# ENERGETICS OF THE SHAD SPAWNING MIGRATION

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WEIGHT LOSS AND ASSOCIATED ENERGY
EXPENDITURE OF AMERICAN SHAD (ALOSA
SAPIDISSIMA, WILSON) DURING THE FRESH-
WATER SPAWNING MIGRATION.

by

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## ABSTRACT

The nature and extent of weight loss and energy utilization by shad (Alosa sapidissima, Wilson), which do not feed in freshwater, was studied in three Atlantic coast rivers. The significance of geographical differences in tissue weight dynamics and bioenergetics was evaluated in terms of adult mortality and of adaptive shifts in the pattern of energy utilization in response to the environment of the home river. Intra-population differences in energy utilization were also examined in relation to timing of migrations.

The variables influencing the rate and extent of energy utilization were distance to spawning areas, water temperature and current velocity, and extent of gonad development in freshwater. Distance was the most important determinant of total energy demand associated with the freshwater migration. The long migration to the spawning grounds in Florida resulted in extensive utilization of energy reserves (70–80%) and complete postspawning mortality. Reduced depletion (30-60%) and postspawning survival were associated with the shorter migrations in Connecticut and Virginia. The greater migration efficiency (kcal expended/kg body weight/km of upriver displacement) in Florida and Virginia (average of 4.5 vs. 6.8 in Connecticut), despite generally higher water temperatures in these southern rivers, was due to reduced current velocities encountered. High water temperatures did account for the reduced migration efficiency of late migrants within the Connecticut population (average of 8.8 vs. 5.7

for earlier migrants) and thus a greater depletion and higher postspawning mortality among these individuals. Extensive gonad development of Connecticut and Virginia shad during active oceanic feeding reduced energy demands for this purpose during the freshwater fast. Conversely, significant increases (20-80%) in the gonad energy content of Florida shad in freshwater clearly taxed the available reserves of these migrants and contributed to complete postspawning mortality.

Shad appear to be highly adapted both energetically and reproductively to their specific home rivers. Larger body size and later mean age at maturity of Connecticut River shad may be an adaptation to increase energy reserves and thereby enhance postspawning survival necessary for population stability in a fluctuating environment. Florida shad maintain a high reproductive potential, despite small body size and complete postspawning mortality, by greatly increasing relative fecundity. Higher fecundity is possible by a reduced allocation of energy per ovum (0.4 cal vs. 1.3 cal for the Virginia and Connecticut populations). Furthermore, the migration rate of shad, near the speed of maximum metabolic efficiency (one body length/sec), may be an adaptation to maximize spawning success and postspawning survival by reducing the energetic cost of swimming.

Extension of the Connecticut River migration to the historical range of the species in the river will significantly alter the population structure. Shad spawning in areas above existing sites will experience significantly higher energy costs and proportionately higher postspawning mortality. Thus an increasing proportion of virgin fish in the Connecticut population is predicted as the restoration program proceeds.

RESUME

L'auteur a étudié dans trois rivières de la côte atlantique la nature et l'importance (1) de la perte de poids corporel, et (2) de l'utilisation des réserves énergétiques, chez l'Alose (Alosa sapidissima, Wilson), qui ne s'alimente pas au cours de sa migration en eau douce. Les changements observés dans le poids des tissus du poisson et dans la bioénergétique de ceux-ci varient d'une rivière à l'autre; la signification de ces différences géographiques a été évaluée en rapport avec la mortalité des adultes et les modifications adaptatives (déterminées par les conditions de vie de la rivière natale) dans le patron d'utilisation des réserves énergétiques. Les différences qui apparaissent également au sein de chaque population dans l'utilisation des réserves énergétiques ont été analysées en relation avec la période d'amorce des migrations.

Le taux et l'importance de l'utilisation des réserves énergétiques sont influencés par les facteurs suivants: l'éloignement des frayères, la température de l'eau et la vitesse des courants, le degré de maturation des gonades en eau douce. La distance à parcourir pour atteindre les frayères est le plus important des facteurs qui déterminent le coût énergétique total de la migration en eau douce. La longue migration vers les frayères de Floride entraîne une importante utilisation des réserves énergétiques (70-80%) et une mortalité post-reproductrice qui atteint la totalité des géniteurs. Dans le Connecticut et en Virginie, la dépense énergétique réduite (30-60%) et l'existence d'une survie post-reproductrice sont à associer aux migrations plus courtes qui s'y déroulent.

La vitesse réduite des courants rencontrés par l'Alose en Floride et en Virginie explique que l'efficacité migratoire (une moyenne de 4.5 en comparaison de 6.8 dans le Connecticut, exprimée en kcal dépensées/kg de poids corporel/km de déplacement en amont) est plus grande dans ces rivières méridionales, bien que les températures y soient généralement plus élevées. Dans le Connecticut, ce sont les températures élevées de l'eau qui sont à l'origine de la diminution dans l'efficacité migratoire des migrateurs tardifs de la population (8.8 en comparaison de 5.7 chez les migrateurs les plus en avance), déterminant ainsi chez ces individus une plus grande dépense énergétique et une mortalité post-reproductrice plus élevée. Un important développement des gonades se produit au cours de la période d'alimentation en mer de l'Alose du Connecticut et de Virginie; cette maturation océanique réduit d'autant le coût énergétique de la migration en eau douce au cours de laquelle l'Alose ne s'alimente pas. Par contre on observe chez l'Alose de Floride des augmentations significatives (20-80%) dans le contenu en énergie des gonades pendant la migration en eau douce; cette maturation continentale grève d'une façon évidente les réserves énergétiques disponibles chez ces migrateurs et contribue à leur importante mortalité post-reproductrice.

L'Alose apparaît profondément adaptée à la rivière natale qui lui est propre, tant d'un point de vue énergétique que reproducteur. L'Alose de la rivière Connecticut présente en effet une taille plus grande et une moyenne plus élevée de l'âge à maturité. Ces caractères pourraient être des adaptations assurant l'augmentation des réserves énergétiques, et de ce fait l'accroissement de la survie post-reproductrice, celle-ci étant nécessaire à la stabilité de la population dans un milieu changeant. Chez l'Alose de Floride, de plus petite taille et dont la mortalité post-reproductrice est totale, l'augmentation adaptative considérable de la fécondité assure malgré tout un potentiel reproducteur élevé. Cette fécondité accrue s'explique par une mise en réserve énergétique réduite au niveau de chaque ovule (0.4 cal en comparaison de 1.3 cal pour les populations des rivières York et Connecticut). Les vitesses de migration de l'Alose sont par ailleurs proches des vitesses d'efficacité métabolique maximale (une longueur de corps/seconde). On peut donc considérer qu'en réduisant ainsi le coût énergétique du déplacement du poisson, la vitesse de migration pourrait être une adaptation qui maximise le succès de la reproduction et la survie post-reproductrice.

Permettre à la migration de la rivière Connecticut qu'elle s'étende à l'ensemble de l'aire de dispersion historique de l'espèce dans cette rivière va entraîner d'une façon significative l'altération de la structure de la population. L'Alose amenée à se reproduire dans des frayères situées en amont des sites présentement occupés à cette fin vont subir des dépenses énergétiques significativement plus grandes et une mortalité post-reproductrice proportionnellement plus élevée. Par voie de conséquence on prédit qu'une proportion croissante de poissons adultes mais n'ayant encore jamais frayé doit apparaître au sein de la population de la rivière Connecticut, au fur et à mesure de l'avancement du programme d'aménagement de l'espèce.

TABLE OF CONTENTS

TABLE OF CONTENTS (cont'd)

LIST OF FIGURES

LIST OF FIGURES (cont'd)

# LIST OF TABLES

# LIST OF APPENDICES

LIST OF APPENDICES (cont'd)

LIST OF APPENDICES (cont'd)

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# STATEMENT OF CONTRIBUTION TO ORIGINAL KNOWLEDGE

The author believes this study has contributed to original knowledge in the following ways:

1. This study has provided the first detailed information on the tissue weight changes and energy costs associated with the spawning migration of American shad.

2. Geographic variation in the bioenergetics of fish migration has been demonstrated for the first time.

3. The estimates of <u>in situ</u> metabolic responses by fish to environmental factors are first reports and corroborate the findings from laboratory studies.

4. The study offers the first evidence that population specific reproductive adaptations by shad may in fact be elaborations of energetic adaptation to local environment.

# PREFACE

This thesis has been written to confirm to section 7, Information Concerning Theses, Faculty of Graduate Studies and Research, McGill University. A paper[1], based on research for this degree and submitted for publication, has been incorporated into the main body of the thesis.

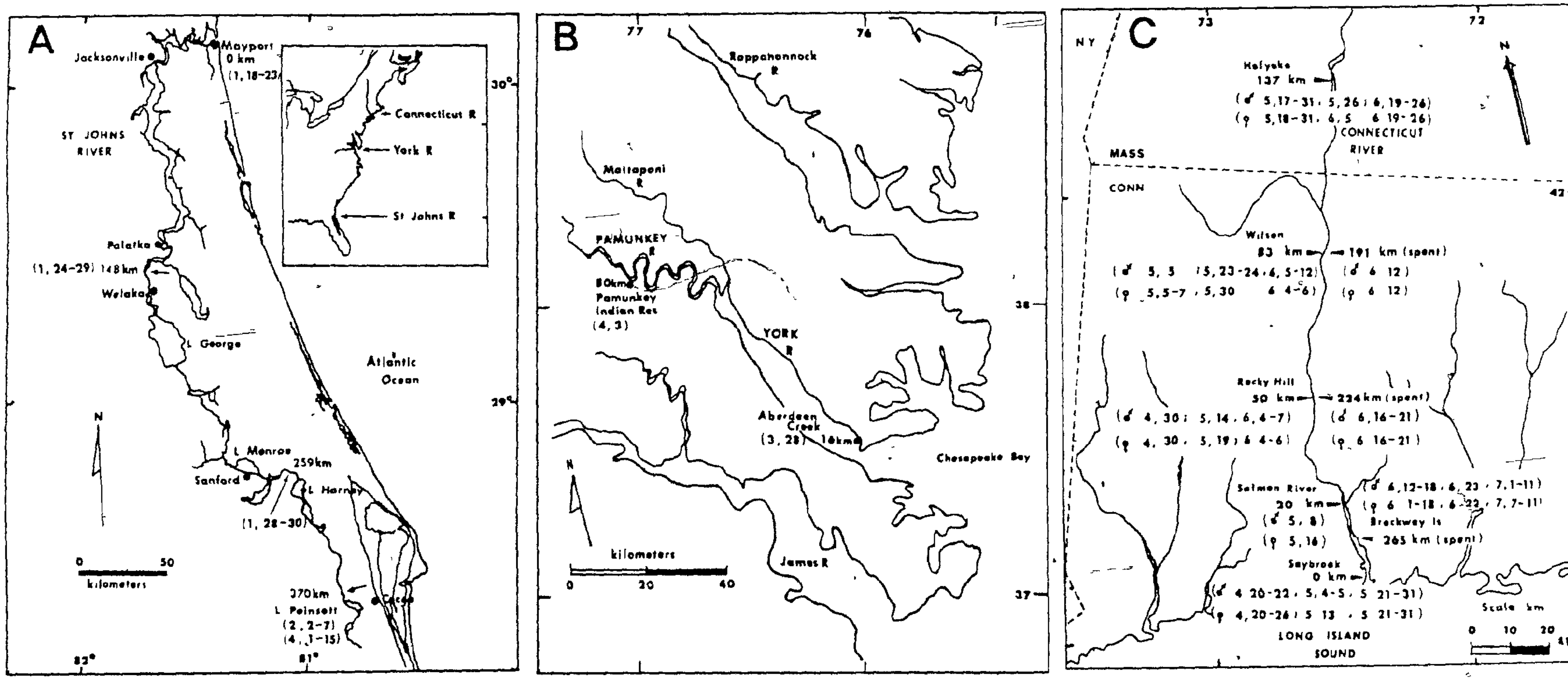
[1] Glebe, B.D., and W.C. Leggett, "Bioenergetics of the Freshwater Spawning Migration of Shad (Alosa sapidissima, Wilson)". J. Fish. Res. Bd. Canada (submitted).

# Introduction

Several anadromous fish species make extensive freshwater migrations without feeding. Concomitant high adult mortality frequently occurs and is often associated with extensive weight loss and energy depletion (Pacific salmon, Idler and Clemens, 1959; Atlantic salmon, Greene, 1926; Belding, 1934; steelhead, Robertson et. al., 1961, Withler, 1966; lamprey, McCay, 1931). American shad (Alosa sapidissima, Wilson) consume little or no food during their extensive freshwater migrations (Leim, 1924; Leach, 1925; Moss, 1946; Atkinson, 1951) and, too, they suffer high, and in some populations complete, mortality at this time. Reported weight losses (Chittenden, 1969; Leggett, 1972) ranging from 30 to 50%, levels associated with death in other species (Belding, 1934), suggest depletion of energy reserves may be a major factor in this mortality. If so, latitudinal variation in spawning mortality, indicated by the clinal change in the proportion of repeat spawners (Leim, 1924; Mansueti and Kolb, 1953; Leggett, 1969), may also result from differential weight loss and energy expenditures during the freshwater migration.

In this study the nature and extent of weight loss and energy utilization by shad during the freshwater migration was determined at three latitudes (Fig. 1) and its significance evaluated in terms of adult mortality and of possible adaptive shifts in the pattern of energy utilization in the three populations. Temporal intrapopulation differences in energy utilization were also examined in relation to varying environmental conditions consequential to the timing of migrations.

Figure 1. Sampling locations and schedule. Total channel distances (round trip distances to Holyoke for spent migrants in the Connecticut River) travelled by shad to each station are given. Collection dates are indicated in parentheses (e.g. (1, 18-23) = January 18-23).



A
Jacksonville
Mayport
0 km
(1, 18-23)
30°
Connecticut R
York R
St Johns R
ST JOHNS
RIVER
Palatka
(1, 24-29) 148 km
Welaka
L George
Atlantic
Ocean
29°
N
L Monroe
259km
Sanford
L Harney
(1, 28-30)
0
50
kilometers
370km
L Poinsett
(2, 2-7)
(4, 1-15)
82°
81°
B
77
76
Rappahannock
R
Mattaponi
R
PAMUNKEY
R
80km
Pamunkey
Indian Res
(4, 3)
YORK
R
38
Aberdeen
Creek
(3, 28)
18km
Chesapeake Bay
N
kilometers
0
20
40
James R
37
C
73
72
N Y
Holyoke
137 km
(♂ 5,17-31, 5,26 ; 6,19-26)
(♀ 5,18-31, 6,5 6 19-26)
CONNECTICUT
RIVER
N
MASS
CONN
42
Wilson
83 km
191 km (spent)
(♂ 5, 5 ; 5,23-24, 6, 5-12)
(♀ 5,5-7, 5,30 6 4-6)
(♂ 6 12)
(♀ 6 12)
Rocky Hill
50 km
224 km (spent)
(♂ 4, 30 ; 5, 14, 6, 4-7)
(♀ 4, 30, 5, 19 ; 6 4-6)
(♂ 6,16-21)
(♀ 6 16-21)
Salmon River
20 km
(♂ 5, 8)
(♀ 5, 16)
(♂ 6,12-18, 6, 23, 7,1-11)
(♀ 6 1-18, 6-22, 7, 7-11)
Brockway Is
265 km (spent)
Saybrook
0 km
(♂ 4 20-22, 5,4-5, 5 21-31)
(♀ 4,20-26 ; 5 13, 5 21-31)
LONG ISLAND
SOUND
Scale km
0
10
20
41

# Materials and Methods

## SAMPLING LOCATIONS

In 1972, 348 shad were collected at eight Connecticut River stations (Fig. 1C) distributed along the freshwater migratory route from Saybrook at the river mouth to Holyoke Dam, the approximate upper limit of the migration for the majority of the population (Marcy, 1972). Gill nets (11.4 and 14.0 cm stretched mesh) were utilized to collect unspent specimens at Saybrook, Salmon River, Rocky Hill, Wilson, and spent downriver migrants at Wilson, Rocky Hill and Brockway Island. Unspent fish collected at Holyoke were taken from a fish lift operated by the Holyoke Water Power Company. In addition 24 spent shad were sampled from a haul seine (7.6 cm stretched mesh) operated at Wilson by the Connecticut Department of Environmental Protection.

In 1973, 367 shad were collected at five Connecticut River stations (Saybrook, Rocky Hill, Wilson, Holyoke and Brockway Island). Collection methods were identical to those employed in 1972.

In the St. Johns River, Florida, 268 shad were collected in 1974 at five stations distributed along the migratory route (Fig. 1A) from Mayport at the river mouth to Lake Poinsett, the upper limit of the spawning migration (Williams and Bruger, 1972). Methods of collection varied from station to station and are summarized below:

| Station | Gear |
|---|---|
| Mayport | - gill nets (11.4, 12.7, and 14.0 cm stretched mesh) |

| | |
|---|---|
| Welaka | - commercial haul seine (6.3 cm stretched mesh) |
| Lake George | - gill nets (11.4 and 12.7 cm stretched mesh) |
| Lake Poinsett | - gill nets (11.4 and 12.7 cm stretched mesh) |
| | - tramel net (25.4 cm and 5.0 cm square meshes) |
| | - angling |

In 1976, 83 adult shad were collected at two stations in the York River system (Fig. 1B) with 12.7 cm (stretched mesh) gill nets.

