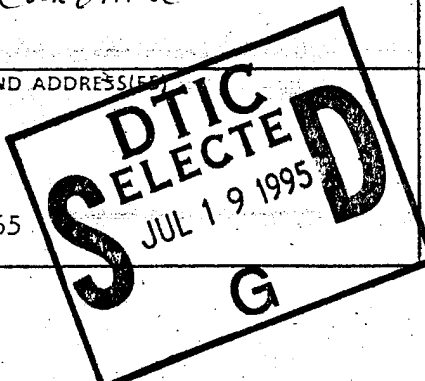


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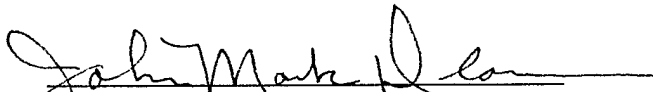
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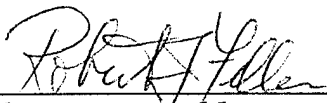
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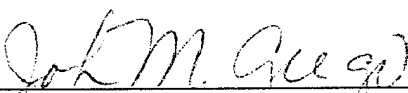
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Table of Contents

	page
List of Figures.....	iii
List of Tables.....	iv
Abstract.....	v
Acknowledgements.....	vi
INTRODUCTION.....	1
MATERIALS AND METHODS.....	10
RESULTS.....	19
DISCUSSION.....	22
CONCLUSIONS.....	33
LITERATURE CITED.....	36
Figures.....	42
Tables.....	58
Appendix 1: Redfin pickerel raw data.....	64

List of Figures

	page
Figure 1: Geographical distribution of <u>Esox americanus</u> complex.....	42
Figure 2: Map of study area in relation to state of South Carolina.....	43
Figure 3: Location of study site in Lee Swamp.....	44
Figure 4: Standard lengths of fish caught per sampling date.....	45
Figure 5: Comparisons of total length and fork length with standard length.....	46
Figure 6: Length-weight relationship for total sample.....	47
Figure 7: Length-weight relationship for fish < 5 cm, 5-10 cm, and > 10 cm.....	48
Figure 8: Length-age relationship.....	51
Figure 9: Data for validation of increment* deposition rate.....	52
Figure 10: Timing of annulus formation.....	53
Figure 11: Distribution of rainfall and hatching of redfin pickerel.....	54
Figure 12: Mean daily air temperature for Sumter, S.C.....	55
Figure 13: Length of fish by hatch date.....	56
Figure 14: Width of first 30 increments by hatch date.....	57

List of Tables

	page
Table 1: Conversion equations for standard length to total length and fork length for redfin pickerel.....	58
Table 2: ANOVA of length-weight regression equations for redfin pickerel.....	59
Table 3: Results from redfin pickerel otolith increment validation experiment.....	60
Table 4: ANOVA of redfin pickerel otolith increment validation experiment.....	61
Table 5: T-test of growth rates of early- and late-spawned redfin pickerel.....	62
Table 6: ANOVA of temperature and rainfall as predictors for spawning.....	63

Abstract

The reproductive strategy of the redbfin pickerel (Esox americanus americanus) in a blackwater system in Sumter County, South Carolina was studied using daily aging techniques derived from otolith analysis. The presence of biannual spawning, a significantly different strategy from that found in the rest of the genus, was expected. One hundred thirty-seven fish were sampled from 15 March to 27 May, 1994 using a backpack electroshocker. Once the presence of daily increments in the sagittal otoliths was confirmed (p-value = 0.0001), daily ages were assigned to each fish based upon the sectioned sagitta. Ages were subtracted from capture dated for each fish to yield a distribution of hatching. This distribution was unimodal, but protracted (from 21 December to 7 March). Fish were divided into two groups based upon batch date, with the date of the lowest temperature of the season used to divide them. Average growth rates of these two groups, as measured by the width of otolith increments, were different (p-value = 0.05). Finally, daily mean temperature and daily rainfall were used to predict spawning activity through analysis of variance. Temperature and cumulative rainfall for 8 - 14 days prior to spawning were significantly correlated with spawning (p-values = 0.0001 and 0.0087, respectively).

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and Bomber's games, I'd still be wandering somewhere on the fourth floor of the library.

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Introduction

During the early 1900's, there was a large increase in interest in the freshwater fishes of the United States. For many years, ichthyologists performed research aimed at describing new species, defining taxonomic relationships, and determining the ranges of species of fish (Heins and Matthews, 1987). Around the same time, the science of ecology was blossoming, and there was a great deal of emphasis placed upon understanding the relationships of organisms and their environments (Brewer, 1988). However, even though fish as a group are well suited for ecological studies due to their great deal of variability and relative abundance, the fields of ichthyology and ecology did not truly converge until about the last twenty years. Only in the recent past have a significant number of studies been performed utilizing freshwater stream fishes to demonstrate more general ecological principles (Heins and Matthews, 1987; Mefee and Sheldon, 1988).

One reason stream fishes are such excellent subjects for ecological and evolutionary studies is that lotic systems, by their very nature, are highly variable. Unlike the ocean environment and even large bodies of freshwater, which change slowly, streams are subject to isolation and dramatic and often very rapid disturbances resulting from flooding, drought, and alteration by man. The effects of these disturbances on the fish communities are unclear. Some studies

indicate that the fish assemblages remain relatively constant (Schlosser, 1987), while others suggest that the population size of a given species can change dramatically from year to year (Brim, 1991). This suggests that species of fish which inhabit small streams have adapted to their unpredictable environment by either being resilient enough to survive a wide range of conditions, or by having the ability to rapidly recolonize an area after disturbance.

The rapid changes in water level that occur seasonally in most small stream systems on the east coast of the U.S. result in large areas of shallow floodplains that are characterized by low flow rates, silt substrates, high productivity from the influx of nutrients (Sheaffer and Nickson, 1986), abundant small food particles, diverse habitat (Copp and Penaz, 1988) and large amounts of emergent and submergent vegetation and structure. It is clear that floodplain habitat is vital for the success of many fish species, for spawning habitat and as nursery areas for young fish (Holland, 1986; Sheaffer and Nickson, 1986; Copp and Penaz, 1988; Brim, 1991). In many species, both the quantity and quality of nursery areas can have a large influence on growth and survival of young fish, and hence the long term health of the population (Holland, 1986). Floodplains provide larval and juvenile fish with protection from current, large amounts of available food, and a haven from predation. In order to take advantage of this habitat, many fish have evolved mechanisms which allow them to exploit

these areas (Welcomme, 1979).

Studies have shown that some species of fish are very dependent upon flooded vegetation for spawning habitat. One group of fish that requires inundated vegetation for successful spawning is the family Esocidae. The northern pike (Esox lucius) is probably one of the most well known and widely studied fish in the northern hemisphere (Doyon, et al., 1988). It is one of the few commercially and recreationally important freshwater fish with a circumpolar distribution, being found in substantial numbers in North America, Europe, and Asia. As a result, the literature base present on this species is enormous, and most aspects of its life history have been studied and recorded (see Carlander, 1969 for review). Likewise, the other large esocids (the muskellunge, the tiger musky, and the chain pickerel) have been studied extensively, because they are important sport trophy fish in the eastern United States, and have been introduced elsewhere (Crossman, 1978).

The importance of flooded vegetation for spawning success for esocids has been well documented. Year classes of northern pike in Bull Club Lake, Minnesota, were strongest in years with high spring water levels (Johnson, 1956). In Lake Oahe, South Dakota, there were several very strong year classes of northern pike soon after impoundment of the Missouri River in 1958, but success was poor once fluctuations in water level ceased and the fish became rare by 1970 (Nelson, 1978). Hassler (1970) reported that in pike in

South Dakota, year class strength was correlated with water level in two reservoirs. He concluded that the success of the spawn was more related to the amount of flooded vegetation present than to the water level itself. In Manitoba, Canada, the abundance of young of the year pike was 4-10 times higher the first year after impoundment of the lake than in the following three years, indicating that flooded terrestrial vegetation only had an effect for the first year (Bodaly and Lesack, 1984). Fabricius and Gustafson (1958) found that in laboratory experiments, the most important factors in stimulating spawning in pike were temperature, daily light intensity, and the presence of suitable vegetation (in Franklin and Smith, 1963).

While these larger members of the pike family are usually found in large bodies of freshwater, the smallest members of the genus, the redbfin pickerel (E. americanus americanus) and the grass pickerel (E. a. vermiculatus) are commonly found in small streams. The redbfin pickerel is distributed along the coastal plain east of the Appalachian Mountains from the St. Lawrence River south to Florida (Figure 1). In Alabama, western Georgia, and Florida, it intergrades with the grass pickerel, which is found west of the Appalachians in the Mississippi River drainage (Crossman, 1978). The redbfin is usually found in sluggish, backwater streams, and prefers leafy, silty habitat with slow flow and submerged vegetation (Mefee and Sheldon, 1988). It reportedly reaches sexual maturity by about age two, and has a

life expectancy of seven to eight years (Crossman, 1962).

After a few weeks of age, the pickerel is a piscivore, sometimes being found with prey in the stomach that are over 50% of the fish's total length (pers. obs.). Unlike the related species, northern pike, relatively little has been published on the ecology of the redfin pickerel, probably because it is not an important commercial or sport fish (Crossman, 1978). It, and the grass pickerel, have been used in several comparative physiological and anatomical studies (Hoyle, et al., 1986; Hoyle and Keast, 1988; Lee and Glimcher, 1991). The redfin pickerel can be a voracious predator, and despite its small size, likely exerts a great deal of influence on prey fish populations in these systems (Buss et al., 1978)

When the redfin and grass pickerel do appear in the literature, it is often in relation to fish usage of floodplain habitat, and the importance of this habitat to the redfin and grass pickerels is readily apparent. In a remarkably large number of studies published on floodplain usage in the central and eastern U.S., one of the most abundant fish found is the redfin or grass pickerel (for example, Angermeier, 1978; Finger and Stewart, 1978; Ross et al., 1978; Ross and Baker, 1983; Kwak, 1988; Mefee and Sheldon, 1988; Brim, 1991). Kwak (1988) found that in an Illinois river system, the most common species of fish found travelling between the main stream channel and both temporary and permanent floodplains was the grass pickerel. The

redfin and grass pickerels are unique among esocids in that they are the most southerly distributed species in the group, and are the only esocids which have adapted primarily to life in small, shallow, stream systems, instead of larger lakes and reservoirs. They also are exceptional in that the females of this complex carry eggs in three different developmental states in the gravid ovaries, instead of only two (Crossman, 1962). Finally, there is some evidence that both the redfin and grass pickerels can spawn over a long time period, from fall to early spring. Lagler and Hubbs (1943) reported the presence of small grass pickerel in August in Michigan, which they believed were spawned in the fall. In addition, Brim (1991) reported the presence of larval redfin pickerel on a South Carolina floodplain in October 1990 following extensive flooding from Tropical Storm Klaus. This behavior is in stark contrast to the other members of the pike family, in which spawning generally takes place over a much shorter time scale, seldom exceeding one to two weeks (Crossman, 1962).

These observations suggest that the Esox americanus complex has developed a different life history strategy than the larger members of the pike family, perhaps as a response to the highly variable nature of the stream systems they inhabit. By maintaining eggs in three distinct developmental states in the ovaries, the redfin and grass pickerels can take advantage of unpredictable flooding events that temporarily provide large amounts of ideal spawning habitat,

thus permitting a biannual spawning strategy that maximizes the chance that a successful year class will be produced. The overall goal of this study is to investigate this life history strategy in the redbfin pickerel. To do so, however, requires an accurate aging technique for the fish which will allow for determination of the effects of short term disturbances in the environment.

In the past, all the research done on the aging of esocids has focused upon the use of scales and the cleithera (Harrison and Hadley, 1983; Casselman, 1974; Diana, 1983). While these methods are common in fisheries science and techniques are well established, they have the disadvantage of only providing annual age estimates, and differences in growth can make interpretation of scale annuli difficult (Mann and Beaumont, 1990). This is satisfactory for studying the adult population dynamics (which is where the commercial importance of these species lies), but it does not allow detailed analysis of age and growth of larval and juvenile fish. One way to examine the timing of spawning, then, is by tracking the gonadal state of the adults over the course of a year and monitoring the site for the presence of larval fish. This is a time consuming and expensive undertaking.

Another way to perform this type of analysis is by tracking the age of juvenile fish. Fortunately, there are methods available for determining the daily age of a fish. In 1971, Pannella published a paper describing the presence of possibly daily growth increments in the otoliths of fish.

This discovery opened up new frontiers in fisheries science. The age and growth rates of larval and juvenile fish can be determined, and the importance of environmental conditions to the survival of these young fish can be studied. This allows researchers to then explore factors affecting recruitment to the adult population. The daily deposition of increments in the otoliths provides a permanent record of information on hatching and other major events in the fish's life, thus eliminating the need for long term sampling.

Since Pannella's paper was published, the number of studies utilizing fish otoliths has grown exponentially (Jones, 1992). The otoliths can supply much more than just age information. The relationship between somatic and otolith growth can be tested, allowing backcalculation of growth rates and calculation of length-at-age data. In addition, timing of significant life history events and recruitment can be determined. By estimating the age of a fish in days, the determination of the spawning date is a simple calculation. Once this information is known, identification of spawning cohorts can be made with comparisons of cohort growth rates and survival. Finally, when the information supplied by daily increments is combined with that provided by annular marks, the timing of annual events in the fish can be determined.

The specific objectives of this project were to test the hypotheses that: 1) the otoliths of redbfin pickerel contain a record of daily growth; 2) spawning cohorts can be

identified through otolith aging; 3) the growth rates of different cohorts are the same; and 4) climatic events are uncorrelated with spawning events.

Materials and Methods

Study Site:

Fish were collected from floodplain habitat located in Lee Swamp, just upstream from its junction with Rocky Bluff Swamp in Sumter County, South Carolina. Rocky Bluff Swamp drains into the Black River, which in turn flows southeast to empty into Winyah Bay in Georgetown, S.C. (Figure 2). The site is located north of the city of Sumter, where State Route 92 crosses Lee Swamp (Figure 3). The drainage is characterized as a blackwater stream, with slow moving water, low dissolved oxygen, low pH, high levels of humic and tannic acid, and relatively low visibility. The location contains a deep main stream channel, bordered by extensive floodplain habitat including large amounts of emergent aquatic vegetation and structure, including cattails, tree stumps, grasses, and submerged aquatic vegetation.

Water level and flow are influenced by a small impoundment upstream of the site (Ardis Pond) (Figure 3), and are buffered by the presence of two beaver dams between the floodplain and main channel. The dams cause the floodplain to maintain a relatively constant state of inundation, for outflow is maintained until the stream below the dam floods to the top of the dam. However, low flow conditions can still result in dramatic reduction in the area of these floodplains. The flow steadily decreased over the course of the ten week sampling period, causing some parts of the floodplain system to dry up entirely, but it appears that at

least some of the floodplain remains inundated throughout the year.

The site yielded a large variety of swamp species besides the redbfin pickerel, including bowfin, warmouth, mosquitofish, eels, mudminnows, various sunfish, and shiners, as well as snakes, tadpoles, snapping turtles, salamanders, and crayfish.

