasing from a single portal at the target temperature, or by mixing water from different portals before it is discharged. Operation of the dam from 1981 to 1989 resulted in warmwater discharge from the epilimnion. A minimum volume of 13.5 x 10^6 m^3 of trout habitat (9.0 percent of total reservoir volume) was maintained in the reservoir during this period (Bugas 1991).

In 1990, operation of the dam was altered to provide a constant coldwater discharge. The resulting release consisted of a single-stage withdrawal from the portal with reservoir water at 14°C (i.e. one of the nine ports located closest to 14.0°C water). This alteration typically resulted in discharge of water from the metalimnion. Reservoir trout habitat was apparently adversely impacted by this discharge alteration. Water quality data collected in the summer and fall of 1990 detailed a severe reduction in habitat. Only 0.3 x 10^6 m^3 of habitat (less than 1 percent of reservoir volume) remained as of 17 September 1990, a reduction of more than 95 percent from previous annual minima (Bugas 1991).

This situation provides the opportunity to study the dynamics of reservoir trout habitat in relation to a change in dam operation. Uncommon natural events, as well as impacts of anthropogenic origin can have a significant influence on reservoir trout habitat. Love (1979) noted that increased reservoir discharge removed all trout habitat (< 21°C, ≥ 4.o mg/L) from Bull Shoals Lake, Arkansas. The operation of pumped-storage hydroelectric facilities can also severely reduce reservoir trout habitat by depleting cold water and returning warm water (Oliver et al. 1977). Reservoir habitat reduction resulting from the upstream release of anoxic water has also been documented (Austin et al. 1978, Weithman and Haas 1984). However, the effects of a metalimnetic constant coldwater release on the trout habitat in a reservoir have not been documented.

The situation also provides an ideal opportunity to study several important effects of habitat limitations that previous studies have not reported. Previous work has focused on detailing seasonal habitat depletion (Stevenson and Hulsey 1961; Oliver et al. 1977; Austin et al. 1978; Love 1979). The effects of these seasonal habitat limitations on trout are not well understood. Love (1979) reported that the distribution of trout in Bull Shoals Lake, Arkansas was limited by seasonal habitat depletion. Weithman and Haas (1984) noted that catch rate and angler effort declined as habitat reached a summer minimum in Lake Taneycomo, Missouri. Analysis of the habitat selection patterns and energetic responses of brown and rainbow trout during habitat degradation will indicate to what degree summer habitat may limit the success and productivity of a reservoir trout fishery.

GOALS AND OBJECTIVES

The goal of this thesis is to document the effects of summer habitat limitations on the distribution and energetics of stocked salmonids in Lake Moomaw, Virginia. Specific objectives of this study are to:

1). Describe the seasonal decline of reservoir trout habitat;

2). Relate the vertical and horizontal distribution of age 1+ and age 2+ brown and rainbow trout to dissolved oxygen and temperature;

3). Determine the degree to which habitat depletion isolates brown and rainbow trout from forage; and

4). Describe the influence of habitat restrictions on growth, condition, and food consumption of two age classes of brown and rainbow trout.

METHODS

Study Area

Sampling was conducted at Lake Moomaw, an impoundment of the Jackson River in Alleghany and Bath Counties of Virginia (Figure 2). The reservoir was formed by the completion of Gathright Dam in 1981 by the U.S. Army Corps of Engineers. Reservoir functions include augmenting low flows to improve downstream water quality in the Jackson and James Rivers and providing flood control. At a normal pool elevation of 523 m, Lake Moomaw covers 1,025 surface hectares and has a maximum depth of 45 m, with a mean depth of 15 m. The reservoir then has 70 km of shoreline, and contains approximately 1.53 X 10^8 m^3 of water. Seasonal fluctuations in reservoir pool elevation are a consequence of augmenting low flows downstream. Reservoir level fluctuations of seven meters have been recorded, but three to five meter fluctuations define the normal seasonal range. Under the usual annual regime, the reservoir is full in spring, with maximum drawdown in fall.

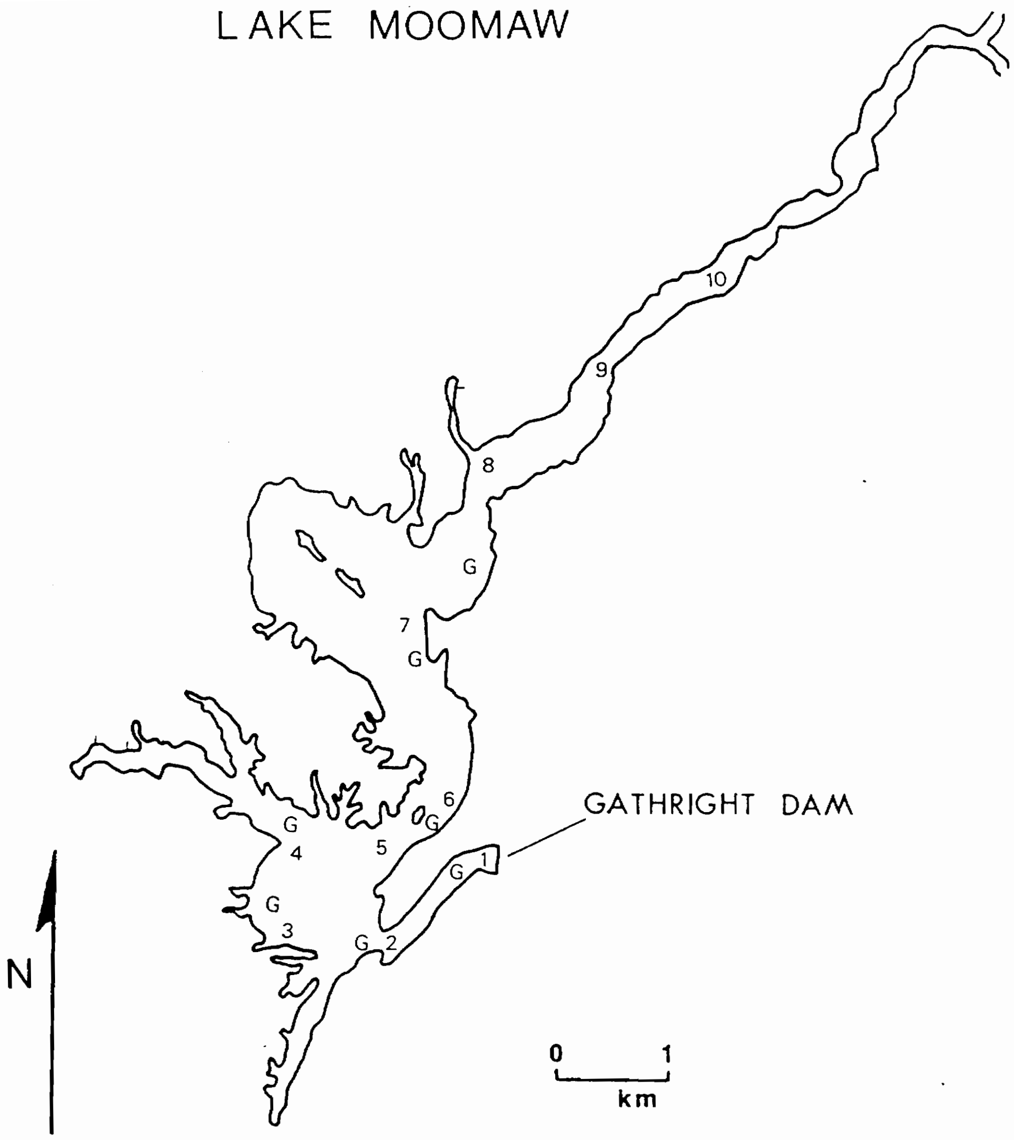


Figure 2. Map of Lake Moomaw, with gillnetting locations (G) from 1991 and 1992. Numbers correspond to limnological sampling stations.

Brown and rainbow trout are stocked annually in December as sub-catchables (150 - 200 mm TL). Current regulations include a 254 mm minimum length limit, and a daily creel limit of six trout. The Lake Moomaw fishery is the state's premier reservoir trout fishery and provides a substantial boost to the local economy. In addition to brown and rainbow trout, the lake supports self-sustaining populations of largemouth and smallmouth bass, chain pickerel, channel catfish, black crappie, yellow perch, alewives, gizzard shad, and a variety of sunfish species (see Table 1 for a list of the scientific names of fish cited by common name in this thesis).

Data Collection

Field sampling incorporated methods that procured data from three critical aspects of the fishery: habitat, fish distribution, and trout performance. Figure 3 displays the three categories of data, the methods employed to collect data, and their logical order of analysis. Describing the seasonal dynamics of trout habitat stored in the reservoir from June to October provided the foundation for subsequent analyses. The effects of these seasonal habitat dynamics on the distributions of trout and alewives was determined by relating fish distributions to ambient temperature and dissolved oxygen.

Table 1. Common and scientific names of all fish species cited by common name in the text.

COMMON NAME	**SCIENTIFIC NAME**
alewife	Alosa pseudoharengus
black crappie	Pomoxis nigromaculatus
brown trout	Salmo trutta
channel catfish	Ictalurus punctatus
chain pickerel	Esox niger
gizzard shad	Dorosoma cepedianum
largemouth bass	Micropterus salmoides
rainbow trout	Oncorhynchus mykiss
smallmouth bass	Micropterus dolomieu
striped bass	Morone saxatalis
sunfish species	Lepomis spp.
yellow perch	Perca flavescens

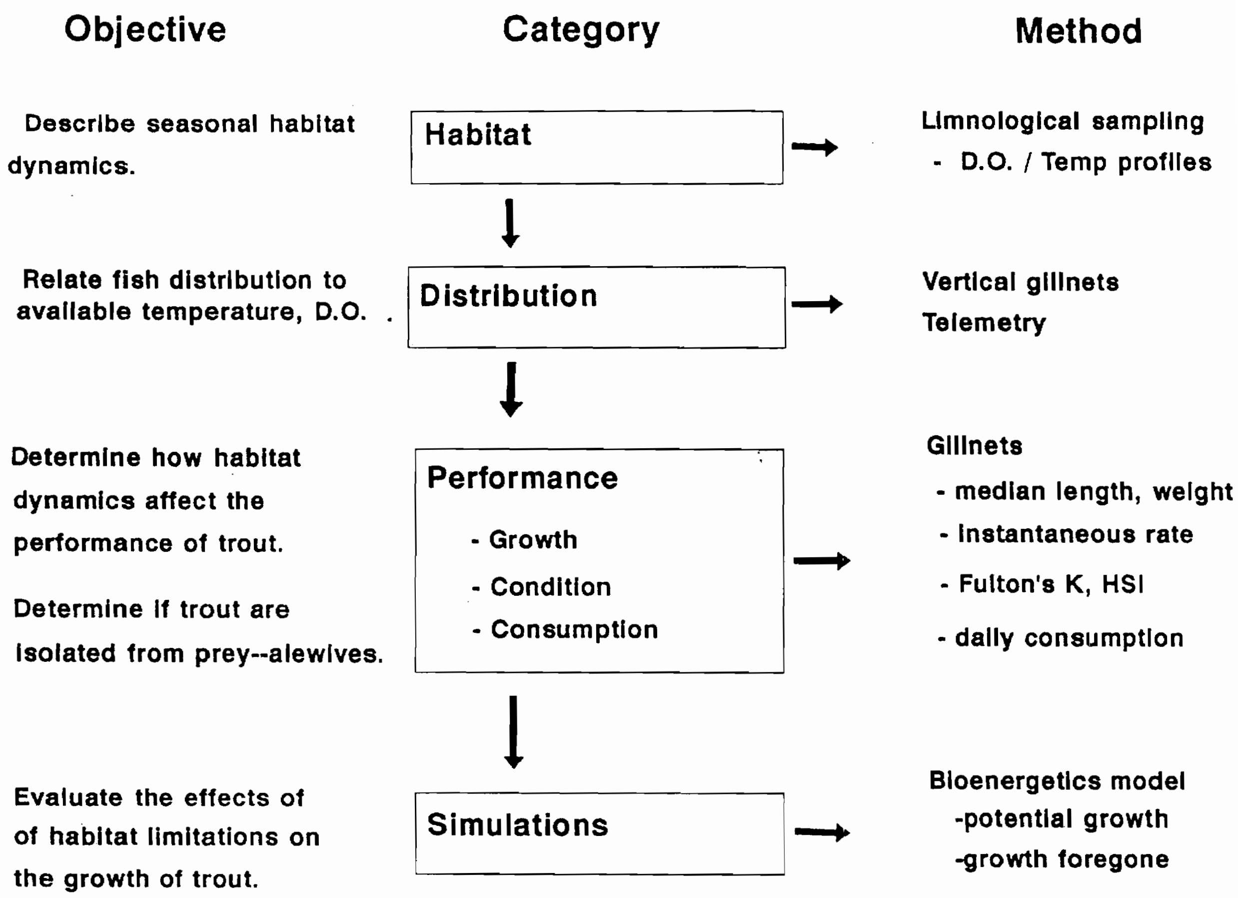


Figure 3. Flow chart depicting the categories of data acquisition and the associated methods.

The growth, condition, and consumption of trout were estimated to evaluate the effect of habitat limitation and restricted distribution on the performance of trout in Lake Moomaw.

A fourth category of data, labeled simulations, was acquired through the use of a bioenergetics model (Figure 3). Bioenergetic simulations provided information that could not be collected in the field: the potential trout growth precluded by habitat limitations and isolation from prey.

Limnological sampling

Dissolved oxygen and temperature profiles were taken at least twice per month during the period (August - October 1991) and (June - October 1992). A Yellow Springs Instrument model number 57 oxygen analyzer with attached thermistor was used to determine profiles from surface to bottom. Dissolved oxygen and temperature were measured at 1-m increments from the surface to a depth of 20 m, and at 5-m increments from 20 m to bottom. Profiles were taken at locations chosen to document the vertical and horizontal availability of trout habitat in the reservoir. (Figure 2). Additional profiles taken coincident with fish sampling provided data to relate fish depth distribution to dissolved oxygen and temperature.

Fish Sampling

Trout sampling. Vertical gillnets were used to collect brown and rainbow trout twice per month (four nights each month) from August to October 1991, and once per month (at least four nights each month) from July to September 1992. Vertical gill net systems were constructed and deployed similar to the descriptions by Kohler et al. (1979). Monofilament nets (3 m X 30 m) of various bar mesh sizes (3.81, 6.35, 10.2 cm) were employed. The nets were set in groups of at least three, and the collective set was anchored by two 8-kg weights.

Vertical gillnet sets were concentrated in the lower section of the reservoir (Figure 2), where depth allowed the nets to stretch from the surface to approximately 30 m. At one location, nets were fished from the surface to 23 m to avoid entanglement with submerged trees. This was accomplished by allowing part of each gillnet to remain on the flotation bar. All vertical nets were marked with numbered plastic labels at 1-m increments to allow determination of depth of capture.

Horizontal gillnets (2.4 m X 30 m) were employed twice per month (four nights each month) from August 1991 to October 1991, and once per month (at least four nights each month) from May 1992 to September 1992 to collect brown and rainbow trout. Nets with different bar mesh sizes (6.35 and 10.2 cm) were suspended at depths and locations based on vertical gill net catches or temperature and dissolved oxygen data. This technique provided increased sampling effort within a specific target zone and effectively increased sample size. Trout collected in horizontal gillnets were not used in the analysis of distribution, but were included in other analyses--growth, condition, and consumption.

In 1991, horizontal gillnets also used to assess the horizontal distribution of trout relative to habitat depletion. Nets were fished in August and September at locations where temperature was below 21°C, and D.O. concentration was below 5.0 mg/L (Figure). Nets were set in the same locations during October to assess the horizontal movement of trout in the recently cooled epilimnion. Horizontal gillnets were not used to assess the horizontal distribution of trout in 1992, because ultrasonic telemetry provided this information.

Only nighttime sets proved successful, and captured fish were removed from the nets at dawn. The depth of capture of fish collected in vertical gill nets was noted. Individual trout were identified to species, weighed (to nearest gram) and measured (to nearest mm), and stomachs were removed for later study. Stomachs were preserved in a 10 percent buffered formalin solution. The liver weights, measured to the nearest

0.1 g (minus the gallbladder), of captured trout were recorded in 1992. Trout were preserved on ice until liver removal was conducted.

Ultrasonic transmitters (16 X 60 mm; 22 g in air) were surgically implanted in nine adult brown trout and five rainbow trout from March to July 1992. Trout were captured by electrofishing tributary streams during the spawning run, and by angling in the reservoir. In a final effort, two trout from a nearby hatchery were implanted with transmitters. Captured fish were anesthetized with MS-222, identified to species, weighed, and measured. A 2-cm incision was made in the hypaxial tissue near the anal vent. The transmitter was inserted into the abdominal cavity, and the incision was closed using a surgical skin stapler (Mulford 1984). After surgical implantation was complete, the trout were released into the reservoir. Fish caught by angling were released at the original capture site. Fish caught by electrofishing were transported to the reservoir and released. The transmitters were labeled with a name and phone number to facilitate the reporting of angler capture.

The temperature-sensitive transmitters (CTT-83, Sonotronics) were calibrated at known temperatures in the laboratory, using a BASIC computer program (CAL1.BAS). The relative position of a fish was determined using a directional hydrophone (DH-2, Sonotronics).

Horizontal distribution of trout was determined by triangulation with a hand-held compass and a topographic map. Vertical distribution of trout was assessed by comparing transmitter temperature data recorded by a digital ultrasonic receiver (USR5B, Sonotronics), with limnological profiles. Temperatures chosen by tagged trout during the study were determined directly by telemetry equipment, whereas depth and dissolved oxygen at each fix were calculated by examining the corresponding limnological profile.

Telemetry observations included assessment of horizontal and vertical location in the reservoir from June to October 1992. Telemetry monitoring occurred at least twice per month. On two occasions (16 July 1992, 15 Sept 1992) brown trout and rainbow trout were monitored over a 24-hour period. During each 24-hour monitoring period, the horizontal position and temperature location of telemetry-implanted fish were recorded at least every eight hours.

Alewife sampling. Two 12.7-mm mesh vertical monofilament gillnets (3 m X 20 m) were used to sample alewife distribution twice per month from August 1991 to October 1991, and once per month from July to September 1992. Because a single 20-m net could not be fished from surface to bottom, one net was fished from the surface to 20 m, while the other net was fished from 15 to 35 meters. This was accomplished by attaching 15 m of rope between the top of the net and the flotation bar. Numbered plastic labels were installed at 1 m increments on both nets, to allow accurate determination of depth of capture. Alewives were removed from the nets at dawn. Depth of capture of individual alewives was recorded.

On three occasions (once per month from May to July 1992) a monofilament cast net (2.3 m diameter; 9.5 mm mesh) was used to collect alewives. The smaller mesh size captured alewives that were too small to be adequately sampled with the gillnets. Alewives were attracted to the surface using a submersible light source. Captured fish were preserved in ice, then frozen for later analysis--derivation of a length-weight regression.

Data Analyses

Trout performance

Growth. The median length and weight of trout were calculated from fish captured in each monthly sampling trip. Plotting these median values versus time depicted the seasonal patterns of growth. Changes in the growth of trout on a monthly basis were also represented in the plot.

To gain more information about the trends of growth between individual months, instantaneous rates of growth were calculated from successive samples. The instantaneous rate of growth was calculated as in Cone and Kreuger (1988):

$$G = \frac{\ln W_{t+1} - \ln W_t}{T} \quad (1)$$

where G is instantaneous growth (g/g/day), W_{t+1} is the median weight of trout (grams) at sampling time t+1, W_t is the median weight of trout (grams) at sampling time t, and T is the amount of time (days) between samples.

Condition. Two indices were used to assess condition of brown and rainbow trout collected in vertical and horizontal gillnets. Because habitat dynamics and fish distribution were similar in both years, condition data from August and September of 1991 and 1992 were pooled. Pooling data from August and September, and including data from October 1991, afforded the assessment of trout condition from May through October. A Fulton-type condition factor (K) was calculated for trout captured in this study using an equation based on length and weight:

$$K = \frac{W}{L^3} \times 10^5 \tag{2}$$

where K is condition, W is weight in grams, and L is total length (mm). Because the Fulton index is only affected by changes in weight, its sensitivity to short term changes in fish condition is suspect (Anderson and Gutreuter 1983). When a fish begins to starve, body tissues are converted to energy, and water replaces the atrophied tissues (Weatherley and Gill 1987). Consequently, the weight of a fish may not change appreciably during relatively short periods of fasting. An ideal index would be more sensitive to short term changes in condition.

The Hepatosomatic Index (HSI) divides the liver weight by total body weight. The HSI can detect changes in short-term condition before impacts to growth are apparent (Adams and McLean 1985). This index is sensitive to short-term nutritional changes because the liver functions as a storehouse for glycogen (Anderson and Gutreuter 1983). Thus, high HSI values correspond to profitable forage and growth conditions. The well-being of trout captured in the 1992 sampling season was estimated using the Hepatosomatic Index.

Consumption. Consumption data from August and September of 1991 and 1992 were also pooled by month to facilitate analysis. Daily consumption was estimated using the reconstructive method (Swenson and Smith 1973). This method is ideal for estimating the consumption of piscivorous fish, as it incorporates data on fish size, prey size, meal size, and evacuation rate. Daily consumption (C_D) is given by the equation:

$$C_D = \sum \frac{C_i \;/\; W_i}{N_t} \qquad (3)$$

Where C_D is average total daily consumption (mg/g/day), C_i is weight of prey (mg) consumed by predator i in 24 hours, W_i is the weight (g) of predator i, and N_t is the number of fish sampled during time period t.

Laboratory Analyses

Trout diet

Composition. Stomach contents of brown and rainbow trout were examined in the laboratory. Diet composition was determined on a percent by weight basis. Insect prey were identified as aquatic or terrestrial, and weighed in aggregate by category to 0.1 g. Each piscine prey was identified to species, measured to 1 mm, and weighed to 0.1 g (Hyslop 1980). Either total length or backbone length of fish prey was measured, depending on the degree of digestion.

Weight of each piscine prey at the time of ingestion was estimated using regression equations developed for the primary prey species--alewife (Table 2). Moore (1988) developed a regression to describe the relationship between backbone length (BL) and total length (TL) for the alewife (Equation 1, Table 2). A length-weight relationship was then developed for alewives collected by castnetting (Equation 2, Table 2). When total length (mm) of prey at the time of ingestion has been estimated, the length-weight regression can be used to estimate prey weight (WT) in grams at the time of ingestion.

Daily consumption. The gastric evacuation rate of piscivorous brown trout has been studied by Elliott (1991) and He and

Wurtzbaugh (unpublished manuscript). A regression equation from He and Wurtzbaugh was used to determine the evacuation rate (g/hour) of brown and rainbow trout feeding on alewives (Equation 3,Table 2). This equation appears applicable to brown and rainbow trout in Lake Moomaw for several reasons. First, the length (352-457 mm standard length) and weight (860-1600 g) of brown trout studied in the laboratory corresponds to the sizes of most of the brown and rainbow trout collected in this study. Second, evacuation rates were determined at temperatures ranging from 4.5 to 21°C. This temperature range is representative of temperature conditions observed in limnological profiles at Lake Moomaw. Third, while evacuation rates were determined using rainbow trout as prey, the weights of individual prey (3.5-7.6 g) are similar to the weights of alewives consumed by trout in Lake Moomaw. Studies have demonstrated that different piscine prey of similar sizes are evacuated at similar rates (Elliott 1991).

Actual stomach contents were corrected to represent the consumption of individual trout over a 24 hour period. The gastric evacuation rate was used to determine the time elapsed since each item had been consumed. Items retained in the stomach longer than 24 hours were deleted from further analysis. At temperatures greater than 18°C, alewives that weighed less than 5 grams (live weight) could be evacuated in less than 24 hours. To avoid underestimating the total daily consumption of trout at these temperatures, stomach contents were multiplied by a factor equal to 24 hours divided by the time to 95 percent digestion at that temperature, e.g. 24 divided by 22.4 (1.07) at 19°C.

Table 2. Equations used to estimate the daily consumption by brown and rainbow trout.

Equation	**r^2**	**Source**
(1) $TL = 1.616\ (BL) - 2.994$	.98	Moore 1988
(2) $\ln WT = -11.38 + 2.93 \ln TL$	.93	Present study
(3) $R = 0.053e^{0.073(t)}$	.98	He and Wurtzbaugh

List of Terms

BL = backbone length in millimeters

TL = total length in millimeters

Wt = weight in grams

R = rate of digestion (g/hr)

t= temperature (°C)

Bioenergetic Simulations

Bioenergetics models are mass-balance equations that can be solved to estimate growth of individual fish. Growth (G) is calculated as the difference between the energy in consumed food (C) and the various energetic costs:

$$G = C - R - W \tag{4}$$

where (R) is equivalent to the energy required for total metabolism, and (W) is the energy lost in waste products.

Numerous reviews of bioenergetics model applications have been published (Brett and Groves 1979; Elliot 1979; Brett 1983; Brafield 1985; Ney 1990). Bioenergetics models have been used to assess the potential limiting effects of temperature and prey availability on the growth of several species (Kitchell et al. 1977; Rice et al. 1983; Brandt et al 1992), but application to brown and rainbow trout energetics is limited. Rand et al. (unpublished manuscript) employed a bioenergetics model to estimate consumption of rainbow trout in Lakes Michigan and Ontario.

A version of the bioenergetics model developed by J. F. Kitchell and colleagues at the University of Wisconsin

(Kitchell et al. 1977; Kitchell and Breck 1980; Stewart et al 1983) was chosen to model the energetics of stocked salmonids in Lake Moomaw. Microcomputer software and a users manual have been developed for the Wisconsin bioenergetics model (Hewett and Johnson 1987; 1992) and are available from the University of Wisconsin Sea Grant Institute, Madison.