SAMPLING SCHEDULE

In the Connecticut River discrete collections of male and female shad were made at the peak of the migration (1972) and early and late in the run (1973). This temporal separation was achieved by plotting the daily catch per unit effort (C/UE) of males and females in an experimental drift gill net fished at the river mouth (Connecticut River Ecological Study (CRES)) during the years 1967 to 1971. Comparison of these trends with the daily C/UE of the same gear fished in 1972 allowed the prediction of the timing of the peak entry of male and female shad into the river in 1972. In 1973, sampling of early male and female migrants at the river mouth coincided with their first appearance in the CRES catches. Sampling for late migrants was initiated when C/UE began to decline rapidly, indicating the approaching termination of the run. The same segment of the population (associated with peak, early and late migrants) was sampled at upriver locations by calculating average rates of upriver migration for males and females from CRES tagging data and timing sampling to this movement. The upriver migration rate was calculated as the slope of the least squares relationship between the average number of days tagged shad were free and the distance travelled to specific upstream recovery sites for the years 1967 to 1971. The timing of the peak entry of shad into the river in 1972 and the realized upstream migration rates for 1972 and 1973 were determined and checked for agreement with predicted values used to determine the sampling sequences.

Upstream migration rates of Florida and Virginia shad are unknown. Therefore, no attempt was made to sample the same segment of these populations at each station. Concurrent sampling of males and females was initiated at the river mouth in late January (Florida) and late March (Virginia) when peak numbers of shad historically enter these rivers (Leggett and Whitney, 1972). Upriver stations were then sampled without delay. Later, the Poinsett Lake station (Florida) was resampled for spent shad. No effort was made to sample spent fish in the York River.

SELECTION OF SHAD FOR SAMPLING

To assess the relationship between weight loss, energy expenditure and body length, shad sacrificed at each Connecticut and Florida location were selected according to predetermined length categories based on reported length ranges (Carlander, 1969). Connecticut River categories were 43-45 cm, 46-48 cm, and 49-51 cm for males and 44-47 cm, 48-51 cm, and 52-55 cm for females. Approximately eight shad were selected in each size category at most stations. Difficulty was experienced in procuring adequate numbers at the Salmon River, Wilson and Rocky Hill stations in 1972, and these stations were dropped from the 1973 sampling schedule. Only unspent fish from catches of upriver migrants, and only fully spent shad from catches of downriver migrants were used in the analyses. The Florida length categories were 33-35 cm, 37-39 cm, and 41-43 cm for males and 38-40 cm, 40-42 cm, and 42-44 cm for females. Approximately ten ripening shad were selected in each size category. However, all spent shad collected at Lake Poinsett were kept because of their scarcity.

In the York River, only one size class of males (37 ± 1.0 cm) and females (42 ± 1.0 cm), representative of the most frequent size class in the population, was sampled. Approximately twenty individuals of each sex were collected at each station.

Water temperature was recorded coincident with sampling in the Connecticut and St. John's Rivers. The Virginia Institute of Marine Science provided water temperature data for the period encompassing the York River shad migration.

The magnitudes of angular displacements during upriver migrations (Khalturin, 1967) were used to indicate relative current velocities experienced by migrants in the three study rivers.

TREATMENT OF SACRIFICED FISH

Immediately after capture all fish were sealed in polyethylene bags. Removal to the laboratory was generally accomplished within six hours of capture. For longer delays (maximum 12 hours) the bags were packed in ice. In the laboratory, fork length was determined to the nearest 0.5 cm.

Gonad, viscera and somatic (eviscerated body) weights were determined to the nearest gram. Somatic tissue was homogenized in a one gallon Waring blender. Approximately 400 g of somatic homogenate, and the entire gonad and viscera were individually sealed in evacuated polyethylene bags and stored at $-34^{\circ}C$ until chemical analyses were performed. Total age, age at maturity and spawning history were determined by scale reading (Cating, 1953; Judy, 1961).

BIOCHEMICAL ANALYSIS OF TISSUE SAMPLES

Proximate analyses of total protein, fat and moisture were performed on the gonad, viscera and somatic tissue of all Florida shad and Connecticut shad collected in 1972. These analyses indicated somatic constituents supplied over 90% of the migratory energy requirements. Therefore only the somatic tissues of the Connecticut samples obtained in 1973 were analyzed. Prior to the analyses, gonads and viscera were homogenized and somatic tissues re-homogenized (to incorporate water separated during frozen storage). Moisture was determined by drying 5-20 g samples (depending on the amount of tissue available) to a constant weight at $90^{\circ}C$. Fat content of the dried viscera and somatic tissue was quantified by the method of Korn and Macedo (1973). Gonad fat was extracted with diethyl ether in a Soxhlet apparatus. Total nitrogen was determined by the nesslerization of Kjeldahl digests (Middleton, 1960) of 1.5 g wet samples using selenium as a catalyst (Strickland and Parsons, 1972). Intensity of the Nessler colour complex was measured on a Unicam SP 600 spectrophotometer using a 4 cm cell. Protein content was estimated by multiplying total nitrogen values by 6.25 (Dowgiallo, 1975). Ash content of all Connecticut River shad tissues collected in 1972 was determined by combusting 1-5 g dry samples to a constant weight (approximately 24 hours of combustion time) at 550$^{\circ}$C in a muffle furnace (Horwitz, 1965). All tissue constituent analyses were performed in duplicate.

Energy expenditures and reallocations by Florida and Connecticut shad were determined by applying caloric equivalents (5.7 kcal/g for protein; 9.5 kcal/g for fat) (Kleiber, 1975) to changes in the energy yielding constituents of the gonad, viscera and somatic tissues. Similar data was obtained for York River shad by combustion of one gram dry samples (no replication) of gonad, viscera and somatic tissue in a Parr non-adiabatic oxygen macro-bomb calorimeter. The equivalence of estimates of tissue energy content using the heat of oxidation method and caloric equivalents of tissue fat and protein content was determined by chi-square analyses of estimates using both methods on 12 tissue samples.

## TISSUE WEIGHT DYNAMICS

Gonad, viscera, and somatic weight changes during the migration in the St. Johns and Connecticut Rivers were studied by comparing regression equations expressing the relationship between these parameters and length at subsequent sampling locations. Simple linear regressions on length were used because logarithmic transformation and polynomial regressions failed to significantly reduce residual variance. Tissue weights (predicted by regression equations) of shad collected at upriver sampling sites were expressed as percentages of the predicted tissue weights of fish of identical size at time of entry into the river (0 km) and the resulting relationships were plotted. Significant differences in temporal and interpopulation changes during the freshwater migration were determined by comparing appropriate pairs of regression equations for equality of slopes and adjusted means by analyses of covariance (Snedecor and Cochran, 1967).

Percentage change in gonad, viscera and somatic weights of York River shad during the migration from the river mouth (km 16) to the spawning grounds was calculated using mean values at each station. The significance of changes was determined using Student's T test (Snedecor and Cochran, 1967).

The extent of gonad development at the time of entry into freshwater was determined by expressing gonad weight as a proportion of somatic weight for shad collected at the river mouth (Vladykov, 1956). In the calculation of this gonad maturity index for Florida and Connecticut shad, gonad and somatic weights predicted from the appropriate regression equations were used.

TISSUE ENERGY DYNAMICS

Simple linear regressions of tissue energy content on fork length were used to calculate proportional and absolute changes in tissue energy content during the migration in the Connecticut and St. Johns Rivers. Proportional changes were determined by comparing the energy content of gonad, viscera and somatic tissues in shad of varying lengths sampled at the river mouth with corresponding energy values for fish of equivalent lengths sampled at upriver locations. Changes in tissue energy content were expressed as proportions of the initial (river entry) energy content. Absolute tissue energy changes during the freshwater migration were calculated only for the "standard" fish (mean length) in the populations.

The significance of temporal and between population differences in tissue energy changes during the freshwater migration were determined by comparing appropriate pairs of regression equations for equality of slopes and adjusted means by analysis of covariance as was done in the analysis of tissue weight dynamics. Because variability in energy content increased relative to tissue weight variability (due to compounding variation by summing protein and fat energy components) fewer length/tissue energy content regressions were significant. However, analysis of covariance remained valid for comparison of non-significant regressions. Only the robustness of the comparisons was lost. Thus, some significant differences in slope and elevation may not have been detected.

Proportional and absolute energy changes in the gonad, viscera and somatic tissues of York River shad were determined in a manner similar to that used in the assessment of energy changes in Florida and Connecticut shad tissues except that sample means for each station rather than predicted values were used in the calculations.

## Results

### UPSTREAM MIGRATION RATES AND SAMPLING SCHEDULE

Upriver migration rates (slopes of regression lines) calculated from the relationship between distance traveled and corresponding days free for tagged migrant shad did not vary significantly from year to year. Therefore a single regression line was fitted to the combined displacement data for the years 1967 to 1971 to determine overall migration rates (5.9 and 6.1 km/day) for males and females respectively (Fig. 2). These rates were used to determine sampling times at successive Connecticut River stations in 1972 and 1973. A posteriori determinations of migration rates indicated that the realized rates were 5.7 and 5.7 km/day for males and 6.8 and 8.2 km/day for females in 1972 and 1973 respectively.

Sampling of male shad in the Connecticut River in 1972 was initiated on May 4. A posteriori analysis of C/UE data indicated the median C/UE actually occurred on May 6. Sampling of females was delayed nine days (May 13) in accord with the average nine day separation between peaks during 1967 to 1971. The calculated median C/UE for females in 1972 coincided with the predicted date (May 13). In 1973 sampling of early and late run fish commenced on April 20 and May 21 respectively.

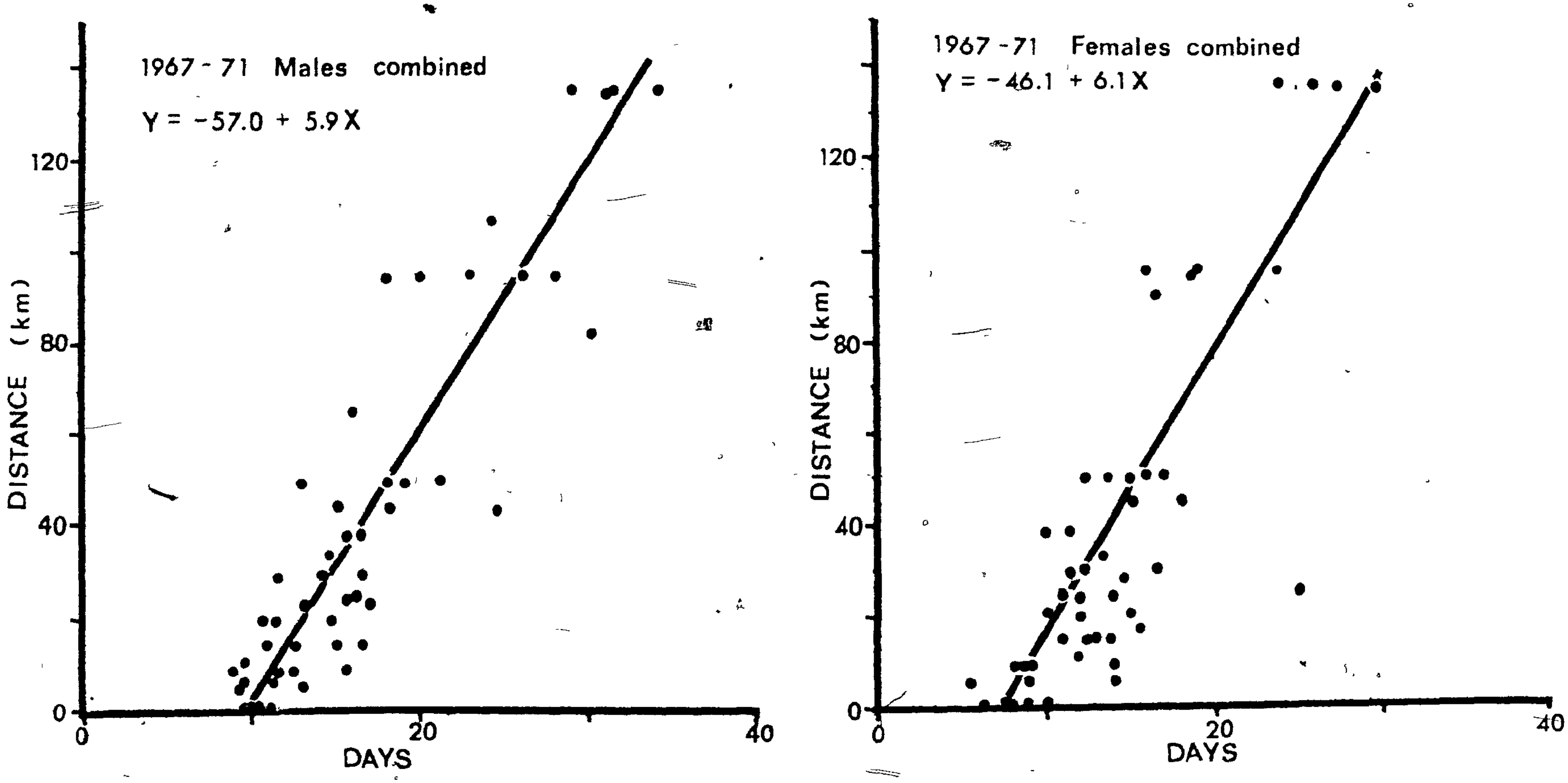
Sampling dates in all three rivers are given in Figure 1.

GONAD MATURITY AND WEIGHT CHANGE

Regression relationships used to analyze changes in gonad weights and relative maturity are given in Table 1.

Significant intra- and interpopulation differences in the degree of gonad development at the time of river entry were found (Fig. 3; Table 2). Within rivers, the ovaries of large Florida and small Connecticut shad were less developed than those of other individuals in their respective populations, while differences in the degree of testes development were small.

Figure 2. The relationship (sexes separate) between days free after tagging (X) and distance travelled (Y) for the years 1967-1971 combined.



1967 - 71 Males combined
Y = -57.0 + 5.9 X
DISTANCE (km)
0
40
80
120
DAYS
0
20
40
1967 - 71 Females combined
Y = -46.1 + 6.1 X
DISTANCE (km)
0
40
80
120
DAYS
0
20
40

Table 1 Linear regression coefficients for body length/tissue weight relationships for Connecticut and St Johns River shad Equations take the form Y = C + bX where Y is predicted tissue weight and X is fork length (* p>0 05)