Sampling:

Sampling was conducted weekly for ten weeks, from 15 March, 1994 to 27 May, 1994. Esox americanus americanus specimens were collected from the floodplain site using a backpack electroshocker supplied by the United States Forest Service. A combination of alternating current (AC) and pulsed direct current (DC) was used, depending upon water depth and conditions. DC is less harmful to the fish and less dangerous to work with, but its range is limited in deep water or when the conductivity is low. AC provides a larger stun field, but generally causes more harm to the fish (Reynolds, 1983; Zalewski and Cowx, 1990). In addition, AC caused immediate flaccid paralysis in the fish, while DC caused spastic paralysis and galvanotaxis, thus making fish easier to locate in low visibility water and areas with large amounts of vegetation (Reynolds, 1983).

The AC was maintained at approximately 400-900 volts, while the DC was provided at approximately 280-630 volts. Stunned fish were removed from the water using insulated dipnets (mesh size = 0.5 cm) and transferred to a bucket in

the field. Fish were subsequently moved to a 48-quart insulated cooler equipped with an airpump for transport to the laboratory.

In the lab, fish which had successfully recovered from the effects of electroshocking were moved to aquaria (at 21°C and 12-hour photoperiod) to be used for the daily increment validation experiment. Remaining fish were sacrificed and frozen for later analysis.

Sample Processing:

Fish were thawed under running water, and measurements of total length (TL), fork length (FL), standard length (SL), head length and snout length were taken to the nearest millimeter. SL was used for all analyses, but conversions from FL and TL are provided, as these measurements are used in other studies on this species (Crossman, 1962). Measurements of head and snout length were used to help in the differentiation of redbfin pickerel and chain pickerel, which are sympatric in these systems and look very similar in juvenile form. Stomach contents were removed and wet weight of the fish was taken to the nearest 0.01 gram, using a Sartorius Model 2354 balance.

Otolith Removal and Preparation:

Both sagittal otoliths were removed by making a longitudinal incision along the top of the head, exposing the brain. When the brain was removed, the sagittal otoliths were visible in the vestibular apparatus, and removed using fine forceps. Otoliths were then cleaned of any adhering

tissue and stored in covered tissue culture trays.

After drying for 24 hours at room temperature, otoliths were weighed using a microbalance, Mettler Model H54AR, to the nearest 0.01 milligram. Both otoliths were weighed, when possible, and their average weight was used in the analyses. Both otoliths were then embedded in low viscosity embedding medium (Embed 812) in accordance with Secor, et al. (1992). Once cured, the block of embedding medium was cut on a Buehler Isomet low-speed saw to remove excess material and mounted on a glass microscope slide with thermo-plastic cement in preparation for sectioning. Left sagitta were sectioned in the transverse plane using 220, 400, and 600 grit wet/dry sandpaper and 0.3 micron polishing alumina on Alpha B polishing cloth to a thin section (Secor, et al. 1992). The right sagitta were maintained for examination of annular marks and measurements of otolith length.

Otolith Analysis:

Three sets of measurements were made on the sectioned otoliths for each fish under 400X magnification on an Olympus BH2 light microscope: number of daily increments, total width of the first 30 increments, and number of increments outside the opaque growth zone (under transmitted light). Two blind sets of counts were made by one individual and averaged to yield the daily age estimates. Individual mean growth rates were calculated by dividing the total length of each fish by its age in days. Otolith lengths were measured from the postrostrum to the rostrum of

the right otoliths, using an ocular micrometer under a magnification of 40x.

The number of visible daily increments was used to assign an age to each fish, and when subtracted from the date of sampling (or date of sacrifice for experimental fish) yield an estimated hatch date. The width of the first 30 increments was used as a measure of somatic growth during the first 30 days of life for each fish, assuming a correlation between otolith and somatic growth exists. The number of increments outside the opaque zone was used to estimate at what time of year the annular mark is deposited. When subtracted from sample date (or sacrifice date), this gave an estimate of the timing of otolith growth zone formation.

Preparations of sectioned otoliths were made for scanning electron microscopy (SEM). Thin-sectioned otoliths were etched using 0.01%-2.0% acetic acid for 5 to 30 seconds to provide surface relief. Otoliths were then sputter coated with gold for 260 seconds, grounded, and examined under SEM at 25 mV.

Validation Experiment:

A laboratory experiment to validate the deposition rate of increments in the otoliths was conducted. Twenty-four fish (young of the year) of roughly equal size (SL = 6.0 - 8.5 cm) were collected on 27 May, 1994, returned to the laboratory, and allowed to recover from the effects of electroshocking and transport. Fish were maintained in aquaria in the laboratory at 21 C and 12-hour light, 12-hour

dark photoperiod, and observed for several days for overall health (general behavior, presence of disease, and willingness to eat). Fish were fed live guppies and/or mosquitofish.

Following this period of acclimation and observation, eleven healthy fish were marked using a solution of alizarin complexone (50 ppm, by mass). Alizarin complexone, a compound absorbed strongly by calcified material, is incorporated into the otoliths and fluoresces under ultraviolet light. Once fish were placed into the alizarin bath, the temperature was lowered to 15 C over a period of several hours.

After a period of 24 hours in the alizarin solution, eight fish were randomly assigned and placed into individual 6 liter plastic containers (35x48x17 cm) fitted with airstones and clear plexiglass covers. These fish were kept at 15 C and 12 hour light, 12 hour dark photoperiod in a climate controlled growth chamber. The remaining three fish were returned to the lab and maintained in a common aquarium at 21 C. Fish were maintained for a period of twenty-one days and fed daily ad libitum with live feeder guppies (obtained commercially from an aquarium supply shop). Each day, the number of live prey fish remaining in each container, the number of dead prey remaining, and the number of new prey fish added were noted. Seven fish that died during the course of the experiment were labelled and frozen for later analysis.

After the three week period, the remaining four fish were sacrificed, and all fish were processed in the same fashion as the field samples. Once the otoliths were prepared, they were observed for the presence of the alizarin mark under ultraviolet light, and increments formed after the mark were counted under 500x magnification under a combination of UV and white light.

Data Analysis:

All statistical analyses were performed using the Statistical Analysis System (SAS, 1985). Length-weight regression was performed on the total pooled sample, as well as on three separate size classes: standard length (SL) < 5 cm, 5 cm - 10 cm, and > 10 cm. Regression was not conducted separately based upon sex, since sexual dimorphism is not apparent until about age V (Crossman, 1962), and no fish large enough to be that old were captured in this study.

Length-frequency histograms were constructed for each two week sampling period. The mean growth rate for the population was estimated by dividing the difference in average length by the number of days between sampling. Frequency histograms were built for the number of fish hatched, the amount of rainfall, and the number of fish forming the annulus, both in daily and 5-day groups. For the validation experiment, the number of visible daily increments was plotted against the number of days the fish were alive, and regression was run to determine the slope of the line (number of increments formed per day).

An ANOVA was used to determine if the slopes of the length-weight regression lines were significantly different for each of the three size classes, and to test if the slope of the line relating number of days and daily increments was significantly different from unity. A t-test was used to test whether the mean lengths of fish from the two spawning cohorts were significantly different and if the mean widths of the first 30 increments (i.e. the growth rates in the first 30 days) were different.

Rainfall and temperature data for Sumter, S.C. were provided by the Climatology Division of the South Carolina Water Resources Commission. Daily rainfall and mean daily temperature for the period from 1 January, 1993 to 8 March, 1994 were used as predictor variables for number of fish hatched per day during the same period. The use of mean air temperature as an estimate of water temperature has been validated (McCombie, 1959). A general linear model was fitted to the data, using a 20-day shift in the hatch data to transform hatch dates into spawning dates (corresponding to the 12-14 days for eggs to hatch (Crossman, 1962) and an estimated 6-7 days for flooding to trigger fish to begin spawning). Five independent variables were tested: day, temperature, and total rainfall from each of the three weeks prior to spawning. Alpha values used to test for significance were 0.05.

Results

Population Data:

A total of 137 individuals were captured at the Lee Swamp site over the period from 15 March, 1994 to 27 May, 1994. The catch per unit effort generally increased over the course of the study (Figure 4). The highest catch rate occurred on 27 May, 1994, when 39 individuals were captured in one hour shocking time. Individuals ranged in size from 2.1 - 21.2 cm SL, and from 0.16 - 124.96 g WW.

The regressions between SL and TL and between SL and FL were significant (Figure 5). The equations for converting between the different length measurements are provided (Table 1) to allow comparisons with other studies.

The length-weight regression based upon the entire sample is not adequately described by the equation:

$$\log (WW) = -0.789 + 1.73 (SL) \quad r^2 = 0.894$$

(Figure 6). When the total sample is divided into the size classes < 5.0 cm, 5.0 - 10.0 cm, and >10.0 cm, and the regression equations calculated (Figure 7), analysis of variance revealed that the slopes of all these lines are significantly different at alpha = 0.05 (Table 2).

The modes of the length-frequency histograms show that the average size of fish captured in each sample increased over the 10 week sampling period, from an average of 5.825 cm on 19 March, to 8.96 cm on 27 May (Figure 4).

Otolith-Fish Relationships:

The average weight of the pair of sagittal otoliths

from a sample of 128 fish was significantly correlated to the fish WW, as described by the equation:

$$\log (\text{OW}) = -3.639 + 0.700 \log (\text{WW}) \quad r^2 = 0.903$$

The mean discrepancy between the two counts of daily age was 9.03 increments, or 6.87 % for each fish. When daily age estimates were assigned to 116 fish, there was a significant relationship between both age and standard length (Figure 8):

$$\log (\text{age}) = 1.599 + 0.055 (\text{SL}) \quad r^2 = 0.813$$

and age and otolith weight:

$$\text{age} = 61.200 + 67083.017 (\text{OW}) \quad r^2 = 0.931$$

Validation Experiment:

The validation experiment lasted 21 days, although fish died at various points throughout the experiment: 0 days (during marking), 4 days, 8 days, 12 days, 16 days (two fish), 17 days, and 21 days (four fish) (Table 3). Prepared otoliths from validation fish displayed a distinct alizarin mark which was apparent in all fish except the one which died during marking. In nine of the eleven fish marked, there was significant growth of the otolith outside the alizarin mark and the number of visible increments could be counted under the light microscope (Table 3). The regression equation for number of days alive vs. number of increments counted is:

$$\text{increments} = -7.80 + 1.418 (\text{days}) \quad r^2 = .697$$

(Figure 9). Analysis showed that the slope of this line is significantly different from zero, but not significantly

different from 1 at $\alpha = 0.05$ (Table 4).

The date of annulus formation for 104 fish ranged from 15 October to 10 April, although over 97% of the fish transitioned to summer growth after 20 February. The mode of the distribution was 15 March (Figure 10).

Spawning Cohorts:

Once daily age estimates were subtracted from sampling date (or sacrifice date), a distribution of hatch dates for 116 fish was obtained (Figure 11). The hatch dates ranged from 21 December, 1992 to 7 March 1994. Of the young of the year (YOY) fish from the '93-'94 season, only 33 fish were hatched before 17 January, 1994 (and none earlier than 25 November, 1993). The maximum number of fish hatched for a single day was 5 fish on 5 February, 1994. The distribution was not bimodal in nature. Since there was no clear distinction between spawning cohorts, a hatch date of 17 January, 1994 was used to delineate between early- and late-spawned fish for the purpose of comparison, since this date represents the minimum temperature during the reproductive season (Figure 12). Thus, fish spawned before this date were generally exposed to falling temperatures, while those spawned after that date experienced rising temperatures during early growth.

The average length for YOY hatched prior to 17 January was 8.7 cm (s.d. = 2.46 cm), while for YOY hatched on 17 January or later, the mean length was 6.26 cm (s.d. = 1.90 cm) (Figure 13). These means are significantly different at

alpha = 0.05.

Growth Rates:

The overall population growth rate, measured by the increase in average length for each sample date, is 4.304 mm/day. The average growth for individual fish, as calculated from length and age data, is 0.699 mm/day, (range = 0.395 - 1.011 mm/day).

A graph of increment width vs. hatch date is shown in Figure 14. The mean width of the first 30 increments for YOY spawned before 17 January, 1994 is 0.118 mm (s.d. = 0.016 mm). For fish spawned after 17 January, the average width of the first 30 increments is 0.125 mm (s.d. = 0.017 mm). These width measurements are different at alpha = 0.05 (p-value = 0.05, Table 5).

Rainfall-Spawning Correlation:

A graph of rainfall and number of fish hatched per 5-day block is shown in Figure 11. Based upon ANOVA, day is a significant predictor for spawning ($p < 0.0001$), as is the temperature ($p < 0.0001$) and the total rainfall from 8-14 days prior to spawning ($p = 0.0087$) at alpha = 0.05. Other variables are not significant (Table 6).

Discussion

Population data:

For a fish that is supposedly very abundant in South Carolina blackwater streams, the redbfin pickerel proved to be elusive and a worthy adversary for our sampling crew. Sampling in sites where large numbers of fish had been captured in previous years was unproductive. It was not until after about six weeks of futile sampling in sites on Church Branch and McGirts Creek (Figure 3) that the Lee Swamp site, with its relative abundance of pickerel, was discovered.

The increase in capture rates for pickerel in the site over the course of the study was remarkable. According to the age estimates, the spawning activity had ended by the time the sampling started. Thus, all fish that were captured during the latter stages of the survey should have been present on the first sampling date. Probably the most important factor resulting in the high capture rates on the final sampling date was that the water level had dropped at the site, causing about two-thirds of the site to dry up. At this point, fish that had not managed to make their way to the main channel of the stream were concentrated in the few remaining pools of water, thus increasing density and making capture much easier. In addition, a change in the water conditions might have played a role. While the physical parameters at the site were not monitored during the study, fluctuations in water temperature, pH, and conductivity could have affected the activity of the fish as well as

the effectiveness of the backpack shocker, causing a change in the number of fish captured over time.

Another possible explanation is experience in using the equipment. During the early part of the study, it was difficult to form an adequate search image which would allow for rapid identification of redbfin pickerel. The enormous number of crayfish in the site was a hinderance in locating fish, since every time the shocker was activated, the flurry of activity from the crayfish tended to distract the sampling crew from finding fish. During the early sampling dates, the water conditions were such that AC was used for all the sampling. One disadvantage of AC is that fish are paralyzed instantly, and thus are not easily visible. As the season progressed, the DC became more effective, and fish were therefore easier to locate and capture.

The range of sample sizes found in this study was slightly smaller than that found in other studies on this species. Crossman (1962) found adult fish up to 28.5 cm (fork length), to which he assigned an age of VI years. Since samples for this study were all collected using the backpack electroshocker, only relatively shallow habitat was sampled (i.e. 1.5 m in depth or less). In northern pike, the adults leave the spawning grounds shortly after eggs are laid (Franklin and Smith, 1963). Since the spawn was mostly complete by the time sampling started, it is likely that adult fish had returned to the deeper water of the main stream channel and vacated the floodplain, thus explaining

the lack of very large fish in the sample.

By comparing the length-frequency distributions over the course of the study, one can see an increase in the average size of the fish captured. Although in previous studies, a two month time span was too short to adequately show length progression (Crossman, 1962), there is an increase in average length over the ten week time frame. The estimated overall population growth rate over this time period of 4.304 mm/day is probably an overestimate, due to the relatively small numbers captured on several of the sampling dates. Crossman (1962) reports a growth rate of 20-30 mm per month for the first two to three months of life for this fish in North Carolina, which corresponds to the individual growth rates of ~ 1 mm/day based upon the length-age relationships found in this study.