Despite considerable effort in the field, successive and adequate samples of adult brown and rainbow trout were difficult to obtain. Small sample sizes (n = 1 in some months) precluded the direct measurement of adult trout growth at Lake Moomaw. A bioenergetics model was used to estimate the potential growth of trout from June 1 to October 1, at preferred temperatures and reasonable forage opportunities.

Solving the bioenergetics model to estimate growth required the input of 23 parameters (Table 3). The model uses specific equations for consumption, respiration, egestion, and excretion. Further description of model equations and details of parameter valuation can be found in Appendix A and Hewett and Johnson (1992). Most parameter values for rainbow trout were taken from Rand et al. (unpublished manuscript). In an attempt to address differences between the species, parameter inputs for consumption by brown trout were derived from the extensive study of brown trout feeding on invertebrates (Elliott 1975a; 1975b; 1976a). When specific values could not be extracted from brown trout literature, parameter values developed for rainbow trout were incorporated.

The model also required the input of site-specific data. Temperature inputs for adult brown and rainbow trout were mean temperatures occupied by telemetry tagged trout. The mean weight (1005 g) of two adult rainbow trout captured in late May 1992 was used as the initial weight (01 June) in model simulations. The initial weight used in the brown trout model was the mean weight (1252 g) of six age 2+ brown trout collected in June 1992.

Because site-specific consumption data was unavailable, a P-value of 0.50 was used to simulate the potential growth of adult brown and rainbow trout from June to October. The P-value (range 0 - 1) is the proportion of maximum consumption consumed by the average fish in one day (see equation A2, Appendix A). A value of 0.50 was chosen for several reasons: (1) it was higher than the maintenance value (0.35), calculated by fitting a P-value to the same beginning and ending fish weight (as described in Hewett and Johnson 1992); (2) a P-value of 0.59 was calculated for age 1+ brown trout based on actual observed growth at Lake Moomaw from May to August; and (3) simulations using the value of 0.50 produced feasible growth rates (3.2 g/day).

The consumption equation of the bioenergetics model allows the inclusion of multiple prey items. Because brown trout fed almost exclusively on alewives, their simulated diet included only alewife forage. To address the observed diversity of rainbow trout diet, invertebrate forage was included as a small component (10 percent) of their diet. This required the input of a digestibility constant (i.e., the amount of consumed food that is indigestible) for the invertebrate portion of the diet (see egestion model, Table 3).

Table 3. Parameter values used in the bioenergetics model. Parameter valuation is discussed in more detail in Appendix A.

Parameter Description	brown trout	rainbow trout
Consumption: C_{max}		
Intercept: C_{max} at T_{opt}	0.239	0.260
Coefficient: C_{max} vs. weight	-0.227	-0.210
Minimum temperature for consumption, CQ	6	5
Optimum temperature for maximum consumption	18	20
Maximum temperature for consumption, CTL	22	24
Proportion of maximum consumption at CQ	0.25	0.33
Proportion of maximum consumption at CTL	0.075	0.20
Metabolism, R		
Intercept: Standard metabolism	0.00264	0.00264
Coefficient: R vs. weight	-0.217	-0.217
Coefficient: R vs. temperature	0.06818	0.06818
Coefficient: R vs. swim Speed	0.0234	0.0234
Swimming Speed, U		
Intercept: U	9.7	9.7
Coefficient: U vs. weight	0.13	0.13
Coefficient: U vs. temperature	0.0405	0.0405
Egestion, F		
Intercept: F vs. temperature, ration	0.212	0.212
Coefficient: F vs. temperature	-0.222	-0.222
Coefficient: P vs. egestion	0.0631	0.0631
Proportion indigestible: invertebrates	---	0.10
Proportion indigestible: fish	---	0.0
Excretion, U′		
Intercept: U′ vs. temperature, ration	0.0314	0.0314
Coefficient: U′ vs. temperature	0.58	0.58
Coefficient: P vs excretion	-0.299	-0.299

Statistical Analyses

Statistical procedures used to analyze data sets in this thesis are listed in Table 4. Preliminary tests (Shapiro - Wilks) revealed that condition (K, HSI) and consumption (C_D) data were not normally distributed ($p < 0.01$) in most months. As habitat was not limited, data collected in May, June, and July were pooled into a single period (MJJ). To represent the period of habitat limitation, data collected in August, September, and October were pooled into a single period (ASO). There was only slightly significant statistical evidence that the pooled data on condition (K, HSI) were not normally distributed ($p = 0.06$). However, there was highly significant statistical evidence that pooled data representing the daily consumption of brown and rainbow trout were not normally distributed ($P < 0.001$). Because parametric statistical analyses can lead to misinterpretation of research results when critical assumptions (e.g. normality) are not met (Pirie and Hubert 1977), nonparametric statistical procedures were used to analyze data sets in this thesis.

Table 4. Statistical procedures applied to analyze various data sets, Lake Moomaw, Virginia, 1991-1992.

Data set	Statistical Procedure
Distribution of monthly data (K, HSI, C_D) vs. normal distribution.	Shapiro - Wilks
Distribution of pooled data (K, HSI, C_D) vs. normal distribution.	Shapiro - Wilks
Condition (K, HSI) of age 1+ brown trout in MJJ vs. condition (K) in ASO.	Wilcoxon's rank sum
Condition (K, HSI) of age 1+ rainbow trout in MJJ vs. condition (K) in ASO.	Wilcoxon's rank sum
Condition (K, HSI) of age 1+ brown trout vs. condition of age 1+ rainbow trout in MJJ.	Wilcoxon's rank sum
Condition (K, HSI) of age 1+ brown trout vs. condition of age 1+ rainbow trout in ASO.	Wilcoxon's rank sum
Daily consumption (C_D) of age 1+ brown trout in MJJ vs. daily consumption of brown trout in ASO.	Wilcoxon's rank sum
Daily consumption (C_D) of age 1+ rainbow trout in MJJ vs. daily consumption of rainbow trout in ASO.	Wilcoxon's rank sum
Daily consumption (C_D) of age 1+ brown trout vs. daily consumption of rainbow trout in MJJ.	Wilcoxon's rank sum
Daily consumption (C_D) of age 1+ brown trout vs. daily consumption of rainbow trout in ASO.	Wilcoxon's rank sum
Percentage of empty stomachs by month for age 1+ trout.	Chi-square

RESULTS

Limnology and Trout Habitat

The temperature profile of Lake Moomaw is characterized by robust stratification: a distinct epilimnion, metalimnion, and hypolimnion were conspicuous beginning in June. The epilimnion typically included temperatures above 21°C from June to mid-September, before cooling as the reservoir destratified. Temperatures in the metalimnion ranged from 21°C at the upper boundary to 12°C at the lower margin. The hypolimnion was characterized by temperatures less than 12°C.

As rising water temperatures caused the epilimnion to enlarge, the depth location of the three zones changed from June to mid-September. For example, the metalimnion comprised depths from 7 to 16 m in July, compared to depths from 10 to 16 m in September. However, the temperatures presented above provided an accurate description of the zones on all sampling dates. Destratification of the epilimnion in late September and early October altered the temperature profile by reducing epilimnetic temperatures to 18°C. The metalimnion was then characterized by temperatures ranging from 16° to 12° C. Temperatures in the hypolimnion were unaffected by destratification in September and October.

The dissolved oxygen concentration in the epilimnion was consistently above 7.5 mg/L--values representing saturation at temperatures greater than 21°C and 523 m elevation (Cole 1983). Dissolved oxygen concentrations in the metalimnion and hypolimnion declined from June to October. Concentrations in some strata of the lower metalimnion and hypolimnion were below 5 mg/L beginning in August.

1991

Trout habitat in Lake Moomaw declined from August to September and recovered in October 1991. Horizontally, habitat depletion proceeded downstream: in late August and early September, the only remaining habitat was located near the dam. Vertically, the best available trout habitat was located near the dam in and adjacent to the original Jackson River channel. All trout habitat was lost in mid-September. Duration of severe habitat limitation was relatively brief, as cooling of the epilimnion, and subsequent reclamation of habitat, began in late September.

During August, available trout habitat was found only in the lower portion of the reservoir (Figure 4). A hypoxic

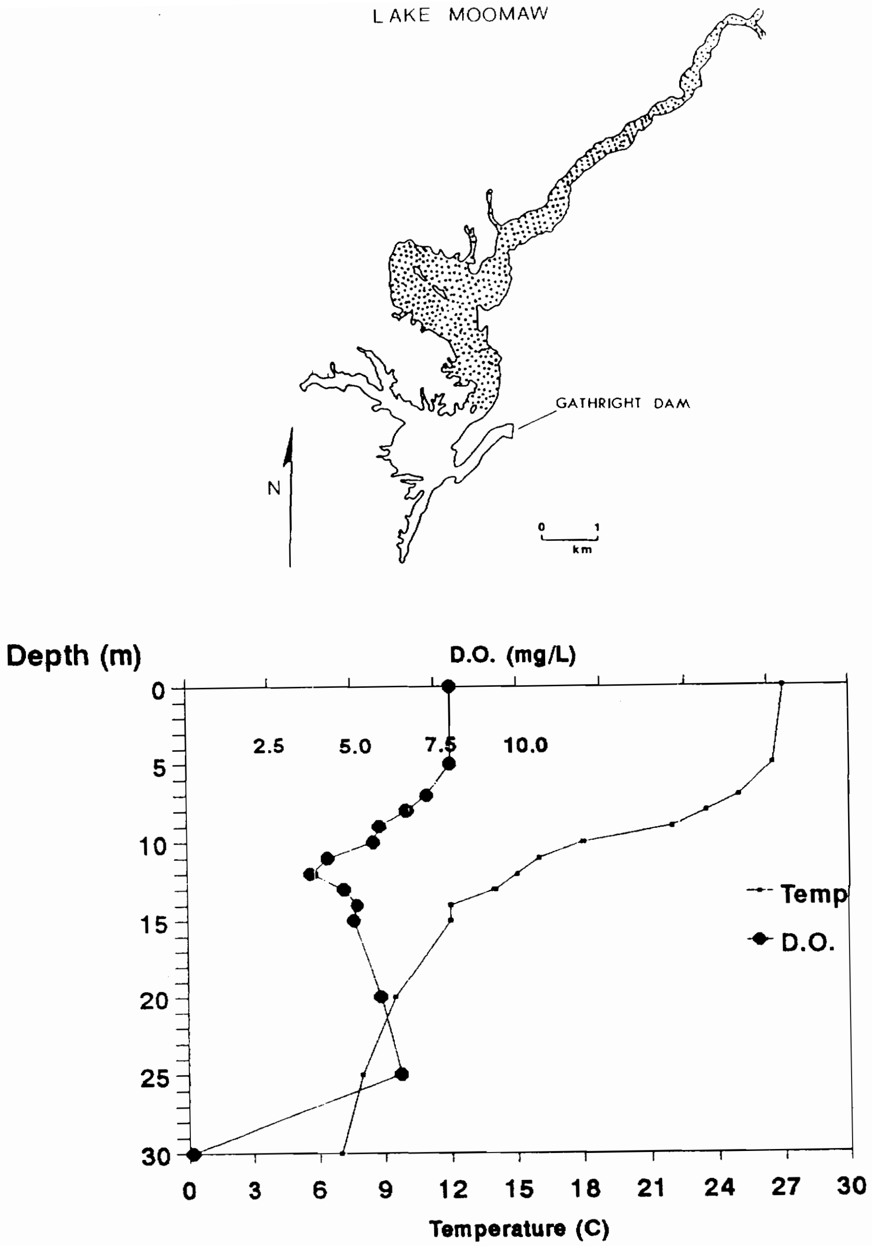


Figure 4. Horizontal and vertical habitat depletion, August 1991. Stippled area on upper panel represents depleted habitat. Limnological profile (lower panel) is from station 1 on 13 August 1991.

stratum developed in the lower metalimnion at depths from 12 to 14 meters and temperatures from 13 to 15°C. The hypoxic stratum formed adjacent to the primary discharge penstock of Gathright Dam, and effectively fragmented existing trout habitat into two segregated vertical components (Figure 4).

On 04 September, trout habit was restricted to an area in and adjacent to the Jackson River channel near the dam (Figure 5). Vertically, habitat was limited to a layer 5-m thick. The layer was located at 20 meters, and was separated from the epilimnion by 10 meters of hypoxic water (Figure 5).

Limnological profiles taken at ten stations on 17 September 1991 indicated that no reservoir strata contained criterion oxygen or temperature. The best available trout habitat was located at station one, near the dam (Figure 6).

Destratification of the reservoir began in late September. The cooler temperatures and increased wind of autumn decreased epilimnetic temperatures below 21 °C. This new volume of trout habitat spanned from the surface to eight meters of depth throughout the reservoir as of 25 September (Figure 7). By 08 October destratification had furhter expanded available trout habitat ; criterion temperature and dissolved oxygen were available from the surface to a depth of 12 meters (Figure 7).

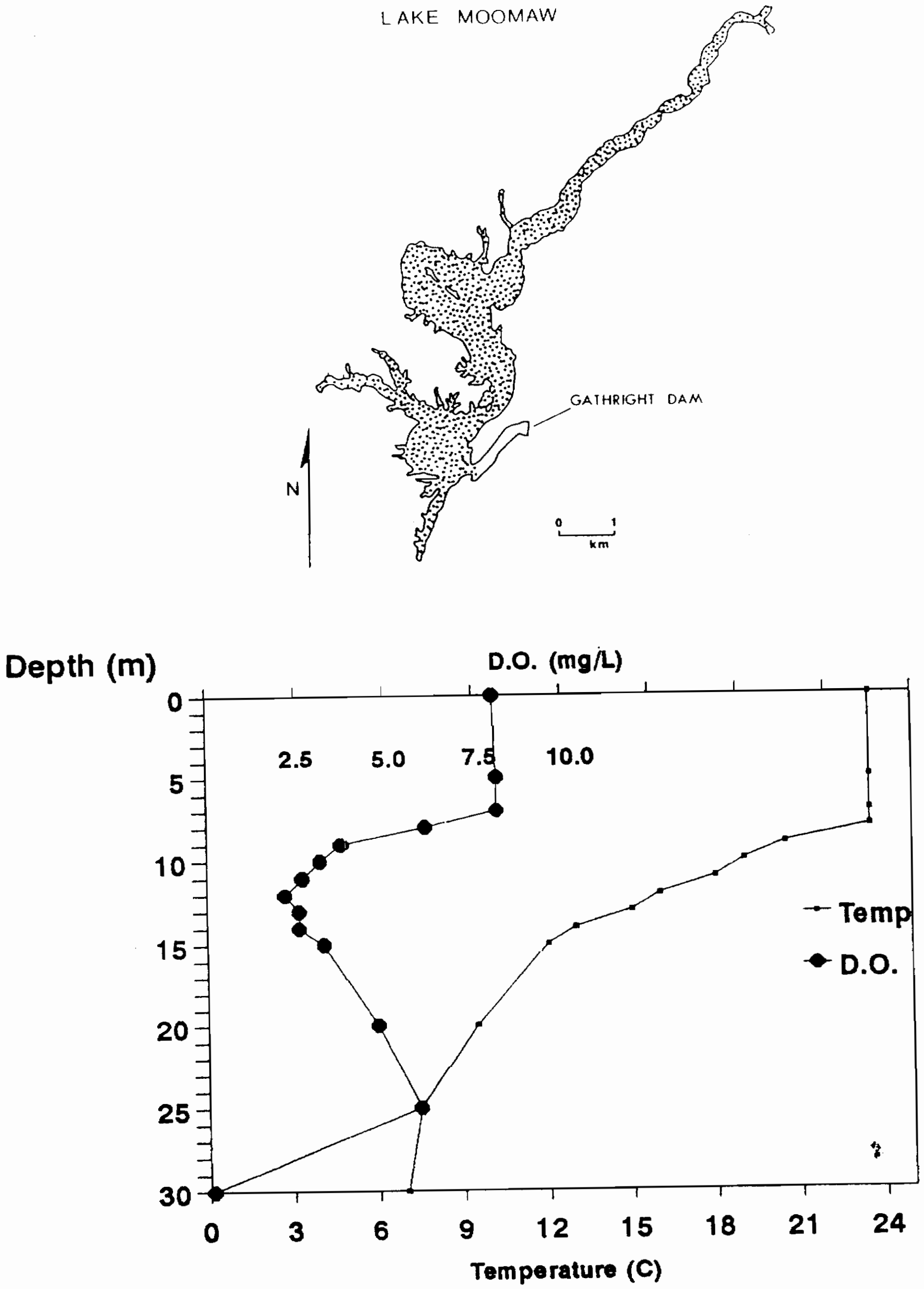


Figure 5. Horizontal and vertical habitat depletion, September 1991. Stippled area on upper panel represents depleted habitat. Limnological profile (lower panel) is from station 1 on 04 September 1991.

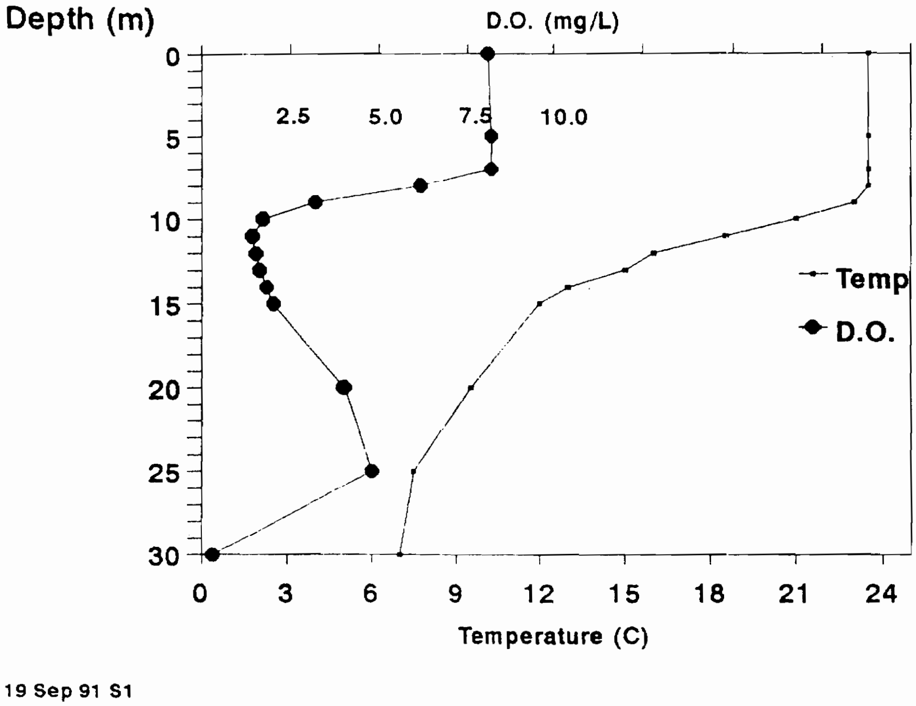
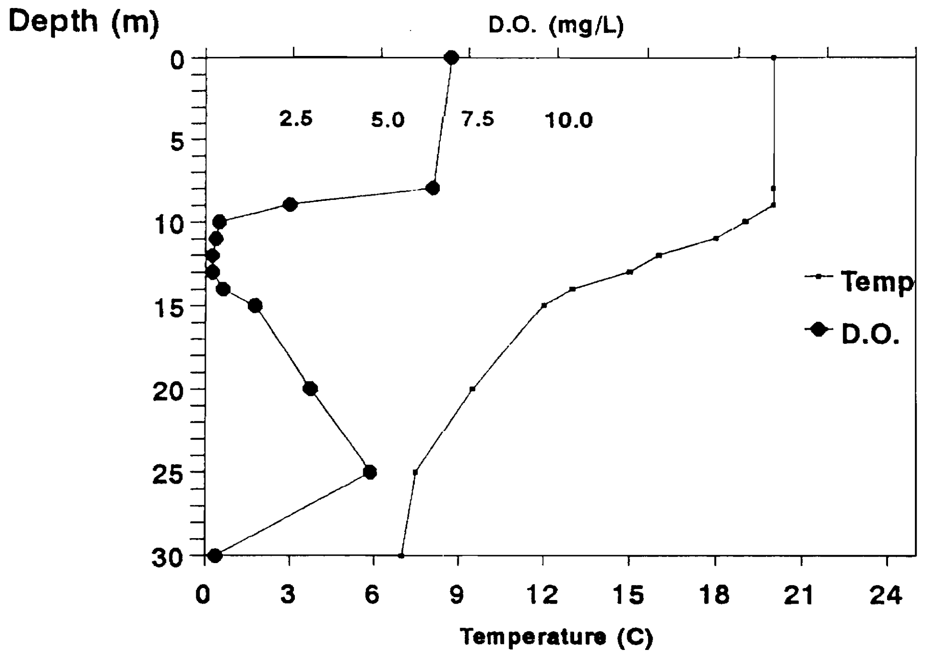


Figure 6. Dissolved oxygen and temperature profile at station 1 on 17 September 1991.



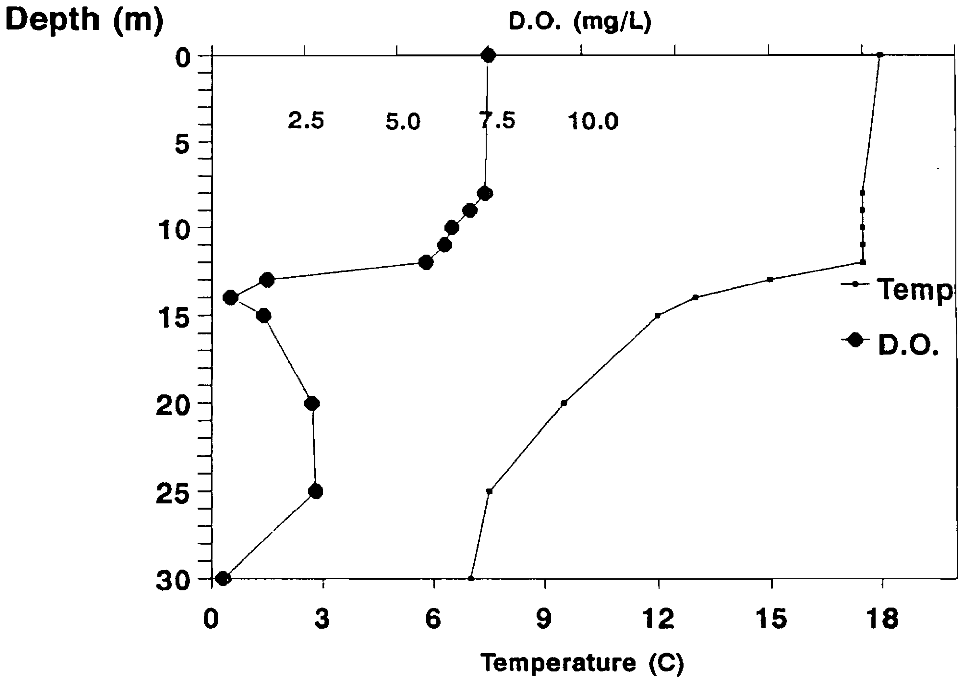


Figure 7. Dissolved oxygen and temperature profiles taken at station 1 on 25 September, 1991 (upper panel), 08 October 1991 (lower panel).

1992

Trout habitat in Lake Moomaw was most abundant in May, declined from June to September, and began to recover in October. As summer progressed, stratification prevented mixing and aeration of the water column, and oxygen demand removed successively greater percentages of the total habitat. Cold, oxygenated water was absent in mid-September, thereafter increasing as the reservoir began to destratify.

The entire reservoir contained cold, well-oxygenated water in May 1992. Vertical habitat reduction began in June, when the temperature exceeded 21° C in the upper two meters of the epilimnion (Figure 8).

Horizontal habitat reduction began in July: shallow and upstream regions of the reservoir no longer contained criterion dissolved oxygen at temperatures below 21°C (Figure 9). The thermally prohibitive epilimnion enlarged to include water from the surface to 6 meters.

Habitat receded further toward the dam in August (Figure 10). Benthic oxygen demand consumed oxygen from the deepest region of the hypolimnion, while a hypoxic stratum in the metalimnion divided remaining habitat into two vertical components. Consistent with 1991 results, the hypoxic layer formed adjacent to the primary discharge portal. Hypolimnetic habitat was separated from metalimnetic habitat by nine meters of hypoxic water on 20 August.

Trout habitat was confined to an area in and adjacent to the original Jackson River channel near the dam in early September. The 10-m hypoxic metalimnetic stratum persisted between shrinking layers of refuge habitat (Figure 11).

On 18 September, limnological profiles taken at six stations indicated that trout habitat was no longer present at any depth in the reservoir. The best available temperature and dissolved oxygen was again located at Station one (Figure 12).

Cooling temperatures and wind-driven aeration created a cold, well-oxygenated epilimnion in October. However, the hypoxic metalimnetic barrier still persisted (Figure 13.)