| Connecticut River | | | | | | | | | St Johns River | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sex and tissue | Reprod stage | Km along mig'n route | Peak (1972) C | Peak (1972) b | Early (1973) C | Early (1973) b | Late (1973) C | Late (1973) b | Sex and tissue | Reprod stage | Km along mig'n route | (1974) C | (1974) b |
| Male | Maturing | 0 | -212 66 | 7 24 | -304 59 | 8 99 | -177 68 | 4 72 | Male | Maturing | 0 | - 73 87 | 2 54 |
| gonad | " | 20 | -179 76 | 6 42 | - | - | - | - | gonad | " | 148 | - 69 69 | 2 64 |
| | " | 50 | -263 39 | 8 37 | -309 05 | 9 23 | - 82 01 | 3 18 | | " | 259 | - 54 57 | 2 42 |
| | " | 83 | -162 33 | 5 97 | -259 25 | 8 11 | - 25 75 | 1 91* | | " | 370 | - 76 48 | 2 71 |
| | " | 137 | -137 40 | 5 01 | -121 40 | 4 84 | -125 09 | 4 02 | | | | | |
| | Spent | 191 | - 84 61 | 2 95 | - | - | - | - | | Spent | 370 | 11 26 | 0 43* |
| | " | 224 | - 79 47 | 2 59 | - | - | - | - | | | | | |
| | " | 265 | - 70 21 | 2 25 | -125 05 | 3 48 | - 23 13 | 1 01* | | | | | |
| Female | Maturing | 0 | -750 50 | 21 18 | -549 65 | 16 24 | -612 67 | 16 94 | Female | Maturing | 0 | - 95 24 | 4 23 |
| gonad | " | 20 | -1000 63 | 26 26 | - | - | - | - | gonad | " | 148 | -293 28 | 9 83 |
| | " | 50 | -436 39 | 14 36 | -572 06 | 17 04 | -197 99 | 2 18* | | " | 259 | -200 58 | 8 45 |
| | " | 83 | -630 59 | 18 93 | -838 57 | 24 04 | -652 70 | 18 09 | | " | 370 | -847 34 | 23 26 |
| | " | 137 | -190 35 | 9 15 | -756 78 | 21 17 | -245 31 | 8 63* | | | | | |
| | Spent | 191 | -469 65 | 11 03 | - | - | - | - | | Spent | 370 | -144 20 | 4 89* |
| | " | 224 | - 68 13 | 2 42* | - | - | - | - | | | | | |
| | " | 265 | - 30 25 | 1 66* | - 62 84 | 2 31* | - 27.59 | 1.71* | | | | | |
| Male | Maturing | 0 | -106 71 | 4.32 | - 91 23 | 4 03 | -143 25 | 4 97 | Male | Maturing | 0 | - 88 96 | 3 44 |
| viscera | " | 20 | - 97 10 | 3 94 | - | - | - | - | viscera | " | 148 | - 79 11 | 3 06 |
| | " | 50 | -138 84 | 4 69 | - 85 02 | 3 46 | - 69 92 | 2 56 | | " | 259 | - 11 65 | 1 02* |
| | " | 83 | - 62 58 | 2 73 | -106 24 | 3 91 | - 99 23 | 3 22 | | " | 370 | - 7 10 | 0 78* |
| | " | 137 | - 63 35 | 2 38 | - 92 61 | 3 05 | -111 07 | 3 33 | | | | | |
| | Spent | 191 | - 97 91 | 3 14 | - | - | - | - | | Spent | 370 | - 1 08 | 0 51* |
| | " | 224 | -103 67 | 3 27 | - | - | - | - | | | | | |
| | " | 265 | -117 46 | 3 54 | -117 37 | 3 57 | -105 43 | 3 18 | | | | | |
| Female | Maturing | 0 | -111 16 | 4 62 | - 75 48 | 3 79 | -106 24 | 4 40 | Female | Maturing | 0 | -123 98 | 4 23 |
| viscera | " | 20 | -151 83 | 5 29 | - | - | - | - | viscera | " | 148 | - 48 11 | 2 35 |
| | " | 50 | -262 77 | 7 30 | -158 73 | 5 16 | -119.27 | 3 94 | | " | 259 | - 53 50 | 2 29 |
| | " | 83 | -145 96 | 4 61 | -314 20 | 8 62 | -151 22 | 4 64 | | " | 370 | - 75 53 | 2 64 |
| | " | 137 | -141 40 | 4 02 | -193 27 | 5 42 | -172 31 | 4 66 | | | | | |
| | Spent | 191 | -140 59 | 4 05 | - | - | - | - | | Spent | 370 | - 71 46 | 2 44 |
| | " | 224 | -150 50 | 4 34 | - | - | - | - | | | | | |
| | " | 265 | -150 24 | 4 23 | -212 19 | 5 70 | -104 21 | 3 22 | | | | | |
| Male | Maturing | 0 | -2617 85 | 90 22 | -2809 11 | 91 92 | -2707.45 | 88 63 | Male | Maturing | 0 | -1762 74 | 68 12 |
| somatic | " | 20 | -2752 51 | 93 97 | - | - | - | - | Somatic | " | 148 | -1803 64 | 67 85 |
| | " | 50 | -2537 26 | 87 58 | -2388 96 | 82 19 | -1793 34 | 64 89 | | " | 259 | -1089 30 | 47 61 |
| | " | 83 | -2310 72 | 82 59 | -2609 79 | 85 89 | -2008 22 | 68 54 | | " | 370 | -1171 88 | 48.03 |
| | " | 137 | -1638 25 | 63 76 | -2078 71 | 71 54 | -2078 01 | 68 13 | | | | | |
| | Spent | 191 | -1818 30 | 63 79 | - | - | - | - | | Spent | 370 | -699 29 | 33 66 |
| | " | 224 | -2138 80 | 70 89 | - | - | - | - | | | | | |
| | " | 265 | -1999 48 | 67.36 | -1432 42 | 52 89 | -1557 31 | 53 33 | | | | | |
| Female | Maturing | 0 | -3581 54 | 111 04 | -2757 86 | 90 84 | -2833 74 | 92 86 | Female | Maturing | 0 | -2555 48 | 87.96 |
| somatic | " | 20 | -3144 29 | 102 78 | - | - | - | - | somatic | " | 148 | -2106 46 | 77 44 |
| | " | 50 | -4566 22 | 131 38 | -2893 62 | 92 58 | -1467 14 | 60 24 | | " | 259 | -1250 37 | 51,74 |
| | " | 83 | -3605 57 | 106 68 | -3726 61 | 110 62 | -2163 57 | 73 64 | | " | 370 | -1835 03 | 63 39 |
| | " | 137 | -3368 28 | 100 85 | -3085 09 | 93 55 | -2319 08 | 73 82 | | | | | |
| | Spent | 191 | -3327 56 | 96 12 | - | - | - | - | | Spent | 370 | -846.70 | 35,28 |
| | " | 224 | -2697 21 | 81 66 | - | - | - | - | | | | | |
| | " | 265 | -2602 21 | 80 01 | -2516 30 | 76 75 | -1474 31 | 51 77 | | | | | |

Figure 3. Relative maturity of gonads at river entry as indicated by the ratio of gonad to somatic weights.

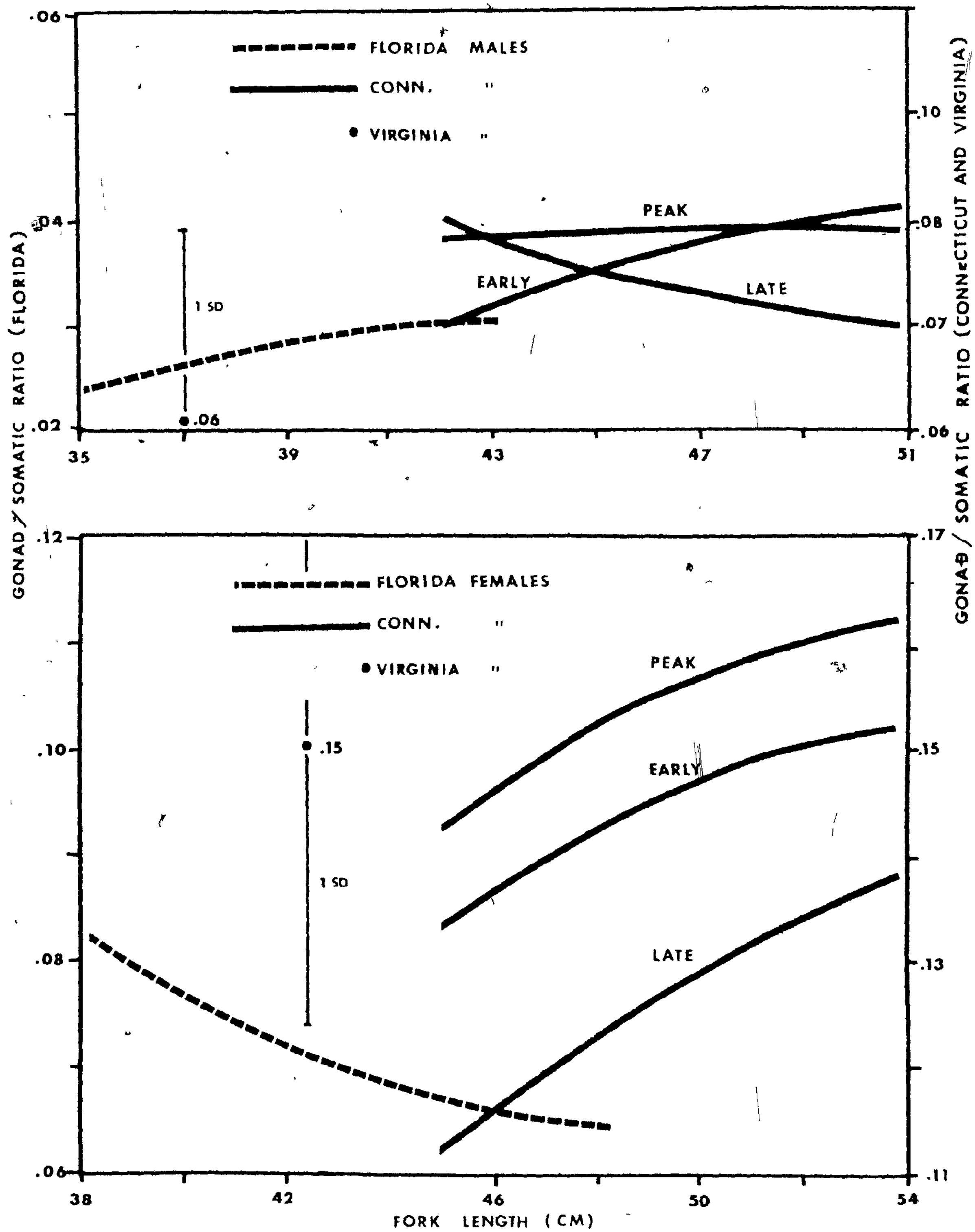

FLORIDA MALES
CONN. "
VIRGINIA "
PEAK
EARLY
LATE
1 SD
.06
.04
.02
35
39
43
47
51
.10
.08
.07
.06
GONAD / SOMATIC RATIO (FLORIDA)
GONAD / SOMATIC RATIO (CONNECTICUT AND VIRGINIA)
FLORIDA FEMALES
CONN. "
VIRGINIA "
PEAK
EARLY
LATE
1 SD
.15
.12
.10
.08
.06
.17
.13
.11
38
42
46
50
54
FORK LENGTH (CM)

Table 2. F values for analysis of covariance of length/gonad weight regressions for fish sampled at the river mouth, at the spawning areas and following spawning. (+) or (-) indicates slopes and elevations of the regressions on the horizontal are significantly greater (+) or less (-) than the slopes and elevations on the vertical ($p<0.01$).

| | Male | | | | | | Female | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Florida | | Conn. Peak | | Conn. Early | | Florida | | Conn. Peak | | Conn. Early | |
| | slope | elevation | slope | elevation | slope | elevation | slope | elevation | slope | elevation | slope | elevation |
| RIVER MOUTH (0 km.) | | | | | | | | | | | | |
| Conn. Peak | 6.2 | 104.8(-) | | | | | 24.5(-) | 50.6(-) | | | | |
| Early | 14.3(-) | 50.6(-) | 0.9 | 5.0 | | | 9.8(-) | 43.0(-) | 0.7 | 7.1 | | |
| Late | 1.1 | 44.2(-) | 1.3 | 10.6(+) | 3.4 | 2.2 | 17.6(-) | 33.0(-) | 0.7 | 25.8(+) | 0.0 | 4.2 |
| MAJOR SPAWNING AREAS (370 km. Florida, 137 km. Conn.) | | | | | | | | | | | | |
| Conn. Peak | 1.3 | 37.7(-) | | | | | 2.3 | 1.4 | | | | |
| Early | 1.8 | 56.1(-) | 0.0 | 2.4 | | | 0.0 | 0.1 | 2.1 | 0.5 | | |
| Late | 0.5 | 0.7 | 0.2 | 29.3(+) | 0.1 | 62.5(+) | 2.8 | 2.4 | 0.0 | 12.5(+) | 1.8 | 14.4(+) |
| SPENT FISH (370 km. Florida, 265 km. Conn.) | | | | | | | | | | | | |
| Conn. Peak | 1.5 | 13.5(-) | | | | | 1.2 | 2.8 | | | | |
| Early | 3.1 | 11.6(-) | 3.0 | 0.6 | | | 1.0 | 5.8 | 0.1 | 0.0 | | |
| Late | 0.1 | 8.2(-) | 2.6 | 12.5(+) | 6.3 | 9.4(+) | 1.1 | 2.5 | 0.0 | 0.5 | 0.1 | 1.0 |

In the Connecticut River only females showed a marked temporal variation in gonad development. Ovaries of females entering the river late in the run were significantly less developed than those migrating at the time of peak abundance or early. Between river comparisons revealed that the gonads of Florida shad were significantly less developed than those of Connecticut migrants (Table 2). The maturity of gonads of Virginia shad was similar to that of Connecticut shad (Fig. 3).

During the upriver migration of St. Johns and York River shad a significant increase in the gonad weight of both males and females occurred (Figs. 4, 5). The maximum increase in testes weight in Florida ranged from 40 to 100%, depending on the size of the individual. The smaller, less mature males experienced the greatest proportional increases. The 21% increase in Virginia shad testes weight was considerably less than testes weight increases of even the smallest Florida males. The maximum observed increase in ovary weight was 20% in Virginia and ranged from 40 to 100% in Florida. The greatest increases were exhibited by the largest St. Johns River females (whose ovaries were least developed at time of entry into the river). In Florida the continued increase in the gonad weight of both sexes to 259 km indicated that little or no spawning occurred below this point. A subsequent significant decrease (covariance $F_{(1,56)} = 21.0$, $p < 0.01$ (males); $F_{(1,48)} = 13.4$, $p < 0.01$ (females)) in the length/gonad weight relationship at 370 km suggested some spawning had occurred between km 259 and 370. This finding is consistent with the reported distribution of spawning areas in the St. Johns River (Williams and Bruger, 1972). Visual comparison of the testes of these

Figure 4. Proportional changes in testes weight (relative to weight at the river mouth) at various distances (km) from the sea. Analysis of covariance F values for differences between slopes and elevations of linear regression lines used to generate the curves (Connecticut and Florida) and t values for comparisons of mean weight at river mouth and spawning grounds (Virginia) are given (→, $p < 0.01$; –, comparisons not made). * indicates % weight change/body length trends were estimated from one non-significant ($p > 0.05$) linear regression (see Table 1). These curves were included to indicate relative elevations which are meaningful.

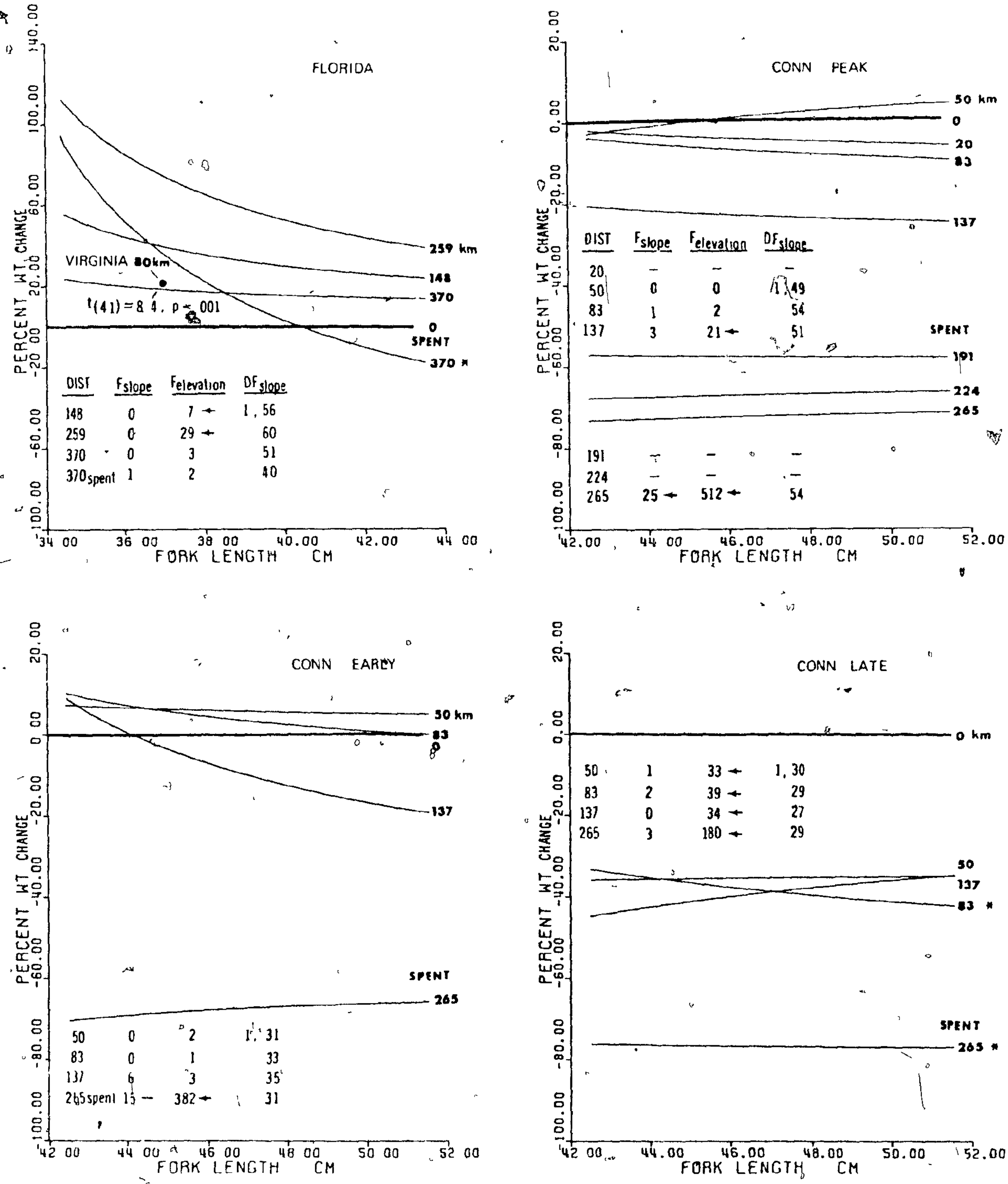
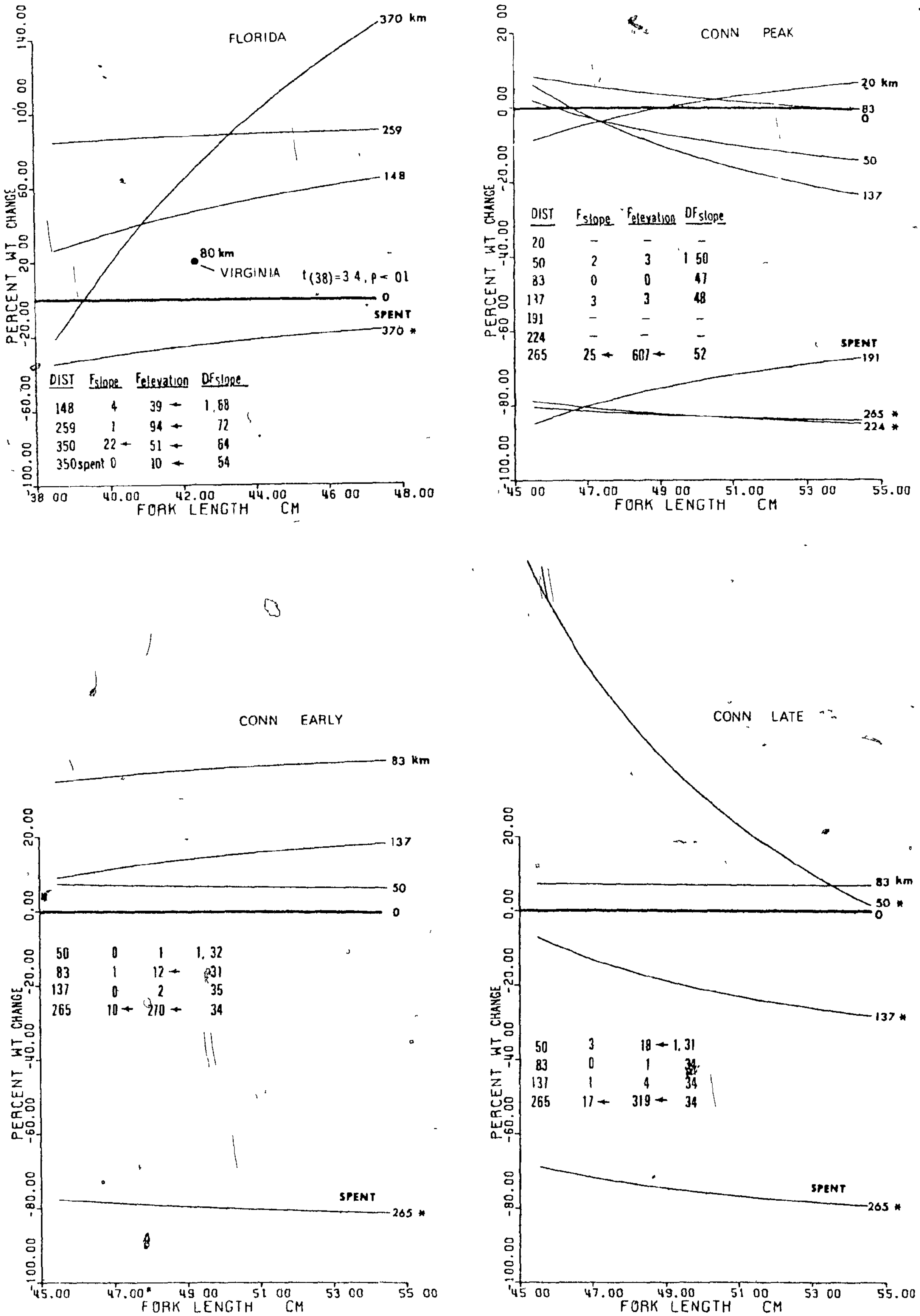