The length-weight data for the fish in this study was unusual in that instead of generating a straight line when graphed on a semilogarithmic scale, the curve was convex (Figure 6). Upon closer examination, there appeared to be three groupings within this curve, each of which appeared linear (Figure 7). The regression was then performed individually within these three groups, and a linear relationship was indeed discovered. Thus, it appears that the length-weight relationship changes during different life history stages of the fish, with the increase in weight per unit length being higher when the fish is very young.

Otolith-Fish Relationships:

The correlations between somatic and otolith measurements are significant in all cases. This means that general predictions can be made about the otolith size and age of the fish based upon measurements that can be made relatively easily, even in the field, and without sacrificing the fish. This will allow for more rapid estimations of population structure in the field, and continued sampling with marked fish can give researchers an idea about the relative abundance of year classes, the survival of different cohorts of fish over time, the population size, and the degree to which these fish move about their habitat and migrate to others.

Validation Experiment:

With the exception of one fish, the regression of number of days the fish were maintained and the number of visible increments counted suggests that increments are formed at the rate of one increment per day (Figure 9). The fact that the intercept term in the equation is negative indicates that there was some lag time between when the marking took place and when the fish started to deposit recognizable increments. This could be caused by stress to the fish, from handling, from the marking itself, from the simultaneous change in temperature, or some combination of these factors. This then can be perceived as a delay in the formation of the increments. It is more likely that the increments are actually deposited, but at such narrow intervals that they could not be discerned using a light microscope,

with which increments < 2 micrometers in width cannot be resolved.

A remarkable finding in this experiment was the individual that laid down almost two increments per day. In looking at the amount of food eaten, it appears that this fish never received a maximum daily ration. On most days, it would eat as many fish as were available to it, even eating up to six guppies before the cover could be replaced on its container (which is as much as most of the other fish ate each day). Other studies have shown that increments are formed at more than daily rates under certain conditions. Fast-growing pink salmon formed increments significantly more often than once per day during their marine residency, and the subdaily increments were indistinguishable from true daily marks (Volk, et al., in press). Campana (1983) found that in steelhead trout, fish fed three times per day formed more subdaily increments than fish fed daily, but claimed that the true daily growth zones were still discernable.

By using live food in this study, the pickerel could feed more than once per day, since prey uneaten in the morning would still be available in the afternoon. If this is the case, this data suggests that feeding period may have an effect on the formation of increments. There is a need for a more intensive validation experiment, utilizing a larger number of fish, for a longer period, and comparing different feeding regimes. In addition, validation of fish in the field would be beneficial, since the use of otoliths is most

common for making inferences about wild fish populations, and growth rates in the laboratory may not accurately reflect conditions in the wild.

Spawning Cohorts:

The estimated hatch dates of young of the year fish ranged from 25 November, 1993 to 7 March, 1994 (Figure 11). For this group of fish, only 33 fish were hatched before 17 Jan 1994, indicating that the fall spawning cohort in this population for this year was relatively unimportant. It is possible that in fact there is not biannual spawning in the redfin pickerel, but rather only a protracted reproductive season, which could be explained as an artifact of the mild climate in this region. This explanation was offered by Crossman (1962), for he found that spawning lasted up to one month in North Carolina. However, the fact that grass pickerel were found to reproduce in the fall in Michigan (Lagler and Hubbs, 1943) tends to invalidate this argument. If reproduction in the fall was only a result of mild climate then one would not expect to see the same phenomenon near the northern part of the fish's range.

Another reason for the apparent lack of a fall cohort is that South Carolina experienced drought conditions throughout the summer and early fall of 1993 (Figure 11). Although the site was not monitored during this period, it is reasonable to believe that the water level was extremely low, since during April and May of 1994, the water level in this site dropped so far that about two-thirds of the flood-

plain dried up entirely. Thus, the amount of flooded vegetation was probably low during the fall, so fish may have reserved their spawning for the spring when water levels, and amount of spawning habitat, were higher.

The significant difference in standard length for the YOY fish indicate that the hatchdate of this species can be roughly estimated based upon its length and the time of capture (Figure 13). This will enable more rapid assessment of relative abundance of cohorts in the field.

Growth Rates:

The analysis of growth rates indicate that there is a difference in the growth rates between the early- and late-spawned fish, with late-spawned fish growing more rapidly (Table 5). The most likely explanation for this is that fish spawned later in the year grow in an environment with rising temperature, while fish spawned earlier in the season faced at least some period of falling temperatures. However, the difference in the width of the first 30 increments is only marginally significant at $\alpha = 0.05$, and the large variation within the two groups suggest that care should be taken when interpreting this result. The amount of variation in the two groups (Figure 14) may mean several things. First, the variation in growth rate from individual to individual might be very high. This could be caused by inherent genetic differences or maternal effects resulting from overall condition of the mother during the time of spawning.

The patchy distribution of food across the sample site may mean that adults which dominate the territory with the highest prey density will produce young that benefit from that habitat during their early growth. This hypothesis assumes that cannibalism is relatively unimportant. While cases of cannibalism were not uncommon with the high fish densities in the laboratory, studies indicate that in natural populations, cannibalism is generally low. For northern pike, cannibalism was recorded at 1.7 % (Franklin and Smith, 1963), and in the redfin pickerel, Crossman (1962) reported only six cases of cannibalism in 237 fish, or about 2.5 %. The fact that adults move off the spawning grounds shortly after releasing their gametes (Franklin and Smith, 1963) may serve to limit the amount of cannibalism that takes place.

In addition, the variation in growth rates may be a result of the technique used to measure this rate. There are several sources of error in this procedure, which may result in not yielding enough power to resolve differences in the actual growth rates. First, the most difficult part of the otolith to read and count is the area around the core (i.e. the early growth of the fish). Therefore, what are considered the first 30 increments may not in fact represent the first 30 days of growth. The timing of yolk sac resorption for larval fish could not be determined in this study, so it was impossible to determine at what time feeding (and growth) became limited by the environment. Secondly, there is inherent measuring error in using the ocular micrometer

to perform measurements. Finally, the exact plane in which the otolith is polished can have an effect on the distance actually measured. For an otolith which is polished in a plane a few degrees different from the rest of the samples, the measurement may not be as accurate. When these factors are considered together, the overall variance may preclude distinguishing small differences in growth.

The use of scanning electron microscopy (SEM) might make this process easier. SEM avoids problems such as artifacts produced by the diffraction of light in the light microscope, as well as allowing higher magnifications and better resolution. However, SEM work is time consuming and expensive (pers. obs.). SEM was attempted to help verify the counts made using light microscopy in this study, but no preparations were produced which yielded less ambiguous information. The process requires trial and error to determine the proper decalcifier and pH to use, the correct amount of etching time, and an acceptable degree of sputter coating with gold. A failure in any of these steps will result in a preparation that provided no contrast and hence no useful information about the otolith. While SEM can be used to supplement light microscopy work and reduce the uncertainty in making counts and measurements, the effort required to obtain this information must be taken into account.

Rainfall-Spawning Correlation:

One of the major hypotheses tested in this study was

that the redbfin pickerel has adapted to its highly variable environment by evolving a life history strategy which allows it to spawn whenever the conditions are most favorable and thus maximize the chances of successful reproduction. If this is truly the case, and one also assumes that the conditions which increase the chance of survival of the larvae are similar to those shown to be important to other esocids, then it should be possible to predict when spawning will occur based upon the climatic conditions. To this end, a regression was performed to test the ability to predict spawning activity through the use of temperature and rainfall data (Table 6).

The fact that temperature is a significant predictor is not surprising. Several studies have indicated that temperature is the trigger for spawning of many species, including other esocids (Hassler, 1970; Craig and Kipling, 1982; Treasurer, 1990). In fact, even in the sparse literature on the redbfin pickerel, it is assumed that temperature is the dominant factor in stimulating reproduction (Crossman, 1962). The fact that the rainfall prior to the spawning date is also a significant predictor indicates that the amount of flooded vegetation is another important factor in reproduction. In many stream systems, there is a lag time between rainfall events and inundation of the floodplains. This seems to be supported by the fact that it is only the second week before spawning that is significant in predicting spawning activity. By running the model repeat-

edly with differing lag times for the delay between rainfall and hatching (the period for fish response time to inundation and for hatching time for the eggs), the best fit was found at 20 days. This indicates that there is a response time for the fish of about 6-8 days, with the incubation time of the eggs making up the rest of this lag period.

There are probably other important factors that influence such a complicated physiological process as reproduction on both the population and individual level. A linear model may not be sophisticated enough to deal with all of these variables and their various levels of impact. The r -squared for this regression was only 0.39, which is not generally considered very significant. However, given the complexity of the system being modeled and the relative simplicity of a linear regression, I think it is reasonable to conclude that the important factors, as indicated by the model, can serve at least as rough predictors of reproductive activity in this species.

Conclusions

Small streams, by their very nature, are highly variable. Environmental and climatic events, such as floods and droughts, and human alterations, like impoundment, development, and pollution, can have sudden and drastic effects on the amount of flow and the productivity of the stream. In order for fish to maintain their population, they must develop some way to deal with this variability.

The redbfin pickerel are part of the only species complex in the family Esocidae that has adapted to life in these highly variable stream environments. The fact that the pickerel spawn over a much longer time period than the other fish in the family is likely an evolutionary response to the unpredictability in the amount of flooded vegetation present during the reproductive season. By having eggs in three developmental states, the pickerel can take advantage of sudden flooding events when advantageous conditions for the growth or survival of larvae are present.

The results from this research suggest that in fact the pickerel spawn over an extended period of time, and that temperature and rainfall are important for the initiation of spawning. While the data do not suggest a truly bimodal reproductive strategy for the season examined, it is possible that this is an artifact of the climatic conditions and may not be a "normal" result for a year with more regular rainfall.

The use of otoliths for age and growth estimation al-

lows an accurate estimation of hatching dates for these fish, and makes possible the comparison of fish from different cohorts and year classes to determine the effect of environmental factors on different life history stages of the fish. In fact, the use of daily ageing techniques will allow various questions about life history strategies and adaptations to various environmental conditions in many other fish.

As with much research, this study has uncovered many more questions that deserve to be tested. First, more extensive validation work will help to clarify the age and growth estimates of the redbfin pickerel. These experiments should focus on the effects of different feeding regimes and different temperatures on growth, and also compare growth in the field with growth in the lab. This will help define the true nature of increment deposition rate and the relationship between otolith and somatic growth.

The presence of spawning cohorts can be further tested by monitoring floodplains for larval pickerel beginning in late fall, using seines, Breder traps, and light traps. In addition, adult fish need to be monitored for gonadal development during the breeding season. The data gained from these observations, along with age data from YOY fish, can resolve the annual spawning schedule. The physical parameters at the site and the climatic conditions can be documented and their relationship to reproductive effort in the population can be defined.

If possible, comparisons with populations along a latitudinal gradient should be made, in order to determine the effects of regional climate and the response of the fish to varying degrees of harshness and uncertainty in the environment. Near the northern limit of the fish's range, it is likely that ice formation completely restricts access to the floodplain during the coldest part of winter. If this is the case, it is possible that spawning might truly be bimodal in cold years, while during mild winters, where access to the floodplains is unrestricted, the spawning can be protracted but unimodal, as in this study.

The understanding of the importance of floodplains to their inhabitants and the effects sudden changes can have on fish populations is crucial to freshwater fisheries ecology. Many of these small stream systems are under constant threat of alteration and destruction by man.

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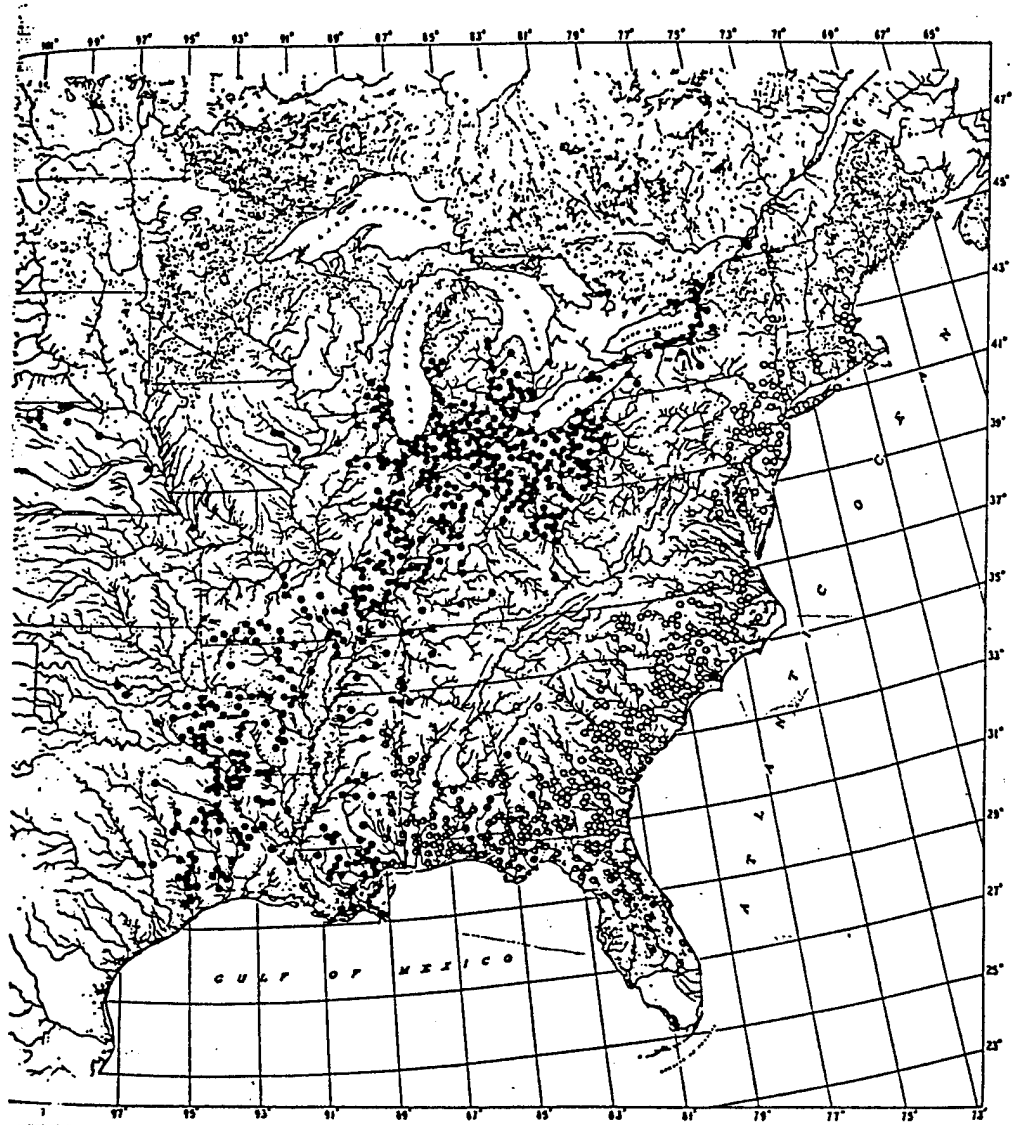
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Figure 1. Geographic distribution of Esox americanus complex (taken from Crossman, 1966).



General distribution of the *Esox americanus* complex as indicated by museum records.
 ○, *E. a. americanus*; ●, *E. a. vermiculatus*; ◐, Intergrades.

Figure 2. Map of study area in relation to South Carolina
(taken from Brim, 1991).