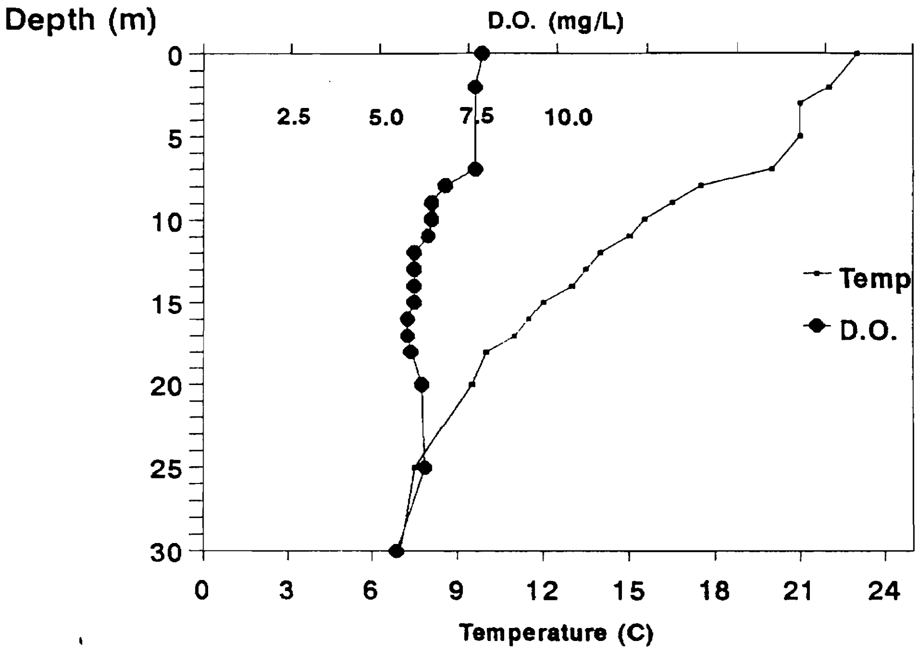


Figure 8. Limnological profile at station 1 of Lake Moomaw on 14 June 1992.

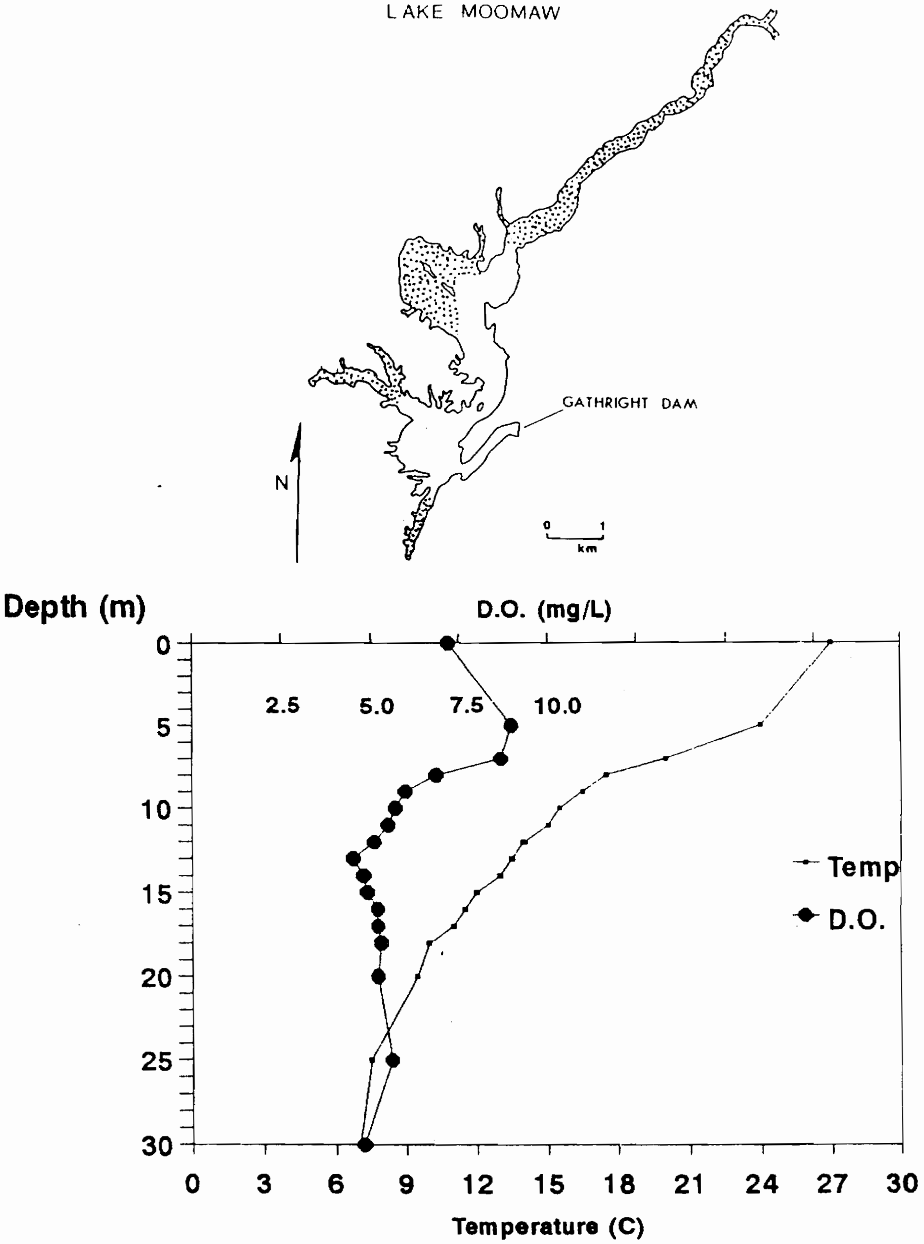


Figure 9. Horizontal and vertical habitat depletion in Lake Moomaw, Virginia, July 1992. Stippled area on upper panel represents depleted habitat. Limnological profile on lower panel is from station 1 on 16 July 1992.

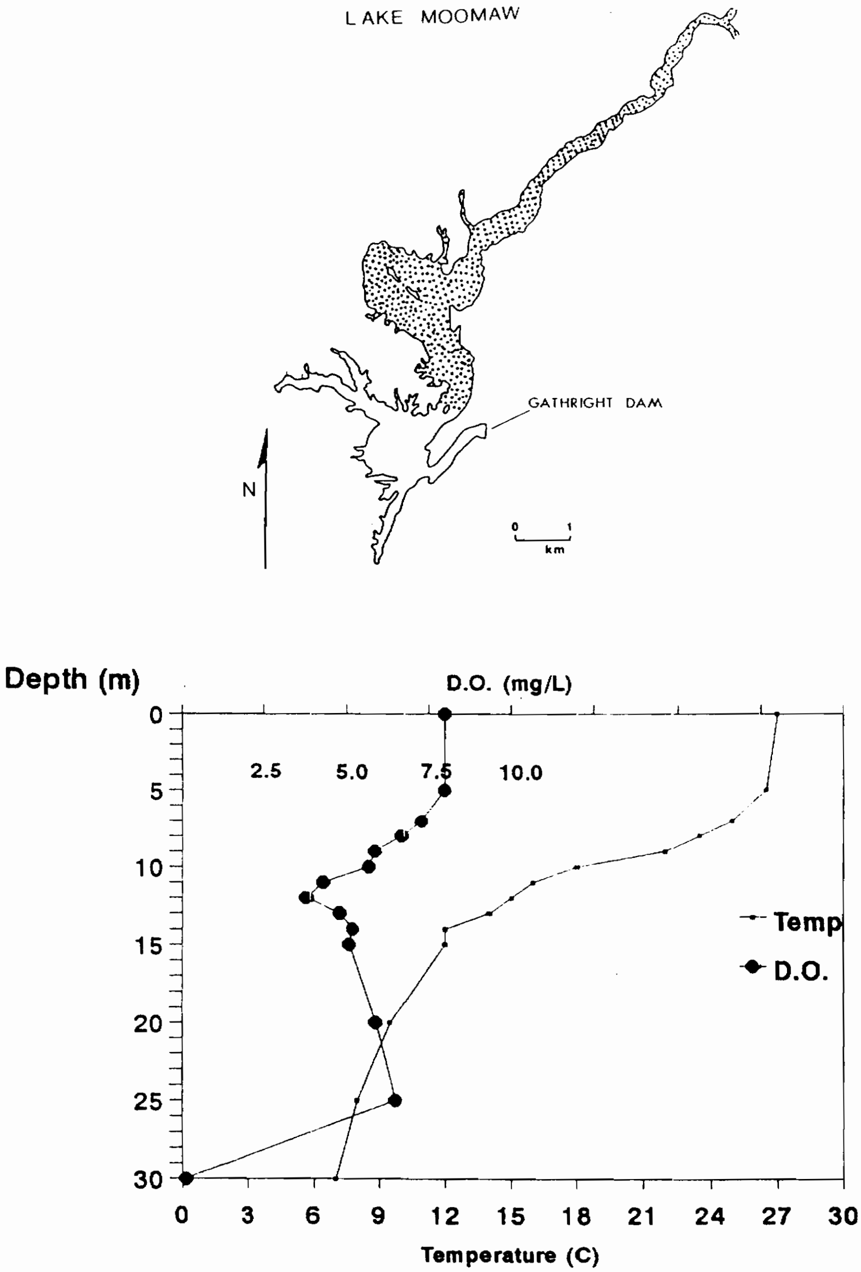


Figure 10. Horizontal and vertical habitat depletion in Lake Moomaw, Virginia, August 1992. Stippled area on upper panel represents depleted habitat. Limnological profile on lower panel is from Station 1 on 20 August 1992

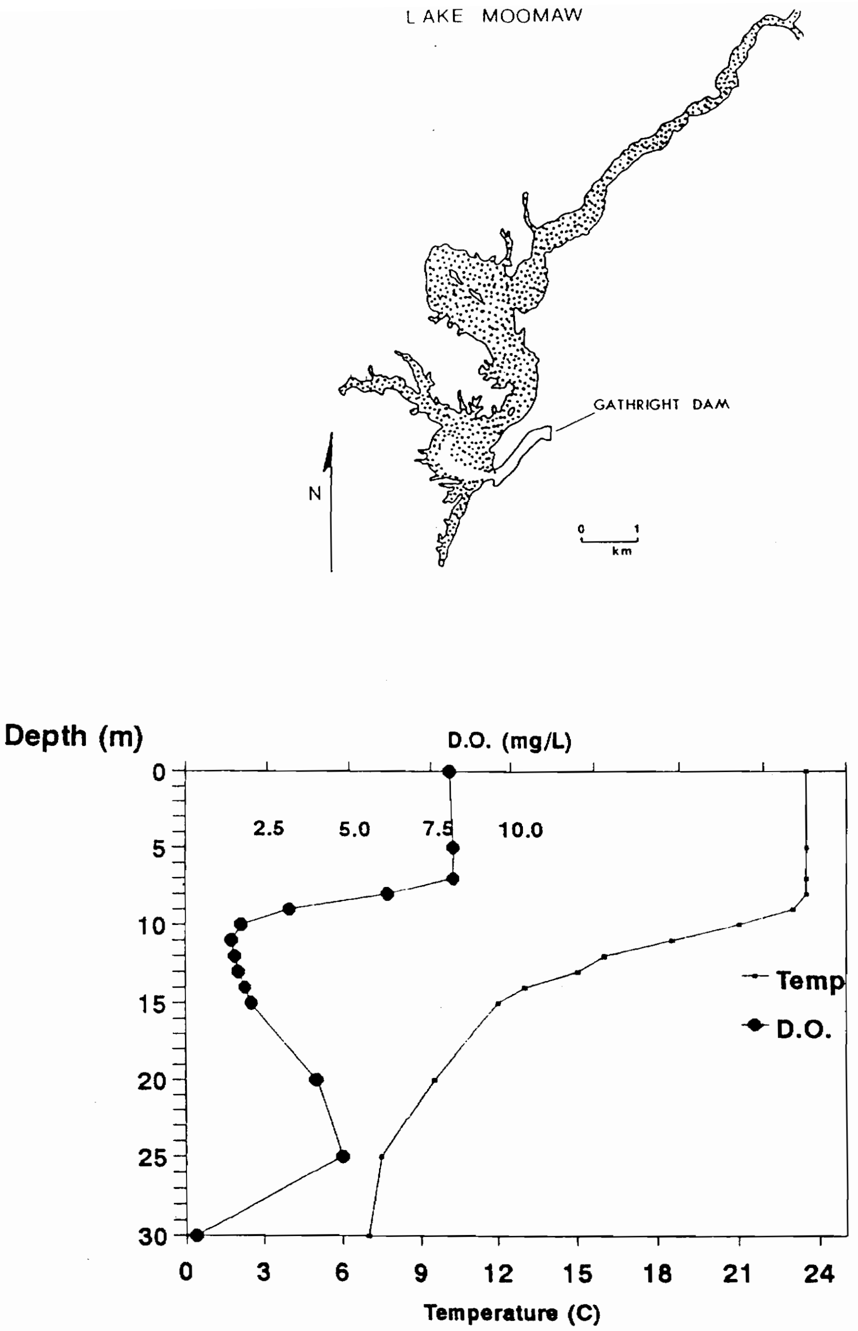


Figure 11. Horizontal and vertical trout habitat depletion, September 1992. Stippled area on upper panel represents depleted habitat. Limnological profile (lower panel) is from station 1 on 03 September 1992.

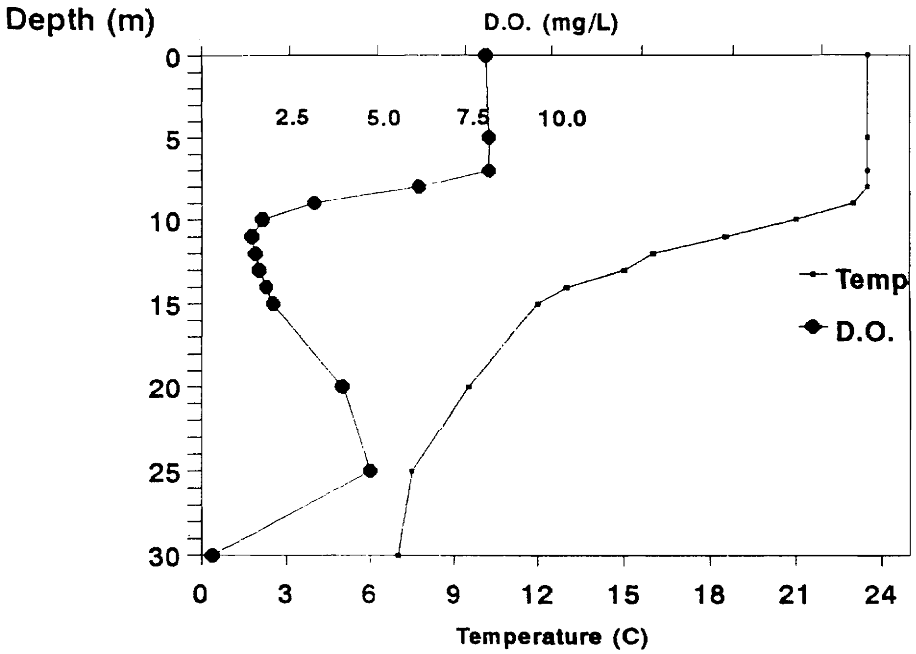


Figure 12. Limnological profile at station 1 on 18 September 1992.

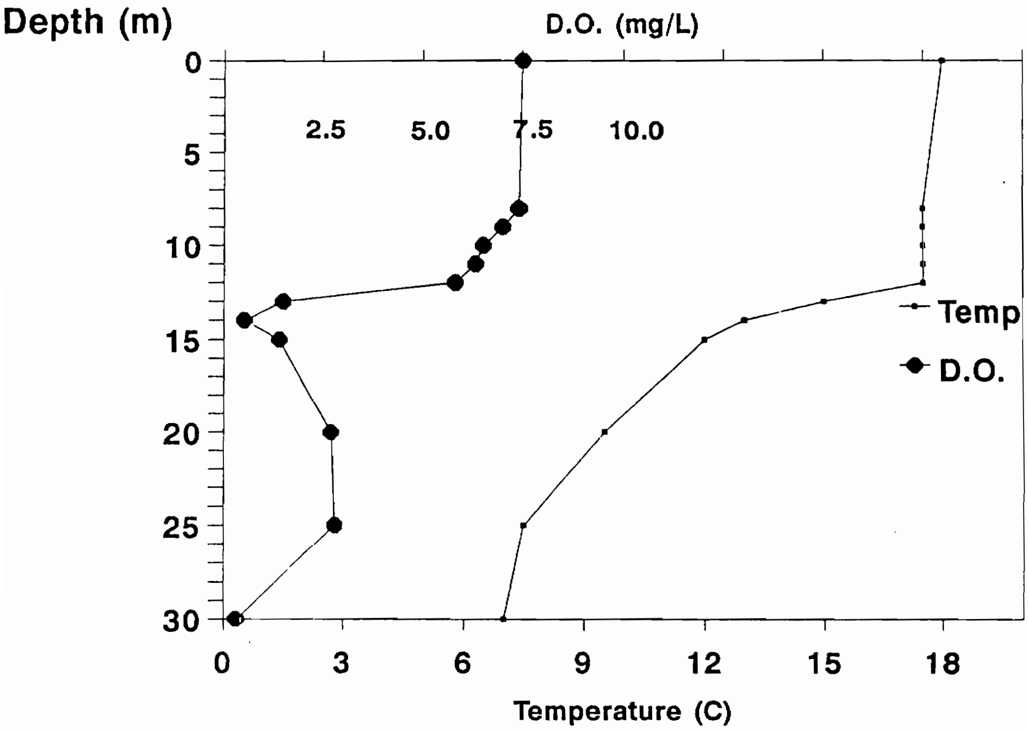


Figure 13. Limnological profile at station 1 on 08 October 1992.

Fish Distribution

Vertical gillnet returns

1991. Ten brown trout and twenty rainbow trout were captured over a range of depths (0 - 25 m) and temperatures (8.0 - 25.0°C) from August to October 1991. Eighty percent of all trout were located at temperatures ranging from 12 to 21°C in 1991 (Figure 14). One trout was captured at 25°C, whereas five trout were captured at temperatures below 14°C.

Capture of 1282 alewives from August to October 1991 afforded the description of prey distribution. Alewives were captured at a range of depths (0 - 17 m) and temperatures (11 - 27°C). About 12 percent of captured alewives were located at temperatures above 21°C, whereas 87 percent were captured at temperatures ranging from 12 to 21°C. Only 11 alewives (less than one percent) were captured at temperatures below 12°C. These distribution data reflect the temperature preferenda (18 - 20°C) of alewife, as reported by Coutant (1977).

Depth distribution of trout and alewives paralleled changes in limnological conditions from August to October. Trout and alewives were captured at successively greater depth, until the epilimnion was destratified in late September. Most age 1+ trout (86 percent) were captured in the metalimnion. One adult rainbow trout was located in the

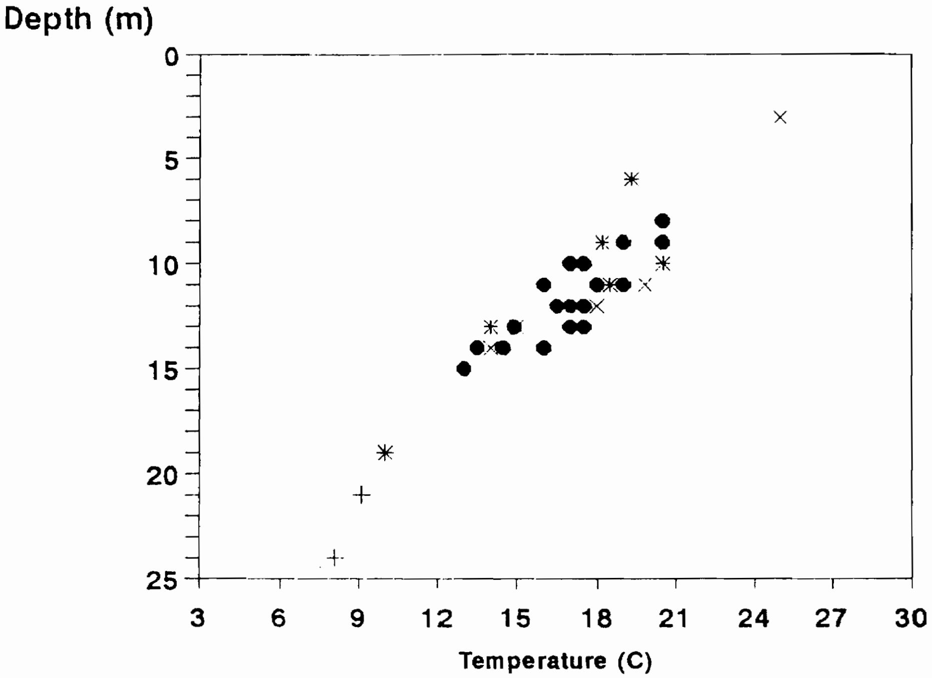


Figure 14. The temperature and depth distribution of brown and rainbow trout captured in vertical gillnets at Lake Moomaw during 1991. Age 1+ brown trout (asterisk), age 2+ brown trout (plus sign), age 1+ rainbow trout (filled circle), and age 2+ rainbow trout (upper case X) are depicted.

heated epilimnion during early September, but most were captured in the metalimnion. Adult brown trout were captured only in the hypolimnion during August and September. Alewives were typically located in the metalimnion and epilimnion, and were rarely captured in the hypolimnion.

Figure 15 depicts the distribution of trout relative to dissolved oxygen in August and September. Depletion of dissolved oxygen in strata containing preferred temperature resulted in distribution of trout at D.O. concentrations below 5 mg/L in August and September. Distribution of trout during September reflected the progressive decline of D.O. in strata with preferred temperature.

All trout and alewives captured in vertical gillnets during October were located in the reclaimed epilimnion. The epilimnion contained ideal habitat, with temperatures near 18°C and dissolved oxygen greater than 8 mg/L. While these data suggest that the effects of habitat limitations have been eased, the results of horizontal gillnetting provide conflicting results. Ten rainbow trout were captured in a horizontal gillnet fished from 20 to 23 meters in October. These fish were isolated from the reclaimed epilimnion by 8 to 10 meters of hypoxic and anoxic conditions. Location at low temperature (8 C) and near lethal dissolved oxygen (2.7 mg/L) placed the isolated trout at physiological risk. The ten trout had empty, constricted stomachs indicative of fasting.

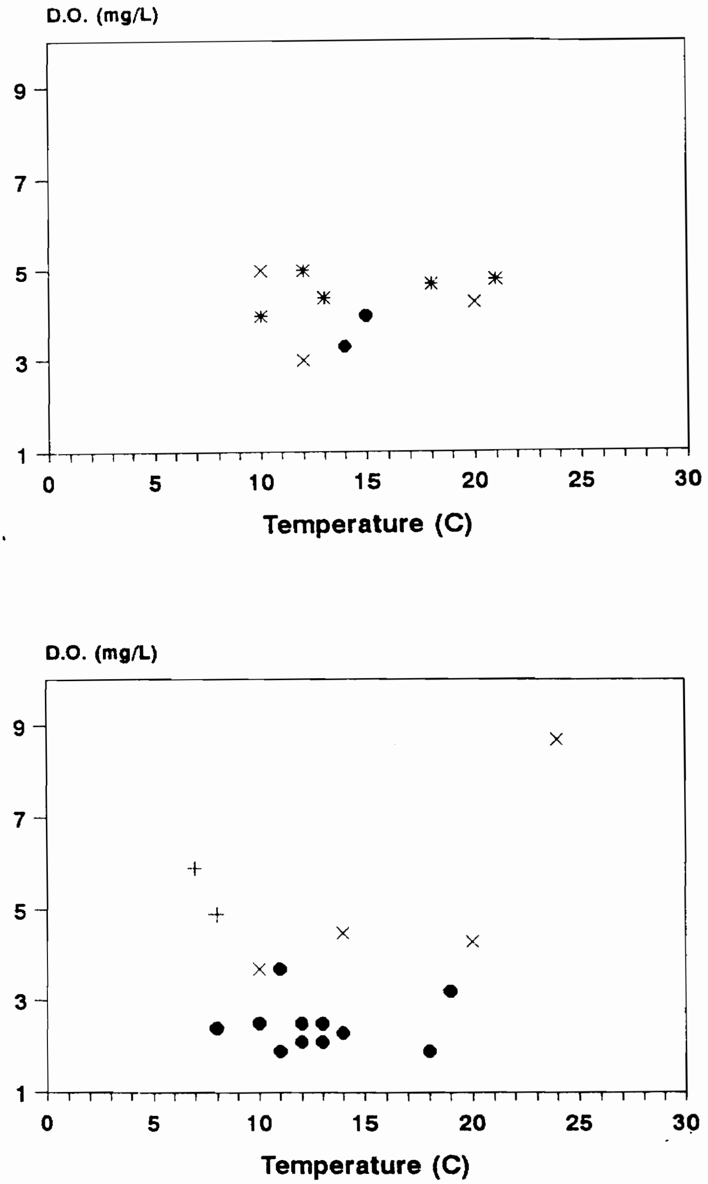


Figure 15. The distribution of brown and rainbow trout relative to dissolved oxygen in (upper panel) August 1991, and (lower panel) September 1991. Age 1+ brown trout (asterisk), age 2+ brown trout (plus sign), age 1+ rainbow trout (empty circle), and age 2+ rainbow trout (upper case X) are depicted.

1992. Twenty-four brown trout and nine rainbow trout were collected in vertical gillnets from July to September 1992. Trout were captured over a wide range of temperatures (8.8 - 26.5°C) and depths (0 - 21 m). Preference for a narrower range of temperature was noted: 76 percent of all trout were caught at temperatures between 12 and 21°C (Figure 16). Capture of two trout at temperatures above 21°C indicates occasional movement into water warmer than their preferred range. That 18 percent of capture trout were distributed at temperatures below 12°C indicated a more pronounced movement to colder temperatures.

Alewife distribution was evaluated from the capture of 292 alewives in vertical gillnets from July to September 1992. About 58 percent of captured alewives were distributed at temperatures greater than 21°C. Forty-one percent of alewives were captured at temperatures ranging from 12 to 21°C. Only 6 alewives (two percent) were captured at temperatures less than 12°C.

Depth distribution of trout and alewives corresponded to changing limnological conditions. Trout and alewives were captured at successively greater depth as the summer progressed (Figure 17). Age 1+ brown trout were typically distributed in the metalimnion. All ages of rainbow trout were captured in the metalimnion from July to September. Adult brown trout were typically captured in the hypolimnion.