FLORIDA
PERCENT WT CHANGE
FORK LENGTH CM
259 km
148
370
0
SPENT
370 *
VIRGINIA 80km
t(41) = 8 4, p < 001
DIST Fslope Felevation DFslope
148 0 7 ← 1, 56
259 0 29 ← 60
370 0 3 51
370spent 1 2 40
CONN PEAK
50 km
0
20
83
137
SPENT
191
224
265
DIST Fslope Felevation DFslope
20 — — —
50 0 0 1, 49
83 1 2 54
137 3 21 ← 51
191 — — —
224 — — —
265 25 ← 512 ← 54
CONN EARLY
50 km
83
0
137
SPENT
265
50 0 2 1, 31
83 0 1 33
137 6 3 35
265spent 15 ← 382 ← 31
CONN LATE
0 km
50 1 33 ← 1, 30
83 2 39 ← 29
137 0 34 ← 27
265 3 180 ← 29
50
137
83 *
SPENT
265 *

Figure 5. Proportional changes in ovary weight during the freshwater migration. Changes associated with specific distances (km) are relative to initial ovary weight. See Fig. 4 for explanation of symbols and terminology.


FLORIDA
370 km
259
148
80 km
VIRGINIA
t(38)=3.4, p<.01
0
SPENT
370 *
DIST Fslope Felevation DFslope
148 4 39 ← 1,68
259 1 94 ← 72
350 22 ← 51 ← 64
350spent 0 10 ← 54
PERCENT WT CHANGE
FORK LENGTH CM
CONN PEAK
20 km
83
0
50
137
DIST Fslope Felevation DFslope
20 – – –
50 2 3 1,50
83 0 0 47
137 3 3 48
191 – – –
224 – – –
265 25 ← 607 ← 52
SPENT
191
265 *
224 *
CONN EARLY
83 km
137
50
0
50 0 1 1,32
83 1 12 ← 31
137 0 2 35
265 10 ← 270 ← 34
SPENT
265 *
CONN LATE
83 km
50 *
0
137 *
50 3 18 ← 1,31
83 0 1 34
137 1 4 34
265 17 ← 319 ← 34
SPENT
265 *

male shad with those of fully spent males sampled later at the same location (370 km) indicated spawning in the former group was incomplete at the time of sampling. The proportional decrease in ovary weight of females less than 43 cm beyond km 259 and the significant reduction (covariance $F_{(1,47)} = 5.9$, $p < 0.05$) in slope of the length/ovary weight relationship at km 370 indicated the smaller females (which were more mature at time of entry into freshwater) were spawning earlier and further downstream than their larger counterparts.

In contrast to the pattern observed in Florida and Virginia, the testes weight of Connecticut River males did not increase during the upstream migration regardless of time of entry into the river (Fig. 4). For females, the pattern of ovary development varied with the time of entry into the river. Early and late migrants exhibited significant increases in ovary weights (ranging from 35-40%) during the migration to the lower limits of the main spawning areas (50-83 km) (Fig. 5). No increases in ovary weights occurred in females entering at the peak of the run presumably because the ovaries of these fish were more fully developed at the time of entry into freshwater.

Spawning of individual Connecticut River shad appeared to be protracted and to occur over a large area. Late migrant males and females experienced significant reductions in gonad weight (Figs. 4, 5) as little as 50 km from the river mouth. Gonad weight losses (indicative of spawning) in early and peak run migrants first occurred approximately 83 km from the river mouth (Figs. 4, 5) and continued to km 137.

The significant increase in gonad weight of Virginia shad between the river mouth and km 80 suggested little or no spawning occurred downstream of km 80. This finding agrees with the reported limited distribution of spawning activity in the York River system (Massmann, 1952).

VISCERA WEIGHT LOSS

Significant interpopulation differences in viscera weights at the time of entry into freshwater were observed. The length/viscera weight relationship of Florida shad was significantly below that of all Connecticut migrants (Table 3) indicating they enter freshwater with smaller viscera energy reserves. Viscera weight losses (approximately 35% (Fig. 6) of initial levels) in females during the upriver migration in the St. Johns River were similar to viscera weight losses experienced by early migrant Connecticut River females but were substantially less than viscera weight losses occurring in Connecticut River females migrating at the peak and late in the run (40-60%). The smaller proportional weight loss of Florida females apparently was a consequence of the reduced viscera reserves carried into the river because the slope and elevation of the length/viscera weight relationships of the Connecticut and Florida shad do not differ at the spawning grounds (Table 3). For males, the viscera weights at entry to both rivers were more similar than the viscera weights of females (Table 3). Consequently, viscera weight losses associated with upriver migration were similar (Fig. 7). The lack of significant decreases in viscera weight after spawning (Figs. 6, 7)

Table 3. F values for analysis of covariance of length/viscera weight regressions for fish sampled at the river mouth, at the spawning areas and following spawning. (+) or (-) indicates slopes and elevations of the regressions on the horizontal are significantly greater (+) or less (-) than the slopes and elevations on the vertical ($p<0.01$).

| | Male | | | | | | Female | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Florida | | Conn. Peak | | Conn. Early | | Florida | | Conn. Peak | | Conn. Early | |
| | slope | elevation | slope | elevation | slope | elevation | slope | elevation | slope | elevation | slope | elevation |
| | | | | | | RIVER MOUTH (0 km.) | | | | | | |
| Conn. Peak | 0.4 | 21.9(-) | | | | | 0.1 | 24.9(-) | | | | |
| Early | 0.2 | 27.2(-) | 0.0 | 0.1 | | | 0.1 | 32.3(-) | 0.2 | 1.0 | | |
| Late | 0.7 | 7.7(-) | 0.1 | 1.6 | 0.2 | 2.6 | 0.0 | 18.0(-) | 0.0 | 1.0 | 0.1 | 0.0 |
| | | | | | | MAJOR SPAWNING AREAS (370 km. Florida, 137 km. Conn.) | | | | | | |
| Conn. Peak | 1.8 | 6.8 | | | | | 0.9 | 1.2 | | | | |
| Early | 3.8 | 3.6 | 0.5 | 0.1 | | | 4.9 | 0.5 | 1.5 | 22.8(-) | | |
| Late | 8.1(-) | 0.3 | 0.7 | 3.8 | 0.1 | 4.5 | 4.8 | 5.1 | 0.3 | 0.1 | 0.6 | 35.9(+) |
| | | | | | | SPENT FISH (370 km. Florida, 265 km. Conn.) | | | | | | |
| Conn. Peak | 1.9 | 0.0 | | | | | 1.7 | 0.4 | | | | |
| Early | 3.6 | 0.4 | 0.0 | 0.2 | | | 6.0 | 0.2 | 2.0 | 9.7(-) | | |
| Late | 6.6 | 0.2 | 0.1 | 1.5 | 0.2 | 5.3 | 0.5 | 0.3 | 0.7 | 1.1 | 4.1 | 16.7(+) |

Figure 6. Proportional changes in female viscera weight during the freshwater migration. Changes associated with specific distances (km) are relative to initial viscera weight. See Fig. 4 for explanation of symbols and terminology.

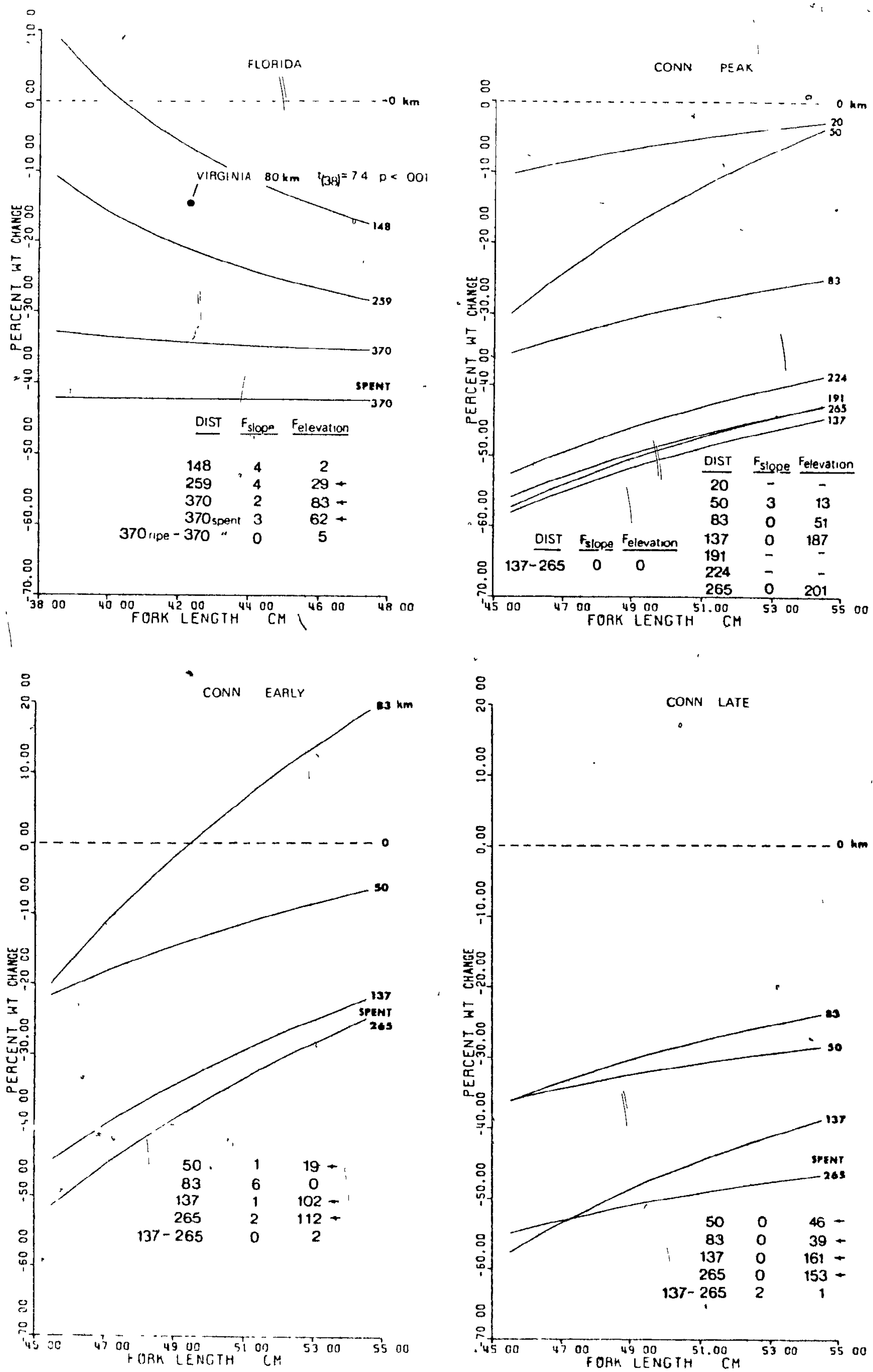
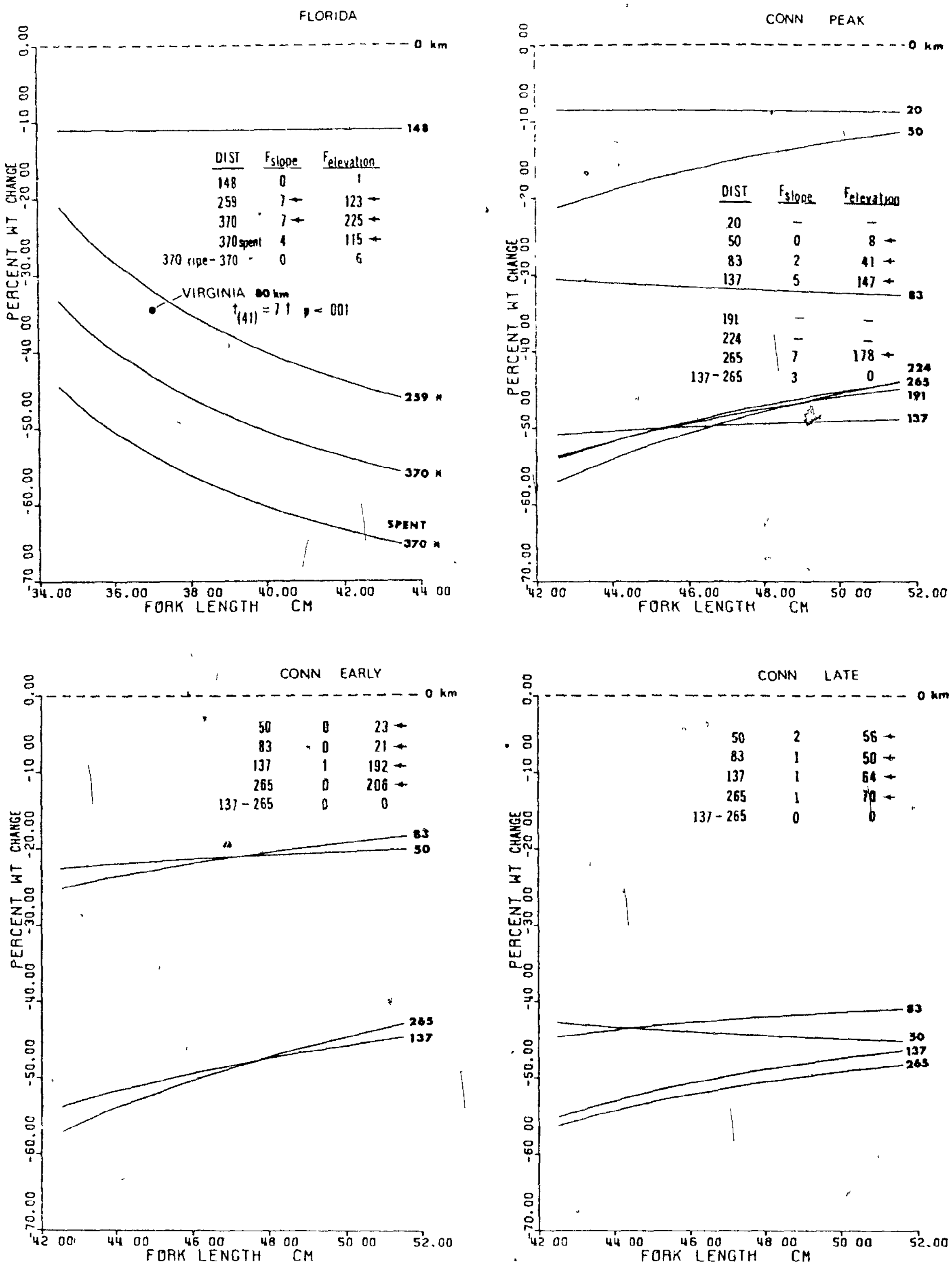

FLORIDA
0 km
VIRGINIA 80 km $t_{(38)}$ = 7.4 p < .001
148
259
370
SPENT
370
DIST F slope F elevation
148 4 2
259 4 29
370 2 83
370spent 3 62
370ripe - 370 " 0 5
PERCENT WT CHANGE
FORK LENGTH CM
CONN PEAK
0 km
20
50
83
224
191
265
137
DIST F slope F elevation
20 - -
50 3 13
83 0 51
137 0 187
191 - -
224 - -
265 0 201
DIST F slope F elevation
137-265 0 0
PERCENT WT CHANGE
FORK LENGTH CM
CONN EARLY
83 km
0
50
137
SPENT
265
50 1 19
83 6 0
137 1 102
265 2 112
137-265 0 2
PERCENT WT CHANGE
FORK LENGTH CM
CONN LATE
0 km
83
50
137
SPENT
265
50 0 46
83 0 39
137 0 161
265 0 153
137-265 2 1
PERCENT WT CHANGE
FORK LENGTH CM

Figure 7. Proportional changes in male viscera weight during the freshwater migration. Changes associated with specific distances (km) are relative to initial viscera weight. See Fig. 4 for explanation of symbols and terminology.