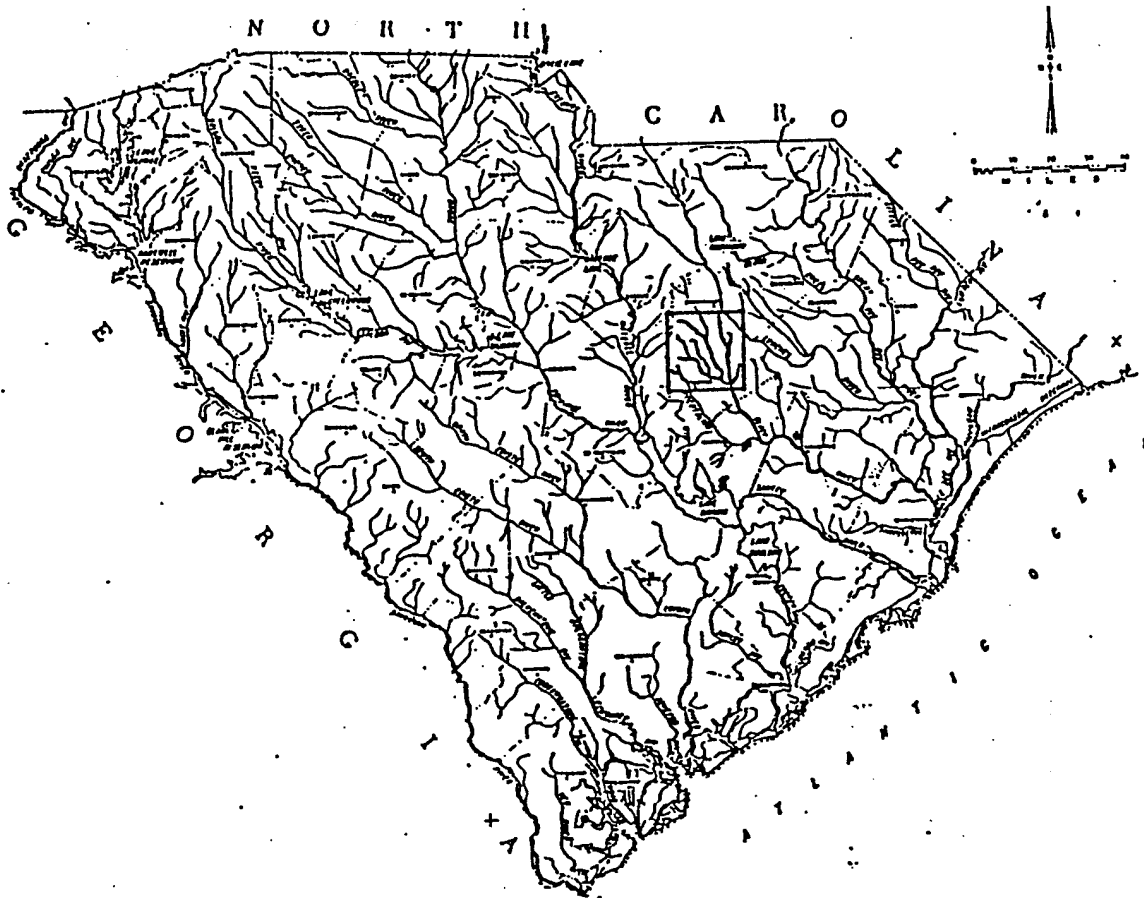


Figure 3. Study site location in Lee Swamp (adapted from
Brim, 1991).

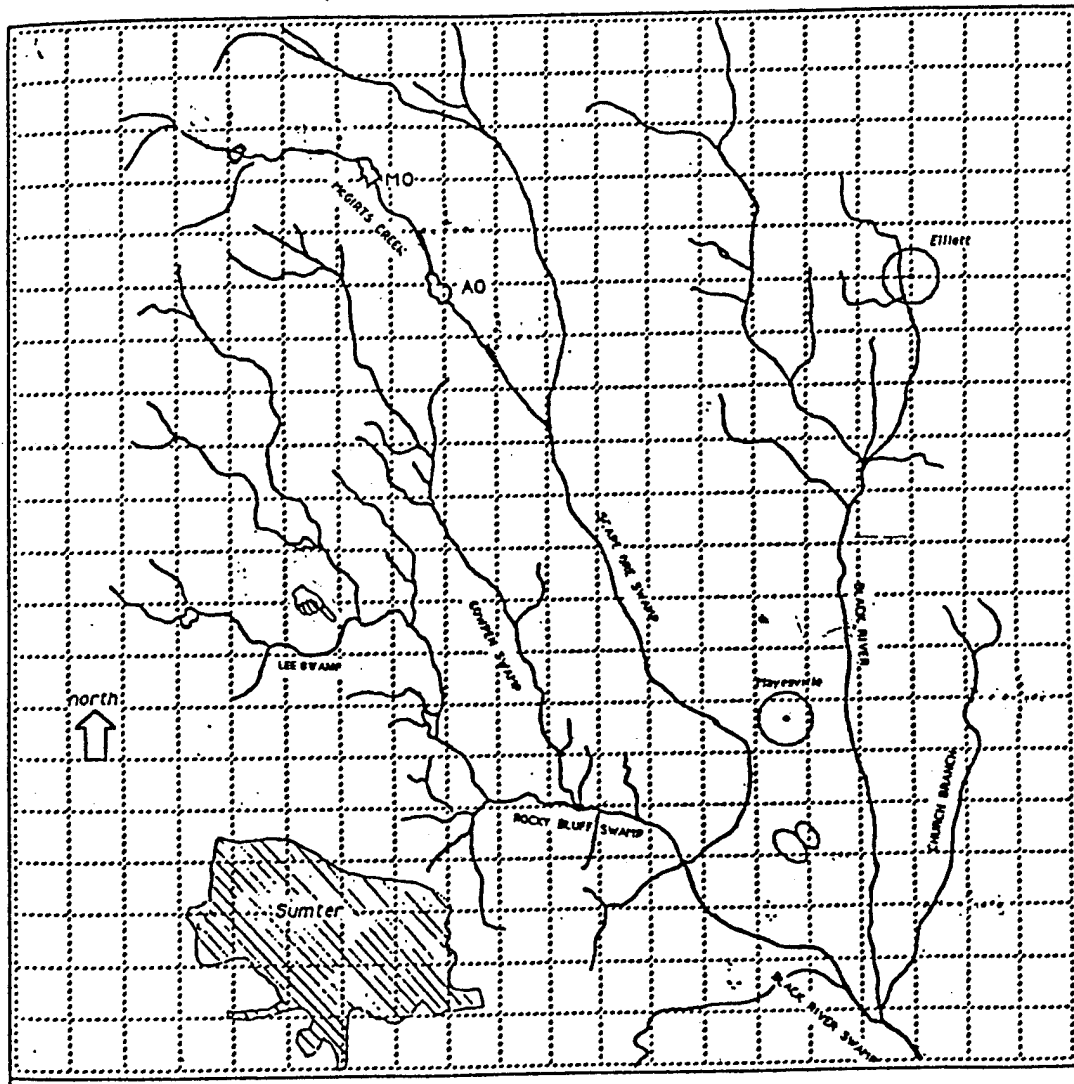


Figure 4. Standard lengths of refin pickerel by sampling date.

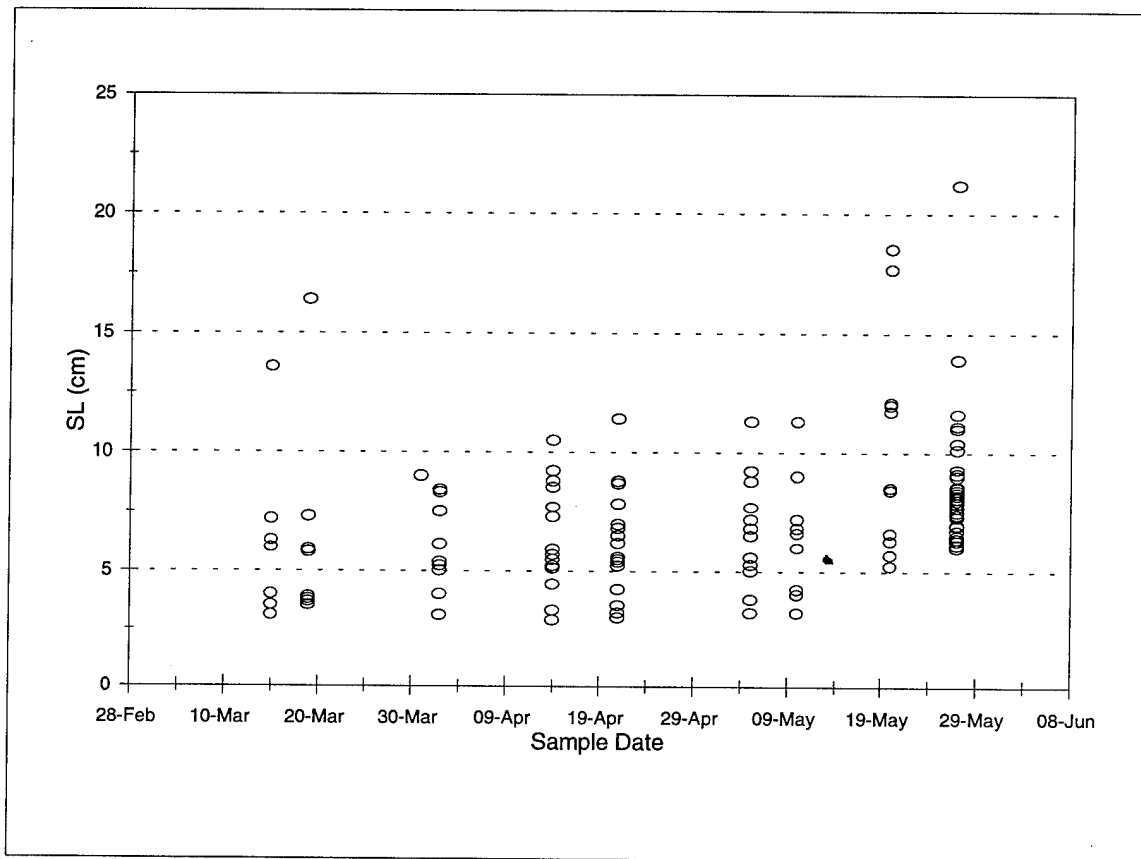
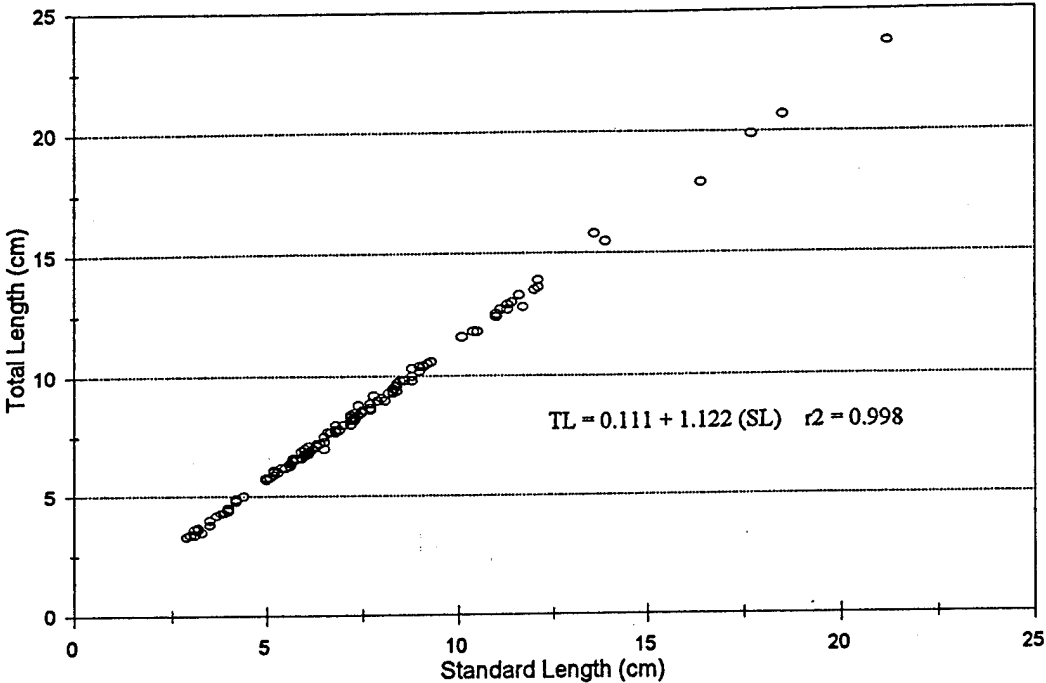


Figure 5. Relationships of standard and total length and standard and fork length for Sumter Co., S.C. redfin pickerel.

Standard Length v Total Length



Standard Length v Fork Length

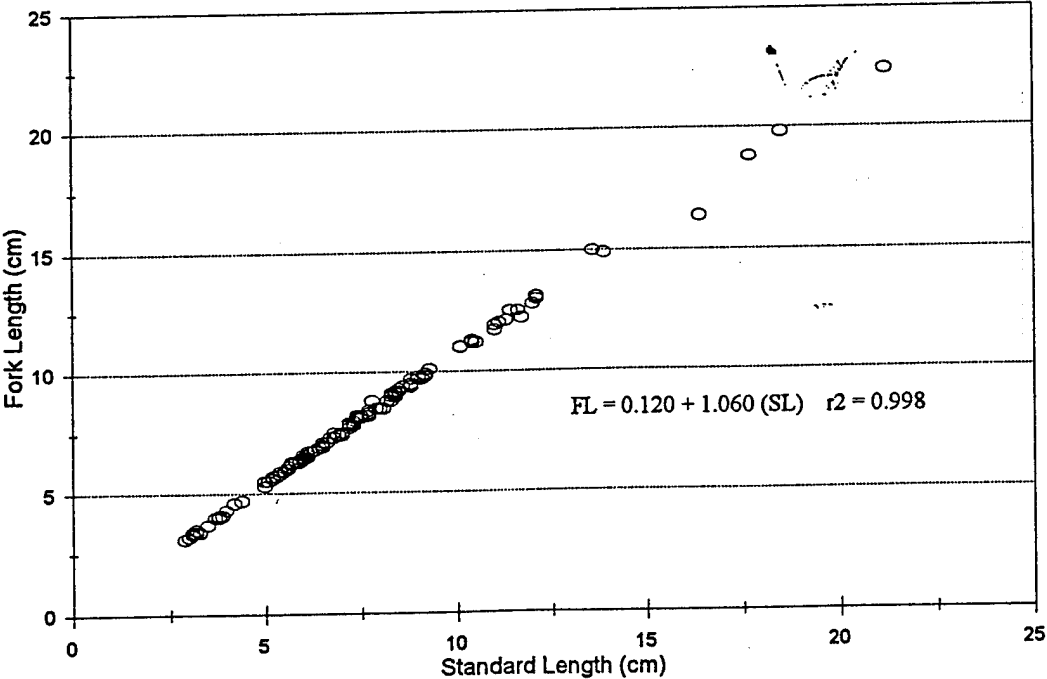


Figure 6. Length vs. weight relationship for 137 Sumter Co., S.C. redbfin pickerel, during March, April, and May, 1994.