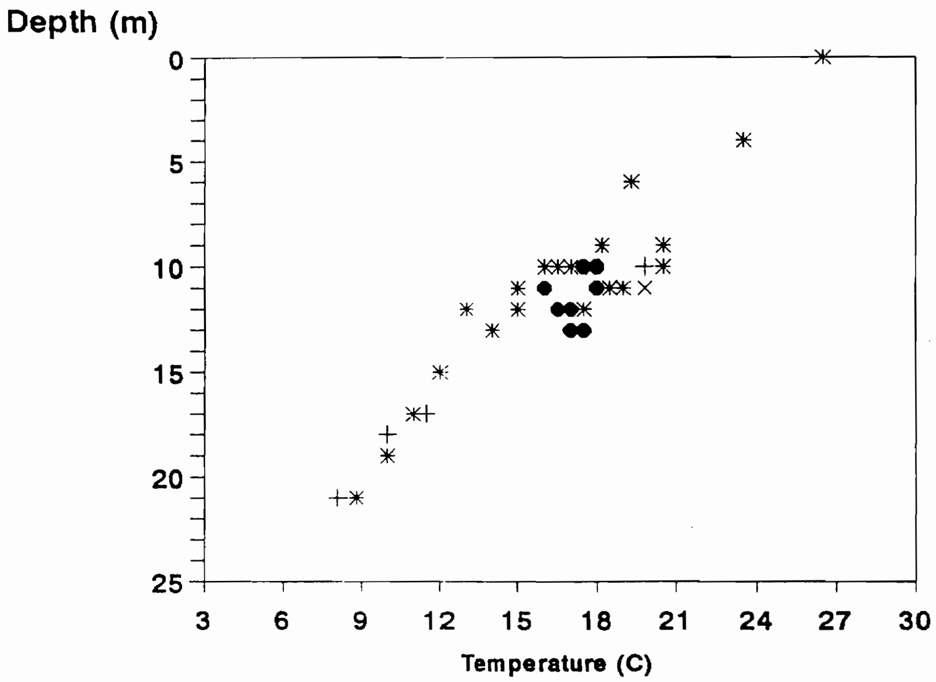


Figure 16. Temperature and depth distribution of brown and rainbow trout captured in vertical gillnets from May to September 1992. Age 1+ brown trout (asterisk), age 2+ brown trout (plus sign), age 1+ rainbow trout (filled circle), and age 2+ rainbow trout (upper case X) are depicted.

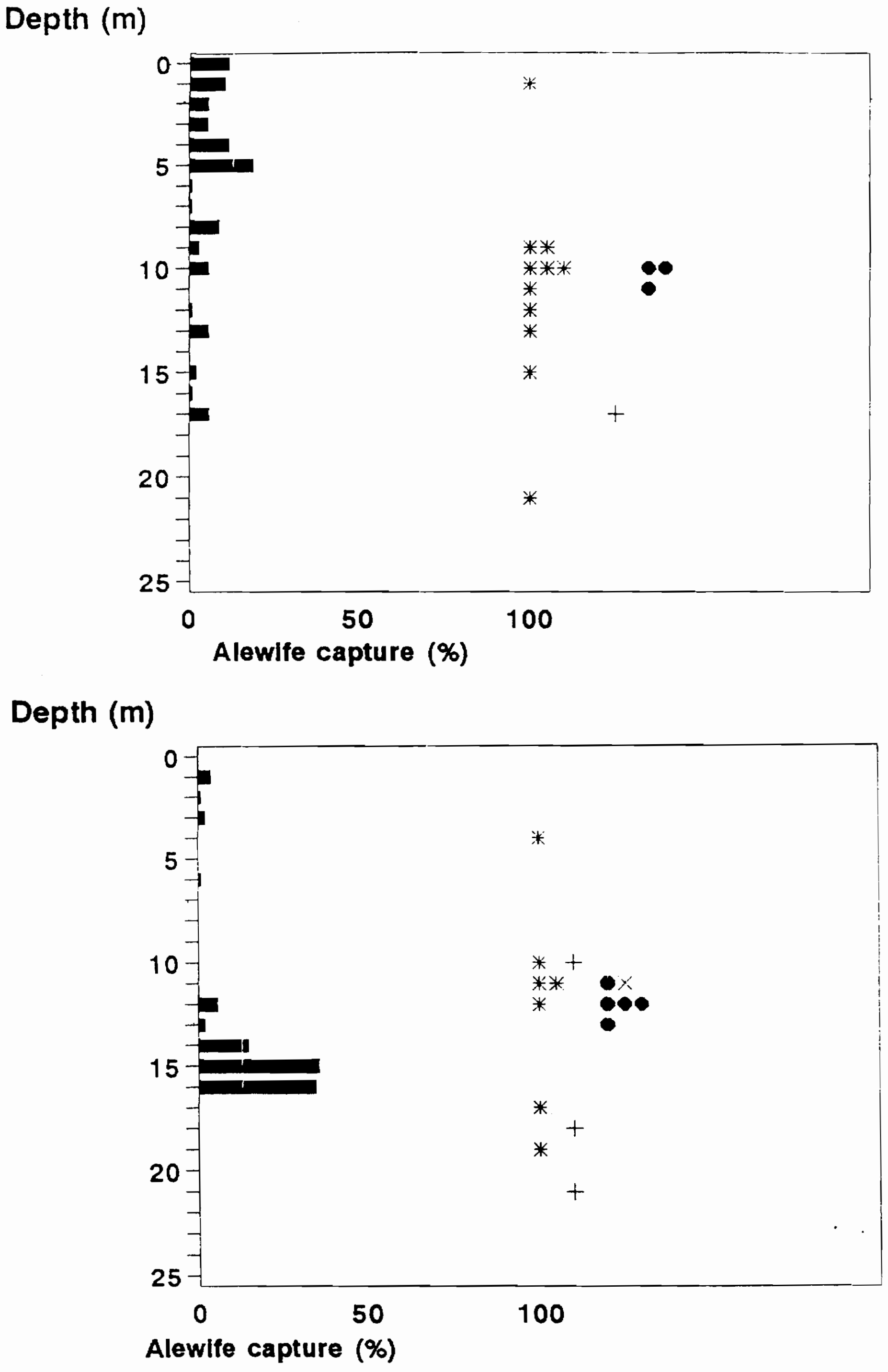


Figure 17. The location of trout and alewives during (upper panel) August, and (lower panel) September 1992. Age 1+ brown trout (asterisk), age 2+ brown trout (plus sign), age 1+ rainbow trout (filled circle), and age 2+ rainbow trout (upper case X) are depicted.

Presence of cold, oxygenated water in the epilimnion in October suggested that the effects of habitat limitation had been alleviated. However, two rainbow trout and one brown trout were captured in horizontal gillnets set from 20 to 23 meters after the epilimnion had been reclaimed. Trout occupying this stratum were separated from the abundant habitat and forage of the epilimnion by eight to ten meters of hypoxic water. Temperature in the stratum was low (9°C), and dissolved oxygen was below criterion (3.9 mg/L). Isolation from preferred prey was apparent: captured trout had empty stomachs, constricted from starvation. These gillnet results indicate that not all trout rapidly relocate from the isolated hypolimnetic stratum to the epilimnion.

Telemetry observations

Ultrasonic transmitters were surgically implanted into a total of nine adult brown trout and five adult rainbow trout. Only six trout, four brown trout and two rainbow trout, provided subsequent tracking information (Table 5). All trout captured by angling in the reservoir (tag numbers 249, 348, and 375) survived surgery and were monitored in this study. Observation of fish number 375 was abbreviated, as an angler harvested the trout on 09 July 1992.

Table 5. Summary information for 1992 ultrasonic telemetry study of brown and rainbow trout in Lake Moomaw, Virginia.

Fish #	Species	Length (mm)	Weight (g)	Release Date	Last Fix	Total Fixes
249	BNT	496	1193	08 Jun	08 Oct	17
348	BNT	518	1579	29 May	18 Sep	16
366	BNT	473	1141	20 Jul	08 Oct	2
375	BNT	527	2130	27 May	08 Jul*	4
384	RBT	412	624	17 Mar	08 Oct	14
456	RBT	546	1325	10 Mar	18 Sep	12

* Fish number 375 was creeled by an angler on 09 July 1992.

The additional stress associated with transportation from capture location to the point of release adversely affected post-surgical survival of trout in this study. Six of the nine trout captured by electrofishing reservoir tributaries apparently died after being released into the reservoir: the implanted transmitters remained at the release site throughout the study. The attempt to stock adult trout from a nearby hatchery was also unsuccessful, as both trout died shortly after their release.

Because age 1+ fish were too small to allow transmitter implantation, telemetry data provided an assessment of adult trout distribution from June to October. The horizontal distribution of tagged brown and rainbow trout contracted as the summer progressed. Tagged trout were located over the entire length of the reservoir during June. Thereafter, trout distribution progressively approached the dam, proceeding at a rate similar to horizontal habitat depletion. Tagged brown trout were located in the lower portion of the reservoir, within one kilometer of the dam from July to September (Figure 18). Distribution of tagged rainbow trout included a larger portion of the reservoir during July, but began to contract toward the dam in August and September (Figure 19).

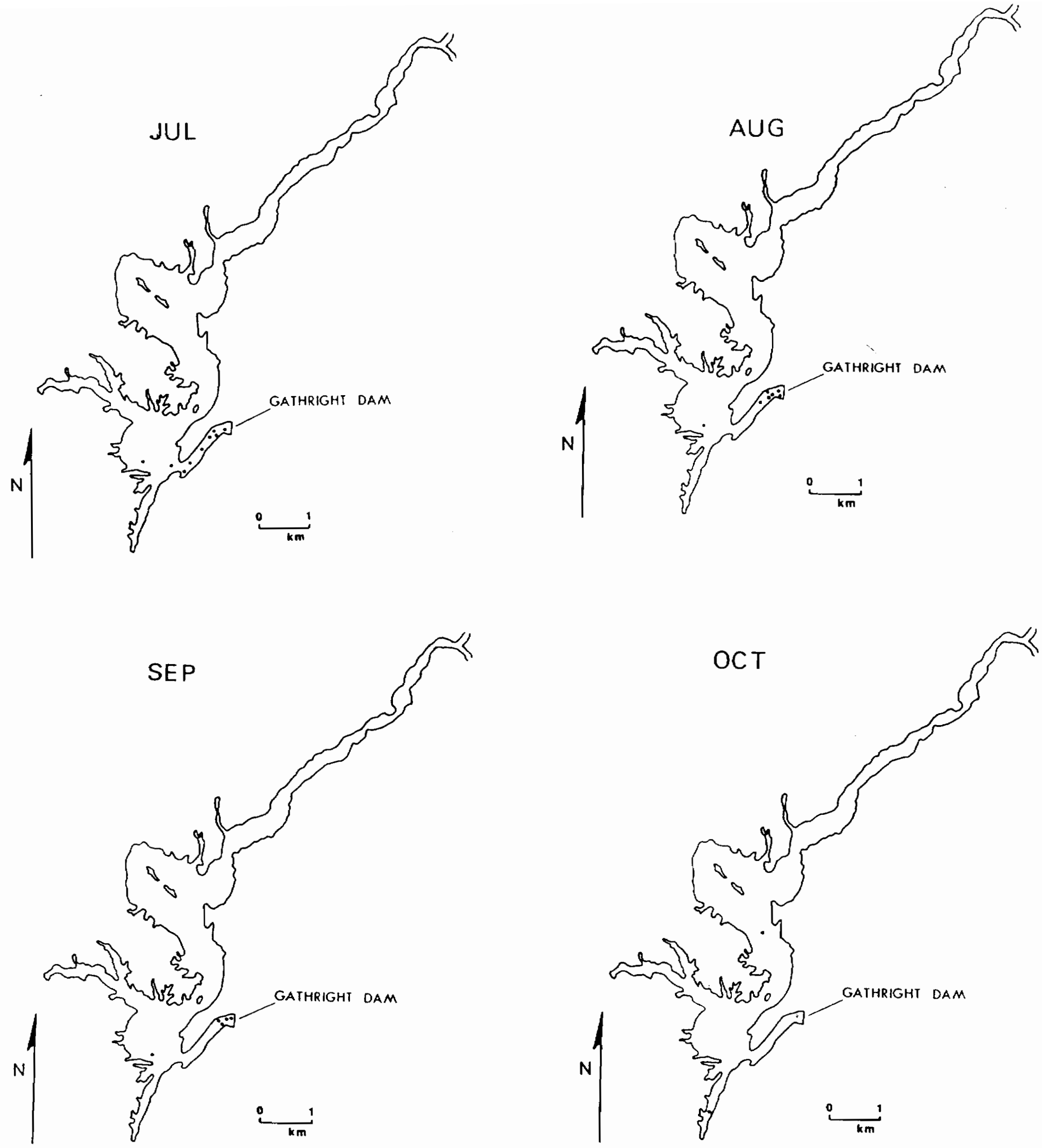


Figure 18. The horizontal location of telemetry-tagged brown trout from July to October 1992.

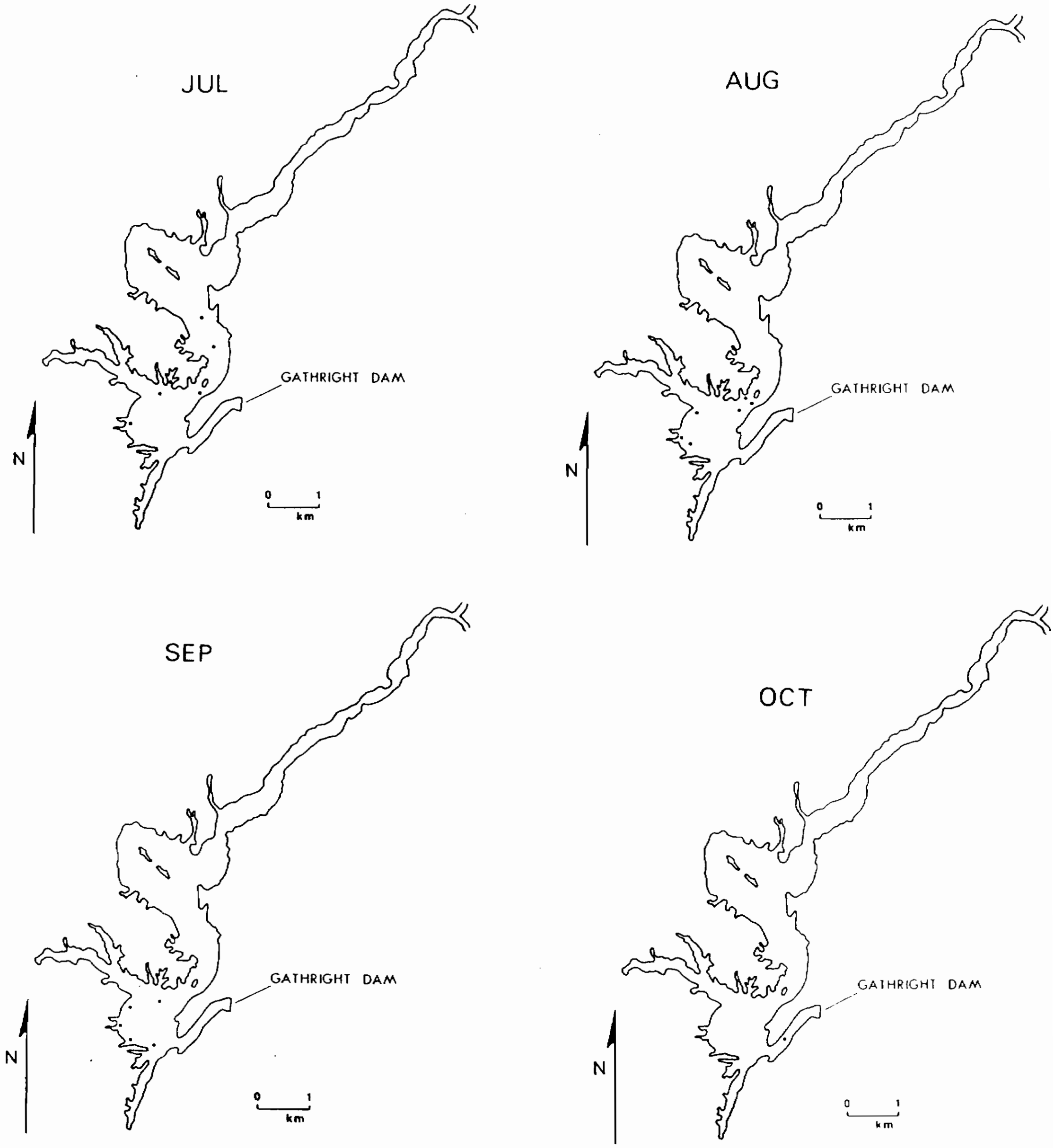


Figure 19. Horizontal distribution of telemetry-tagged rainbow trout from July to October 1992.

Cooling of the epilimnion preceded the horizontal redistribution of trout in early October (Figures 18-19). The location of two tagged trout could not be determined in October. The entire reservoir was searched without success. A 100-m reach of the Jackson River downstream of the dam was examined to evaluate possible emigration from the reservoir. There was no report of angler capture.

The mean temperature and dissolved oxygen selected by brown trout declined until the well-oxygenated epilimnetic waters cooled below 21 C in October (Table 6). However, the mean depth occupied by tagged brown trout increased. Tagged brown trout that were distributed in the lower metalimnion during June and July moved to the hypolimnion during August and September, and relocated in the cooled epilimnion in October. The mean dissolved oxygen at depths chosen by brown trout during the study was above 5 mg/L, with the exception of September.

The location of individual tagged brown trout relative to temperature and oxygen varied during the study (Figures 20 - 22). Location of brown trout at extreme depth during August and September is congruent with gillnet results, and affords additional evidence of isolation from preferred forage. Proximity to tributary streams in October suggests that the urge to spawn may motivate an exodus from the hypolimnion to the epilimnion.

Table 6. Summary of depth, temperature, and oxygen occupied by telemetry tagged brown and rainbow trout from June to October 1992.

Mon	n	# fixes	Mean depth (m)	Mean Temp. (C)	Range	Mean D.O. mg/L	Range
					Brown trout		
Jun	3	7	10	14.6	10.3-16.3	7.0	5.7-7.7
Jul	3	9	15	12.3	8.7-14.6	5.1	4.9-5.7
Aug	3	10	16	11.3	9.0-13.2	5.0	4.5-5.6
Sep	3	12	25	8.1	7.5- 9.5	3.7	2.7-4.9
Oct	2	2	5	17.8	17.6-18.0	7.5	7.2-7.8
					Rainbow trout		
Jun	2	4	10	15.1	14.5-16.5	6.8	6.1-7.1
Jul	2	8	14	13.0	7.6-17.9	5.5	4.7-7.2
Aug	2	5	12	14.5	12.7-16.5	4.1	3.4-6.0
Sep	2	7	14	14.4	11.0-16.1	2.6	2.1-2.9
Oct	1	1	20	9.3	---	3.1	---

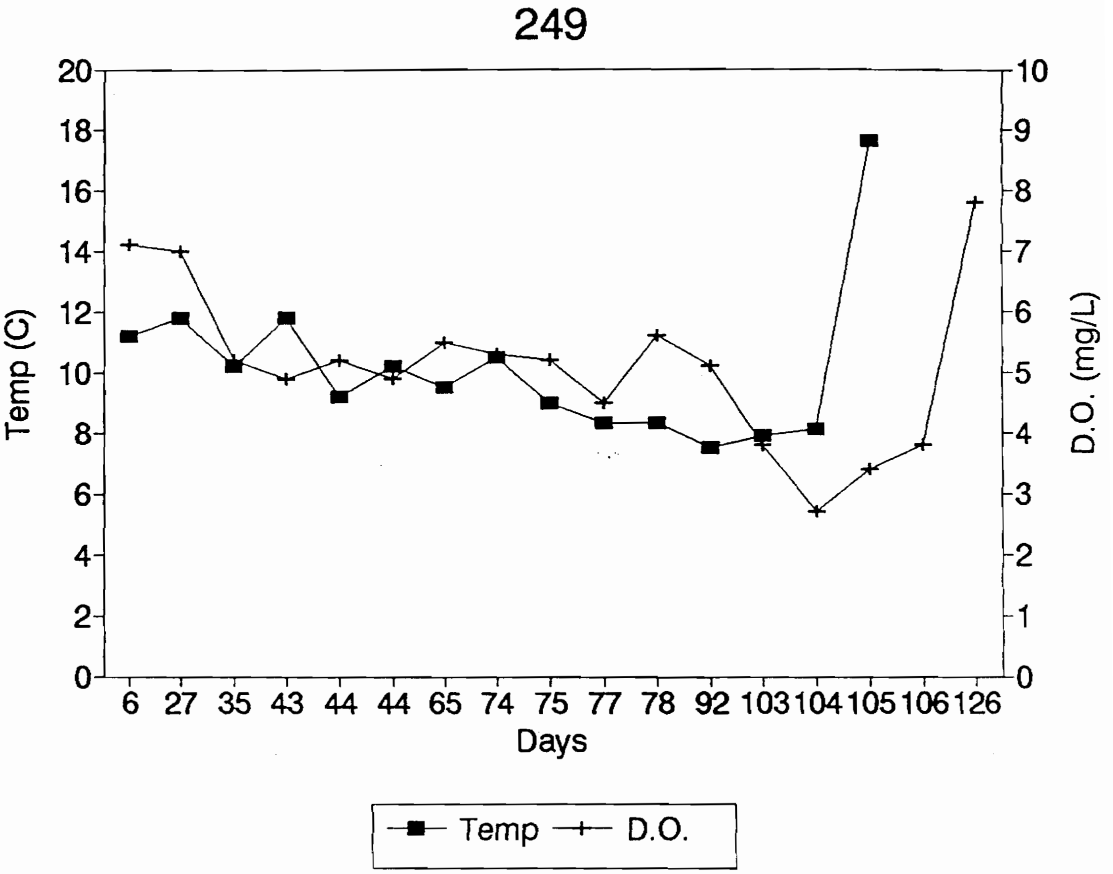


Figure 20. Temperatures and dissolved oxygen concentrations selected by telemetry-tagged brown trout number 249.

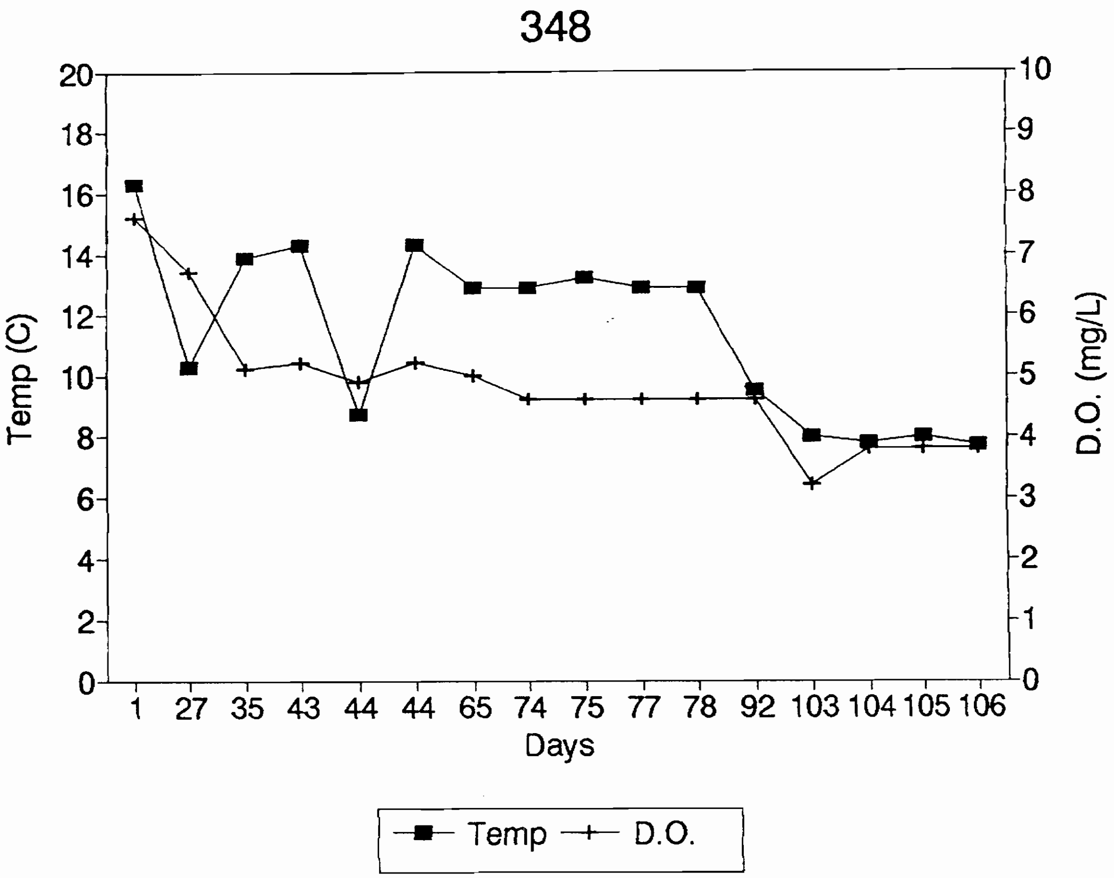


Figure 21. Temperatures and dissolved oxygen concentrations selected by telemetry-tagged brown trout number 348.