FLORIDA
0 km
148
DIST
Fslope
Felevation
148 0 1
259 7 123
370 7 225
370spent 4 115
370 ripe-370 0 6
VIRGINIA 80 km
t(41) = 7.1 p < .001
259 km
370 km
SPENT
370 km
PERCENT WT CHANGE
FORK LENGTH CM
CONN PEAK
0 km
20
50
DIST
Fslope
Felevation
20 – –
50 0 8
83 2 41
137 5 147
191 – –
224 – –
265 7 178
137-265 3 0
83
224
265
191
137
PERCENT WT CHANGE
FORK LENGTH CM
CONN EARLY
0 km
50 0 23
83 0 21
137 1 192
265 0 206
137-265 0 0
83
50
265
137
PERCENT WT CHANGE
FORK LENGTH CM
CONN LATE
0 km
50 2 56
83 1 50
137 1 64
265 1 70
137-265 0 0
83
50
137
265
PERCENT WT CHANGE
FORK LENGTH CM

in males and females suggests they exploited viscera reserves maximally during upriver movement. Proportional viscera weight losses during total freshwater stay in Connecticut and Florida were comparable (40-60%).

Mean viscera weights at entry to the York River (48 g, SD = 9 for males of mean length 37.0 cm, SD = 0.6; 67 g, SD = 10 for females of mean length 42.3 cm, SD = 0.6) are intermediate to viscera weights predicted for Connecticut and Florida shad of equivalent lengths at the river mouth (Table 1). Subsequent viscera weight losses (Figs. 6, 7) incurred during the migration to the York River spawning area were substantially less than losses by either Florida or Connecticut shad during travel to their respective major spawning sites. Viscera reserves may thus be available for the downstream migration of York River shad.

SOMATIC WEIGHT LOSS

Covariance analysis revealed no significant differences in the slope or elevation of the length/somatic weight relationship of males and females from the Florida and Connecticut populations at the time of entry into the rivers (Table 4). Similarly, mean somatic weights of males (790 g, SD = 71) and females (1202 g, SD = 76) entering the York River system approximated the predicted weights of Florida males (758 g) and females (1165 g) of comparable lengths entering the St. Johns River (Table 1). Subsequent somatic weight losses experienced in attaining the spawning grounds were similar in Florida and Connecticut (15-25%; Figs. 8, 9) in spite of the greater distances travelled by Florida fish. In Virginia, where the spawning migration is shortest, the magnitude of

Table 4. F values for analysis of covariance of length/somatic weight regressions for fish sampled at the river mouth, at the spawning area and following spawning. (+) or (-) indicates slopes and elevations of the regressions on the horizontal are significantly greater (+) or less (-) than the slopes and elevations on the vertical (p<0.01).

| | Male | | | | | | Female | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Florida | | Conn. Peak | | Conn. Early | | Florida | | Conn. Peak | | Conn. Early | |
| | slope | elevation | slope | elevation | slope | elevation | slope | elevation | slope | elevation | slope | elevation |
| RIVER MOUTH (0 km.) | | | | | | | | | | | | |
| Conn. Peak | 6.4 | 2.3 | | | | | 3.7 | 0.1 | | | | |
| Early | 4.8 | 0.2 | 0.0 | 19.9(+) | | | 0.1 | 3.8 | 1.6 | 14.5(+) | | |
| Late | 2.5 | 2.3 | 0.0 | 28.9(+) | 0.1 | 1.3 | 0.2 | 1.4 | 1.1 | 9.6(+) | 0.0 | 0.4 |
| MAJOR SPAWNING AREAS (370 km. Florida, 137 km. Conn.) | | | | | | | | | | | | |
| Conn. Peak | 1.0 | 17.5(-) | | | | | 3.3 | 2.3 | | | | |
| Early | 4.9 | 2.3 | 0.5 | 6.2 | | | 2.7 | 0.8 | 0.2 | 2.9 | | |
| Late | 2.8 | 2.9 | 0.1 | 38.4(+) | 0.1 | 32.2(+) | 0.4 | 0.1 | 2.8 | 43.6(+) | 2.1 | 25.6(+) |
| SPENT FISH (370 km. Florida, 265 km. Conn.) | | | | | | | | | | | | |
| Conn. Peak | 4.0 | 0.5 | | | | | 11.3(-) | 5.5 | | | | |
| Early | 2.9 | 0.2 | 4.6 | 21.2(+) | | | 7.0 | 2.4 | 0.1 | 4.8 | | |
| Late | 1.5 | 4.0 | 2.5 | 48.2(+) | 0.0 | 19.1(+) | 1.0 | 1.9 | 5.0 | 59.1(+) | 2.8 | 20.8(+) |

Figure 8. Proportional changes in male somatic weight during the freshwater migration. Changes associated with specific distances (km) are relative to initial somatic weight. See Fig. 4 for explanation of symbols and terminology.

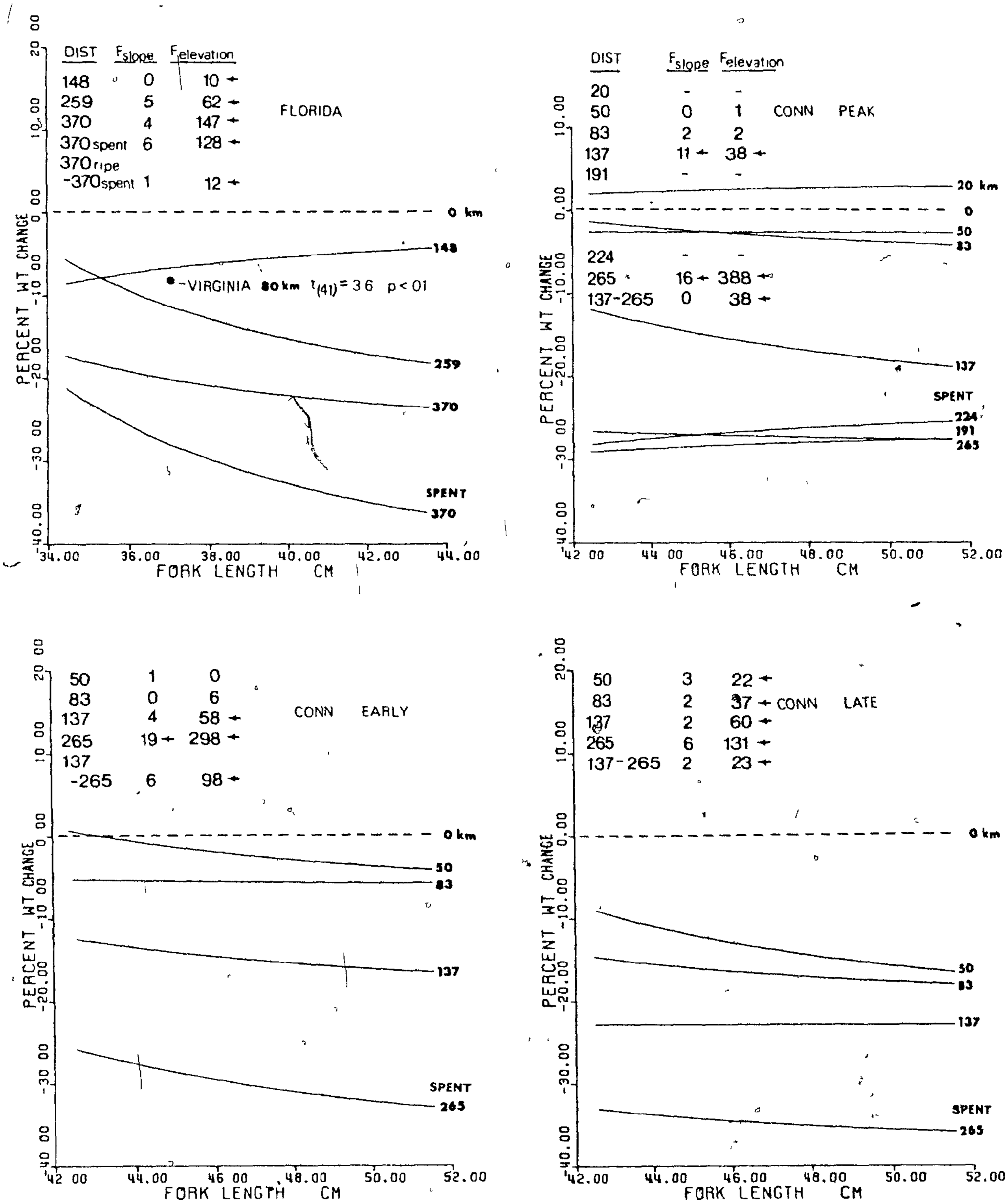
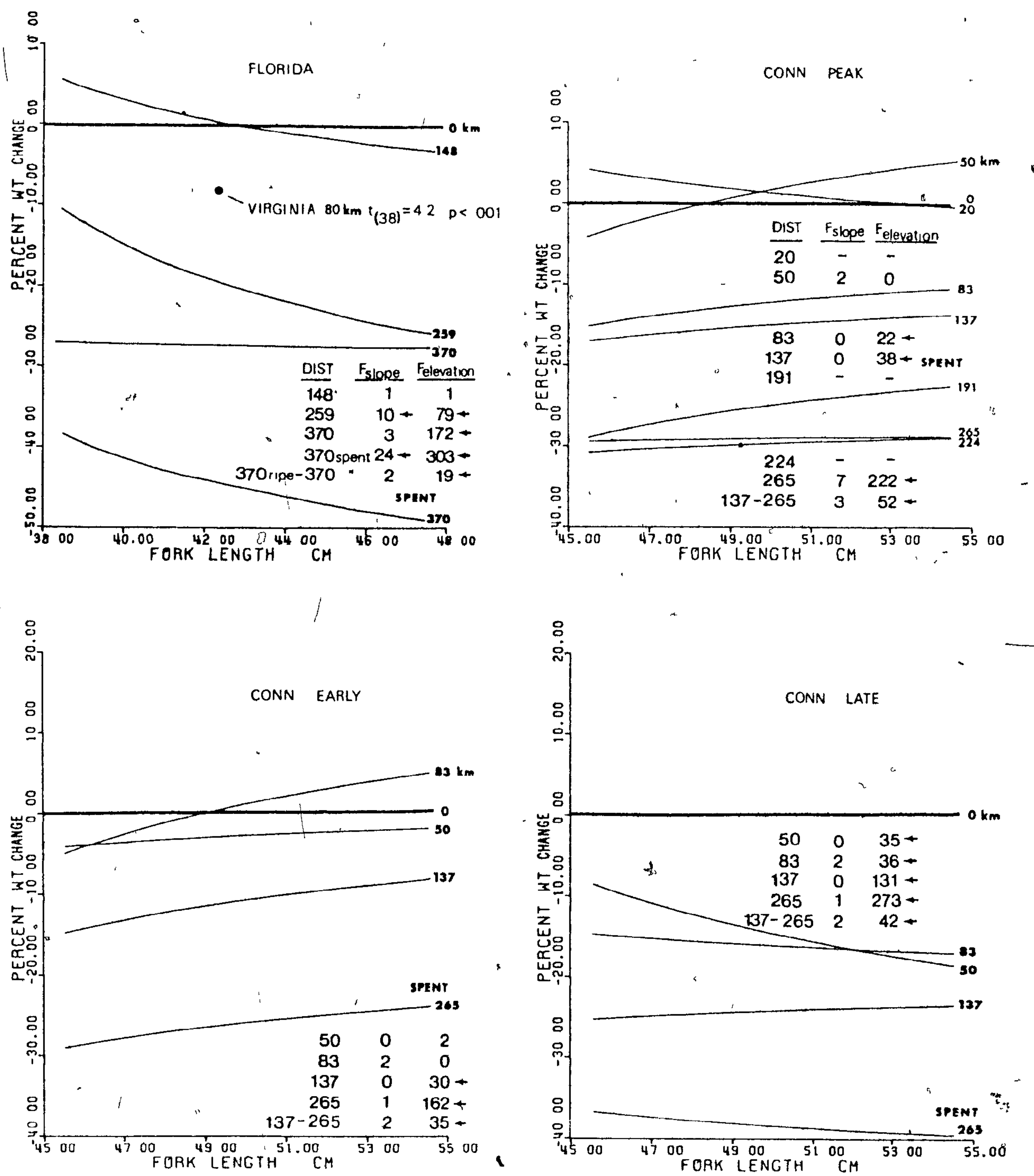

DIST Fslope Felevation
148 0 10
259 5 62
370 4 147
370 spent 6 128
370 ripe
-370 spent 1 12
FLORIDA
0 km
148
259
370
SPENT
370
•-VIRGINIA 80 km t(41)=3.6 p<.01
PERCENT WT CHANGE
FORK LENGTH CM
DIST Fslope Felevation
20 - -
50 0 1
83 2 2
137 11 38
191 - -
224 - -
265 16 388
137-265 0 38
CONN PEAK
20 km
0
50
83
137
SPENT
224
191
265
PERCENT WT CHANGE
FORK LENGTH CM
50 1 0
83 0 6
137 4 58
265 19 298
137
-265 6 98
CONN EARLY
0 km
50
83
137
SPENT
265
PERCENT WT CHANGE
FORK LENGTH CM
50 3 22
83 2 37
137 2 60
265 6 131
137-265 2 23
CONN LATE
0 km
50
83
137
SPENT
265
PERCENT WT CHANGE
FORK LENGTH CM

Figure 9. Proportional changes in female somatic weight during the freshwater migration. Changes associated with specific distances (km) are relative to initial somatic weight. See Fig. 4 for an explanation of symbols and terminology.



FLORIDA
PERCENT WT CHANGE
0 km
148
VIRGINIA 80 km t(38)=4 2 p< 001
259
370
DIST Fslope Felevation
148 1 1
259 10 ← 79 ←
370 3 172 ←
370spent 24 ← 303 ←
370ripe-370 2 19 ←
SPENT
370
FORK LENGTH CM
CONN PEAK
PERCENT WT CHANGE
50 km
0
20
DIST Fslope Felevation
20 – –
50 2 0
83
137
83 0 22 ←
137 0 38 ← SPENT
191 – –
191
265
224
224 – –
265 7 222 ←
137-265 3 52 ←
FORK LENGTH CM
CONN EARLY
PERCENT WT CHANGE
83 km
0
50
137
SPENT
265
50 0 2
83 2 0
137 0 30 ←
265 1 162 ←
137-265 2 35 ←
FORK LENGTH CM
CONN LATE
PERCENT WT CHANGE
0 km
50 0 35 ←
83 2 36 ←
137 0 131 ←
265 1 273 ←
137-265 2 42 ←
83
50
137
SPENT
265
FORK LENGTH CM

somatic weight losses associated with attainment of spawning sites was less (approximately 8%; Figs. 8, 9). Significant differences in somatic weight losses between the Connecticut and St. Johns Rivers occurred during the postspawning period. Spent shad sampled at the spawning grounds in Florida experienced proportional weight losses as great (males) or greater than (females) spent fish sampled at the river mouth just prior to the return to sea in Connecticut. Florida males and females consumed 20-35% and 40-50% respectively of their somatic tissues (Figs. 8, 9). Connecticut River shad weight losses during the entire migration ranged from 30 to 40%. No comparable data was available for York River migrants. Significant temporal differences in the length/somatic weight relationships of Connecticut River shad occurred at the river mouth (Table 4). Shad migrating at the "peak" of the run entered the river with significantly larger somatic reserves, however the length/somatic weight relationships of shad entering early or late in the run did not differ significantly. The consistently lower length/somatic weight relationships of late run shad at 137 km (spawning area) and 265 km (spent shad leaving the river) (Table 4) indicates these fish utilized a significantly greater proportion of their body reserves during the migration.