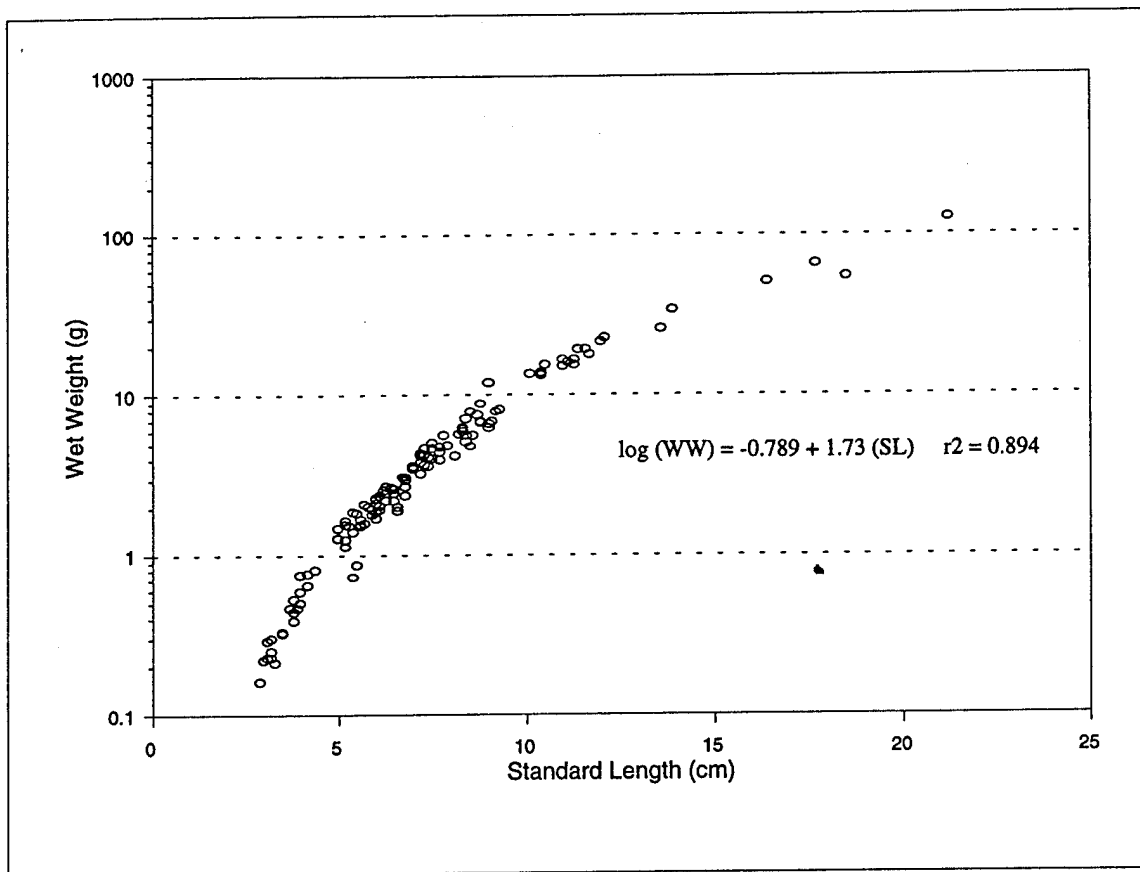
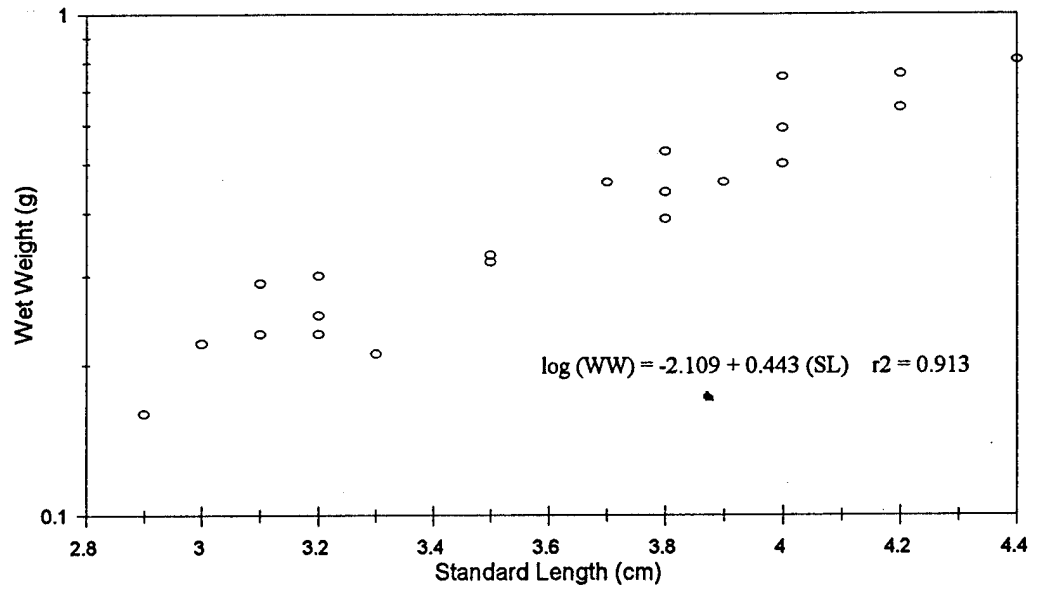
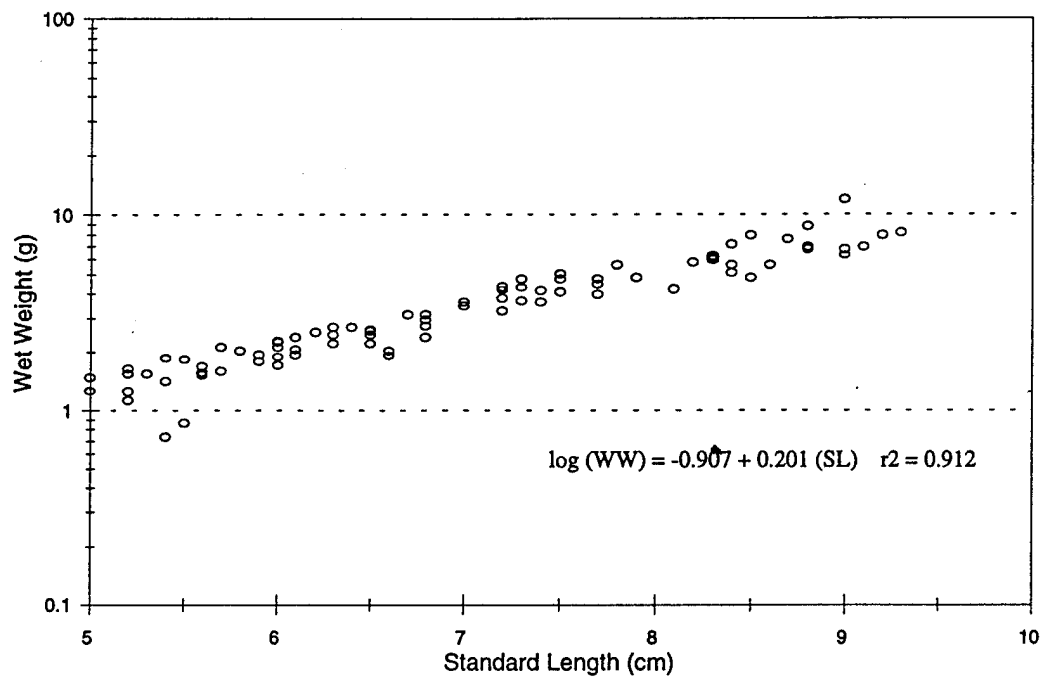


Figure 7. Length vs. weight relationship for three size classes of redfin pickerel: < 5 cm, 5 - 10 cm, and > 10 cm (SL).

SL < 5 cm



SL = 5-10 cm



SL > 10 cm

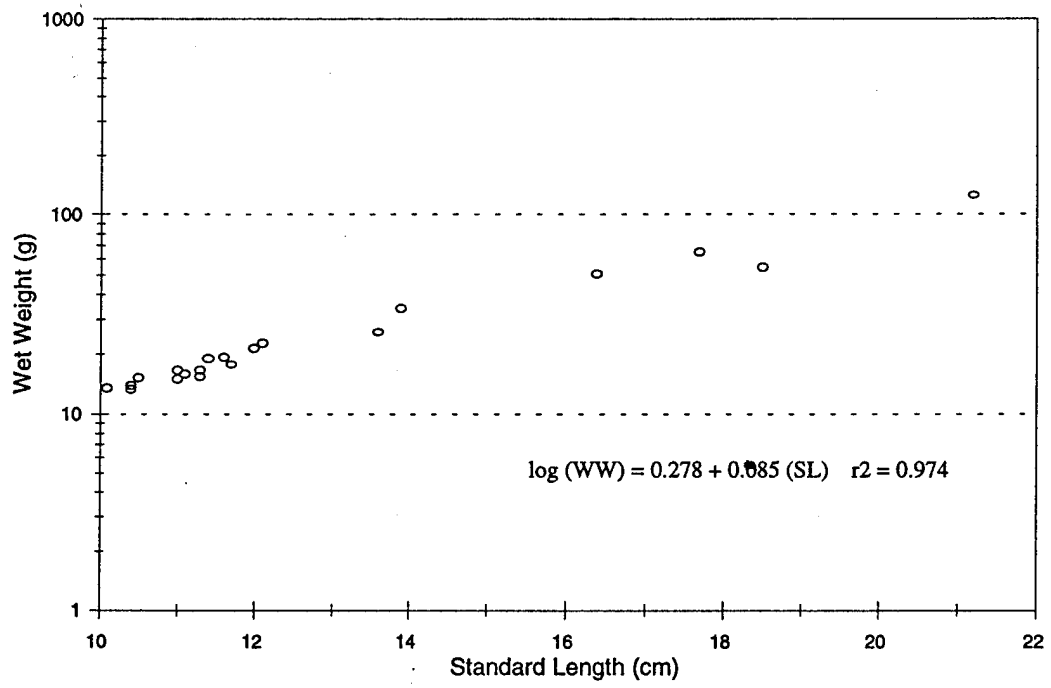


Figure 8. Standard length vs. age relationship for Sumter Co., S.C. redfin pickerel, based on otolith daily increment analysis.

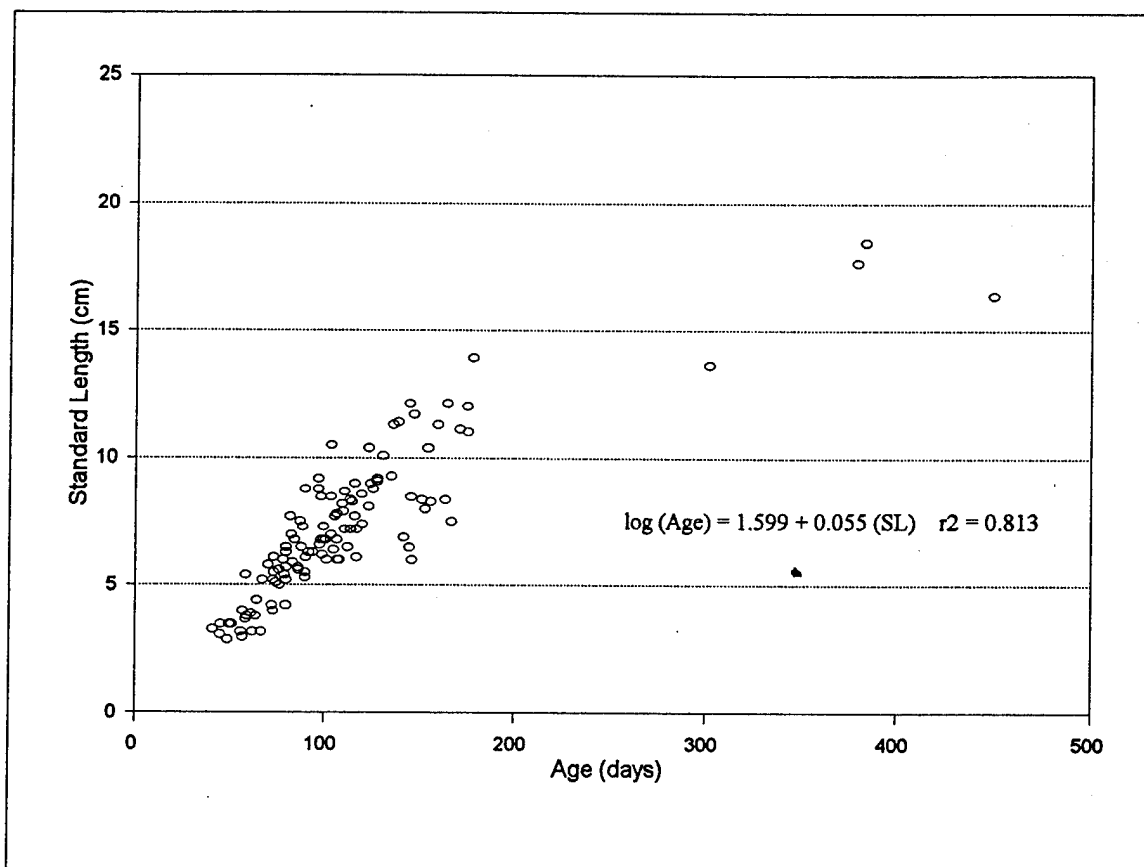


Figure 9. Results of otolith increment validation experiment in redfin pickerel: number of visible increments formed vs. number of days maintained in experiment.

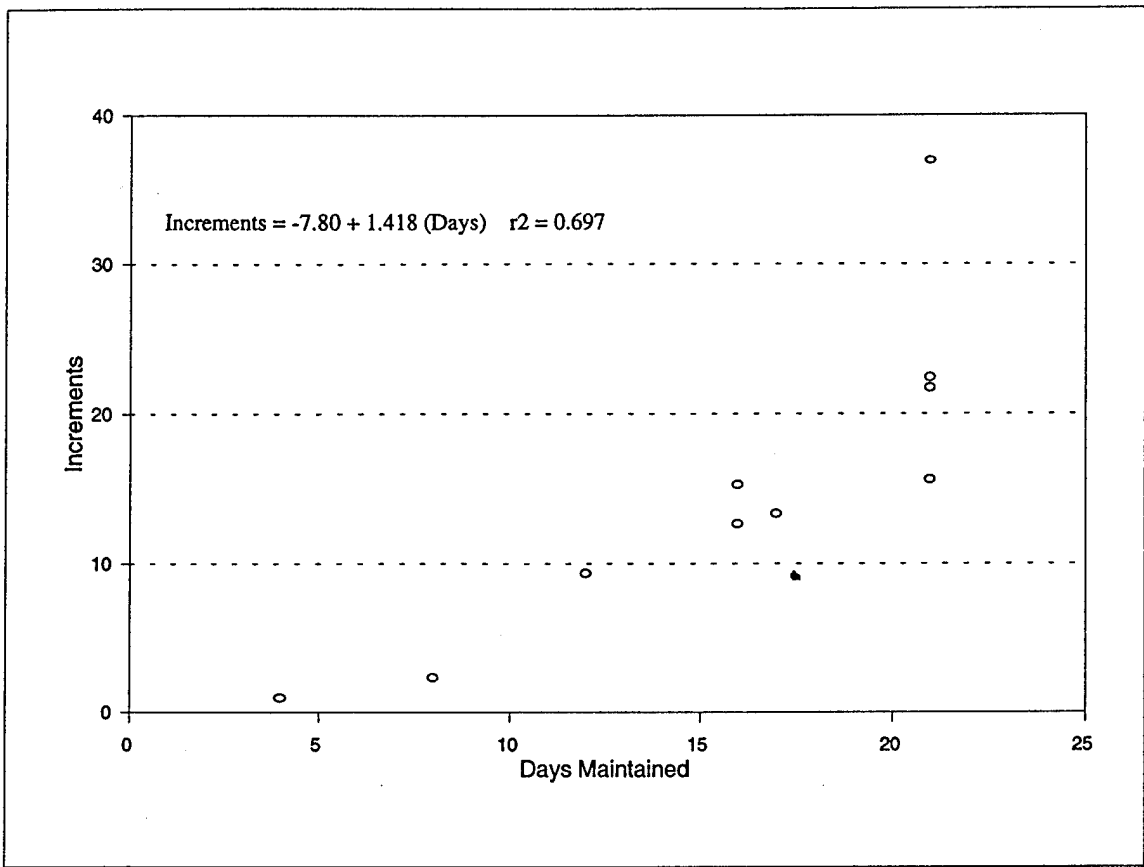


Figure 10. Timing of annulus formation in otoliths of Sumter Co., S.C. redbfin pickerel: number of fish forming annulus per day. Dates are grouped in 5-day intervals.