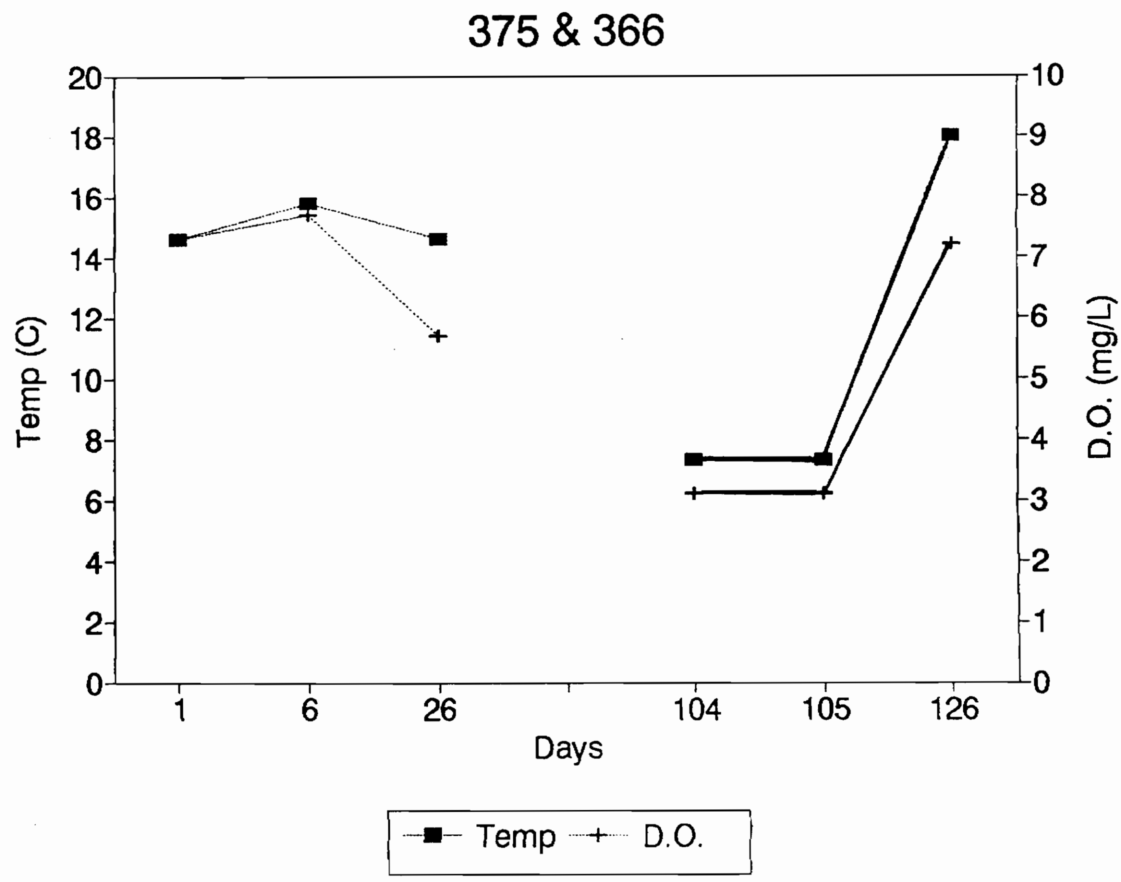


Figure 22. Temperatures and dissolved oxygen concentrations selected by telemetry-tagged brown trout number 375 (dotted lines) and number 366 (solid lines).

In contrast to brown trout, tagged rainbow trout did not collectively occupy progressively deeper, colder water (Table 6). Tagged rainbow trout were typically located in the metalimnion from June to September (Figures 23 and 24.). The one tagged rainbow trout located in October (# 384) was residing in the hypolimnion. Distribution in the metalimnion subjected rainbow trout to low dissolved oxygen during August and September. Failure to relocate in the epilimnion during October extended the duration in hypoxic waters.

Temperatures selected by tagged trout over a 24-hour period in July revealed diel vertical migration in two of the four fish (Figure 25). Vertical migration from the hypolimnion (7.6°C) to the metalimnion (14.6°C) indicated that no barrier existed between adult trout and alewives during July. The same tagged trout, plus one additional brown trout, were monitored for a 24-hour period during September. Vertical movement of tagged rainbow trout within the metalimnion was noted (Figure 25). However, tagged brown trout remained sedentary in the hypolimnion. The presence of a hypoxic stratum in the lower metalimnion seemed to prohibit vertical movement between the hypolimnion and metalimnion, thus separating tagged brown trout from their preferred prey.

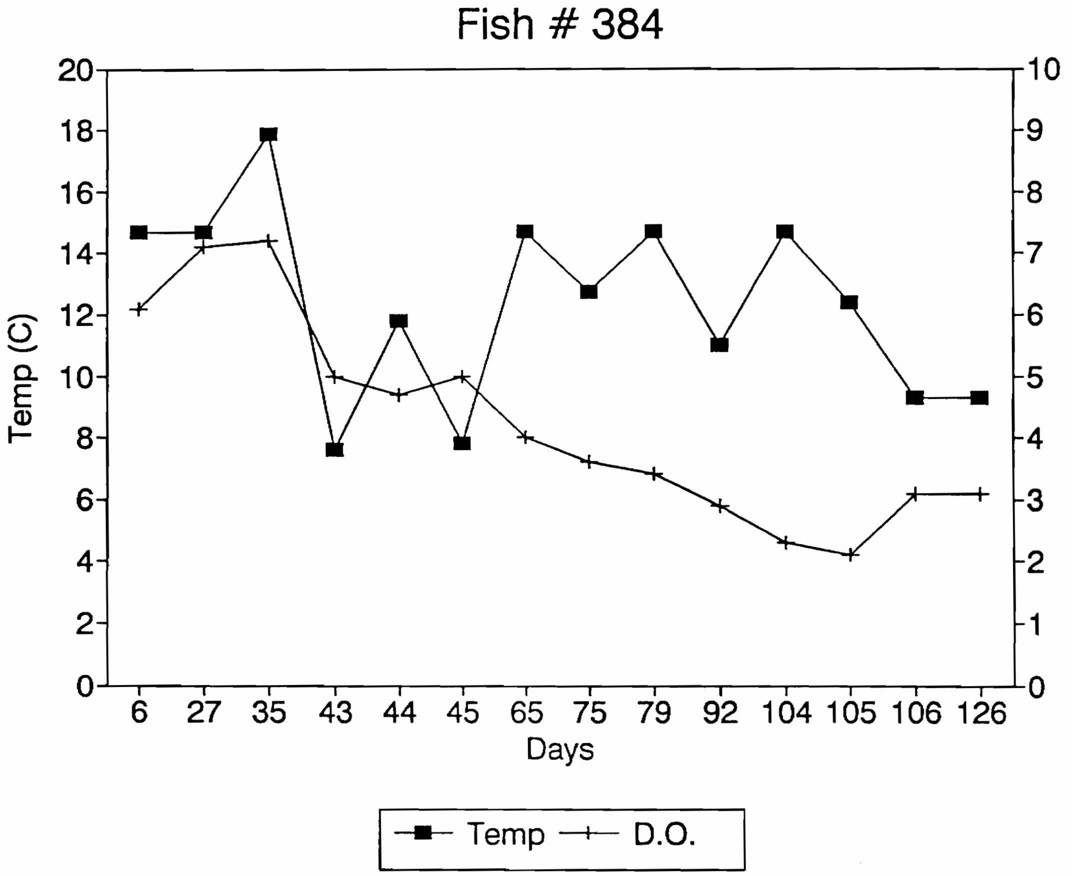


Figure 23. Temperatures and dissolved oxygen concentrations selected by telemetry-tagged rainbow trout number 384.

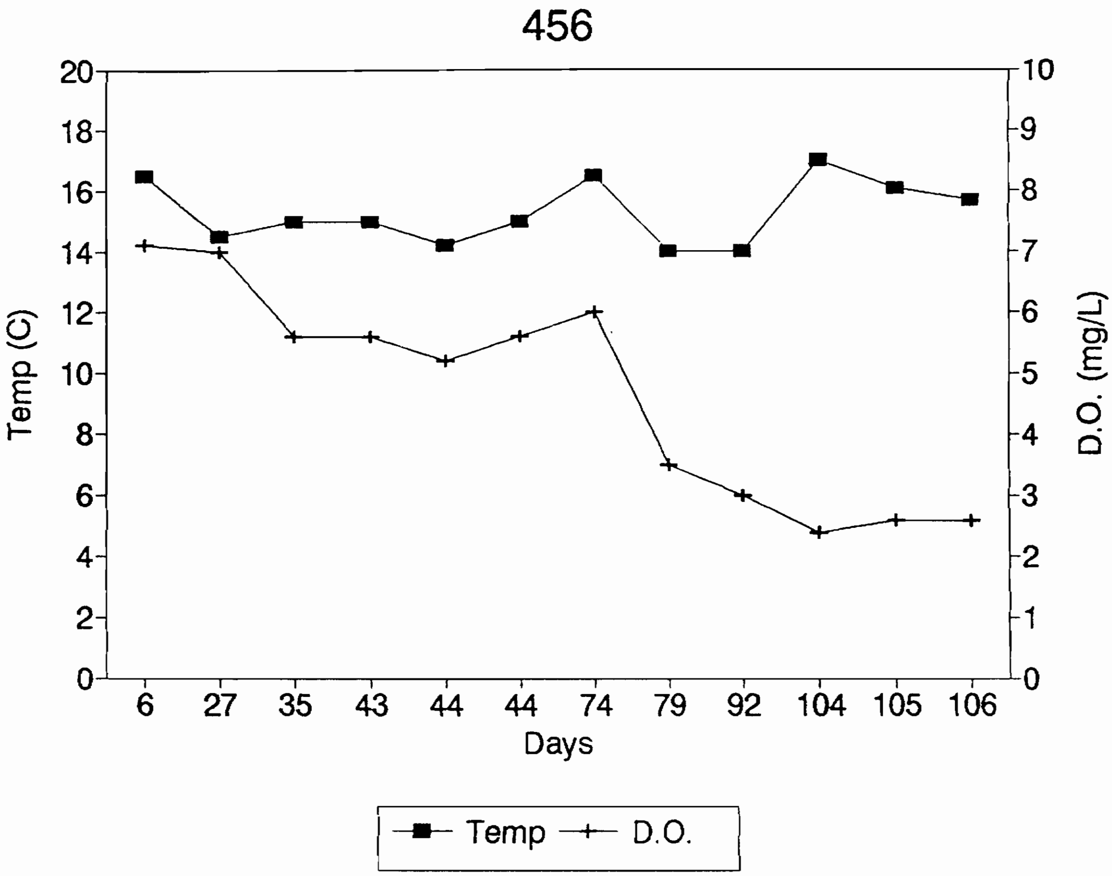


Figure 24. Temperatures and dissolved oxygen concentrations selected by telemetry-tagged rainbow trout number 456.

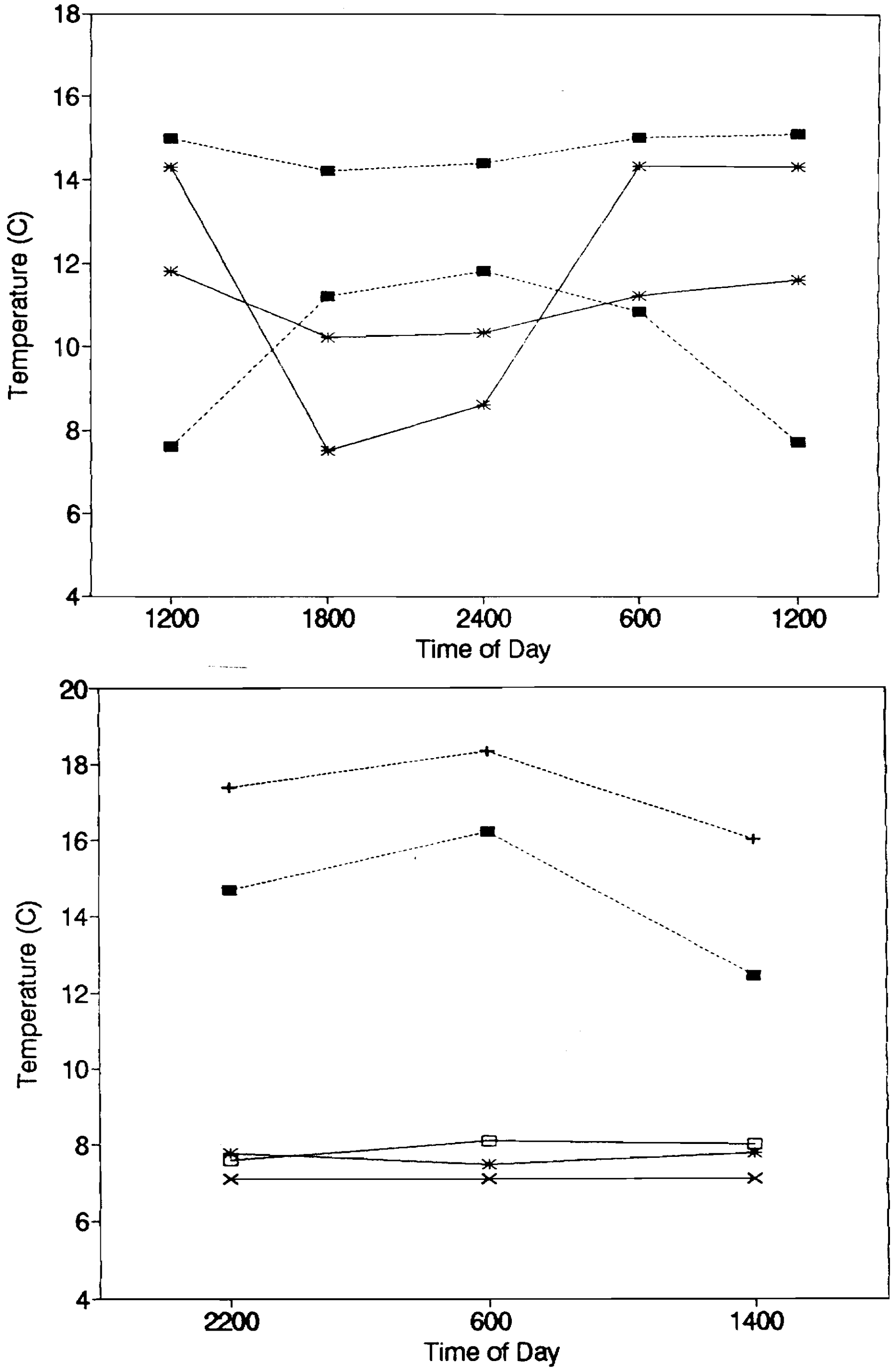


Figure 25. The temperatures selected by tagged brown trout (solid lines) and tagged rainbow trout (dotted lines) over a 24-hour period in (upper panel) July 1992, and (lower panel) September 1992.

Performance of Trout

Growth

1991. The median lengths and weights of age 1+ brown and rainbow trout captured in gill nets from August to October 1991 are listed in Table 7. Age 1+ brown trout increased steadily in length and weight. The median length of age 1+ rainbow trout remained virtually unchanged over the period, but their median weight declined in September, and increased in October.

Despite considerable effort in the field, successive samples of adult brown and rainbow trout were difficult to obtain. Sample sizes were regrettably small. Consequently, estimation of seasonal growth with any degree of confidence was impossible.

Capture of brown trout from the 1989 year class (marked before stocking) afforded a cursory assessment of brown trout growth in the second year of reservoir residence. The six age 2+ brown trout captured in gillnets during 1991 ranged in length from 476 to 546 mm, and weighed from 1.14 to 1.73 kg. The average age 2+ brown trout (1.45 kg) had added more than 1,400 grams of weight in the 20 months since stocking. Assuming that their first year growth was similar to that observed for age 1+ brown trout in Lake Moomaw during this study, the 1989 year class of brown trout grew about 85 grams per month in their second year of reservoir residence.

Table 7. Median lengths and weights of age 1+ brown and rainbow trout collected from August to October 1991

		Length (mm)		Weight (g)	
Month	n	median	range	median	range
		Brown trout			
August	12	315	282-375	320	238-628
September	7	319	288-355	374	226-511
October	3	357	315-370	432	320-598
		Rainbow trout			
August	11	331	275-363	372	212-607
September	14	325	267-387	329	204-655
October	5	332	305-358	377	250-448

1992. The median lengths and weights of age 1+ brown trout collected from May to September of 1992 are depicted in Figure 26. An apparent summer growth depression from July to August separates periods of rapid growth (Table 8). Rate of growth in length was greatest from June to July, whereas growth in weight peaked from August to September.

A disparate pattern of growth was observed for cohort one rainbow trout (Figure 27). The maximum rate of growth in length and weight was observed from June to July (Table 8). This was the only period of positive growth in weight for rainbow trout.

The inability to collect successive samples of adequate size precluded the assessment of seasonal growth of adult brown and rainbow trout in Lake Moomaw. Capture of marked brown trout from the 1989 year class provided data to assess the growth of brown trout during their third year of reservoir residence. Four age 3+ brown trout captured in 1992 ranged in length from 607 to 665 mm, and weighed from 2.72 to 3.37 kg. The average age 3+ brown trout (3.19 kg) had added approximately 1,740 grams in the third year of reservoir residence, an average of 145 grams per month.

Condition (K) and HSI

Indices of well-being are considered to be more sensitive to the short-term energetic responses of fish than direct

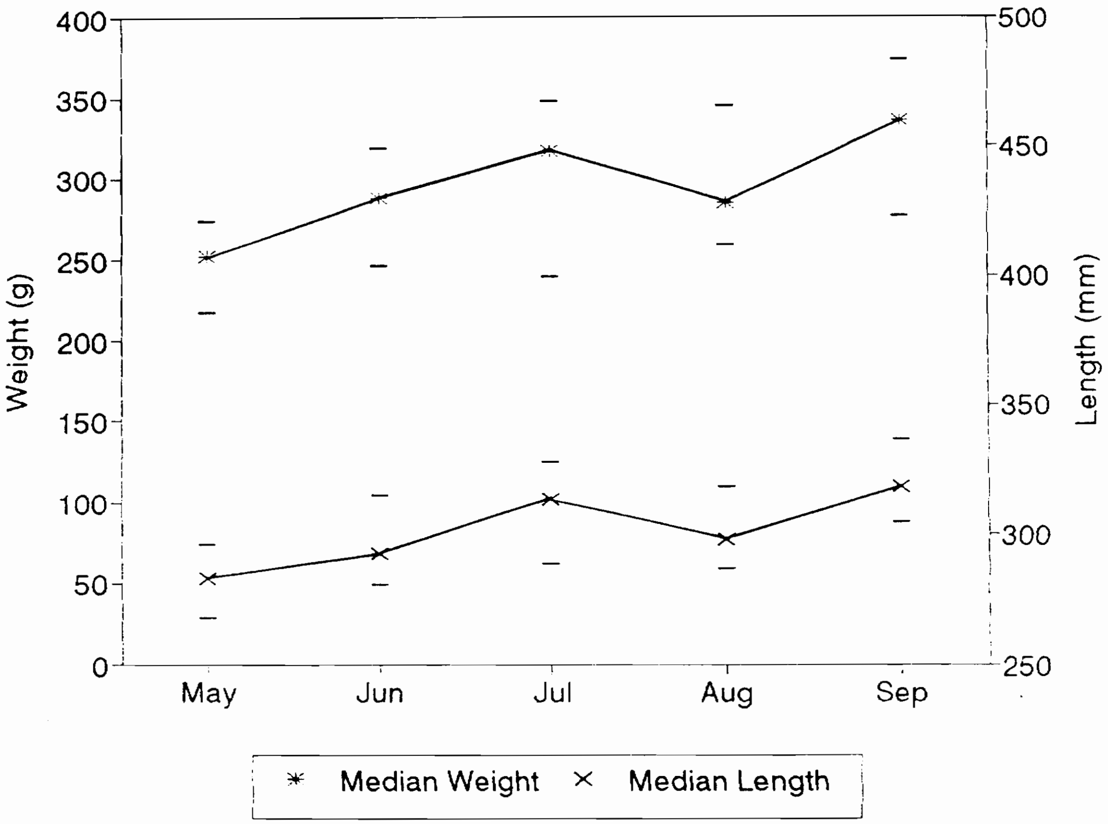


Figure 26. Median Lengths, weights, and interquartile ranges of age 1+ brown trout collected in 1992.

Table 8. Instantaneous growth rates (g/g/day; mm/mm/day) for age 1+ brown and rainbow trout in Lake Moomaw, Virginia, May through September 1992.

Age 1+ Species	Time Interval	Growth Rate Weight	Growth Rate Length
Brown trout	May - Jun	0.00477	0.00118
	Jun - Jul	0.00355	0.00253
	Jul - Aug	-0.00500	-0.00187
	Aug - Sep	0.00505	0.00238
Rainbow trout	May - Jun	-0.00209	0.000819
	Jun - Jul	0.00842	0.00112
	Jul - Aug	-0.00460	-0.00010
	Aug - Sep	-0.00151	-0.00188

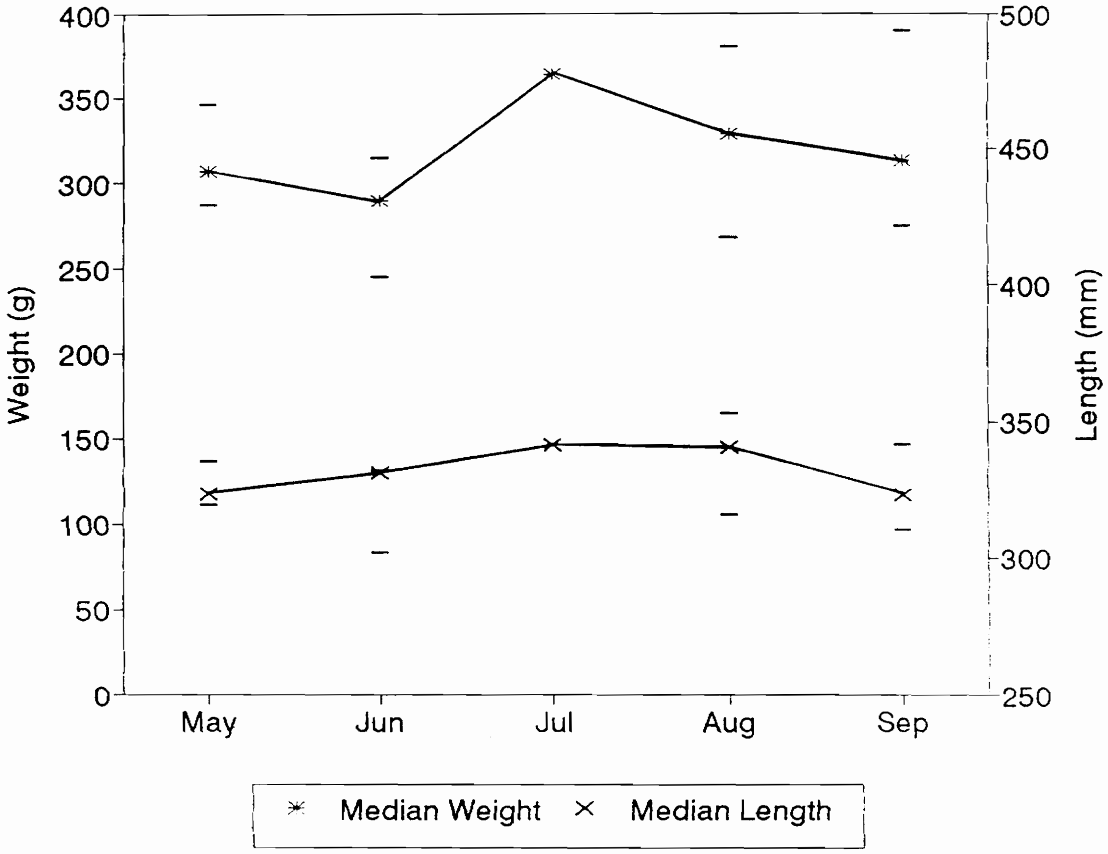


Figure 27. Median lengths, weights, and interquartile ranges of age 1+ rainbow trout collected in 1992.

measurements of growth (Anderson and Gutreuter 1983). In particular, the hepatosomatic index is championed as a means of detecting physiological response before growth is visibly affected (Adams and McLean 1985).

Because habitat conditions were similar, and to facilitate statistical analysis, condition (K) and consumption (C_D) data collected in both years for age 1+ trout were pooled into two categories: data from May, June, and July (MJJ) represent unlimited habitat conditions; data from August, September, and October (ASO) represent conditions of limited habitat.

The condition (K) of young brown trout during ASO was significantly less than condition (K) in MJJ ($P = 0.02$). However, age 1+ rainbow trout condition (K) in ASO was not significantly different from condition in MJJ ($P > 0.50$). The condition (K) of age 1+ rainbow trout was significantly lower than brown trout condition during each period ($P < 0.001$). These results are consonant with the observed disparity between the growth of age 1+ brown trout and age 1+ rainbow trout at Lake Moomaw.

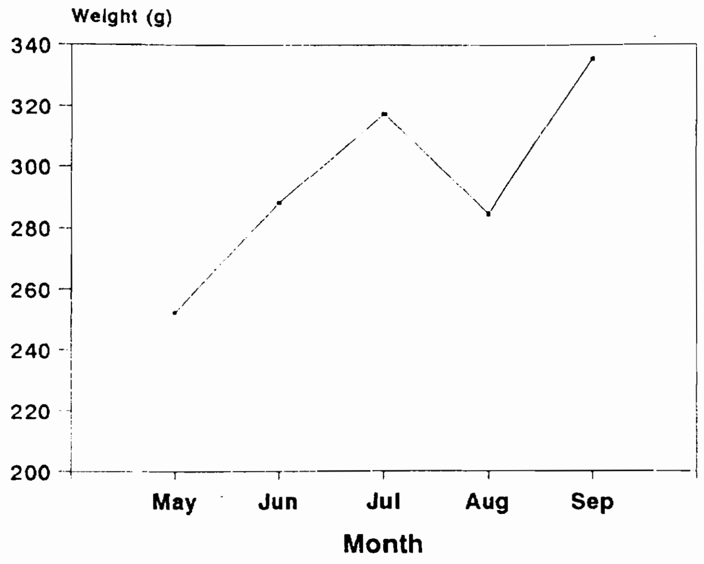
Relative liver weights (HSI) of age 1+ brown trout were significantly higher in ASO as compared to MJJ ($P = 0.04$). For young rainbow trout, there was no significant difference in the HSI value during ASO as compared to their HSI in MJJ

($P = 0.40$). The HSI values of age 1+ rainbow trout were significantly lower than the HSI of young brown trout in each period ($P < 0.01$).