## INTERACTIVE CHANGES IN TISSUE WEIGHTS

A temporal sequence in tissue utilization was indicated by the relative changes in the elevation of the length/viscera weight and length/somatic weight relationships during the migration. In the Connecticut River population significant decreases in the elevation of the length/

viscera weight relationships occurred between km 0 and km 50 (Table 3), the absolute decrease being greatest (30-45%) for late migrants (Figs. 6, 7). Significant reductions in the somatic weight of early and peak run shad (Table 4) occurred only after the viscera weight loss reached its maximum, suggesting a preferential use of viscera tissues early in the migration. In contrast, the viscera and somatic weight loss in late run migrants occurred simultaneously throughout the early stages of the migration. During the downstream migration following spawning somatic tissues were used exclusively (Figs. 8, 9). Somatic weight losses during the downstream migration were of similar magnitude to losses incurred during the upstream migration.

Florida shad were similar to late migrant Connecticut shad in that they utilized somatic and viscera reserves simultaneously during the upriver migration. Significant declines in the elevation of the length/somatic weight relationships of Florida shad occurred closer to (between 0 and 140 km) or at the same distance from (148-259 km for females) the river mouth as the decreases in elevations of the length/viscera weight relationships (Figs. 6, 7, 8, 9). Following spawning, like their Connecticut counterparts, Florida shad utilized somatic tissues exclusively.

The paucity of sampling locations prevented a definitive assessment of interactive changes in shad viscera and somatic weights during upstream progress in the York River. However, reduced viscera and somatic weight losses by Virginia migrants relative to losses experienced by Connecticut and Florida shad during travel to spawning sites suggested that, unlike

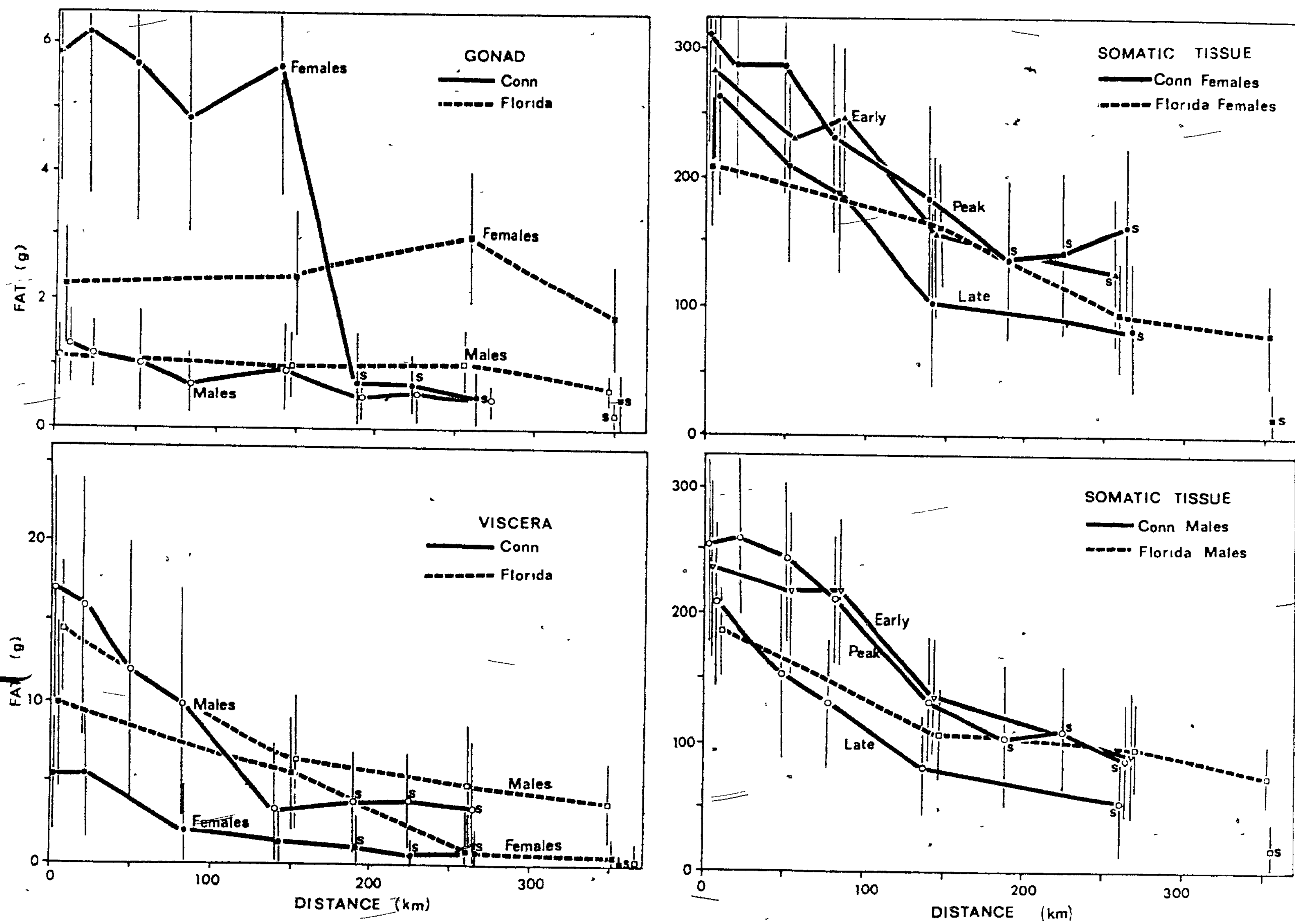
Connecticut and Florida migrants, Virginia shad may have both viscera and somatic energy reserves available for the postspawning downstream migration.

BODY COMPOSITION CHANGES

Fat dynamics Trends in gonad fat changes during the migration were similar for Connecticut males and females, although absolute levels of fat in the gonads varied between sexes. The ovarian fat content remained relatively constant (5-6 g for the "standard" female (population mean length = 50 cm); Fig. 10) during the upriver movement. A subsequent sharp decline (85%) was associated with spawning. Similarly, testicular fat content remained constant (range 1.2 to 0.8 g for the standard male (45 cm)) during the upstream migration. Postspawning fat content fell to 70% of prespawning levels.

Trends and absolute changes in gonad fat content during the freshwater migration in Florida differed from those in Connecticut. Testicular fat reserves were greater upon entry to the St. Johns River, the smaller Florida males (standard length = 40 cm) having reserves (1.1 g) equivalent to that of the much larger (45 cm) Connecticut males. Subsequent changes in testicular fat levels with distance were slight (ranging from 1.1 g at 0 km to 0.6 g at 370 km). Fat losses associated with spawning (68%) were similar to losses in Connecticut. In contrast to the constant ovarian fat levels in upstream migrant Connecticut shad, the ovarian fat content of the Florida standard female (42 cm) increased by 35% during upriver movement (Fig. 10). Subsequent reductions of ovarian fat (90%) associated with spawning were comparable in both Florida and Connecticut shad.

Figure 10. Mean fat content of gonad, viscera and somatic tissues at various distances along the freshwater migration in the St. Johns and Connecticut Rivers. Mean shad lengths associated with specific river locations did not vary more than 1.0 cm around the "standard" length. "S" = spent shad; vertical bar = 1 S.D.


GONAD
Conn
Florida
Females
Males
FAT (g)
VISCERA
SOMATIC TISSUE
Conn Females
Florida Females
Early
Peak
Late
Conn Males
Florida Males
DISTANCE (km)

Significant sex related differences in viscera fat content at the time of river entry occurred in both populations. Connecticut males, despite their smaller size, had three times the viscera fat reserves of females (Fig. 10). Differences in Florida shad were less extreme. At the river mouth, male viscera fat content was approximately 40% higher than that of females.

Viscera fat levels declined rapidly in both populations during upriver movement. However, during the postspawning period in the river, little change occurred.

Obvious differences in the somatic fat content of Florida males and females existed at entry to the river. Despite their generally smaller body size, males began the migration with absolute fat reserves comparable to those of females (Fig. 10). In contrast, the somatic fat reserves of Connecticut females at initiation of the river migration was greater than that of males, as would be expected from the larger relative body size of the females.

A rapid decline in somatic fat content of all shad occurred during upriver movement (Fig. 10). During this period of the Connecticut River migration, late run males and females suffered the most extreme reduction (60%) in somatic fat levels. Losses of a similar magnitude were experienced by St. Johns River males and females before the spawning grounds were attained. Postspawning losses by all shad were small in comparison to prespawning losses. Connecticut "early", "peak" and "late" migrant males utilized from 10 to 20% of their somatic fat reserves during the seaward migration. Florida males utilized considerably more fat (37%)

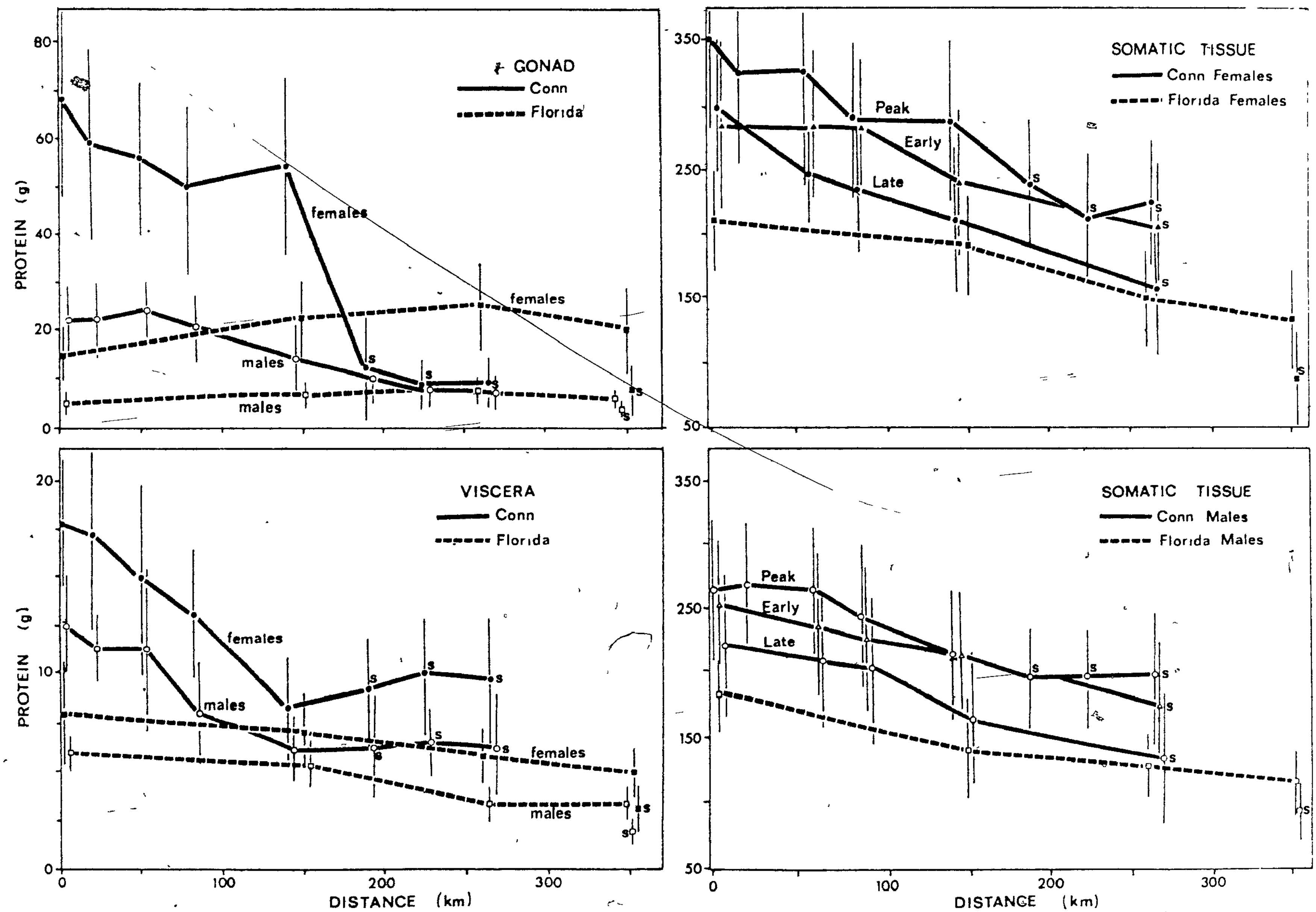
during the same period. The postspawning fat expenditures of early and late run Connecticut females and Florida females ranged from 10 to 35%. Peak migrant females in the Connecticut River experienced no reduction in somatic fat following spawning.

The somatic tissue was the most important source of fat during the Florida and Connecticut migrations, supplying up to 150 g for metabolic purposes. In comparison, a maximum of 12 g of fat was utilized from visceral sources.

Protein dynamics The protein content of the gonads of male and female Connecticut River shad was relatively stable during the upriver migration (Fig. 11). An abrupt decline of 71% for males and 87% for females occurred during spawning. In contrast, the ovary and testes protein content of Florida shad increased approximately 30% during upriver movement. Decreases in gonad protein content associated with spawning (50-73%) were of lesser magnitude relative to decreases in gonad protein content of Connecticut shad.

The viscera protein content of shad declined rapidly during the upstream migration with little or no decrease after spawning. In Connecticut, the trends in initial protein depletion were similar; the viscera protein of both males and females being reduced approximately 45% (Fig. 11). No decline occurred after spawning. The reduction in viscera protein of Florida shad was more gradual during upriver movement. Although the proportional losses of Florida migrants were greater (50% for males; 75% for females) than those of Connecticut shad, the absolute reduction in protein content of 3 g over 370 km of river travel was far

Figure 11. Mean protein content of gonad, viscera and somatic tissues at various distances along the freshwater migration in the St. Johns and Connecticut Rivers. "S" = spent shad; vertical bar = 1 S.D.



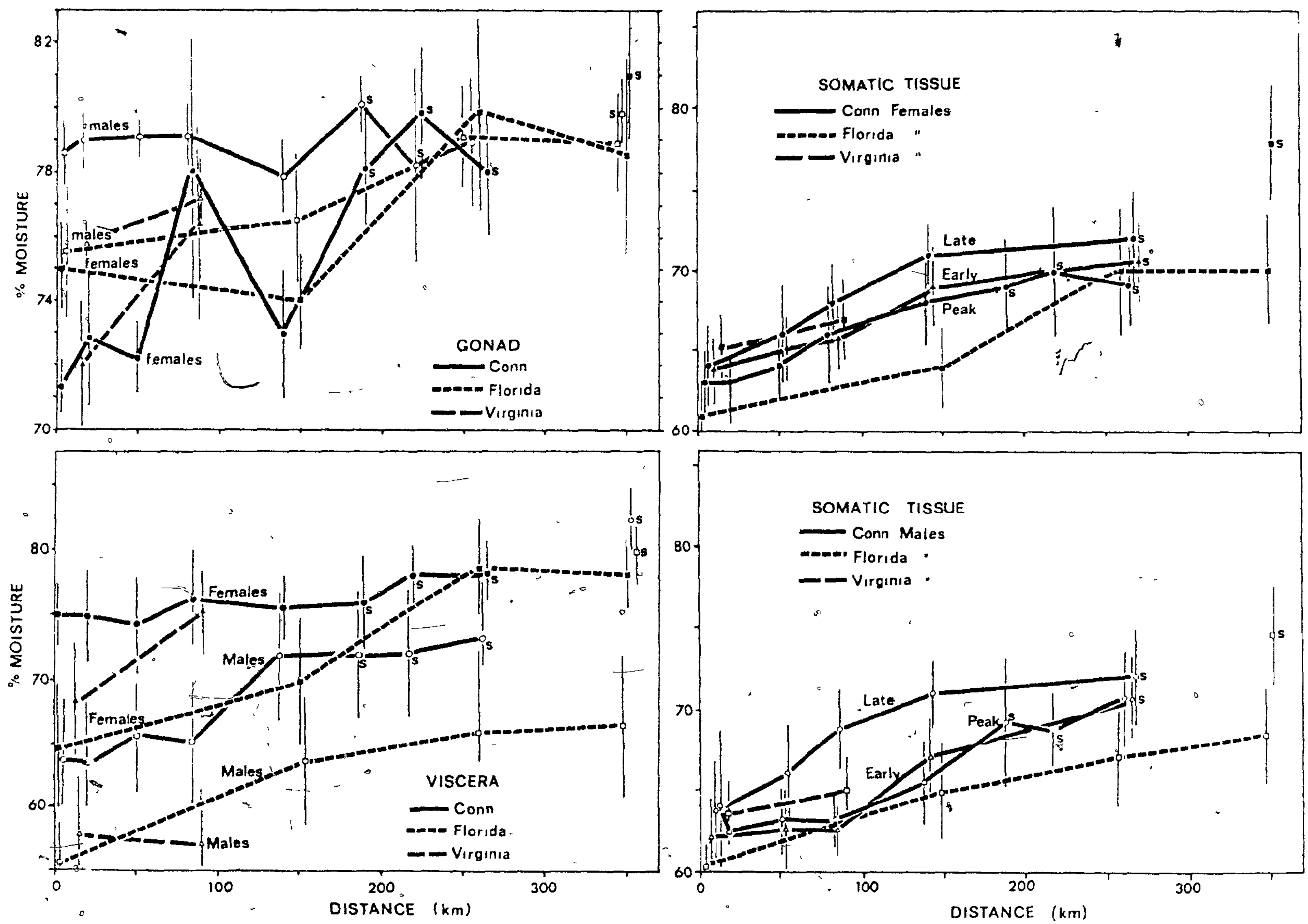
GONAD
Conn
Florida
females
males
PROTEIN (g)
SOMATIC TISSUE
Conn Females
Florida Females
Peak
Early
Late
VISCERA
Conn
Florida
females
males
SOMATIC TISSUE
Conn Males
Florida Males
Peak
Early
Late
DISTANCE (km)
DISTANCE (km)

less than losses by Connecticut shad (6 and 10 g for males and females respectively) over a comparatively shorter migration distance. After spawning, the viscera protein of Florida males and females decreased an additional 17 and 25% respectively.