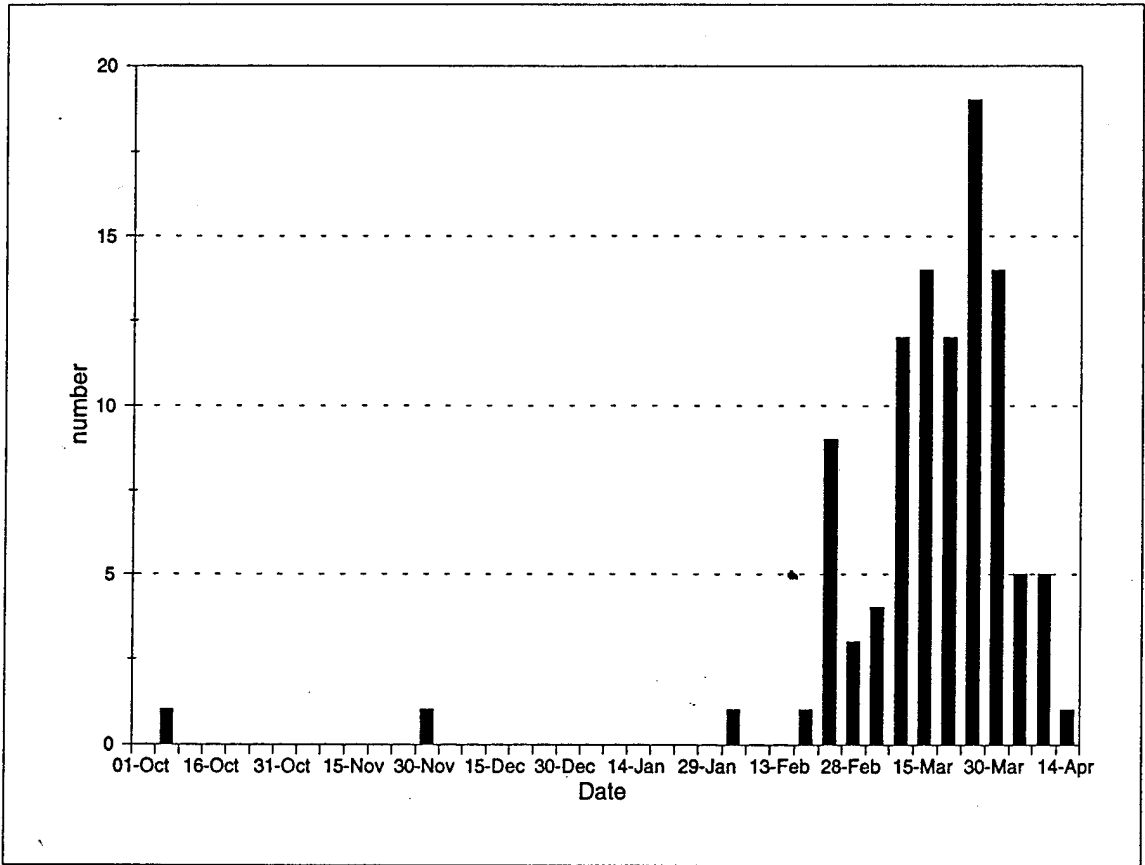


Figure 11. Comparison of rainfall and hatch date distributions: number of fish hatched with rainfall per day. Dates are grouped in 5-day intervals.

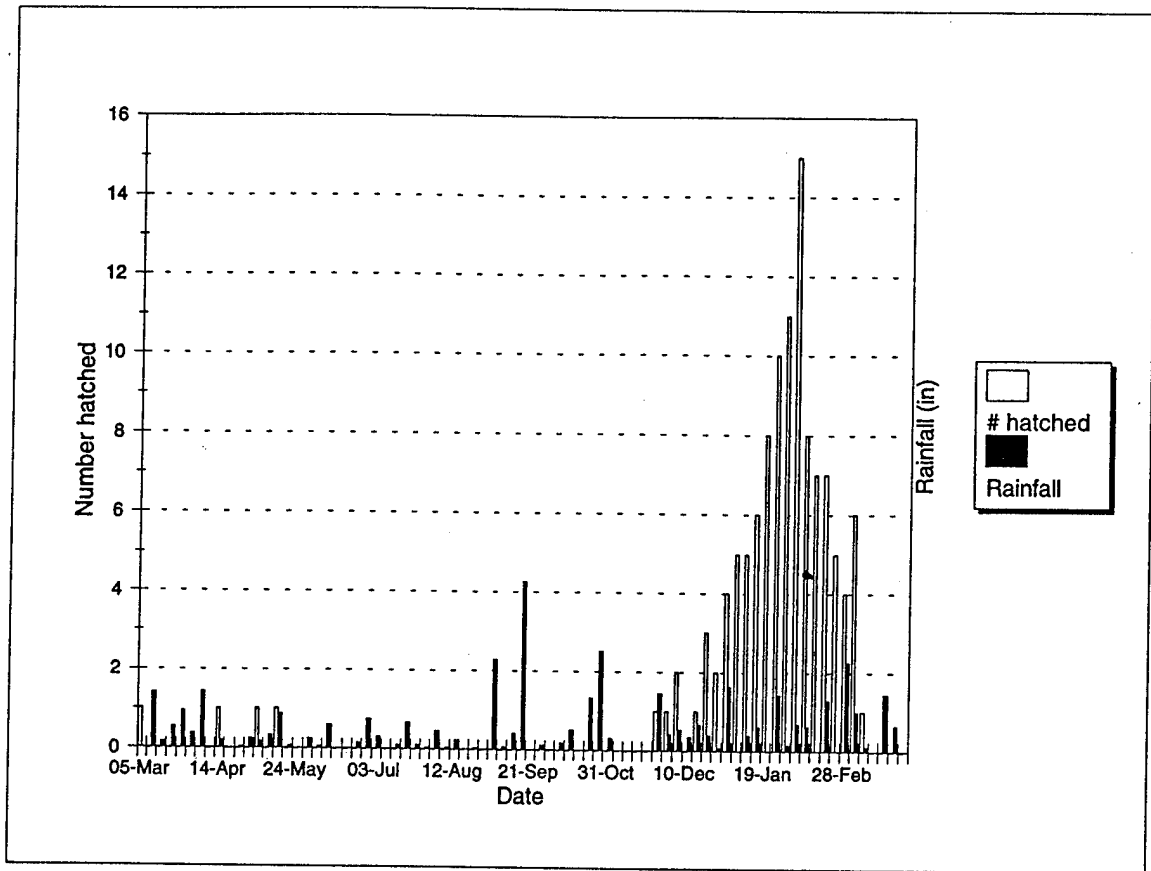


Figure 12. Mean daily air temperature for Sumter, S.C., from
1 January, 1993 to 30 April, 1994.

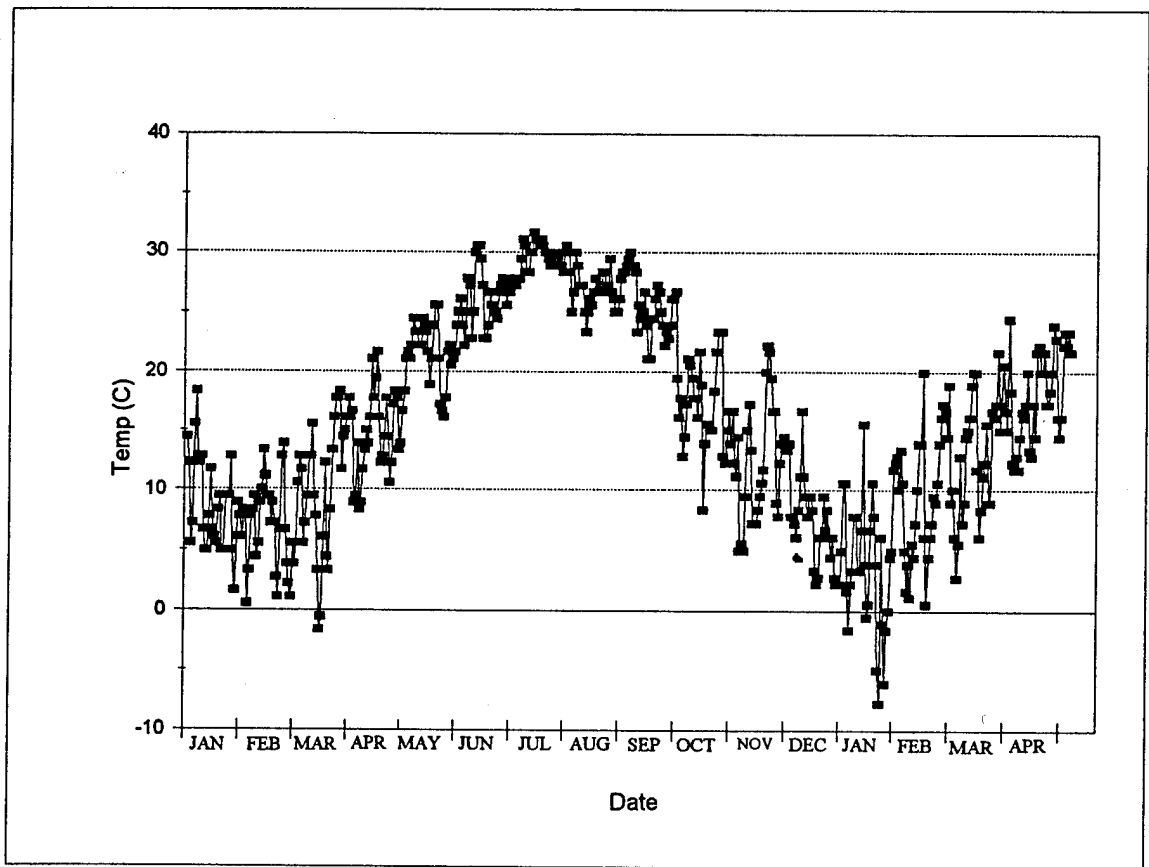


Figure 13. Standard length vs. hatch date for Sumter Co., SC
redfin pickerel.

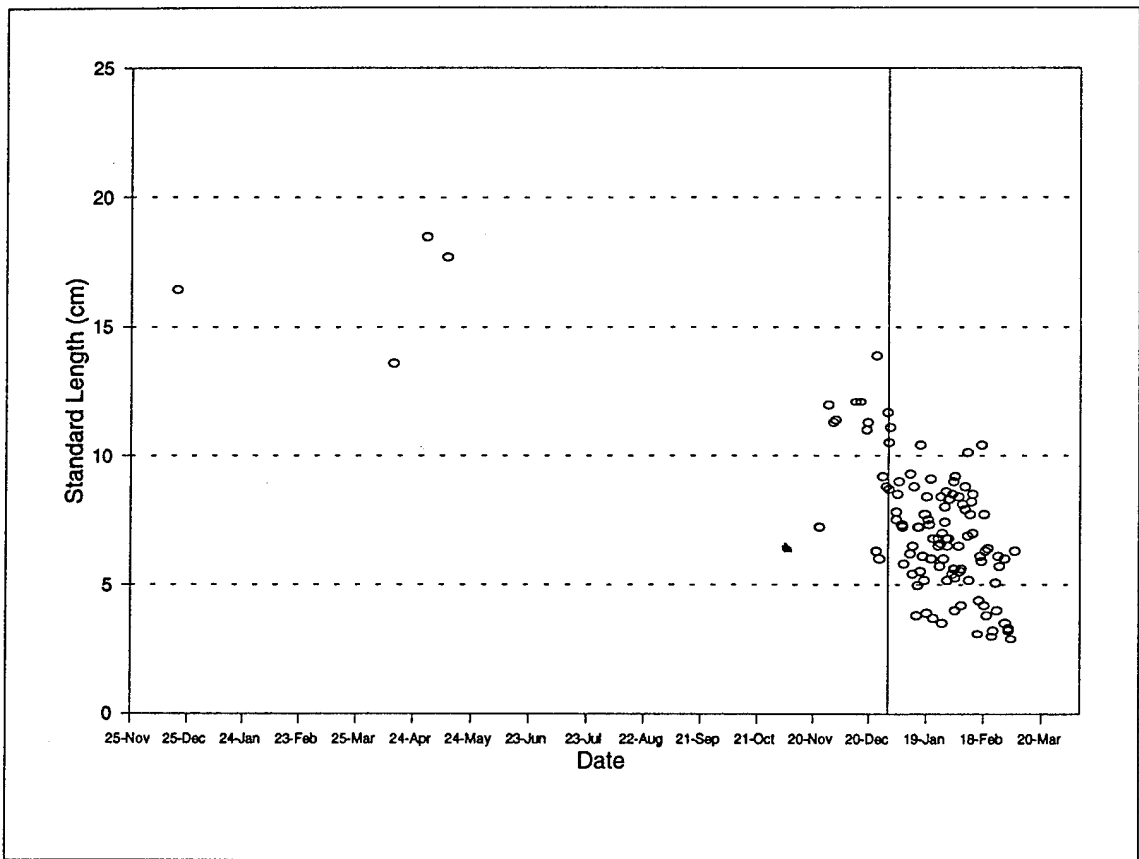


Figure 14. Early growth rates of Sumter Co., S.C. redbfin
pickerel: width of first 30 daily otolith increments vs.
hatch date.