An interesting relationship exists between monthly trends in the growth of age 1+ brown trout and monthly changes in the indices of well-being (Figure 28). Changes in condition (K) and relative liver weight (HSI) during one month consistently preceded changes in the growth of young brown trout in the next month. Poor growth observed from July to August corresponds to a prior decline in K and HSI from June to July. The conspicuous increase in K and HSI from July to August predates the surge of growth from August to September.

Because habitat availability and trout distribution were similar in both years, and to improve sample size, condition (K) data for adult brown and rainbow trout collected from August to October 1991 were pooled with data from August to October 1992. Sample size remained regrettably small, and consequently precluded statistical analysis.

Condition (K) of adult trout from August to October was relatively stable (Figure 29). Brown trout condition increased gradually over the period, but was lower (1.13 versus 1.50) than the mean condition of six brown trout collected in May, June, and July 1992. Condition (K) of age 2+ rainbow trout remained relatively constant from August to



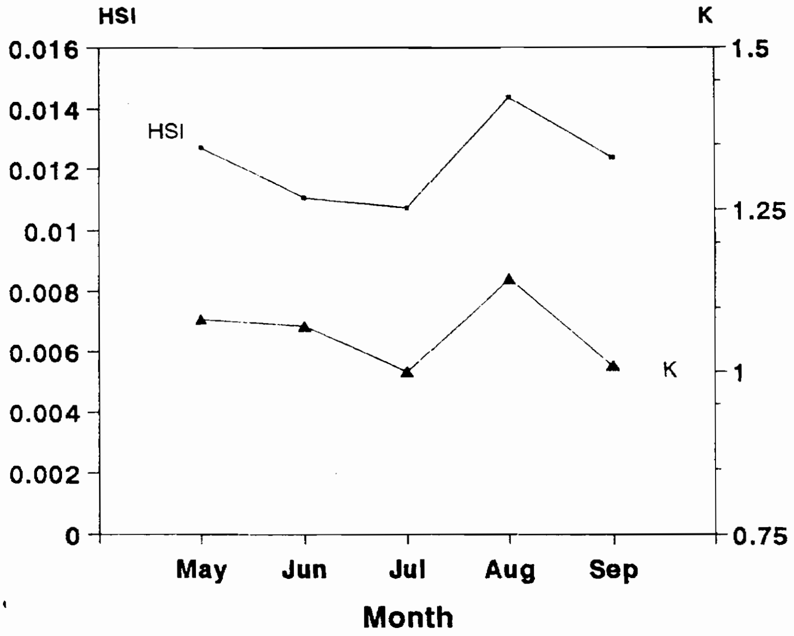


Figure 28. The observed growth, condition (K), and relative liver weight (HSI) of age 1+ brown trout collected in 1992.

October, and was higher (1.05 versus 0.84) than the mean condition of two rainbow trout captured in May 1992 (Figure 29).

The relative liver weight (HSI) of age 2+ brown trout collected in 1992 increased from August to September, but declined from September to October (Figure 30). The HSI of the one adult brown trout collected in August (0.0148) was similar to the mean HSI (0.0138) of six adult brown trout captured in June 1992. The relative liver weight of adult rainbow trout increased from August to September, before decreasing from September to October (Figure 30). The relative liver weight of the single adult rainbow trout collected in August (0.0087) was very similar to the mean HSI (0.0090) of two adult rainbow trout collected in May 1992.

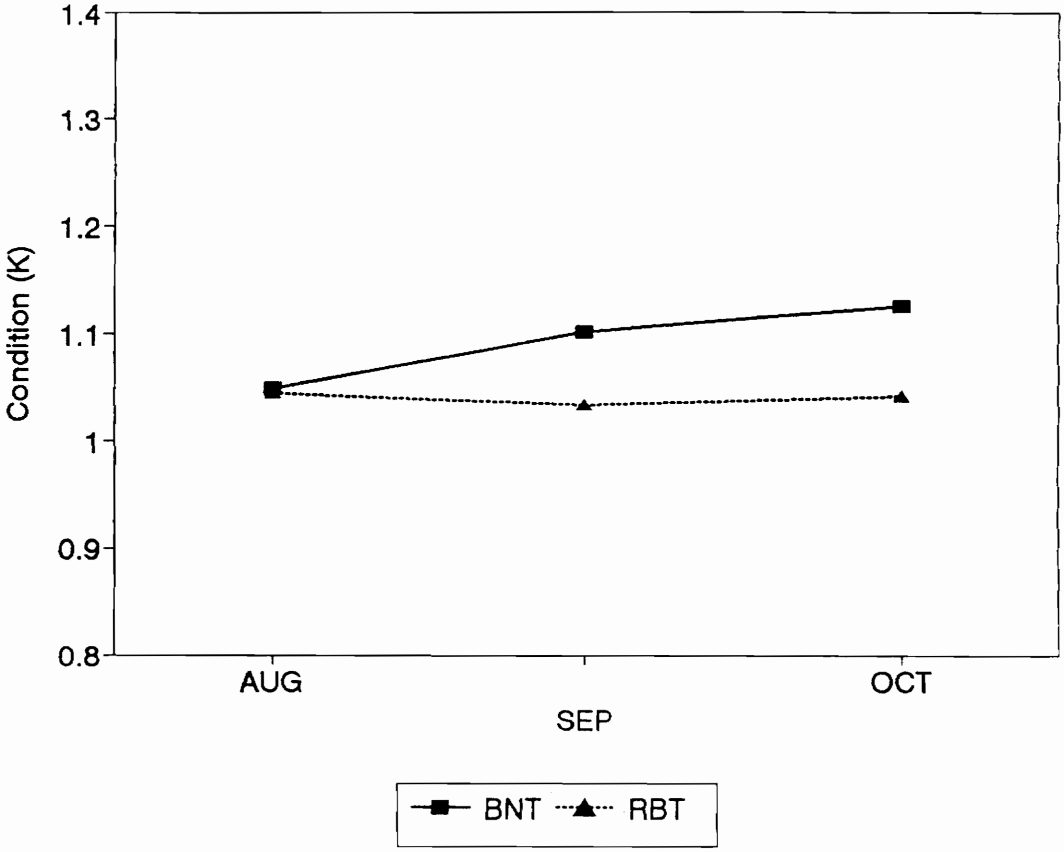


Figure 29. The Fulton-type condition (K) index for adult brown trout (solid line) and adult rainbow trout (dotted line). Data from August to October was pooled from 1991 and 1992.

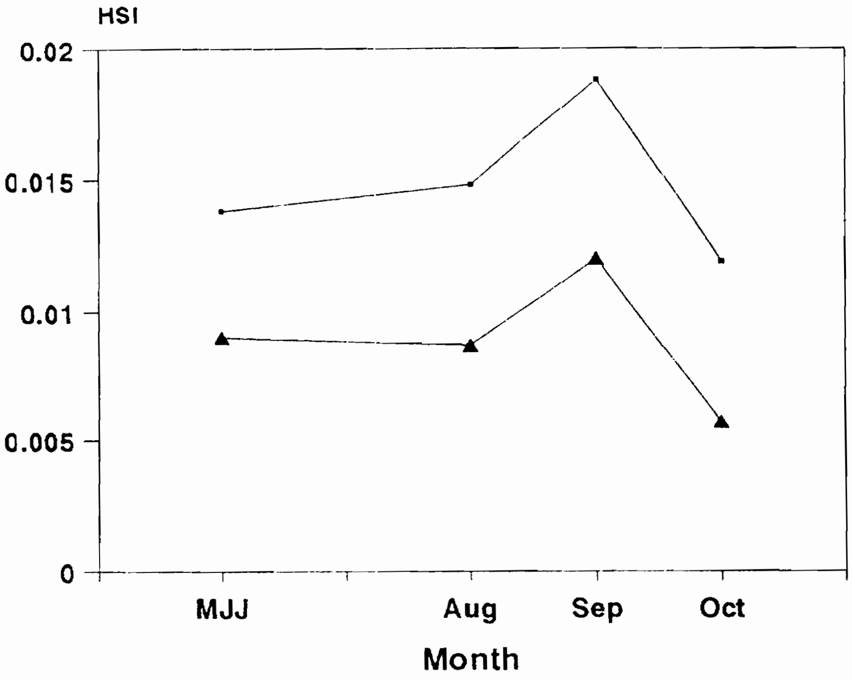


Figure 30. Relative liver weights (HSI) of adult brown trout (filled square) and rainbow trout (triangle) collected at Lake Moomaw in 1992.

Food Consumption

Trout diet. Alewives were the primary prey (by weight) of age 1+ brown trout from May to October (Table 9). Aquatic and terrestrial insects were present only in trace amounts, with the exception of July, when aquatic insects constituted 11 percent of the total diet. *Chironomus* was the most frequently consumed aquatic insect. A similar percentage of age 1+ brown trout stomachs were empty in each month ($P > 0.10$).

The diet of age 1+ rainbow trout was more diverse. Alewives provided the major forage (by weight) in four of the six months, but aquatic and terrestrial insects constituted a notable percentage of the diet (Table 10). The percentage of age 1+ rainbow trout stomachs that contained no food was statistically similar from May to October ($P >.05$).

Accurate assessment of adult trout diet composition from May to July was precluded by the lack of successive samples. Pooling data from August, September, and October of 1991 and 1992 improved sample size, and allowed the assessment of diet composition from August to October.

Only one of 16 age 2+ brown trout stomachs contained food (Table 11). Most age 2+ rainbow trout (18 of 22) also had empty stomachs. Alewives were the major prey by weight in the diet of adult rainbow trout in August, but aquatic insects (*Chaoborus spp.*) dominated in September (Table 11).

Table 9. Diet composition (by weight), and daily consumption (C_D; mg/g/day) of age 1+ brown trout from May to October. August, September, and October data are pooled from 1991 and 1992.

			Percentage	**by**	**Weight**	
Month	n	% empty	alewife	Aquatic Insects	Terrest. Insects	C_D
May	14	57	99.0	1.0	0.0	10.6
Jun	12	42	99.8	0.2	0.0	18.0
Jul	10	60	89.0	11.0	0.0	4.1
Aug	40	26	99.0	0.3	0.7	9.4
Sep	31	53	97.5	2.5	0.0	5.0
Oct	3	67	100.0	0.0	0.0	1.0

Table 10. Diet composition (by weight), and daily consumption (C_D; mg/g/day) of age 1+ rainbow trout from May to October. August, September, and October data are pooled from 1991 and 1992.

			Percent	**by**	**Weight**		
Month	n	% empty	alewife	Aquatic Insects	Terrest. Insects	Cray-fish	C_D
May	7	29	78.0	22.0	0.0	0.0	6.9
Jun	5	40	72.0	28.0	0.0	0.0	7.2
Jul	4	50	0.0	100.0	0.0	0.0	0.4
Aug	24	12	81.8	11.1	3.6	3.6	7.3
Sep	29	52	97.0	3.0	0.0	0.0	8.4
Oct	5	60	0.0	33.0	67.0	0.0	1.6

Table 11. Diet composition (by weight), and daily consumption (C_D; mg/g/day) of adult brown and rainbow trout. Data were pooled from 1991 and 1992.

				Percent by Weight		
Species	Month	n	Percent Empty	Alewife	Aquatic Insects	C_D
Brown trout	Aug	3	67	0.0	100.0	0.4
	Sep	7	100	0.0	0.0	0.0
	Oct	6	100	0.0	0.0	0.0
Rainbow trout	Aug	5	60	100.0	0.0	6.0
	Sep	8	75	33.2	66.8	4.3
	Oct	9	100	0.0	0.0	0.0

Daily consumption. There was no significant difference in the estimated daily consumption (mg/g/day) by age 1+ brown trout during ASO as compared to consumption during MJJ (P = 0.36). The daily consumption by young rainbow trout was also similar in each period (P = 0.45). Although there was disparity among their growth, condition and diet composition, age 1+ rainbow trout daily consumption was not significantly different from age 1+ brown trout consumption during MJJ (P = 0.97), or during ASO (P = 0.74).

The daily consumption by age 1+ brown trout (Table 9; Figure 31) follows a seasonal pattern similar to that exhibited by condition (K) and HSI (see Figure 28). Decreases in mean daily consumption from June to July are congruent with decreases in K and HSI, and are followed by poor growth in the subsequent period (July - August). Increases in consumption from July to August also predate the rapid growth of age 1+ brown trout from August to September.

The mean daily consumption (mg/g/day) by age 1+ rainbow trout was less dynamic (Figure 32). Disregarding the July minimum, daily consumption was relatively constant.

The daily consumption by age 2+ brown trout was near zero from August to October (Table 11). The daily consumption of adult rainbow trout was detectable during August and September, but none of the nine adult rainbow trout collected in October had food in their stomachs.

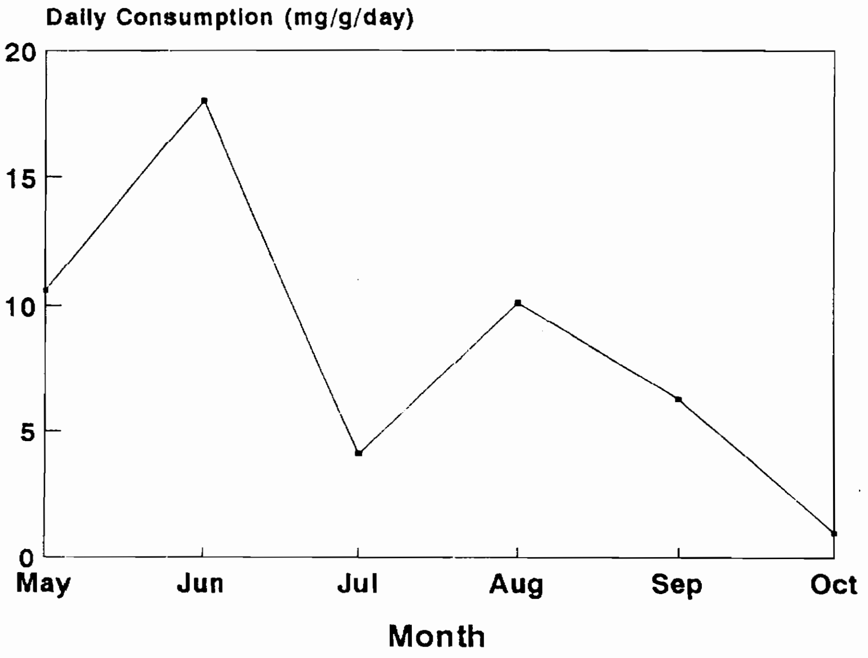


Figure 31. Seasonal variation in the estimated daily consumption (C_D) of age 1+ brown trout in Lake Moomaw. Data were pooled from 1991 and 1992 were pooled by month (August and September).

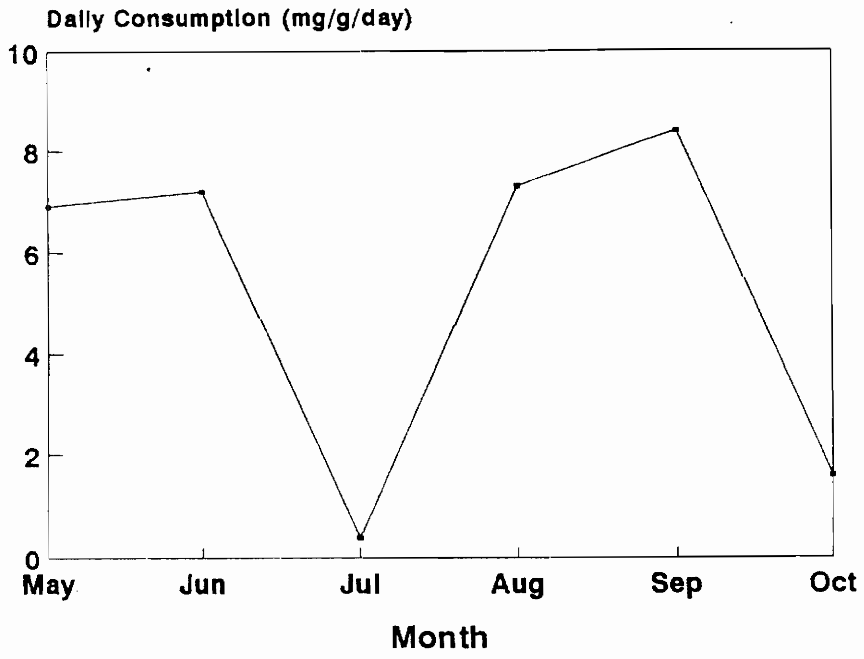


Figure 32. Estimated daily consumption (C_D) of age 1+ rainbow trout at lake Moomaw from May to October. Data from 1991 and 1992 were pooled for August and September.

Bioenergetic Simulations

The bioenergetics model was used to estimate potential growth of adult trout for the period 01 June to 01 October. Potential growth without habitat limitation was determined by using a constant P-value of 0.50, and the temperature occupied by telemetry-tagged adult trout in June and July. To determine the potential effects of isolation from prey, inputs were adjusted to approximate conditions observed in the isolated stratum at Lake Moomaw: (P) was set to zero, and temperature was changed to 10°C. Inputs were altered for the last 15, 30, and 45 days of the simulation period, to approximate habitat restriction beginning on 15 September, 01 September, and 15 August respectively.

An adult brown trout that weighed 1252 grams on 01 June would gain a potential 388 g from June to October in the absence of habitat limitations (Figure 33). This growth rate (3.2 g/day) is slightly higher than the estimated second year growth (2.8 g/day) of age 2+ brown trout from the 1989 year class. Segregation from prey for the final 15 days of simulation reduced potential growth by 65 percent: an age 2+ brown trout weighed only 1,384 grams on 01 October. The final weight (1,234 g) of fish that were isolated for 30 days was less than their initial weight four months earlier. An adult brown trout that was isolated from mid-August to early October

(45 days) would not only forego the potential growth of 388 grams, but would also lose 12 percent of the initial weight accumulated before 01 June.

An adult rainbow trout (1,005 g) would gain a potential 821 grams during the four months of simulation (Figure 34). Isolation that lasted for 15 days reduced potential growth by 342 grams (42 percent). An additional 214 grams (total of 68 percent) of potential weight gain was precluded by a 30-day fast. Adult rainbow trout that were sequestered without food at low temperature for 45 days would grow 85 grams in four months, a 90 percent reduction of potential growth.

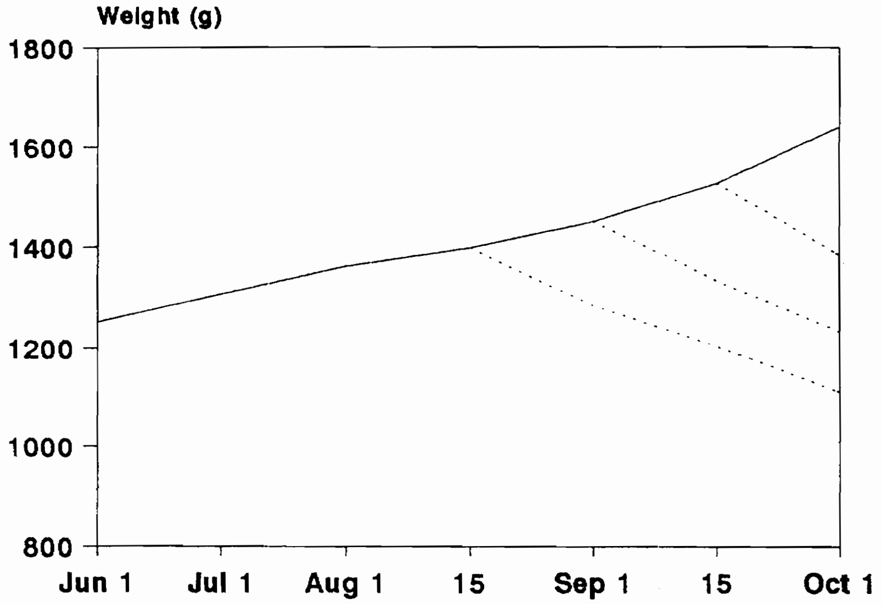


Figure 33. Predicted growth of adult brown trout from June to October, without habitat limitation. Descending slopes (dotted) depict pattern of growth loss due to different durations of isolation.

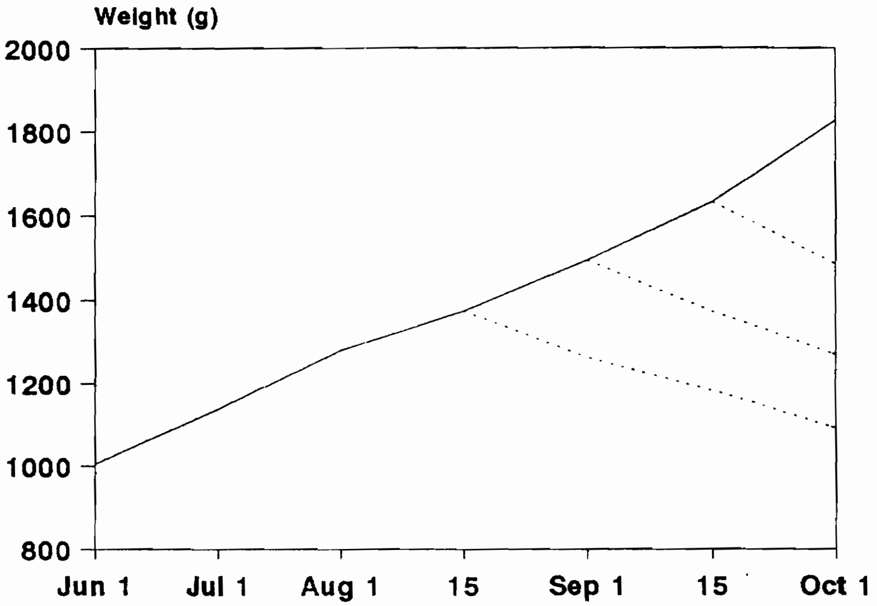


Figure 34. Predicted growth of adult rainbow trout from June to October, without habitat limitation. Descending slopes (dotted) depict the pattern of growth loss due to different durations of isolation.

DISCUSSION

Trout Habitat Dynamics

Lake Moomaw retained enough winter-cooled water in the metalimnion and hypolimnion during summer months to allow trout survival all year long. However, trout habitat (< 21°C, ≥ 5.0 mg/L) in Lake Moomaw disappeared in September.

Water temperatures in the shallow, upstream portions of the reservoir increased more rapidly than in the deeper waters near the dam. Because thermal stratification effectively prevented mixing of strata below the epilimnion, low dissolved oxygen limited the available trout habitat in the metalimnion and hypolimnion. Dissolved oxygen was depleted less rapidly in the lower portion of the reservoir because of greater volume and lower productivity. Other researchers have reported the horizontal recession of trout habitat toward the dam, and the vertical compression of habitat into narrow strata (Stevenson and Hulsey 1961; Kirkland and Bowling 1966; Baker and Mathis 1967; Axon 1971; Love 1979). Trout habitat loss at Lake Moomaw can be attributed to three major factors: elevated water temperature, dissolved oxygen depletion, and export of potential habitat through operation of the dam. All three factors played critical roles in the depletion of habitat at Lake Moomaw.

Water temperatures were elevated beyond the criterion (21°C) in the epilimnion beginning in June. Epilimnetic temperatures were at a maximum (27°C) in July and August and did not decline appreciably until late September.

Dissolved oxygen depletion began eliminating trout habitat from the upstream portion of the reservoir in July. Depletion then proceeded toward the dam, reducing D.O. concentrations below criterion ($\geq$ 5.0 mg/L) in the metalimnion and hypolimnion.

The operation of Gathright Dam from June to October typically resulted in discharge of 14°C water from the metalimnion, thus exporting potential trout habitat from the reservoir. Under this discharge regime, Gathright Dam discharged approximately 2.0×10^6 m^3 of potential reservoir trout habitat to meet mandated downstream flow requirements in the summer of 1992 (Larry Mohn, Virginia Department of Game and Inland Fisheries, unpublished manuscript).

Albeit the observed seasonal decline of trout habitat was expected, two aspects of the habitat dynamics at Lake Moomaw warrant further discussion. First, the formation of a hypoxic stratum in the lower metalimnion is of critical concern, as it seems to restrict the distribution of adult trout. Second, the apparent absence of criterion temperature and oxygen from mid-September to October could have deleterious effects on the trout fishery.

The development of the hypoxic stratum within the lower metalimnion could be the result of mechanisms of D.O. depletion described by Gordon and Skelton (1977). Changes in the density of water retard the vertical descent of seston and debris through this stratum. Decomposition of these organics consumes dissolved oxygen at an accelerated rate. However, that the depths and temperatures of the initial hypoxic stratum coincided with the location of the primary discharge penstock of Gathright Dam is suspect. Limnological data from years predating the coldwater release at Lake Moomaw did not detect the presence of a hypoxic metalimnetic stratum (Virginia Department of Game and Inland Fisheries; Virginia Water Control Board, unpublished data).

The formation of a similar hypoxic stratum in Bull Shoals Reservoir, Arkansas was reported by Love (1979). The hypoxic stratum also developed at depths adjacent to the primary discharge penstock. Love compared the stored trout habitat to changes in water release from 1963 to 1973, and concluded that increased discharge in 1973 contributed to the development of the hypoxic stratum.

Love (1979) concluded that the increased discharge of water from Bull Shoals Reservoir in 1973 was related to increased rainfall. However, the timing and intensity of hypoxic stratum development at Lake Moomaw were consistent in both a low rainfall year (1991) and a higher rainfall year (1992). This suggests that current discharge regime of Gathright Dam contributes to the development of the hypoxic stratum irrespective of climatic conditions.