Somatic protein declined both prior to, and after spawning in both rivers, with the declines being approximately equal in the two intervals (Fig. 11). The decrease in protein content of early migrant females (14%) was comparable to losses suffered by "peak" migrant females (17%). Late migrants entered the River with reduced tissue protein levels and subsequent losses (30%) were greatest among Connecticut River migrants. The same temporal trends in protein loss existed for males, and the absolute reductions in protein were similar despite their smaller size. The average protein content of "early" and "peak" migrant males decreased 18% between 0 and 137 km and finally 6% between 137 km and 265 km. Late male migrants, like late females, entered the river with reduced protein reserves. Subsequent losses (23% and 14% between 0 and 137 km and between 137 km and 265 km respectively) were more extensive than those of earlier migrants. Florida males utilized less somatic protein both prior to (34%) and after spawning (15%) than did Florida females (respectively 38% and 19% for the same intervals).

<u>Moisture dynamics</u> Ovary moisture content increased steadily prior to spawning in all rivers (Fig. 12). In the Connecticut this increase was associated with ripening fascicules of ova (personal observation) on the Wilson spawning grounds (83 km). In comparison, female shad sampled at Holyoke (137 km) exhibited reduced ovary moisture (arcsine transformed

Figure 12. Mean percent moisture in gonad, viscera and somatic tissues at various distances along the freshwater migration in the St. Johns, Connecticut and York Rivers. "S" = spent shad; vertical bar = 1 S.D.



% MOISTURE
GONAD
Conn
Florida
Virginia
males
males
females
females
SOMATIC TISSUE
Conn Females
Florida "
Virginia "
Late
Early
Peak
VISCERA
Conn
Florida
Virginia
Females
Males
Females
Males
Males
SOMATIC TISSUE
Conn Males
Florida "
Virginia "
Late
Peak
Early
DISTANCE (km)
DISTANCE (km)

proportions, $t_{(49)} = 4.8$, $p < 0.001$. Upstream movement was active at this stage and no obvious ripening of the ova was occurring in this area. The increase in ovary moisture during the 80 km migration in the York River system was similarly significant (arcsine transformed proportions, $t_{(38)} = 5.5$, $p < 0.001$). No change in ovary moisture was observed during the early stages (0-148 km) of upstream migration in Florida despite increases in gonad weight. However, between 148 and 359 km ovary moisture increased dramatically suggesting a rapid maturation of ova (arcsine transformed proportions, $T_{(55)} = 7.2$, $p < 0.001$).

In Florida trends in testes moisture changes were similar to those observed for ovaries. Testes moisture content increased approximately 5% (from 75 to 80%) between km 0 and 259, coincident with an increase in testes weight. A minor increase in testes moisture (1.3%) accompanying an increase in gonad weight was also apparent during the migration in Virginia. The percent testes moisture of Connecticut shad remained constant (approximately 78%) throughout the migration.

Reciprocal moisture and fat changes were apparent in viscera and somatic tissues in both the St. Johns and Connecticut Rivers (Figs. 10, 12). Increases in male viscera moisture of 8 and 14% for Connecticut and Florida males respectively accompanied corresponding fat depletions of 75 to 93%. In Florida, female viscera moisture increased 15% as fat content declined by 90%. Connecticut females, which entered the river with reduced fat reserves relative to those of Connecticut males, had a much higher moisture content (75%) and, as a result, increases were moderate (3%) and coincided with reduced viscera fat loss. The moisture content of the somatic tissue of Connecticut peak and early migrants increased approximately 7% (from 63 to 70%) as fat content declined by 50%. The moisture increase was greatest (approximately 8%) for late migrants (from 64 to 72%) and approximately 7% more fat was utilized by these fish. The greatest moisture increase (17%) occurred in Florida females and accompanied a decline in somatic fat content of 95%. Among males, the Connecticut "peak", "early" and "late" migrants experienced similar somatic moisture increases (8%) associated with an average fat reduction of 65%. The highest moisture increase (15%) and greatest fat decrease (90%) occurred in the somatic tissue of Florida males.

Ash dynamics Somatic and viscera ash content remained relatively constant during the freshwater migration (Fig. 13). Gonad ash content decreased in concert with spawning activity as expected.

ENERGY UTILIZATION

Chi square analysis ($\chi^2 = 21.1$, 11 d.f., $p = 0.025$) indicated heat of oxidation and caloric equivalents of fat and protein provided comparable measures of tissue energy content. Therefore, bomb calorimetry estimates of tissue energy content (Virginia shad) were compared directly with estimates based on proximate composition (Florida and Connecticut shad).

Gonad energy change Despite increases in the gonad weight of both sexes during the upriver migration of Florida shad only the energy content of the ovaries increased significantly (Fig. 14). Moreover, trends in proportional ovary energy increases suggested among females the large

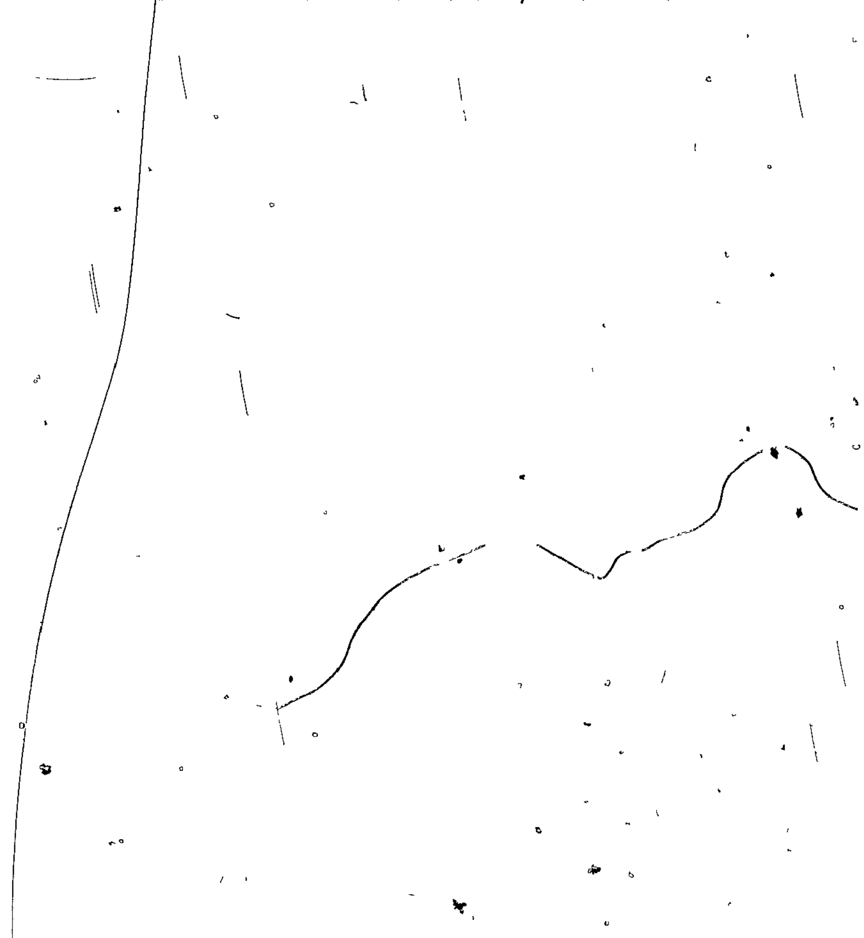


Figure 13. Mean ash content of gonad, viscera and somatic tissues at various distances along the freshwater migration in the Connecticut River. "S" = spent shad; vertical bar = 1 S.D.

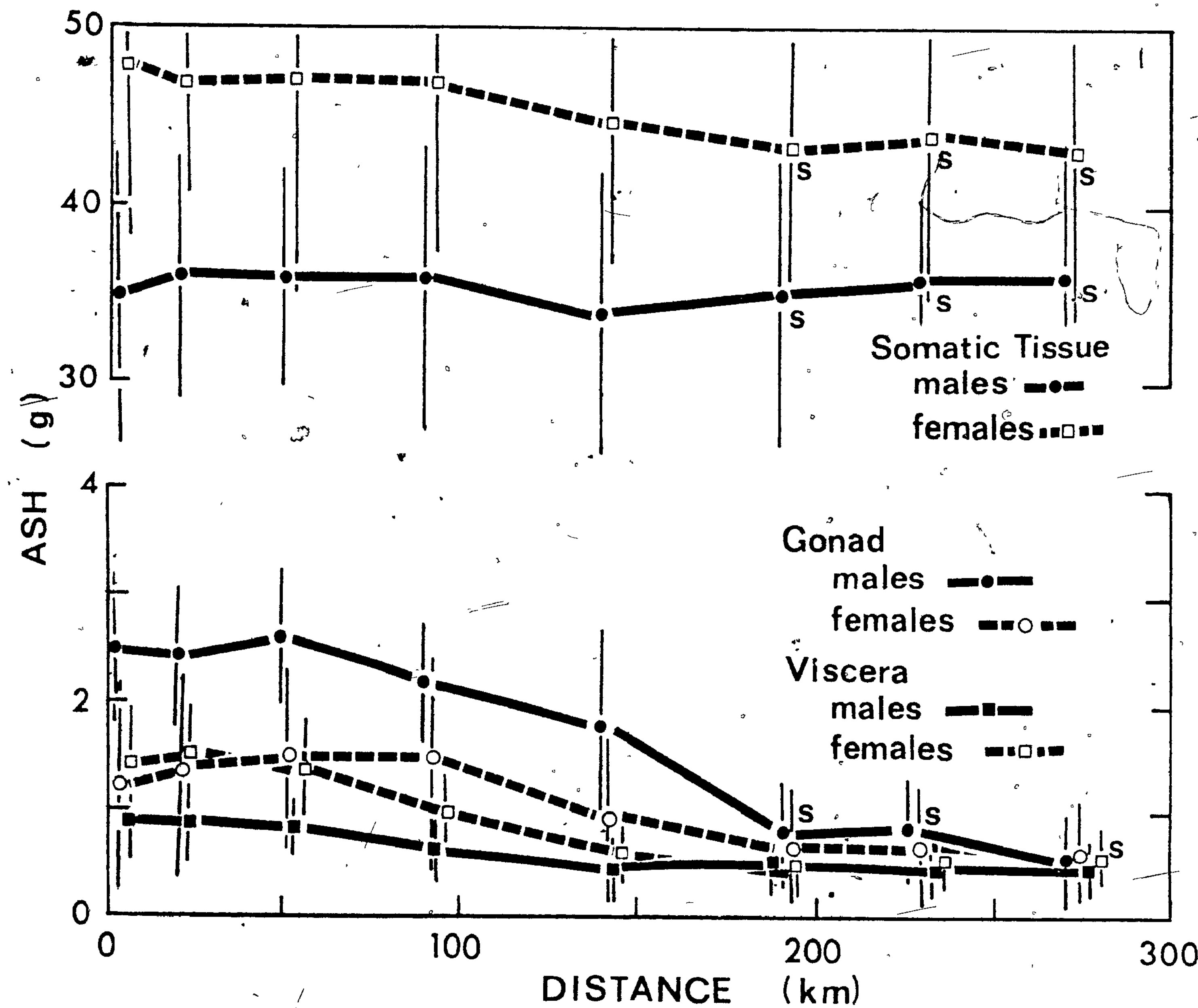
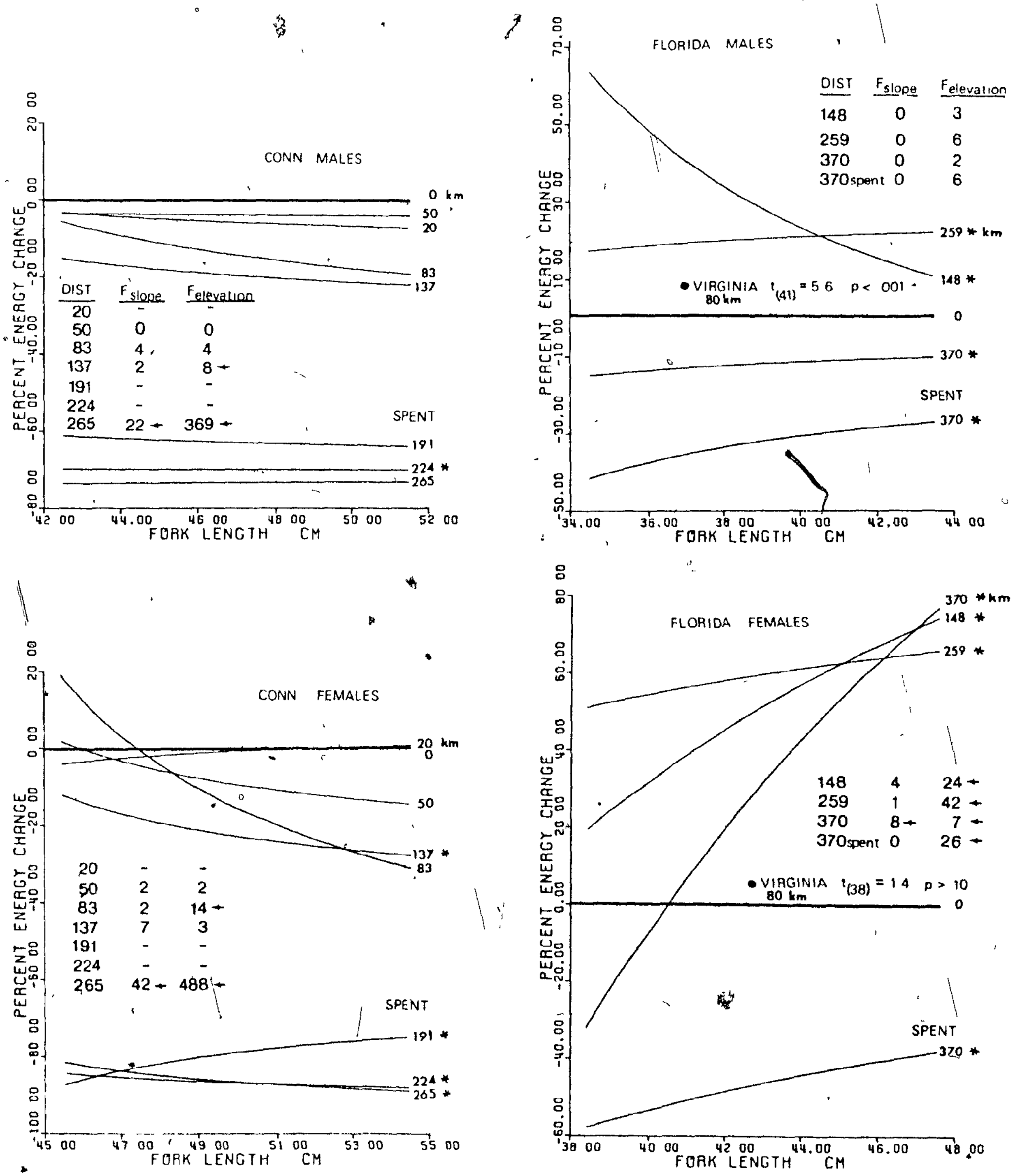

50
40
30
ASH (g)
4
2
0
0
100
200
300
DISTANCE (km)
Somatic Tissue
males
females
Gonad
males
females
Viscera
males
females
S

Figure 14. Proportional changes in gonad energy content during the freshwater migration. Changes associated with specific distances (km) are relative to initial gonad energy content. See Fig. 4 for explanation of symbols and terminology.



CONN MALES
PERCENT ENERGY CHANGE
FORK LENGTH CM
DIST F slope F elevation
20 - -
50 0 0
83 4 4
137 2 8
191 - -
224 - -
265 22 369
SPENT
0 km
50
20
83
137
191
224 *
265
FLORIDA MALES
DIST F slope F elevation
148 0 3
259 0 6
370 0 2
370spent 0 6
259 * km
148 *
VIRGINIA 80 km t(41) = 5 6 p < 001
0
370 *
SPENT
370 *
CONN FEMALES
20 - -
50 2 2
83 2 14
137 7 3
191 - -
224 - -
265 42 488
20 km
0
50
137 *
83
SPENT
191 *
224 *
265 *
FLORIDA FEMALES
148 4 24
259 1 42
370 8 7
370spent 0 26
370 * km
148 *
259 *
VIRGINIA 80 km t(38) = 1 4 p > 10
0
SPENT
370 *

individuals were shunting more energy into the gonads. The increase in ovary energy content during the early stages of migration (km 0 to km 148) was 70% for 48 cm females compared to 20% for 38 cm females. Because this finding was consistent with disparate ovary maturity at river entry and disproportionate increases in ovary weight with upriver movement, these trends in ovary energy increases were accepted as real despite the use of non-significant regression lines in their calculation (Fig. 14). Subsequent spawning by the large individuals was apparently delayed, as indicated by the significant increase in the slope of the ovary energy content/length relationship at 370 km. This increase reflected the earlier losses of gonad energy resulting from spawning in small females.