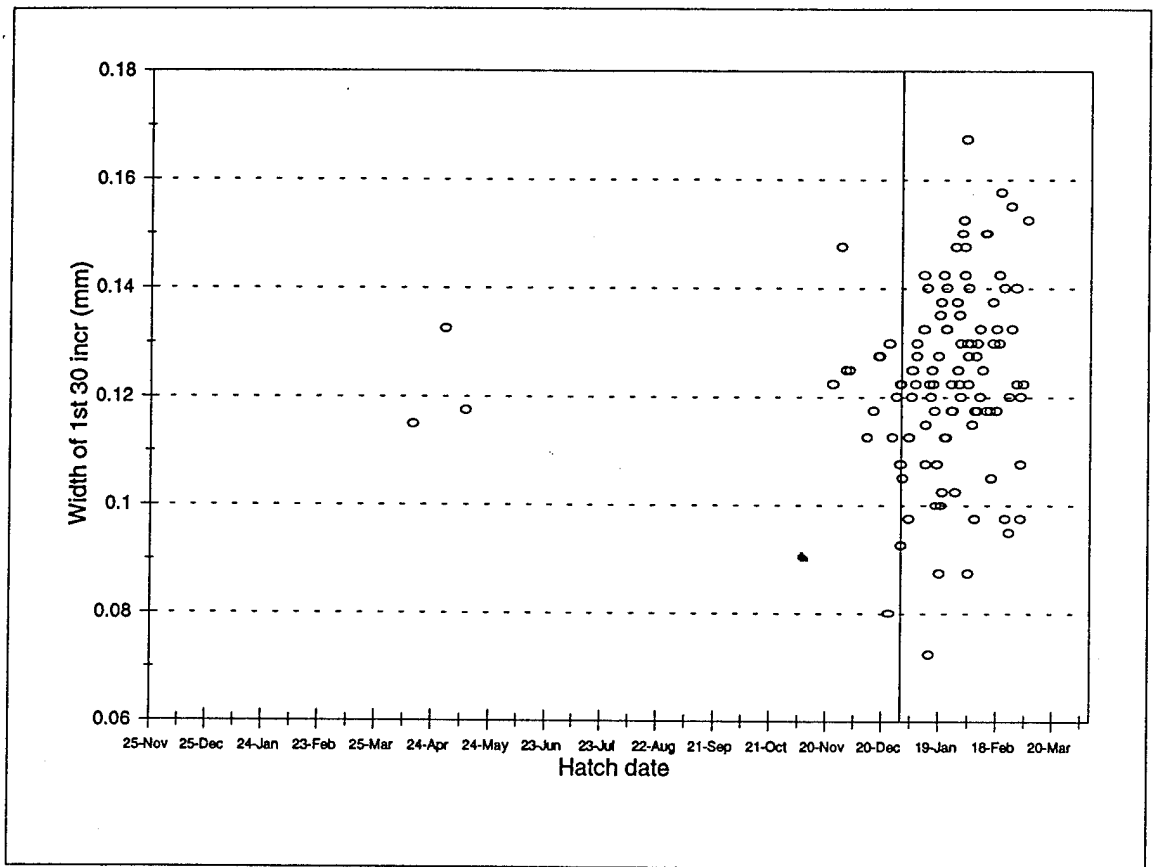


Table 1. Conversion equations for standard length to total length and standard length to fork length for redfin pick-
erel. All lengths in centimeters.

Conversion	Equation	r2
SL - TL:	$TL = 0.111 + 1.122 \cdot (SL)$	0.998
SL - FL:	$FL = 0.121 + 1.060 (SL)$	0.998

Table 2. ANOVA for length-weight regression of three size classes: SL < 5 cm, 5 - 10 cm, and > 10 cm.

General Linear Models Procedure

Dependent Variable: LOGWT

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	41.72436739	8.34487348	1719.28	0.0001
Error	124	0.60185815	0.00485369		
Corrected Total	129	42.32622554			

R-Square	C.V.	Root MSE	LOGWT Mean
0.985780	14.56465	0.069668	0.47833953

Source	DF	Type I SS	Mean Square	F Value	Pr > F
LENGTH	1	37.81932356	37.81932356	7791.86	0.0001
X1	1	2.46864234	2.46864234	508.61	0.0001
X2	1	0.03624397	0.03624397	7.47	0.0072
LENGTH*X1	1	0.38267047	0.38267047	78.84	0.0001
LENGTH*X2	1	1.01748704	1.01748704	209.63	0.0001
X1*X2	0	0.00000000	.	.	.
LENGTH*X1*X2	0	0.00000000	.	.	.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
LENGTH	1	1.34091488	1.34091488	276.27	0.0001
X1	1	1.25201436	1.25201436	257.95	0.0001
X2	1	1.06073833	1.06073833	218.54	0.0001
LENGTH*X1	1	0.50282137	0.50282137	103.60	0.0001
LENGTH*X2	1	1.01748704	1.01748704	209.63	0.0001
X1*X2	0	0.00000000	.	.	.
LENGTH*X1*X2	0	0.00000000	.	.	.

Parameter	Estimate	T for H0: Parameter=0	Pr > T	Std Error of Estimate
INTERCEPT	0.278537403	4.14	0.0001	0.06723939
LENGTH	0.084893868	16.62	0.0001	0.00510754
X1	-2.297876241	-16.06	0.0001	0.14307317
X2	-1.186055690	-14.78	0.0001	0.08023007
LENGTH*X1	0.357922582	10.18	0.0001	0.03516564
LENGTH*X2	0.116324539	14.48	0.0001	0.00803421
X1*X2	0.000000000 B	.	.	.
LENGTH*X1*X2	0.000000000 B	.	.	.

NOTE: The X'X matrix has been found to be singular and a generalized inverse was used to solve the normal equations. Estimates followed by the letter 'B' are biased, and are not unique estimators of the parameters.

Table 3. Redfin pickerel otolith increment validation
experiment results: number of days maintained and number of
increments formed for each fish

Fish Number	# Days Alive	# Increments Formed
1	0	0
2	4	1
3	8	2
4	12	9
5	16	13
6	16	15
7	17	13
8	21	16
9	21	22
10	21	22
11	21	37

Table 4. ANOVA for redfin pickerel otolith increment validation experiment.

General Linear Models Procedure

Dependent Variable: COUNT

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	1619.976296	1619.976296	59.77	0.0001
Error	26	704.737990	27.105307		
Corrected Total	27	2324.714286			
	R-Square	C.V.	Root MSE	COUNT Mean	
	0.696850	35.21153	5.206276	14.7857143	

Source	DF	Type I SS	Mean Square	F Value	Pr > F
DAYS	1	1619.976296	1619.976296	59.77	0.0001
Source	DF	Type III SS	Mean Square	F Value	Pr > F
DAYS	1	1619.976296	1619.976296	59.77	0.0001

Parameter	Estimate	T for H0: Parameter=0	Pr > T	Std Error of Estimate
INTERCEPT	-7.798351356	-2.53	0.0178	3.08253037
DAYS	1.417833717	7.73	0.0001	0.18339950

Table 5. T-test for comparison of early- and late-spawned
redfin pickerel from Sumter Co., S.C.: width of first 30
daily otolith increments.

Increment Width

14:07 Thursday, August 18, 1994⁶

TTEST PROCEDURE

Variable: INCRWID

COHORT	N	Mean	Std Dev	Std Error
1	33	0.11848485	0.01590916	0.00276943
2	76	0.12539474	0.01708826	0.00196016

Variances	T	Method	DF	Prob> T
Unequal	-2.0366	Satterthwaite	65.1	0.0458
		Cochran	.	0.0484
Equal	-1.9795		107.0	0.0503

For H0: Variances are equal, $F' = 1.15$ DF = (75,32) Prob>F' = 0.6660

Table 6. ANOVA for temperature and rainfall as predictors
for spawning in redfin pickerel.

General Linear Models Procedure

Dependent Variable: HATCH

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	6	79.57166457	13.26194410	38.88	0.0001
Error	343	116.98833543	0.34107386		
Corrected Total	349	196.56000000			

R-Square	C.V.	Root MSE	HATCH Mean
0.404821	208.5769	0.584015	0.28000000

General Linear Models Procedure

Dependent Variable: HATCH

Source	DF	Type I SS	Mean Square	F Value	Pr > F
TEMP	1	43.01649135	43.01649135	126.12	0.0001
WEEK1	1	0.86957430	0.86957430	2.55	0.1112
WEEK2	1	0.09123183	0.09123183	0.27	0.6054
WEEK3	1	0.63510508	0.63510508	1.86	0.1733
DAY	1	32.15664418	32.15664418	94.28	0.0001
TEMP*WEEK2	1	2.80261784	2.80261784	8.22	0.0044

Source	DF	Type III SS	Mean Square	F Value	Pr > F
TEMP	1	6.77724479	6.77724479	19.87	0.0001
WEEK1	1	1.05554215	1.05554215	3.09	0.0794
WEEK2	1	2.37721133	2.37721133	6.97	0.0087
WEEK3	1	0.61929846	0.61929846	1.82	0.1787
DAY	1	33.42652859	33.42652859	98.00	0.0001
TEMP*WEEK2	1	2.80261784	2.80261784*	8.22	0.0044

Parameter	Estimate	T for H0: Parameter=0	Pr > T	Std Error of Estimate
INTERCEPT	1.630007380	8.06	0.0001	0.20223397
TEMP	-0.012679980	-4.46	0.0001	0.00284457
WEEK1	-0.071345096	-1.76	0.0794	0.04055557
WEEK2	0.490100098	2.64	0.0087	0.18564152
WEEK3	-0.054344713	-1.35	0.1787	0.04033031
DAY	0.003163247	9.90	0.0001	0.00031953
TEMP*WEEK2	-0.008692148	-2.87	0.0044	0.00303228

Appendix 1.

Redfin Pickerel Raw Data

Num	CapDate	SacDate	TL	FL	SL	HL	SnL	WW	Oto Weights		Age 1	Age 2	Avg age	Hatch Date	otolith length (mm)	30 incr width(mm)	incr in translucent zone	
									Left	Right								Average
1	09-FEB	11 FEB	15.8	15	13.6			25.66	0.00327	0.00327	312	292	302	14-Apr	2.8625	0.115	130	
2	15 MAR	15 MAR	8	7.7	7.2			3.8	0.00039	0.00039	102	119	110.5	24-Nov	1.1875	0.1225	21	
3			4.4	4.3	4			0.75			44	47	45.5	27-Jan	0.775	0.1025	6	
4			3.8	3.7	3.5			0.32										
5			3.4	3.3	3.1			0.23										
6			6.8	6.5	6			2.27	0.00028	0.00028	74	83	78.5	26-Dec	1.1	0.1125	19	
7			7.1	6.8	6.3			2.45	0.00026	0.00026	74	86	80	24-Dec	1.175	0.08	18	
8			17.9	16.4	16.4			50.28	0.00614	0.00614	415	484	449.5	20-Dec	3.5		106	
9	19 MAR	20 MAR	4.3	4.1	3.8			0.44										
10		20 MAR	6.6	6.3	5.9			1.93	0.00024	0.00024								
11		20 MAR	6.6	6.3	5.8			2.01	0.0003	0.0003	67	74	70.5	07-Jan	1.175	0.1275	20	
12		20 MAR	4.3	4	3.8			0.39			65	63	64	14-Jan	0.65	0.0725	24	
13		21 MAR	4	3.7	3.5			0.32			51	52	51.5	27-Jan	0.7425	0.1025	12	
14		23 MAR	4.2	4	3.7			0.46			55	62	58.5	22-Jan	0.775	0.1125	6	
15		23 MAR	4.3	4.1	3.9			0.46			59	64	61.5	19-Jan	0.8	0.0875	9	
16		20 APR	8.2	7.9	7.3	2.4	1		0.00039	0.00042	0.00041	88	89	88.5	20-Jan	1.4825	0.1	31
17		11 JUN	10.4	9.8	9	3.2	1.2	11.92										
18	31 MAR	31 MAR	9.7	9.1	8.4	3	1.2	5.55	0.00057	0.00058	0.00058							
19	02 APR	02 APR	9.5	9.1	8.3	2.8	1.1	6.1	0.00068	0.00068	0.00068							
20		02 APR	8.6	8.2	7.5	2.6	0.9	4.7	0.00047	0.00049	0.00048	83	92	87.5	03-Jan	1.45	0.1125	26
21		02 APR	6.9	6.6	6.1	2.1	0.7	2.05	0.0002	0.00027	0.00024	74	73	73.5	17-Jan	1.1825	0.1	25
22		02 APR	6.2	5.9	5.4	1.8	0.6	1.86	0.00019	0.00024	0.00022	80	78	79	12-Jan	1.1425	0.1075	40
23		02 APR	4.5	4.3	4	1.3	0.5	0.59	0.0001	9E-05	9.5E-05	50	64	57	03-Feb	0.8	0.0875	14
24		02 APR	6	5.7	5.2	1.8	0.6	1.25	0.0002	0.0002	0.0002	72	74	73	18-Jan	1.0925	0.1075	32
25		02 APR	6.2	5.8	5.4	1.8	0.6	1.4	0.00017	0.00016	0.00017	58	59	58.5	01-Feb	1.0575	0.1475	29
26		02 APR	5.7	5.3	5	1.8	0.7	1.26	0.00023	0.00024	0.00024	78	75	76.5	14-Jan	0.9875	0.1225	61
27		02 APR	3.6	3.4	3.1	1.1	0.4	0.29	7E-05	5E-05	6E-05	47	43	45	15-Feb	0.675	0.1175	19
28		10 MAY	10	9.5	8.8	2.7	1	6.85	0.00055	0.00054	0.00055	91	89	90	08-Feb	1.55	0.1175	60
29	14 APR	14 APR	3.5	3.4	3.3	1.1	0.4	0.21	4E-05	4E-05	4E-05	42	40	41	03-Mar	0.6575	0.12	19
30		14 APR	9.8	9.3	8.5	3.1	1.2	7.84	0.00067	0.00067	0.00067	99	98	98.5	04-Jan	1.8	0.12	34
31		14 APR	11.8	11.2	10.5	3.6	1.2	15.18	0.00085	0.00087	0.00086	105	102	103.5	30-Dec	1.8425	0.1225	50
32		17 APR	8.5	7.8	7.3	2.5	0.9	4.3	0.0006	0.00064	0.00062	101	98	99.5	06-Jan	1.6625	0.1225	26
33		17 APR			5.5	2	0.8	0.86	0.00037	0.00042	0.0004	92	88	90	16-Jan	1.3925	0.1225	37