The second critical concern, the complete loss of trout habitat, has also been documented in other two-story reservoirs. Van Velson (1974) documented the decline and eventual absence of trout habitat in Lake McConaughy, Nebraska, but no mortality was noted coincident to the loss of habitat. Jones (1982) reported epidemic trout mortality as a result of the complete loss of reservoir trout habitat in Laurel River Lake, Kentucky. Dissolved oxygen levels below 4.0 mg/L were recorded during late September and early October. The lake destratified in November, but intensive sampling provided no evidence of trout survival.

Extensive trout mortality was also observed after complete habitat loss in Bull Shoals Reservoir, Arkansas (Love 1979). Trout habitat was severely reduced in mid-September, and absent in October. Dissolved oxygen concentrations were below 3.0 mg/L in October. Dead and moribund trout were noted at the surface of the reservoir.

Fortunately, no conspicuous mortality was noted coincident to the complete loss of trout habitat in Lake Moomaw. The duration of habitat loss was brief, about two weeks. Cooling and aeration of the epilimnion occurred at a similar rate and time in both years: about fifty percent of the total trout habitat was reclaimed by early October.

Fish Distribution

The vertical distribution of trout in Lake Moomaw was apparently determined more by temperature than D.O. concentration. Trout were located at a consistent range of temperatures (10° - 21°C) even when D.O. concentrations declined. Alternative distribution in the epilimnion (>21°C) would have provided dissolved oxygen concentrations at or above saturation from June to September. However, trout were rarely captured in the epilimnion during the same period.

Age 1+ brown and rainbow trout were consistently located in the metalimnion at temperatures higher than adult trout--a distribution that overlapped with alewife distribution. Alewife distribution in the metalimnion at Lake Moomaw reflects their temperature preferenda (18 - 20°C) as reported by Coutant (1977).

Adult rainbow trout were also distributed in the metalimnion from June to September, but were located in the hypolimnion during October. Adult brown trout were located in the metalimnion during June and July, whereas they were distributed in the hypolimnion in August and September. Distribution of adult trout in the hypolimnion was at low temperatures and D.O. concentrations, and resulted in segregation from alewife forage in the metalimnion and epilimnion.

The frequent capture of brown and rainbow trout over a narrow range of temperatures (12 - 21°C) is consistent with the results of other studies of trout distribution (Jones 1982: Nettles et al. 1987: Bevelhimer 1990; Stables and Thomas 1992). This range includes the preferred temperatures (14 - 18°C) of brown and rainbow trout as determined in laboratory studies (Cherry et al. 1977; Coutant 1977). The consumption and growth of brown trout are also maximized within this temperature range (Elliott 1976b; Spigarelli et al. 1982). Occasional capture of trout in water warmer than 21°C at Lake Moomaw indicated that thermal barriers are not impermeable. Capture of rainbow trout in waters warmer than 21°C has been reported by Bevelhimer (1990) and Stables and Thomas (1992). In addition, distribution of both brown and rainbow trout in the heated effluents of Lake Michigan has been documented (Spigarelli and Thommes 1978). The presence of alewives and terrestrial insects in the warmer waters of the epilimnion affords a potential explanation of why a few trout were captured at temperatures greater than 21°C. In the laboratory, rainbow trout frequently enter thermally prohibitive water to obtain food rewards (Munson et al. 1989).

Distribution of adult trout in Lake Moomaw at greater depth and lower temperature than age 1+ trout indicated age segregation. The results of many laboratory studies list disparate temperature preferenda for different aged fish of the same species (Ferguson 1958; Coutant 1977). Most adult brown trout in Lake Moomaw were distributed in the hypolimnion at low temperature from mid-August to early October, whereas age 1+ brown trout were located in the metalimnion during the same period. Age segregation of rainbow trout was evident in October, when adult fish were distributed in the hypolimnion at lower temperatures than age 1+ rainbow trout. These results concur with other studies of trout distribution. Haraldstat and Jonsson (1983) reported age segregation of brown trout in a Norwegian lake: adult brown trout were often located in the deep pelagic and benthic zones, whereas age 1 brown trout were typically distributed in shallow areas. Spigarelli and Thommes (1978) reported that small rainbow trout (< 1 kg) selected warmer temperatures than larger rainbow trout (> 1 kg) in Lake Michigan. Selection of colder temperatures may represent behavioral thermal regulation, as metabolic costs decline at colder temperatures (Warren 1971).

The horizontal distribution of trout in Lake Moomaw visibly responded to changes in dissolved oxygen concentration. No trout were caught in horizontal gillnets fished at upstream locations in the reservoir during August and September of 1991. In addition, the horizontal distributions of telemetry-tagged brown and rainbow trout were restricted to the lower portion of the reservoir during August and September of 1992.

The vertical distributions of age 1+ brown and rainbow trout in Lake Moomaw responded to changes in the temperature profile, but did not respond to changes in dissolved oxygen concentration. Age 1+ brown and rainbow trout were captured at progressively greater depth as summer temperatures altered the location of the metalimnion. However, young brown and rainbow trout maintained their vertical distribution within the metalimnion (12 - 21°C) during August and September, when D.O. concentrations fell below 5.0 mg/L. Similar results were reported in recent literature. The vertical distribution of small rainbow trout (172 -242 mm fork length) in Spada Lake, Washington, was also unaffected by dissolved oxygen concentrations that declined below 5.0 mg/L (Stables and Thomas 1992).

In contrast, the vertical distribution of adult brown and rainbow trout in Lake Moomaw was visibly affected by dissolved oxygen depletion. Temperatures selected by telemetry-tagged brown trout in June and July (12.3-14.6°C) indicated distribution in the lower metalimnion. Dissolved oxygen concentrations in these strata began to decline below 5.0 mg/L in mid-August, and adult brown trout distribution promptly changed. Tagged brown trout were located in the hypolimnion during August and September.

The October distribution of adult rainbow trout was affected by dissolved oxygen depletion. Telemetry-tagged rainbow trout that were distributed in the metalimnion in September, descended to colder temperatures in the hypolimnion. Gillnet capture of adult trout yielded harmonious results.

Adult brown trout relocated to the cold, oxygenated epilimnion in October faster than rainbow trout. Telemetry-tagged brown trout had evacuated the hypolimnion by early October, whereas tagged rainbow trout remained in the isolated stratum of the hypolimnion. Rainbow trout were also captured more frequently in gillnets fished in the isolated stratum.

The spawning urge probably motivated a brown trout exodus from the isolated stratum. This theory is supported by the results of the ultrasonic telemetry study, as tagged brown trout were located near reservoir tributaries in October.

Gillnet capture of adult brown trout at upstream locations in the reservoir in October of 1991 provides additional evidence of a spawning migration. In addition, telemetry-tagged brown trout are known to migrate toward tributaries of Lake Ontario in late fall (Nettles et al. 1987).

Performance of Trout

Growth and Condition

Brown trout experienced excellent growth in Lake Moomaw. In fact, the specific growth rates of age 1+ brown trout from May to June (0.0047 g/g/day), and from August to September (0.0051 g/g/day) in 1992 compare favorably with rates reported under controlled conditions in the laboratory.

Data presented in Table 1 of Spigarelli et al. (1982) indicate that brown trout (365 - 401 g) feeding on dead alewives (to satiation) in the laboratory grew at a different rates depending on the temperature regime. Lake Moomaw brown trout grew faster than brown trout held at constant (ideal) temperature (0.0044 g/g/day), and at temperatures approximating Lake Michigan conditions (0.0037 g/g/day). Growth rate of age 1+ brown trout at Lake Moomaw was only slightly lower than the reported maximum growth rate (0.0061 g/g/day) achieved by brown trout exposed to a fluctuating temperature regime.

Lake Moomaw brown trout grew at approximately the same rate as brown trout fed Gammarus pulex to satiation. Data presented in Elliot (1975b) detail a maximum growth rate of 0.0047 g/g/day for a 248 g brown trout fed to satiation.

The growth of age 1+ brown trout experienced seasonal variation. Increased growth of young brown trout during May to June was indicative of ideal habitat and forage conditions. The poor growth apparent from July to August could be the result of a combination of factors. The synchronous decline of daily consumption, condition (k), and relative liver weight (HSI) of age 1+ brown trout in July suggested that the poor growth could be related to diminished foraging success in July. Increased mortality during and after June spawning probably reduced adult alewife abundance, whereas young-of-the-year alewives were too small to provide profitable forage in July. Diet composition results support this theory. July was the only month in which alewives constituted appreciably less than 100 percent (by weight) of age 1+ brown trout stomach contents.

In addition to reduced overall abundance, alewives in Lake Moomaw may be of less energetic value in July. The caloric density of alewives in Lake Michigan varies seasonally (Flath and Diana 1985). Stewart and Binkowski (1986) reported that the energetic content of Lake Michigan alewives was at an annual minimum in July. Therefore, depressed growth from

July to August is probably related to reduced prey abundance and energy content.

The surge in growth of age 1+ brown trout from August to September could be the result of increased prey abundance and foraging success. Young-of-the-year alewives were present in the stomachs of age 1+ trout beginning in August. The growth surge is predated by condition (K) and relative liver weight (HSI) in August. The hepatosomatic index (HSI), and condition (K) seemed to be sensitive to short term changes in nutrition, and as such were an accurate predictor of brown trout growth in the subsequent period. A similar 1-month lag relationship between HSI and growth has also been reported in studies of largemouth bass in a Tennessee reservoir (Adams and McLean 1985).

That the relative liver weight (HSI) of age 1+ brown trout was significantly higher in the period of habitat limitation (ASO) than in the unlimited habitat period (MJJ) indicates that habitat limitations do not adversely affect the energetics of age 1+ brown trout in Lake Moomaw. This is not surprising, as distribution in the upper metalimnion locates young brown trout at ideal temperature and profitable forage abundance. It is enigmatic, however, that the condition (K) of age 1+ brown trout was significantly lower in ASO than in MJJ. In view of the previous discussion of the distribution, growth, consumption, and relative liver weight (HSI) of young brown trout in Lake Moomaw, it seems unlikely that the observed difference in the condition (K) of age 1+ brown trout represents a deleterious effect of habitat limitation.

The growth and condition of age 1+ rainbow trout were less dynamic. Poor summer growth of rainbow trout, compared to brown trout, probably results because age 1+ rainbow trout diet typically includes a higher proportion of invertebrate forage. The energy density of most invertebrates, 207 to 1058 calories per gram wet weight, is much lower than the values reported by Hewett and Johnson (1992) as the energy content of alewives (1200 - 2270 cal/g).

No significant difference was noted in the condition (K) or relative liver weight (HSI) of age 1+ rainbow trout between the two periods. Both indices remained relatively constant during this study, and consequently did not provide any prediction of growth. A potential explanation of the inadequacy of the hepatosomatic index as a predictor of rainbow trout growth is detailed in a study of rainbow trout physiology. Weatherley and Gill (1981) noted that the growth of liver tissue did not respond to nutritional changes faster than somatic tissue in rainbow trout. Instead, the visceral tissue provided the most punctual response to short-term changes in nutrition. Therefore, the visceral-somatic index may provide a better index of rainbow trout condition, and should be included in future studies of the short-term energetic response of this species.

Evaluation of the growth of adult brown and rainbow trout was precluded by an inability to collect adequate, successive samples from May to September. Capture of brown trout from the 1989 year class during their second (1992) and third year (1993) of reservoir residence provided evidence of the excellent overall growth potential of adult trout in Lake Moomaw.

Pooling data from 1991 and 1992 afforded improved assessment of adult trout condition from August to October. That the condition (K) of adult brown trout increased from August to October despite decreased growth and consumption, indicates that the index is not always sensitive to changes in short-term energetic response. The efficacy of a Fulton-type condition factor (K) is affected by the production of gonadal tissue (Anderson and Gutreuter 1983). In addition, the index can be affected by physiological changes that result from fasting. During periods of starvation, fish are forced to break down lipids and proteins stored in body tissues in order to provide energy for metabolism. These degenerated tissues are replaced by water (Weatherley and Gill 1987). Thus, the total weight of a fasting trout may not change appreciably.

In contrast to age 1+ brown trout results, the hepatosomatic index was not an accurate predictor of adult brown trout growth in the next month. This may be the result of random variation due to small sample size. However, Adams and McClean (1985) reported similar findings--the HSI was less effective as a predictor of the growth of adult largemouth bass. This phenomenon probably results because mature fish channel a substantial portion of their consumed energy into gonadal production rather than lipid storage in the liver.

The condition (K) of adult rainbow trout remained relatively constant from August to October. Accuracy of the Fulton-type condition factor is subject to the constraints detailed above. Notably, the production of gonadal products (gravid female rainbow trout were captured in gillnets), and the uptake of water to replace degenerated tissue adversely affect the index.

Changes in the relative liver weight (HSI) of adult rainbow trout corresponded to changes in distribution from August to October. Adult rainbow trout were distributed at preferred temperatures in the metalimnion during August and September. Condition (HSI) during these months should be higher than condition in October, when captured trout were located at conditions of low temperature (9°C), diminished oxygen (3.9 mg/L), and limited food.

Food Consumption

Trout diet. Alewives were the primary forage of brown and rainbow trout at Lake Moomaw in most study months. The affinity of brown and rainbow trout for alewives is well documented in studies of the Great Lakes salmonid fisheries (Stewart et al. 1981; Jude et al. 1987; Nettles et al. 1987). That brown trout of both ages preyed almost exclusively on alewives is also consistent with the results of these studies (Jude et al. 1987; Nettles et al. 1987).

Aquatic and terrestrial insects constituted a notable portion of age 1+ rainbow trout diet, even though alewives were abundant and their distributions overlapped. The tendency of reservoir young rainbow trout to consume substantial amounts of invertebrate forage when clupeid prey is readily available has also been noted in Tellico Reservoir, Tennessee (Bivens and Strange 1985). This phenomenon is probably related to a size-based diet switch. Scott and Crossman (1973) detailed a size and age-based shift from invertebrate diet to piscivority in rainbow trout in Canadian systems. Jude et al. (1987) reported that Lake Michigan rainbow trout less than 300 m in length consumed a higher proportion of invertebrate forage than rainbow trout larger than 300 mm.

Analysis of adult brown and rainbow trout diet was complicated by the lack of successive samples from May, June, and July. The high percentage of empty stomachs made assessment of their diet composition from August to October relatively easy. Adult brown effectively did not feed during this period. One of 16 stomachs contained a trace amount of chaoborids. The diet of adult rainbow trout included only alewives in August, but consisted of aquatic insects and alewives in September.

Daily consumption. Daily consumption by age 1+ brown trout was statistically similar in both periods. There was also no significant difference between the daily consumption by young rainbow trout in each period. In contrast to condition (K) and relative liver weight (HSI), there was also no significant statistical difference between the consumption by age 1+ rainbow trout and age 1+ brown trout. That consumption by young trout was similar in both periods further reflected the minimal effects of habitat limitations on young trout. Distribution in the upper metalimnion located age 1+ brown and rainbow trout at profitable temperatures and prey abundance.

Monthly estimates of daily consumption indicated that age 1+ brown trout consumption followed a bimodal distribution, with peaks in June and August. The same trend was evident in the seasonal changes in age 1+ brown trout condition (K) and relative liver weight (HSI). That these indices promptly responded to apparent changes in age 1+ brown trout consumption bolstered the concept of their sensitivity to the short-term energetic responses of fish.

Peaks in the daily consumption by young brown trout corresponded to improved foraging conditions at Lake Moomaw. Alewives were probably more susceptible to predation in June, when they were affected by the rigors of spawning. The recruitment of young-of-the-year alewives in August increased prey abundance dramatically, and improved the foraging success of age 1+ brown trout. The observed decline in daily consumption by age 1+ brown trout in July was probably related to alewife population dynamics. Alewife abundance should be at an annual minimum in July. Mortality incurred during and after their June spawning would reduce adult alewife abundance, whereas young-of-the-year alewives would be too small to provide meaningful forage.

The daily consumption of age 1+ rainbow trout peaked in September. The September peak is probably the result of increased piscivory, as alewives constituted 97 percent of rainbow trout diet in September. The increase in piscivory coincides with the increased abundance of small (young-of-the-year) alewives. Increased piscivority in young rainbow trout (< 300 mm) during the fall was also noted in Lake Michigan (Jude et al. 1987).

Results of this study indicated that adult brown trout at Lake Moomaw effectively did not feed from August to October.

The fasting of adult brown trout during this period provided further evidence of isolation from their preferred prey, alewives. The stomach of only one adult brown trout contained food--a minimal amount of chaoborids. Diurnal vertical migration of chaoborids through the water could expose these insects to potential predation by trout isolated in the hypolimnetic stratum (Merritt and Cummins 1984).

Daily consumption by adult rainbow trout was also limited; eighteen of the 24 stomachs examined were empty. Daily consumption declined from August to September, and was near zero in October. Distribution of adult rainbow trout in the metalimnion during August and September afforded ample foraging opportunities, whereas distribution in the hypolimnion during October resulted in effective isolation from alewife forage.

Estimates of daily consumption were subject to the constraints of several assumptions. It must be assumed that gillnet capture is without bias, i.e. that fish with empty stomachs are not more likely to be collected than fish with full stomachs. In addition, daily consumption estimates assume no regurgitation of stomach contents.

Daily consumption estimates presented in this thesis are probably overestimates. Consumption estimates included only the stomach contents that had been consumed in the last 24 hours. This method produces an overestimate, because feeding ceased at the time of capture. For example, a trout that remained the net for 12 hours was unable to feed for fifty percent of the daily consumption period. Daily consumption estimates based on consumption during 24 hours preceding the removal from the net would actually include only 12 hours of feeding. Thus the method could potentially underestimate daily consumption.

Simulations

Because age 2 + brown and rainbow trout constitute most of the trophy fishery at Lake Moomaw, evaluation of the effects of habitat limitations on their growth is particularly relevant to this study. The inability to collect successive samples of sufficient size impeded efforts to directly assess these effects. A bioenergetics model was used to estimate the potential adult trout growth from June to October. With a potential growth established, the growth foregone due to various duration of isolation from prey could be estimated.

Ultrasonic telemetry data and limited vertical gillnet data indicated that adult brown trout were located in the hypolimnion from mid-August to October (45 days), whereas age 1+ trout were distributed in the metalimnion. Adult rainbow trout were also located in the hypolimnion for at least 15 days (mid-September to October). Distribution in the hypolimnion was at suboptimal temperatures (< 10°C) and low D.O. concentrations (< 5.0 mg/L). As the hypoxic stratum developed in the lower metalimnion, fish located in the hypolimnion suffer an increased risk of isolation from prey. Thus habitat limitations affect adult brown and rainbow trout more than age 1+ trout of both species. Trends in the daily consumption of trout from August to October support this theory: estimated daily consumption by adult brown trout was zero from August to October, and adult rainbow trout consumption declined to zero from September to October. Age 1+ brown and rainbow trout continued to forage in the same period.

Bioenergetics model predictions suggested that even brief isolation from prey could substantially reduce the seasonal growth of adult brown trout. This happens because isolation from prey precludes any intake of extrinsic energy, and starvation induces the mobilization of intrinsic energy--lipids and proteins stored in body tissues (Weatherley and Gill 1987). Thus no energy is being stored as growth, and energy stores accumulated prior to fasting are being consumed.

Stomach content analysis indicated that adult brown trout at Lake Moomaw were not feeding from mid-August to October (45 days). Simulations that mimicked conditions in the isolated stratum indicated that this duration of fasting would preclude all potential growth in weight from June to October. In fact, the degeneration of tissue accumulated before June would result.

The growth of adult rainbow trout from June to October was also simulated. Evaluation of daily consumption indicated that rainbow trout continued to forage from August to mid-September, but were spatially segregated from alewives from September to October. Gill net capture suggested that the shortest duration, 15 days, was the most probable scenario. However, telemetry observations indicate that isolation may persist for a longer duration.

Model simulations provide an improved assessment of the potential effects of habitat limitations on the growth of adult rainbow trout in Lake Moomaw. Rainbow trout that endured a 15-day isolation precluded 42 percent of their potential growth from June to August. A 45-day fast reduced growth potential by about 90 percent.

The bioenergetics model predicted disparate results for adult brown trout and adult rainbow trout. This is not enigmatic, given that model equation inputs reflect differences in the two species. Components of the consumption equation are considerably different for each species (See Table 3). Most of the disparity in model results arise from the these differences, as running the model with identical temperature and weight data yields different results for the two species.

Several inadequacies of the bioenergetics model should be noted. The model does not incorporate the effects of dissolved oxygen on fish growth. Because oxygen can act as a limiting factor to the growth of fish (Kramer 1987), inclusion of an oxygen component would improve the overall validity of the model. Low D.O. concentrations are known to decrease the swimming speed of fish (Beamish 1978), and to increase the rate of standard respiration (Weatherley and Gill 1987). The two effects are antithetical. To procure necessary oxygen, more water must be passed over the gills. This results in a net increase in standard respiration. Since more time and energy are spent in the acquisition of oxygen, less energy is available for locomotion. As both swimming speed and standard respiration are included as components of the bioenergetics model used in this study, the inclusion of D.O. parameters could alter the results of model simulations.

Both factors would reduce the daily consumption of trout subjected to low dissolved oxygen. Because model simulations were designed to mimic conditions in the hypolimnetic strata (P-value = 0.0), factors that influence daily consumption would not have any effect on model simulations in this study. However, inclusion of the effects of low D.O. concentrations in the bioenergetics model would have offered additional information relevant to this study. For example, age 1+ trout distributed in the metalimnion were subjected to low D.O. concentrations beginning in mid-August. The refined model could simulate these conditions, and estimate the potential energetic costs of living at dissolved oxygen lower than 5.0 mg/L. This information would allow improved evaluation of the effects of seasonal habitat limitation on trout energetics.

Another inadequacy of the model is related to caloric density. In the current model, caloric density of the predator is modeled either as a constant, or as a function of fish weight (Hewett and Johnson 1992). The potential problem is related to the physiological changes that accompany starvation in fish. When a fish starves, high caloric density tissues (lipids and proteins) are replaced by water (Weatherley and Gill 1987). Therefore, the caloric density of a starving fish changes, but probably not analogous to changes in weight. It is feasible that the uptake of water by a fasting fish could obscure any detectable change in total weight.

A final inadequacy of the model is related to selection of a P-value. The ideal scenario would have been to use the actual daily consumption observed during June and July in Lake Moomaw. Unfortunately, small sample size precluded the direct estimation of the daily consumption of adult trout in this study. A P-value of 0.50 seems reasonable though, as it produced a growth rate similar (3.2 vs 2.8 g/day) to a gross estimate for age 2+ brown trout in Lake Moomaw.

Despite apparent limitations, model simulations allowed some degree of assessment when direct measurement was not possible. A bioenergetics model was included in this study to estimate the amount of growth forgone due to periodic isolation of trout from their prey; information that could not be obtained by direct sampling at Lake Moomaw.

SUMMARY AND CONCLUSION

1. Trout habitat at Lake Moomaw was defined as water with temperature less than 21°C and dissolved oxygen greater than or equal to 5.0 mg/L. Limnological profiles taken twice per month from August to October 1991, and from May to October 1992 described the horizontal and vertical availability of trout habitat.

2. Trout habitat at Lake Moomaw was most abundant in May, and declined from June to August. For the first time since the reservoir was filled in 1981, trout habitat was absent in September. Habitat availability began to improve in October, as much of the epilimnion cooled below 21°C.

3. The distributions of stocked brown and rainbow trout were determined using vertical gillnets from August to October 1991. Ultrasonic telemetry and vertical gillnets were used to assess the horizontal and vertical distributions of brown and rainbow trout from May to October 1992.

4. Primarily age 1+ brown and rainbow trout were captured in the gillnets; few age 2+ and older trout were collected. However, ultrasonic telemetry data from June to October 1992 detailed the distributions of age 2+ brown and rainbow trout.

5. The vertical distribution of age 1+ brown and rainbow trout was apparently unaffected by seasonal habitat dynamics. Most age 1+ brown and rainbow trout maintained distribution in the metalimnion (12 - 21°C) from May to October, even though dissolved oxygen in some strata of the metalimnion was below 5.0 mg/L during August and September.

6. The distributions of age 2+ brown and rainbow trout were altered by seasonal habitat limitations. The horizontal distribution of telemetry-tagged age 2+ brown and rainbow trout contracted toward the dam as suitable habitat was depleted from the upstream portion of the reservoir. In terms of vertical distribution, tagged brown trout were located in the metalimnion during June and July. When dissolved oxygen concentrations in the metalimnion declined in August and September, tagged brown trout were distributed in the hypolimnion (< 12°C). Tagged brown trout had relocated to the cooled epilimnion in early October. Tagged rainbow trout were typically distributed in the metalimnion from June to September, but were located in the hypolimnion in October.

7. The growth, well-being, and food consumption of brown and rainbow trout captured in the gillnets were noted relative to seasonal habitat dynamics. Consecutive samples of sufficient size allowed estimation of incremental growth rates for age 1+ brown and rainbow trout. Small monthly sample sizes ($n = 0$ to 6) for age 2+ brown and rainbow trout precluded estimation of growth rates.

8. Instantaneous rates of growth in weight (g/g/day) were calculated for age 1+ brown and rainbow trout. Growth in weight of age 1+ brown trout was variable, but peaked from August to September. The growth in weight of age 1+ rainbow trout was highest from June to July, and remained consistently poor thereafter.

9. Condition factor (K) and relative liver weight (HSI) were calculated as indices of well-being. The condition (K) of age 1+ brown trout was significantly higher ($p = 0.02$) in the period May, June, and July than in the period August, September, and October. However, the relative liver weight (HSI) of age 1+ brown trout was significantly higher ($p = 0.04$) in the August to October period than in the period from May to July. The condition (K) and the relative liver weight (HSI) of age 1+ rainbow trout were not significantly different ($p > 0.10$) in either period.