34	17 APR	6.6	6.3	5.7	1.9	0.7	2.1	0.00041	0.00037	0.00039	79	81	80	26-Jan	1.3425	0.1175	30
35	20 APR	6.1	5.6	5.2	1.7	0.7	1.55	0.00029	0.0003	0.0003	68	67	67.5	10-Feb	1.2	0.125	25
36	22 APR	5	4.7	4.4	1.5	0.5	0.81	0.00024	0.00018	0.00021	62	67	64.5	15-Feb	1.0075	0.105	34
37	23 APR	3.3	3.1	2.9	1.1	0.3	0.16	5E-05	7E-05	6E-05	49	49	49	04-Mar	0.7375	0.1225	49
38	11 MAY	5.8	5.5	5.1	1.7	0.7		0.00023	0.0003	0.00027	72	77	74.5	24-Feb	1.2075	0.095	32
39	12 MAY	8.7	8.3	7.7	2.1	0.9	3.94	0.0007	0.00068	0.00069	82	82	82	18-Feb	1.725	0.1325	59
40	12 MAY	10.5	9.8	9.2	2.9	1		0.00081	0.00079	0.0008	91	103	97	03-Feb	1.85	0.1275	43
41	12 MAY	6.9	6.4	5.9	2	0.7	1.79	0.00039	0.00037	0.00038	85	82	83.5	16-Feb	1.2575	0.13	49
42	12 MAY	6.2	5.8	5.4	1.8	0.7	0.73	0.00029		0.00029							
43	21 APR	9.2	8.8	7.8	2.7	1.1	5.6	0.0006	0.00056	0.00058	99	114	106.5	03-Jan	1.6425	0.0975	56
44	21 APR	8	7.4	7	2.4	0.9	3.6	0.00053		0.00053	73	92	82.5	27-Jan		0.1475	
45	21 APR		6.8	6.5	2.1	0.8	2.61	0.00053	0.00055	0.00054	79	90	84.5	25-Jan	1.475	0.1225	40
46	21 APR	13	12.5	11.4	3.9	1.5	18.96	0.0102	0.001	0.00101	145	132	138.5	03-Dec	2.0875	0.125	47
47	21 APR		8.7	8.7	3.5	1.2	7.57	0.00067	0.00066	0.00067	109	112	110.5	30-Dec	1.825	0.0925	
48	21 APR	10.3	9.7	8.8	3.1	1.2	8.76	0.00074	0.00068	0.00071	89	105	97	13-Jan		0.14	43
49	21 APR	7	6.9	6.5	2.1	0.8	2.61	0.00038	0.00037	0.00038	77	83	80	30-Jan	1.375	0.13	30
50	21 APR	3.6	3.5	3.2	1.2	0.5	0.23	8E-05	6E-05	7E-05	52	60	56	23-Feb	0.725	0.0975	56
51	21 APR		3.5	1.2	0.4	0.33	9E-05	9E-05	9E-05	9E-05	49	51	50	01-Mar	0.7625	0.1225	15
52	21 APR	6.4	6.1	5.6	1.7	0.5	1.68	0.00041	0.00045	0.00043	68	85	76.5	02-Feb	1.3375	0.13	40
53	21 APR	3.4	3.2	3	1.1	0.3	0.22	7E-05	5E-05	6E-05	57	57	57	22-Feb	0.7125	0.14	57
54	21 APR	4.9	4.6	4.2	1.4	0.6	0.76	0.0002	0.00032	0.00026	70	75	72.5	06-Feb	1.025	0.1175	
55	21 APR	6.3	6	5.6	1.9	0.8	1.57	0.00028	0.00025	0.00027	73	79	76	03-Feb	1.2325	0.1225	39
56	21 APR	6.2	5.9	5.5	1.9	0.8	1.83	0.00021	0.00019	0.0002	77	70	73.5	05-Feb	1.225	0.115	30
57	21 APR	7	6.7	6.2	2.2	0.9	2.54	0.00041	0.00038	0.0004	101	97	99	11-Jan	1.45	0.1425	37
58	21 APR	5.9	5.6	5.2	1.7	0.7	1.64	0.00027	0.00024	0.00026	79	81	80	30-Jan	1.2	0.12	34
59	21 APR		3.8	1.4	0.5	0.53	0.0001*	0.0001*	0.00013	0.00012	59	60	59.5	19-Feb	0.8625	0.13	27
60	05 MAY	3.6	3.4	3.2	1.1	0.4	0.25	8E-05	0.0001	9E-05	62	63	62.5	02-Mar	0.825	0.1075	41
61	05 MAY	5.8	5.5	5	1.9	0.7	1.48	0.00045	0.00043	0.00044					1.3925		
62	05 MAY	6.3	6	5.6	2	0.7	1.52	0.00033	0.00037	0.00035	84	89	86.5	06-Feb	1.3875	0.0975	45
63	05 MAY	6	5.7	5.3	1.9	0.7	1.54	0.00034	0.00031	0.00033	87	93	90	03-Feb	1.4575	0.14	51
64	05 MAY	8.9	8.4	7.7	2.7	1	4.76	0.00072	0.0007	0.00071	102	109	105.5	18-Jan		0.1275	53
65	05 MAY	10.5	9.9	9.2	3.1	1.1	7.86	0.0009	0.00098	0.00094	128	127	127.5	28-Dec	2	0.12	75
66	05 MAY	12.7	12.1	11.3	3.7	1.4	16.62	0.00158	0.00157	0.00158	134	138	136	19-Dec	2.45	0.1275	63
67	05 MAY	8	7.5	6.8	2.5	0.9	3.09	0.00061	0.0006	0.00061	97	105	101	23-Jan	1.65	0.14	41
68	05 MAY	8.4	7.9	7.2	2.5	0.9	4.32	0.00073	0.00077	0.00075	114	120	117	07-Jan	1.825	0.13	57

69	05 MAY	7.5	7.1	6.5	2.2	0.8	2.58	0.00042	0.00042	0.00042	0.00042	0.00042	0.00042	90	86	88	05-Feb	1.4875	0.13	36
70	05 MAY	9.8	9.4	8.8	2.9	1	6.69	0.00086	0.00081	0.00084	0.00084	0.00084	0.00084	131	120	125.5	30-Dec	2	0.1225	49
71	05 MAY	7.5	6.9	6.5	2.3	1	2.2	0.00044	0.00044	0.00044	0.00044	0.00044	0.00044	111	113	112	12-Jan	1.525	0.115	41
72	05 MAY	7.7	7.1	6.6	2.3	1.1	1.91	0.00044	0.00043	0.00044	0.00044	0.00044	0.00044	99	96	97.5	26-Jan	1.4375	0.1175	36
73	10 MAY	3.7	3.5	3.2	1.1	0.4	0.3	0.00011	0.00013	0.00012	0.00012	0.00012	69	65	67	03-Mar	0.8575	0.0975	43	
74	10 MAY	4.5	4.3	4	1.4	0.5	0.5	0.0002	0.00019	0.0002	0.0002	0.0002	77	77	73	25-Feb	1.0925	0.1175	41	
75	10 MAY	4.8	4.6	4.2	1.5	0.5	0.65	0.0002	0.00036	0.00037	0.00037	0.00037	82	78	80	18-Feb	1.4675	0.1025	46	
76	10 MAY	6.9	6.5	6	2.1	0.8	1.88	0.00037	0.00046	0.00048	0.00048	0.00048	109	107	108	21-Jan	1.4625	0.1125	59	
77	10 MAY	6.9	6.5	6	2.1	0.7	2.24	0.0005	0.00056	0.00057	0.00057	0.00057	108	106	107	22-Jan	1.6	0.135	40	
78	10 MAY	6.9	6.5	6	2.2	0.8	2.12	0.00058	0.00053	0.00055	0.00055	0.00055	99	100	99.5	29-Jan	1.5875	0.13	41	
79	10 MAY	7.7	7.3	6.8	2.3	0.8	2.71	0.00056	0.00057	0.00057	0.00057	0.00057	93	104	98.5	30-Jan	1.525	0.12	62	
80	10 MAY	7.7	7.3	6.8	2.3	0.9	2.36	0.00056	0.00063	0.00062	0.00062	0.00062	111	117	114	15-Jan	1.725	0.1325	46	
81	10 MAY	8.2	7.8	7.2	2.6	1	3.25	0.00061	0.00059	0.00061	0.00061	0.00061	105	108	106.5	22-Jan	1.5675	0.125	51	
82	10 MAY	7.8	7.3	6.8	2.4	0.9	2.94	0.00062	0.00071	0.0007	0.0007	0.0007	108	119	113.5	15-Jan	1.7425	0.125	45	
83	10 MAY	8.3	7.8	7.2	2.6	0.9	4.16	0.00069	0.00103	0.00105	0.00105	0.00105	119	129	124	05-Jan	2.1575	0.125	53	
84	10 MAY	10.2	9.7	9	3.1	1.2	6.67	0.00106	0.00156	0.00157	0.00157	0.00157	151	168	159.5	01-Dec	2.3875	0.1175	55	
85	10 MAY	12.9	12.1	11.3	3.9	1.5	15.34	0.00158	0.00155	0.00153	0.00153	0.00153	141	148	144.5	16-Dec	1.2675	0.1325	59	
86	10 MAY	13.9	13.1	12.1	4.1	1.6	22.59	0.0015	0.00022	0.00024	0.00023	0.00023	308	460	384	01-May	3.0875	0.1475	62	
87	20 MAY	5.6	5.2	1.8	0.8	1.13	2.01	0.00043	0.00516	0.00511	0.00511	0.00511	110	117	113.5	26-Jan	1.9625	0.1425	45	
88	20 MAY	7.7	7.1	6.6	2.4	1	2.01	0.00043	0.00098	0.00093	0.00093	0.00093	174	176	175	28-Nov	2.525	0.1075	77	
89	21 MAY	20.7	19.8	18.5	5.9	2.2	54.17	0.00505	0.00156	0.00157	0.00156	0.00156	92	96	94	19-Feb	1.5825	0.15	58	
90	21 MAY	9.2	8.4	3	1.1	5.1	2.7	0.00088	0.00055	0.00053	0.00053	0.00053	86	87	86.5	26-Feb	1.4325	0.1175	61	
91	23 MAY	13.5	12.8	12	4.2	1.6	21.37	0.00157	0.00132	0.00131	0.00131	0.00131	145	149	147	30-Dec	2.3	0.1125	67	
92	25 MAY	7.2	6.8	6.3	2.1	0.7	2.7	0.00055	0.00158	0.00157	0.00157	0.00157	165	164	164.5	13-Dec	2.5	0.1175	67	
93	25 MAY	6.5	6.2	5.7	1.9	0.7	1.59	0.00038	0.00405	0.00407	0.00406	0.00406	330	429	379.5	12-May	3	0.15	58	
94	27 MAY	12.8	12.2	11.7	3.8	1	17.73	0.0013	0.00072	0.00072	0.00072	0.00072	97	110	103.5	12-Feb	1.75	0.1175	61	
95	27 MAY	13.6	13	12.1	4.1	1.6	22.66	0.00156	0.00061	0.00061	0.00061	0.00061	98	109	103.5	12-Feb	1.7625	0.1525	60	
96	27 MAY	19.9	18.8	17.7	5.5	2.1	65.02	0.00405	0.00056	0.00057	0.00057	0.00057	110	119	114.5	31-Jan	2.225	0.1325	63	
97	28 MAY	8.5	8	7.5	2.8	1	4.79	0.00072	0.00076	0.00076	0.00076	0.00076	124	146	135	11-Jan	2.6125	0.155	63	
98	28 MAY	8	7.5	7	2.4	0.9	3.45	0.00061	0.00057	0.00057	0.00057	0.00057	86	95	90.5	25-Feb	1.5925			
99	27 MAY	8.4	8.1	7.4	2.5	0.9	4.14	0.00056	0.00075	0.00076	0.00076	0.00076	110	119	114.5	31-Jan	1.7625			
100	27 MAY	9.3	8.8	8.3	2.7	1	5.9	0.00076	0.00117	0.00118	0.00118	0.00118	124	146	135	11-Jan	2.225			
101	27 MAY	10.6	10.1	9.3	3.1	1.2	8.05	0.00119	0.00166	0.00162	0.00162	0.00162	86	95	90.5	25-Feb	1.5925			
102	27 MAY	13.3	12.5	11.6	3.9	1.5	19.21	0.00157	0.00058	0.00057	0.00057	0.00057	110	119	114.5	31-Jan	1.7625			
103	28 MAY	6.8	6.5	6.1	2.1	0.8	2.39	0.00058	0.00057	0.00057	0.00057	0.00057	86	95	90.5	25-Feb	1.5925			

104	30 MAY	8.3	7.9	7.3	2.4	0.9	3.67	0.00063	0.00067	0.00065	118	122	120	29-Jan	1.7375	0.125	77
105	30 MAY	8.8	8.2	7.4	2.6	0.9	3.63	0.00089	0.00096	0.00093	118	122	120	29-Jan	1.8125	0.125	77
106	30 MAY	9	8.5	7.9	2.6	1	4.83	0.00084	0.00086	0.00085	106	114	110	08-Feb	1.85	0.13	69
107	30 MAY	9.8	9.4	8.6	3.1	1.1	5.62	0.001	0.00104	0.00102	113	126	119.5	29-Jan	2.0625	0.1225	79
108	30 MAY	10.4	9.7	9	3	1.1	6.25	0.00114	0.00121	0.00118	110	122	116	02-Feb	2.15	0.1675	77
109	30 MAY	10.4	9.7	9.1	3	1.1	6.82	0.0012	0.0012	0.0012	127	128	127.5	21-Jan	2.0875	0.1425	70
110	2 JUN	12.4	11.9	11	3.7	1.5	15.01	0.00155	0.00145	0.0015					2.375		
111	2 JUN	9.3	8.8	8.2	2.8	1	5.74	0.00082	0.00082	0.00082	104	114	109	12-Feb	1.875	0.15	69
112	6 JUN	7.2	6.9	6.4	2.2	0.7	2.67	0.00059	0.00056	0.00058	105	105	105	20-Feb		0.1575	65
113	7 JUN	7.2	6.8	6.3	2.3	0.8	2.22	0.00064	0.00062	0.00063	90	94	92	06-Mar	1.5625	0.1525	60
114	7 JUN	8.6	8.1	7.5	2.8	1.1	4.07	0.00092	0.00095	0.00094					1.9625	0.135	
115	8 JUN	8.6	8.2	7.7	2.5	1	4.46	0.00087	0.00085	0.00086					1.825		
116	8 JUN	8.6	8.2	7.7	2.6	1	3.96	0.00074	0.00074	0.00074	112	120	116	11-Feb	1.7675		59
117	11 JUN	6.7	6.4	6	2	0.8	1.71	0.00042	0.00044	0.00043	100	103	101.5	28-Feb	1.4875	0.14	60
118	11 JUN	9	8.5	8.1	2.7	1	4.2	0.00077	0.00078	0.00078	120	126	123	07-Feb	1.8825	0.1275	71
119	13 JUN	12.5	11.7	11	3.6	1.3	16.5	0.00147	0.00148	0.00148	163	188	175.5	19-Dec	2.3125	0.1275	76
120	14 JUN	7.1	6.7	6.1			1.92	0.00053	0.00055	0.00054	122	112	117	16-Feb	1.5675	0.1375	76
121	16 JUN **	7.7	7.3	6.7	2.3	0.9	3.09	0.0007	0.0007	0.0007					1.7125		
122	20 JUN **	7.3	7	6.5	2.2	0.8	2.45	0.00056	0.00057	0.00057	154	135	144.5	25-Jan	1.625	0.1175	79
123	21 JUN	11.8	11.2	10.4	3.4	1.2	13.31	0.0013	0.00129	0.0013	122	124	123	17-Feb	2.1575		85
124	21 JUN	11.8	11.3	10.4	3.4	1.3	13.82	0.0015	0.00156	0.00153	150	159	154.5	16-Jan	2.4	0.1175	105
125	21 JUN	11.6	11	10.1	3.5	1.3	13.55	0.00149	0.00144	0.00147	127	134	130.5	09-Feb	2.2575	0.12	80
126	21 JUN	12.7	12	11.1	3.6	1.5	15.92	0.00148	0.00144	0.00146	168	174	171	31-Dec	2.275	0.105	77
127	21 JUN	15.5	14.9	13.9	4.6	1.7	33.71	0.00191	0.00197	0.00194	177	179	178	24-Dec			
128	21 JUN	23.7	22.4	21.2	6.6	2.3	125	0.00627	0.00643	0.00635							
129	24 JUN **	7	6.6	6	2.1	0.8	2.26	0.0007	0.0007	0.0007	142	150	146	28-Jan		0.1375	
130	28 JUN **	9.8	9.2	8.5	2.8	1		0.001	0.00094	0.00097	142	149	145.5	01-Feb		0.1425	
131	02 JUL **	7.8	7.4	6.9	2.4	0.8		0.00069	0.00065	0.00067	140	143	141.5	09-Feb		0.1325	
132	02 JUL **	9.1	8.5	8	2.5	0.9		0.00082	0.00084	0.00083	147	159	153	29-Jan		0.125	
133	03 JUL **	9.4	9	8.4	2.7	0.9		0.00098	0.00104	0.00101	158	169	163.5	19-Jan		0.135	
134	07 JUL **	8.5	8.1	7.5	2.7	1	5.01	0.00083	0.00089	0.00086	163	171	167	20-Jan		0.1375	
135	07 JUL **	9.6	9	8.4	3	1.1	7.06	0.00088	0.00085	0.00087	150	152	151	05-Feb		0.13	
136	07 JUL **	9.4	9	8.3	2.8	1	6.22	0.00086	0.00085	0.00086	157	155	156	31-Jan		0.15	