10. Alewives were the major forage found in age 1+ brown trout stomachs in all months. The estimated daily consumption (mg/g/day) by age 1+ brown trout peaked in June, declined in July, and increased in August. There was no significant difference ($p = 0.36$) in the daily consumption by age 1+ brown trout in the period August to October, as compared to the period from May to July.

11. Age 1+ rainbow trout also fed primarily on alewives, but aquatic and terrestrial insects contributed notably to their diet in most months. Estimated daily consumption by age 1+ rainbow trout (mg/g/day) peaked in September. There was no significant difference ($p = 0.45$) in the daily consumption by age 1+ rainbow trout from August to October, as compared to the period from May to July.

12. Only one of sixteen age 2+ brown trout stomachs collected from August to October contained food, suggesting that age 2+ brown trout did not feed during the period. Most age 2+ rainbow trout stomachs collected (18 of 22) were also empty. Alewives were the primary forage of age 2+ rainbow

trout in August, but aquatic insects dominated in September. None of the nine age 2+ rainbow trout stomachs collected in October contained food.

13. A bioenergetics model was used to estimate the potential growth (in weight) of age 2+ brown and rainbow trout from June to October. Growth foregone due to isolation from prey was also predicted.

14. Ultrasonic telemetry and gillnet results indicated that age 2+ brown trout at Lake Moomaw were isolated in the hypolimnion from mid-August to October (45 days). Stomach content analysis suggested that age 2+ brown trout did not feed during this period of isolation. The bioenergetics model estimated that without habitat limitation an age 2+ brown trout could add 388 grams from June to October. Model predictions also indicated that an age 2+ brown trout subjected to a 45-day fast from mid-August to October would forfeit all potential growth from June to October, and some of the growth achieved before June.

15. Study results suggested that age 2+ rainbow trout at Lake Moomaw were isolated from their primary forage for at least 15 days, from mid-September to October. Bioenergetic simulations estimated that without habitat limitations age 2+ rainbow trout could gain 821 grams from June to October. Isolation from prey for 15 days reduced potential growth by 42 percent. An age 2+ rainbow trout sequestered for 45 days would add only 85 grams of weight from June to October, reducing potential growth by about 90 percent.

The results of this study indicated that seasonal habitat limitations affect adult trout more than younger trout, and adult brown trout more than adult rainbow trout. The metalimnetic distribution of age 1+ brown and rainbow trout reduced their risk of being isolated from prey. In contrast, Adult brown and rainbow trout were often distributed in the hypolimnion, where they suffered an increased risk of isolation from their preferred prey, alewives.

The results of the bioenergetics model predicted that even brief isolation can substantially reduce the potential growth of trout. Prolonged isolation can negate growth achieved in previous periods. Thus, seasonal habitat limitations could have an adverse effect on the trophy trout fishery at Lake Moomaw. If current trends in habitat depletion persist or worsen, the success of the trophy fishery will most likely decline.

Any effort that retards the depletion of trout habitat in Lake Moomaw should improve the success of the trout fishery. Changes in the operation of Gathright Dam could increase the amount of trout habitat stored in the reservoir during summer and fall months. The mandated coldwater release could be achieved by mixing hypolimnetic and epilimnetic strata before discharge, rather than drawing directly from the metalimnion. The proposed change would not only decrease the total amount of ideal trout habitat exported from the reservoir, but should also decrease the magnitude of the hypoxic metalimnetic stratum that segregates adult trout from alewives.

If the threat of annual habitat deprivation can be allayed, efforts to increase the abundance of age 2+ trout would improve the trophy fishery. The current size regulation (254-mm minimum length limit) allows the harvest of age 1+ trout long before their growth potential is realized. The results of this study indicated that the average brown and rainbow trout stocked in December exceeded 254 mm before May. Thus, under current regulation the reservoir is actually managed on a put-and-take basis, rather than a put-grow-and-take basis.

Because trout in Lake Moomaw reach trophy sizes during their second year of reservoir residence, an effort should be made to protect brown and rainbow during their first year of reservoir residence. A 406-mm minimum length limit would protect most age 1+ brown and rainbow trout through October of their first season.

Release (hooking) mortality is a valid concern, but the results of this study and others suggest that it should not be catastrophic for age 1+ trout. Numerous age 1+ trout, angled while attempting to collect telemetry specimens, were released without evidence of mortality during May, June, and July.

Excessive temperatures in the epilimnion in July, August, and September could increase the risk of release mortality. However, distribution and diet composition reveal voluntary periodic movement toward the surface during this period. In addition, both angler effort and catch rate typically decline after July (personal observation).

Continued research at Lake Moomaw is warranted, both to protect the trout resource, and to promote the continued success of the fishery. Limnological sampling should be conducted to detail the dynamics of trout habitat relative to any future changes in the operation of Gathright Dam.

Annual evaluation of the distribution, consumption, and condition of brown and rainbow trout should be implemented so that future management decisions can be based on contemporary data. Vertical gillnet sampling conducted in September should detail the distribution of trout during the period of severe habitat limitation, whereas October sampling could reveal any prolonged effects of habitat limitation. The percent of captured trout with empty stomachs should provide an indication of consumption by trout during September and October. The Hepatosomatic Index and the Visceral-somatic index should adequately describe the condition of brown and rainbow trout collected during September and October.

LITERATURE CITED

Adams, S.M., and R.B. Mclean. 1985. Estimation of largemouth bass, Micropterus salmoides, growth using the liver somatic index and physiological variables. Journal of Fish Biology 26:111-126.

Anderson, R.O., and S.J. Gutreuter. 1983. Length, weight, and associated structural indices. In L.A. Nielsen and D.L. Johnson, editors. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland, USA.

Austin, R.S., E.L. Morgan, and J.T. Browning. 1978. United States Department of Agriculture, Forest Service. Southeastern trout resource: Ecology and management. Symposium proceedings. Southeast Forest Experimental Station, Asheville, North Carolina.

Axon, J.R. 1971. An evaluation of the trout fishery in Lake Cumberland, Kentucky. Pp. 235-242 in Reservoir Fisheries and Limnology, Gordon E. Hall editor. Special publication no. 8. American Fisheries Society.

Baker, R.F., and W.P. Mathis. 1967. A survey of Bull Shoals Lake, Arkansas, for the possibility of an existing two-story lake situation. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 20:360-368.

Beamish, F.W.H. 1978. Swimming capacity. Pages 101-187 in W.S. Hoar and D.J. Randall (eds.) Fish Physiology, Vol VII. Academic Press, London.

Beauchamp, D.A., D.J. Stewart, and G.L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. Transactions of the American Fisheries Society 118:597-607.

Bevelhimer, M.S. 1990. Habitat selection by kokanee salmon and smallmouth bass in thermally heterogenous environments: the importance of growth maximization to diel habitat shifts. PhD dissertation. University of Tennessee, Knoxville, Tennessee.

Bevelhimer, M.S., R.A. Stein, and R.F. Carline. 1985. Assessing significance of physiological differences among three esocids with a bioenergetics model. Canadian Journal of Fisheries and Aquatic Sciences 42:57-69.

Bivens, R.D., and R.J. Strange. 1987. Evaluation of a southeast two-story rainbow trout. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 41:187-196.

Brafield, A.E. 1985. Laboratory studies of energy budgets. Pages 257-281 _in_ P. Tytler and P. Calow (eds.), Fish Energetics: New perspectives. Johns Hopkins University Press, Baltimore.

Brandt, S.B., D.M. Mason, and E.V. Patrick. 1992. Spatially-explicit models of fish growth rate. Fisheries 17:23-33.

Brett, J.R. 1979. Environmental factors and growth. Pages 599-675 _in_ W.S. Hoar, D.J. Randall and J.R. Brett (eds.) Fish Physiology, Vol VIII: Bioenergetics and growth. Academic Press, New York.

Brett, J.R. 1983. Life energetics of sockeye salmon, _Oncorhynchus nerka_. Pages 29063 _in_ W.P. Aspey and S.I. Lustwick (eds.), Energetics: Vertebrate costs of survival. Ohio State University Press, Columbus.

Brett, J.R., and J.M. Blackburn. 1981. Oxygen requirements for growth of young coho (_Oncorhynchus kisutch_) and sockeye (_O. nerka_) salmon at 15°C. Canadian Journal of Fisheries and Aquatic Sciences 38:399-404.

Brett, J.R. and T.D.D. Groves. 1979. Physiological energetics. Pages 279-352 _in_ W.S. Hoar, D.J. Randall, and J.R. Brett (eds.), Fish physiology, Vol VIII: Bioenergetics and growth. Academic Press, New York.

Brodeur, R.D., R.C. Francis, and W.G. Pearcy. 1992. Food consumption of juvenile coho (_Oncorhynchus kisutch_) and chinook salmon (_O. tshawytscha_) on the continental shelf off Washington and Oregon. Canadian Journal of Fisheries and Aquatic Sciences 49:1670-1685.

Bugas, P.E., Jr. 1991. Virginia Department of Game and Inland Fisheries. Unpublished manuscript.

Burdick, G.E., M. Litshvetz, H.G. Dean, and E.J. Harris. 1954. Lethal oxygen concentrations for trout and smallmouth bass. New York Fish and Game Journal 1:84-97.

Cherry, D.S., K.L. Dickson, J. Cairns Jr., and J.R. Stauffer. 1977. Preferred, avoided, and lethal temperatures of fish during rising temperature conditions. Journal of the Fisheries Research Board of Canada 34:239-246.

Cole, G.A. 1983. Textbook of limnology, Third edition. Waveland Press, Prospect Heights, Illinois.

Cone, R.S., and C.C. Kreuger. 1988. Comparison of survival, emigration, habitat use, marking mortality, and growth between two strains of brook trout in Adirondack Ponds. North American Journal of Fisheries Management 8:497-504.

Coutant, C.C. 1977. Compilation of temperature preference data. Journal of Fisheries Research Board of Canada 34:739-745.

Coutant, C.C. 1987. Poor reproductive success of striped bass from a reservoir with reduced summer habitat. Transactions of the American Fisheries Society 116:154-160.

Daniel, W.W. 1987. Biostatistics: A foundation for analysis in the health sciences. John Wiley and Sons Press, New York.

Davis, J.C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. Journal of the Fisheries Research Board of Canada 32:2295-2332.

Elliott, J.M. 1975a. Numbers of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding for brown trout, _Salmo_ _trutta_, L. Freshwater Biology 5:287-303.

Elliott, J.M. 1975b. The growth rate of brown trout (_Salmo_ _trutta_ L.) fed on maximum rations. Journal of Animal Ecology 44:805-821.

Elliott, J.M. 1976a. Energy losses in the waste products of brown trout (_Salmo_ _trutta_ L.) Journal of Animal Ecology 45:561-580.

Elliott, J.M. 1976b. The energetics of feeding, metabolism, and growth of brown trout (Salmo trutta L.) in relation to body weight, water temperature and ration size. Journal of Animal Ecology 45:923-948.

Elliott, J.M. 1979. Energetics of freshwater teleosts. Pages 29-61 in P.J. Miller (ed.), Fish phenology: Anabolic adaptiveness in teleosts. Symposia of the Zoological Society of London 44.

Elliott, J.M. 1991. Rates of gastric evacuation in piscivorous brown trout, Salmo trutta. Freshwater Biology 25:297-305.

Ferguson, R.G. 1958. The preferred temperature of fish and their midsummer distribution in temperate lakes and streams. Journal of the Fisheries Research Board of Canada 15(4):607-624.

Flath, L.E., and J.S. Diana. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. Transactions of the American Fisheries Society 114:328-337.

Fry, F.E.J. 1951. Some environmental relations of the speckled trout (Salvelinus fontinalis). Report of the Proceedings of the Northeast Atlantic Fisheries Conference, May 1951.

Gordon, J.A., and B.A. Skelton. 1977. Reservoir metalimnion oxygen demands. Journal of the Environmental Engineering Division, ASCE 103:1001-1011.

Gordon, J.A., and W.R. Nicholas. 1977. Effects of impoundments on water quality: observation of several mechanisms of dissolved oxygen depletion. TVA E-EP-77-1.

Haraldstat, O., and B. Jonsson. 1983. Age and sex segregation in habitat utilization by brown trout in a Norwegian Lake. Transactions of the American Fisheries Society 112:27-37.

He, E., and W.A. Wurtzbaugh. Gastric evacuation rates in fish: an empirical model of the effects of temperature and prey size, and an analysis of digestion in piscivorous brown trout. Unpublished manuscript.

Hewett, S.W., and B.L. Johnson. 1987. A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute publication WIS-SG-87-245. Madison, Wisconsin.

Hewett, S.W., and B.L. Johnson. 1992. An upgrade of a generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute publication WIS-SG-92-250. Madison, Wisconsin.

Hutchinson, G.E. 1957. A treatise on limnology, Volume 1. John Wiley and Sons. New York, New York.

Hyslop, E.J. 1980. Stomach contents analysis - a review of methods and their application. Journal of Fish Biology 17:411-419.

Jones, A.R. 1982. The "two-story" rainbow trout fishery at Laurel River Lake, Kentucky. North American Journal of Fish Management 2:132-137.

Jude, D.J., F.J. Tesar, S.F. Deboe, and T.J. Miller. 1987. Diet and selection of major prey species by Lake Michigan salmonines, 1973-1982. Transactions of the American Fisheries Society 116:677-691.

Kirkland, L., and M. Bowling. 1966. Preliminary observations on the establishment of a reservoir trout fishery. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 20:364-374.

Kitchell, J.F., D.J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (_Perca flavescens_) and walleye (_Stizostedion vitreum vitreum_). Journal of the Fisheries Research Board of Canada 34:1922-1935.

Kitchell, J.F., and J.E. Breck. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (_Petromyzon marinus_). Canadian Journal of Fisheries and Aquatic Sciences 37:2169-2174.

Kohler, C.C., J.J. Ney, and A.A. Nigro. 1979. Compact, portable vertical gill net system. The Progressive Fish Culturist 41(1):34-35.

Kohler, C.C., J.J. Ney, and W.E. Kelso. 1986. Filling the void: development of a pelagic fishery and its consequences to littoral fishes in a Virginia mainstream reservoir. Pages 166-177 In G.E. Hall, editor, Reservoir Management Strategies for the Eighties. Southern Division of the American Fisheries Society.

Kramer, D.L. 1987. Dissolved oxygen and fish behavior. Environmental Biology of Fishes 18:81-92.

Love, W.T. 1979. Effects of a high rainfall year on trout habitat in Bull Shoals Reservoir. Proceeding of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 33:331-343.

Merritt, R.W., and K.W. Cummins. 1984. An Introduction to the Aquatic Insects of North America, second edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Moore, C.M. 1988. Food habits, population dynamics, and bioenergetics of four predatory fish species in Smith Mountain Lake, Virginia. Ph.D. dissertation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

Mulford, C.J. 1984. Use of a surgical skin stapler to quickly close incisions in striped bass. North American Journal of Fisheries Management 4:571-573.

Munson, B.H., J.H. McCormick, and H.L. Collins. 1980. Influence of thermal challenge on conditioned feeding forays of juvenile rainbow trout. Transactions of the American Fisheries Society 109:116-121.

Nettles, D.C., J.M. Haynes, R.A. Olson, and J.D. Winter. 1987. Seasonal movements and habitats of brown trout (Salmo trutta) in southcentral Lake Ontario. Journal of Great Lake Research 13(2):168-177.

Ney, J.J. 1990. Trophic economics in fisheries: Assessment of demand-supply relationships between predators and prey. Reviews in Aquatic Sciences 2(1):55-81.

Oliver, J.L., P.L. Hudson, and J.P. Clugston. 1977. Effects of a pumped storage hydroelectric plant on reservoir trout habitat. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 31:449-457.

Pirie, W.R., and W.A. Hubert. 1977. Assumptions in statistical analysis. Transactions of the American Fisheries Society 99(2):440-443.

Rand, P.S., D.J. Stewart, P.W. Seelbach, M.L. Jones, and L.R. Wedge. Modeling steelhead trout population energetics in Lakes Michigan and Ontario. Unpublished manuscript.

Rao, G.M.M. 1968. Oxygen consumption of rainbow trout (*Salmo gairdneri*) in relation to activity and salinity. Canadian Journal of Zoology 46:781-786.

Rao, G.M.M. 1971. Influence of activity and salinity on the weigh-dependent oxygen consumption of the rainbow trout *Salmo gairdneri*. Marine Biology 8:205-212.

Rice, J.A., J.E. Breck, S.M. Bartell, and J.F. Kitchell. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environmental Biology of Fishes 9:263-275.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184.

Spigarelli, S.A., and M.M. Thommes. 1978. Temperature selection by brown trout residing in a thermal discharge area. Pages 33-36 *in* Radiological and Environmental Research Division annual report, January-December 1978. Argonne National Laboratory, ANL-78-65, Part III, Argonne, Illinois.

Spigarelli, S.A., M.M. Thommes, and W. Prepejchal. 1982. Feeding, growth, and fat deposition by brown trout in constant and fluctuating temperatures. Transactions of the American Fisheries Society 111:199-209.

Stables, T.B., and G.L. Thomas. 1992. Acoustic measurement of trout distributions in Spada Lake, Washington using stationary transducers. Journal of Fish Biology 40:191-203.

Stevenson, J.H., and A.H. Hulsey. 1961. Vertical distribution of dissolved oxygen and water temperature in Lake Hamilton with special reference to suitable rainbow trout habitat. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 15:245-255.

Stewart, D.J. 1980. Salmonid predators and their forage base in Lake Michigan: a bioenergetics modeling synthesis. Ph.D. dissertation, University of Wisconsin-Madison, Madison, Wisconsin.

Stewart, D.J., and F.P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: and energetics-modeling synthesis. Transactions of the American Fisheries Society 115:643-661.

Stewart, D.J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-1988. Canadian Journal of Fisheries and Aquatic Sciences 48(5):909-922.

Stewart, D.J., W.D.V. Rottiers, and T.A. Edsall. 1983. An energetics model for lake trout, Salvelinus namaycush: Application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40(6):681-698.

Swenson, W.A., and L.L. Smith. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (Stizostedion vitreum vitreum). Journal of the Fisheries Research Board of Canada 30:1327-1336.

Thorton, K.W., and A.S. Lessem. 1978. A temperature algorithm for modifying biological rates. Transactions of the American Fisheries Society 107(2):284-287.

Van Velson, R.C. 1974. Self-sustaining rainbow trout (Salmo gairdneri) population in McConaughy Reservoir, Nebraska. Transactions of the American Fisheries Society 103:59-64.

Warren, C.E. 1971. Biology and water pollution control. W.B. Saunders Company. Philadelphia, Pennsylvania, USA.

Weatherley, A.H., and H.S. Gill. 1981. Recovery growth following periods of restricted rations and starvation in rainbow trout Salmo gairdneri Richardson. Journal of Fish Biology 18:195-208.

Weatherley, A.H., and H.S. Gill. 1987. The biology of fish growth. Academic Press, London.

Weihs, D. 1973. Optimal fish cruising speed. Nature 245:48-50.

Weithman, A.S., and M.A. Haas. 1984. Effects of dissolved oxygen depletion on the rainbow trout fishery in Lake Taneycomo, Missouri. Transactions of the American Fisheries Society 113:109-124.

Ware, D.M. 1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. Journal of the Fisheries Research Board of Canada 33:33-41.

Wilkins, P. 1965. Doe Creek rainbows. The Tennessee Conservationist 31(4):3-5.

Wilkins, P., L. Kirkland, and A. Hulsey. 1967. The management of trout fisheries in reservoirs having a self-sustaining warm water fishery. Pp. 444-451 in Reservoir Fishery Resources Symposium, Reservoir Committee, Southern Division American Fisheries Society.

Wooton, R.J. 1990. Ecology of teleost fishes. Chapman and Hall, London.

APPENDIX A

COMPONENTS OF THE BIOENERGETICS MODEL

Components of a Bioenergetics Model

The bioenergetics model used to estimate growth of brown and rainbow trout in Lake Moomaw was based on an equation solved for the average member of the population (as in Ney 1990):

$$G = C - R_S - R_A - R_D - F - U \qquad \textbf{(A1)}$$

where G = growth, C = consumption, R_S = standard metabolism, R_A = activity metabolism, R_D = specific dynamic action (heat increment), F = egestion, and U = excretion. Model equations and parameter inputs are discussed in detail in Hewett and Johnson (1992).

Consumption equation

The Wisconsin model determines the daily consumption of a fish (C_D) as a function of both weight and temperature, and as a proportion of the physiological maximum consumption (C_{max}):

$$C_D = C_{\max} \cdot P \cdot r_c \qquad \textbf{(A2)}$$

where C_{max} is the maximum consumption at the optimum temperature, P is the proportion of maximum consumption (range 0-1), and r_c is a temperature dependent scaler of consumption rate.

C_{max} is calculated as an allometric function of weight:

$$C_{\max} = aW^{b} \qquad \textbf{(A3)}$$

where a is the intercept of maximum consumption at optimum temperature, W is the wet weight in grams, and b is the weight dependence exponent of maximum consumption. A value of .239 for a, and -.227 for b was the best fit to data on the maximum daily consumption of brown trout at optimum temperatures (Elliot 1975a). The value of a can be interpreted as the percent of maximum daily ration consumed by a 1 gram brown trout. A value of 23.9 percent is reasonable, and similar to values derived for other salmonids (Hewett and Johnson 1992). Because maximum consumption declines on a specific (g/g) basis as weight increases, b is negative. The weight dependence exponent (-.227) is similar to values derived for other salmonids (Hewett and Johnson 1992).

The model of Thornton and Lessem (1978) was used to describe the temperature dependence of consumption, r_c. This model equation provides a better fit for coldwater species (Hewett and Johnson 1992). The model was fit to the data reported for brown trout feeding on invertebrates (Elliot 1975a). The results described the optimum temperature at 18°C with consumption declining as temperature increased or decreased. Precipitous declines in consumption occurred at 6°C and 22°C, where brown trout consumed 25 and 7.5 percent of optimum temperature C_{max} respectively.

Respiration equation

Standard and activity metabolism were modelled based on an equation developed by Stewart et al. (1983):

$$R = a_2 W^{b_2} \cdot e^{pT} \cdot e^{vU} \qquad \textbf{(A4)}$$

where R = total metabolism, W = wet weight (g), T = temperature experienced by the fish, U = optimal swimming speed, and a_2, b_2, p, v are constants. This model has been used to calculate metabolic costs in a number of salmonid studies (Beauchamp et al. 1989; Stewart and Ibarra 1991; Brodeur et al. 1992; Rand et al. unpublished).

Stewart (1980) derived values for rainbow trout from the work of Rao (1968, 1971), Weihs (1973) and Ware (1975). These values were assumed applicable to reservoir brown trout, and were incorporated into the model used in this study (Table 3).

Specific dynamic action, R_D, was calculated as a constant proportion of consumption. A value of .172 was assigned to R_D, as in most models of energetics for piscivorous fish (Hewett and Johnson 1992).

Egestion equation

Energy lost in egestion (F) is calculated as a function of water temperature and feeding rate, such that:

$$F = a_F \cdot T^{bF} \cdot e^{yF \cdot P\text{-}val} \cdot C \tag{A5}$$

where a_F is the intercept of egestion versus temperature and ration, b_f is the exponent of the temperature dependence of egestion, y_F is the exponent of feeding level (P) dependence of egestion, T is water temperature, and C is consumption. This equation is most appropriate when diet consists of all fish. Values of a_F, b_f, and y_F are taken from Elliot (1976), and represent the standard inputs used in most models of salmonid energetics (Hewett and Johnson 1992).

Excretion equation

The model of excretion (U) follows the basic form of the egestion equation:

$$U = a_U \cdot T^{bU} \cdot e^{yU \cdot P\text{-}val} \cdot (C-F) \qquad \textbf{(A6)}$$

where a_U is the intercept of excretion versus temperature and ration, b_U is the exponent of the temperature dependence of excretion, y_U is the exponent of feeding level (P) dependence of excretion, T is water temperature, C is consumption, and F is egestion. Again, values are from Elliot (1976), and are the standard values used in the modeling of salmonid energetics.

Energy density

Predator energy density was assumed to be constant over the annual cycle. Caloric density of brown trout was calculated as a function of weight, and was approximated by a linear regression developed for coho salmon in Lake Michigan (Stewart and Ibarra 1991):

$$CD = A + BW \tag{A7}$$

where CD is caloric density (cal/g wet weight), A is the intercept, B is the slope, and W is the wet weight (g) of the predator. Values of A and B were calculated as 1377 and .2356 respectively.

Caloric density of the primary prey, alewives, varies seasonally. Stewart and Binkowski (1986) reported the seasonal variation of alewife energy density in Lake Michigan, based on the original data of Flath and Diana (1985). Changes in the energy density of alewives during the simulation period were approximated using this data (Table A1).

Table A1. Caloric density of alewives, as used in the bioenergetics model. Data is from Stewart and Binkowski (1986), based on the original data of Flath and Diana (1985).

Date	Day of Simulation	Caloric content (cal/g wet weight)
June 1	1	1380
July 1	30	1255
August 1	61	1370
September 1	92	1677
October 15	122	2069

VITA

Thomas Marvin Hampton was born in Wise County, Virginia on February 9, 1969. He grew up on the banks of Rumley Creek, near Pound, Virginia. In 1987, Tom graduated from Pound High School, and then continued his education at the Virginia Polytechnic Institute and State University. He earned a B.S. degree in May 1991, graduating Cum Laude in Forestry and Wildlife. In January 1992, Tom became a candidate for an M.S. in Fisheries and Wildlife Sciences at V.P.I.& S.U. He took a position as a District Fisheries Biologist with the Virginia Department of Game and Inland Fisheries in May 1993. Tom currently resides in Farmville, Virginia.

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