The gonad energy content of Connecticut shad which were more mature at time of entry into freshwater, did not increase during the migration (Fig. 14). A significant decrease in testes and ovary energy content between km 0 and km 137 suggested upriver migrants captured at Holyoke may have engaged in limited spawning activity before reaching this point. No body size dependent trends in spawning were apparent for Connecticut migrants.

The ovaries of Virginia shad which, like those of Connecticut females, were at an advanced stage of maturity at river entry did not significantly increase in energy content during the migration (Fig. 14). However, the testes of Virginia shad, intermediate in maturity to the gonads of Connecticut and Florida migrants, did experience a significant increase in energy content.

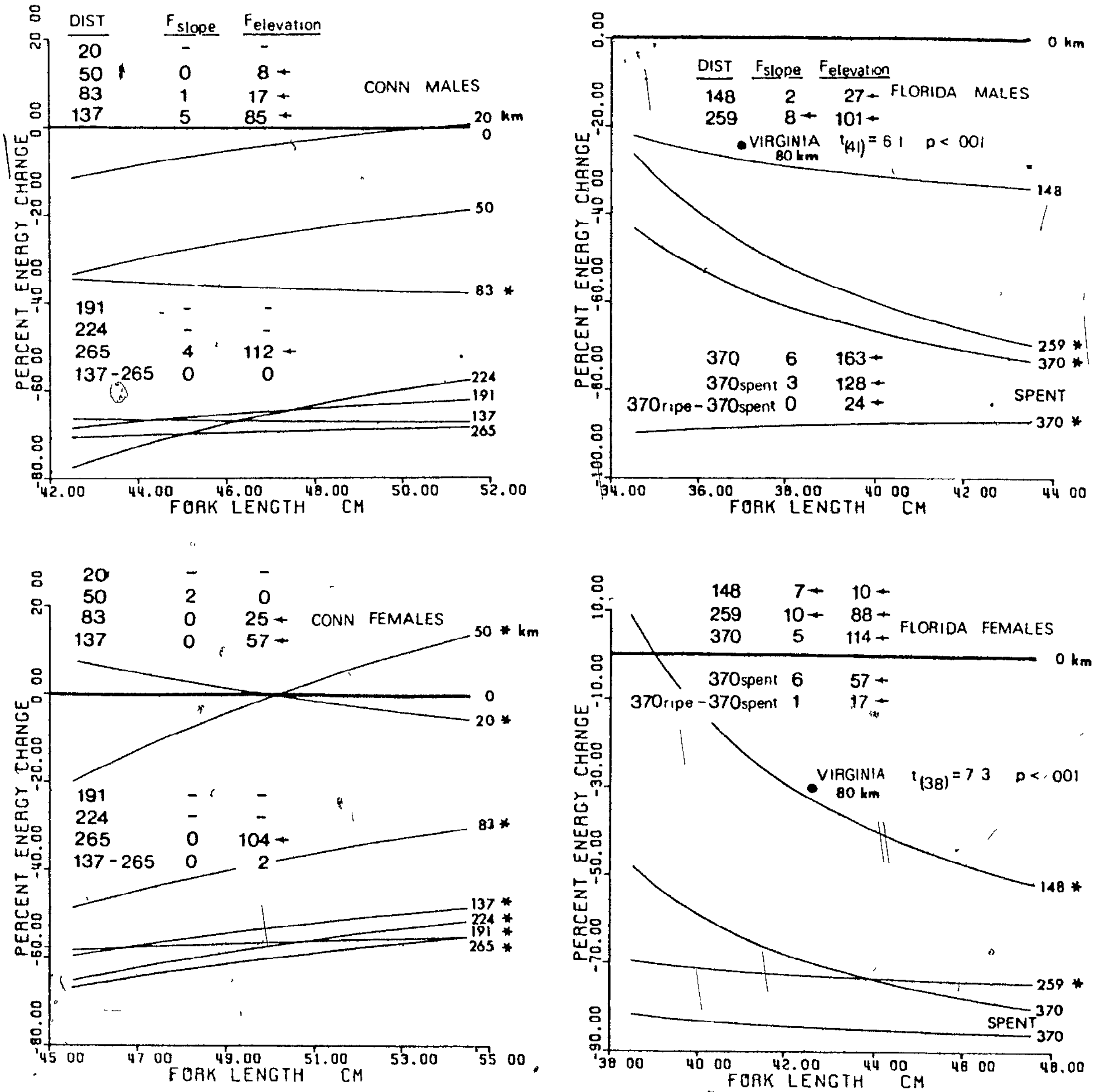
A comparison of regression elevations at 0 km indicated Connecticut shad entered the river with greater gonad energy reserves than Florida migrants (Table 5). Despite increases in the gonad energy of Florida shad, this disparity persisted at the spawning areas. Mean testes energy content at entry to the York River (61 kcal, SD = 15) approximated the calculated value for Connecticut River males of equivalent length (54 kcal). However, initial ovary energy content (307 kcal, SD = 78) was 116% greater than that of Connecticut females of comparable length. In the York River, only testes energy increased significantly with upriver movement (Fig. 14).

Viscera energy change The viscera energy reserves of Florida shad were equivalent to or greater than reserves of the Connecticut migrants at the time of entry into freshwater (Table 5). The viscera reserves of Virginia shad at the river mouth (males: 125 kcal, SD = 19; females: 109 kcal, SD = 18) approximated those calculated for Connecticut shad of equivalent length (males: 123 kcal; females: 105 kcal). Subsequent proportional viscera energy losses associated with upriver migration were least in the York River (25-30%; Fig. 15). The extent of viscera reserve depletion in the Connecticut and St. Johns Rivers was similar (60-80%; no statistical difference in regression elevation at upriver stations and upon completion of the freshwater migration (Table 5)). The proportionally greater viscera energy losses experienced by Florida females (Fig. 15) upon completion of the migration was a consequence of the greater initial reserves.

Table 5. F values for analysis of covariance of length/gonad energy and length/viscera energy regressions for Connecticut (peak) and Florida shad sampled at the river mouth, at the spawning area and following spawning. (+) or (-) indicates slopes and elevations of regressions for Connecticut migrants are greater (+) or less (-) than the equivalent regressions of Florida shad ($p<0.01$).

| Location | Tissue | Male | | Female | |
|---|---|---|---|---|---|
| | | slope | elevation | slope | elevation |
| River mouth (0 km.) | gonad | 5.4 | 48.5(+) | 28.7(+) | 29.4(+) |
| | viscera | 0.0 | 0.1 | 7.4(-) | 11.2(-) |
| Spawning area (137 km. Conn.) (370 km. Florida) | gonad | 1.3 | 29.4(+) | 0.5 | 10.7(+) |
| | viscera | 0.6 | 0.0 | 0.1 | 0.0 |
| Spent Fish (265 km. Conn.) (370 km. Florida) | gonad | 0.0 | 2.1 | 0.7 | 0.5 |
| | viscera | 0.1 | 1.4 | 1.0 | 0.3 |

Figure 15. Proportional changes in viscera energy content during the freshwater migration. Changes associated with specific distances (km) are relative to initial viscera energy content. See Fig. 4 for explanation of symbols and terminology.


CONN MALES
DIST
F slope
F elevation
20 - -
50 0 8
83 1 17
137 5 85
191 - -
224 - -
265 4 112
137-265 0 0
20 km
0
50
83 *
224
191
137
265
PERCENT ENERGY CHANGE
FORK LENGTH CM
FLORIDA MALES
DIST
F slope
F elevation
148 2 27
259 8 101
VIRGINIA 80 km
$t_{(41)}$ = 6 1 p < 001
0 km
148
259 *
370 *
370 6 163
370spent 3 128
370ripe - 370spent 0 24
SPENT
370 *
PERCENT ENERGY CHANGE
FORK LENGTH CM
CONN FEMALES
20 - -
50 2 0
83 0 25
137 0 57
191 - -
224 - -
265 0 104
137 - 265 0 2
50 * km
0
20 *
83 *
137 *
224 *
191 *
265 *
PERCENT ENERGY CHANGE
FORK LENGTH CM
FLORIDA FEMALES
148 7 10
259 10 88
370 5 114
370spent 6 57
370ripe - 370spent 1 17
0 km
VIRGINIA 80 km
$t_{(38)}$ = 7 3 p < 001
148 *
259 *
370
SPENT
370
PERCENT ENERGY CHANGE
FORK LENGTH CM

Greater total viscera energy stores were associated with the retarded gonad development of large Florida females. These large individuals had reserves up to 198% greater than the reserves of the smallest females. Subsequent viscera energy losses by the large females were greater early in the migration (157 kcal were utilized by 48 cm females compared to an expenditure of 25 kcal by 38 cm females between km 0 and 148) as more energy was required for gonad maturation. "Peak" run Connecticut females did not transfer energy to the gonads during upriver movement. In the Connecticut River smaller fish utilized up to 12% more energy from viscera sources.

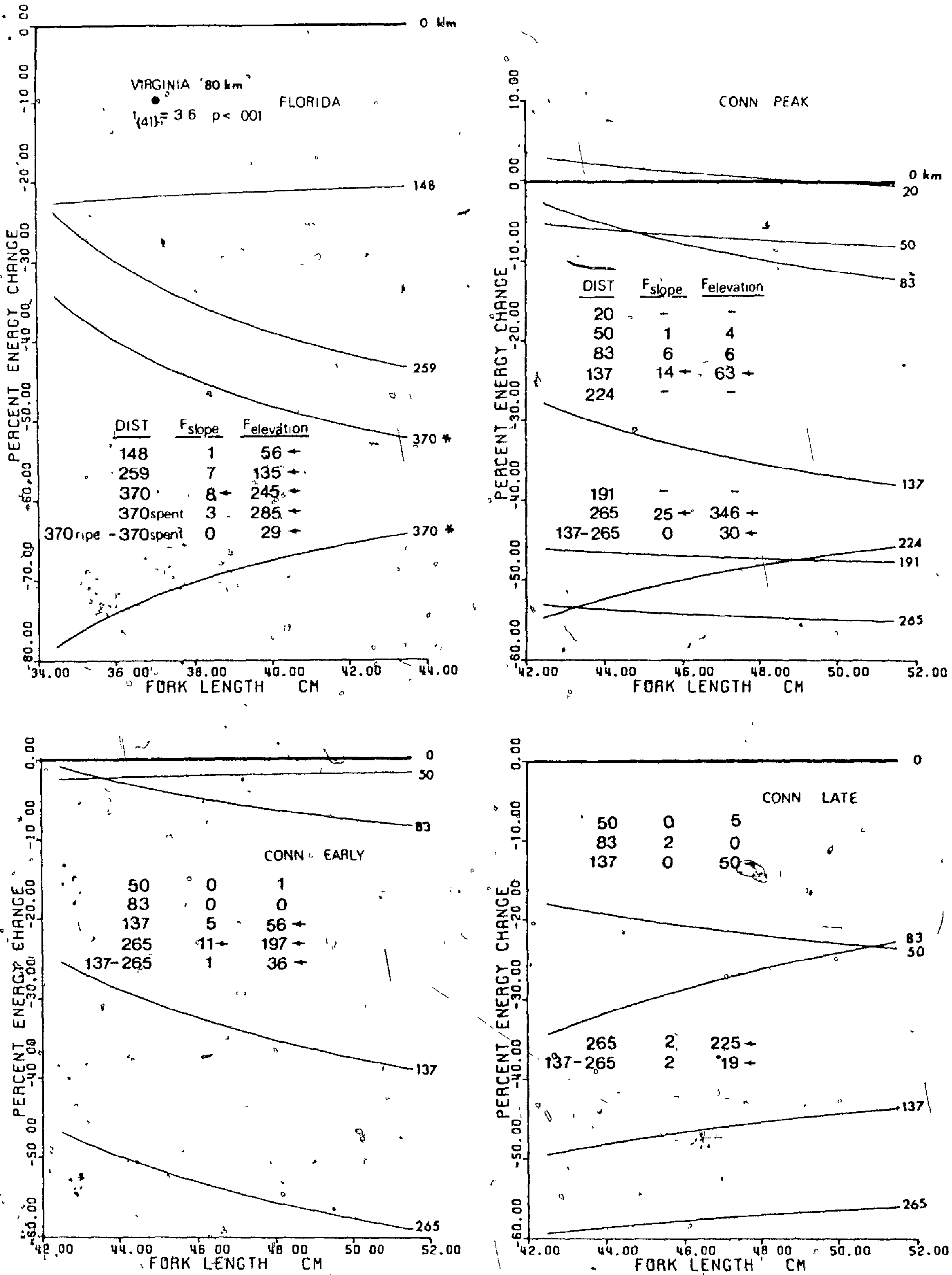
Somatic energy changes Florida and Connecticut males began the migration with comparable somatic energy reserves (Table 6). The mean somatic energy content of Virginia males at entry to the river (1933 kcal, SD = 181) agreed with the calculated somatic reserves of Florida males of equivalent length (1994 kcal). Depletion of reserves during total freshwater residence was greatest for Florida males (65-80% vs. a maximum of 60% for Connecticut males; Fig. 16). Virginia males experienced the least depletion during upstream movement (10% vs. a minimum of 25% for Connecticut and Florida migrants). In the Connecticut River, "late" migrants expended more energy in reaching all upriver locations than did "early" and "peak" migrants.

Florida females entered freshwater with significantly greater somatic energy reserves than "early" and "late" run Connecticut migrant females of equivalent sizes and with reserves equivalent to those of Connecticut "peak" migrants (Table 6). The mean somatic energy content of Virginia

Table 6. F values for analysis of covariance of length/somatic energy regressions for Connecticut and Florida shad sampled at the river mouth, at the spawning areas and following spawning. (+) or (-) indicates slopes and elevations of regressions on the horizontal are significantly greater (+) or less (-) than the slopes and elevations on the vertical ($p<0.01$).

| | Male | | | | | | Female | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Florida | | Conn. Peak | | Conn. Early | | Florida | | Conn. Peak | | Conn. Early | |
| | slope | elevation | slope | elevation | slope | elevation | slope | elevation | slope | elevation | slope | elevation |
| RIVER MOUTH (0 km.) | | | | | | | | | | | | |
| Conn. Peak | 2.3 | 2.0 | | | | | 0.1 | 3.6 | | | | |
| Early | 0.2 | 4.5 | 0.8 | 12.6(+) | | | 4.1 | 22.5(+) | 3.1 | 6.8 | | |
| Late | 0.0 | 3.6 | 2.3 | 24.9(+) | 0.1 | 0.2 | 1.7 | 8.5(+) | 1.6 | 6.8 | 0.2 | 2.1 |
| MAJOR SPAWNING AREAS (370 km. Florida, 137 km. Conn.) | | | | | | | | | | | | |
| Conn. Peak | 0.9 | 9.4(-) | | | | | 3.2 | 0.1 | | | | |
| Early | 0.3 | 5.3 | 0.4 | 2.6 | | | 0.0 | 2.0 | 4.6 | 8.6(+) | | |
| Late | 5.0 | 0.6 | 3.4 | 2.4 | 5.0 | 0.0 | 0.6 | 2.1 | 2.6 | 37.5(+) | 2.5 | 0.0 |
| SPENT FISH (370 km. Florida, 265 km. Conn.) | | | | | | | | | | | | |
| Conn. Peak | 0.0 | 2.1 | | | | | 7.0 | 4.3 | | | | |
| Early | 0.5 | 7.8(-) | 2.4 | 2.8 | | | 0.3 | 8.7(-) | 6.2 | 7.1 | | |
| Late | 0.4 | 0.0 | 0.9 | 0.0 | 5.9 | 3.7 | 0.0 | 9.6(-) | 10.9(+) | 54.8(+) | 0.5 | 0.7 |

Figure 16. Proportional changes in male somatic energy content during the freshwater migration. Changes associated with specific distances (km) are relative to initial somatic energy content. See Fig. 4 for explanation of symbols and terminology.



0 km
VIRGINIA '80 km'
$t_{(41)} = 3.6$ p< .001
FLORIDA
148
259
370 *
370 *
DIST Fslope Felevation
148 1 56
259 7 135
370 8 245
370spent 3 285
370ripe - 370spent 0 29
PERCENT ENERGY CHANGE
FORK LENGTH CM
CONN PEAK
0 km
20
50
83
137
224
191
265
DIST Fslope Felevation
20 - -
50 1 4
83 6 6
137 14 63
224 - -
191 - -
265 25 346
137-265 0 30
CONN EARLY
0
50
83
137
265
50 0 1
83 0 0
137 5 56
265 11 197
137-265 1 36
CONN LATE
0
83
50
137
265
50 0 5
83 2 0
137 0 50
265 2 225
137-265 2 19

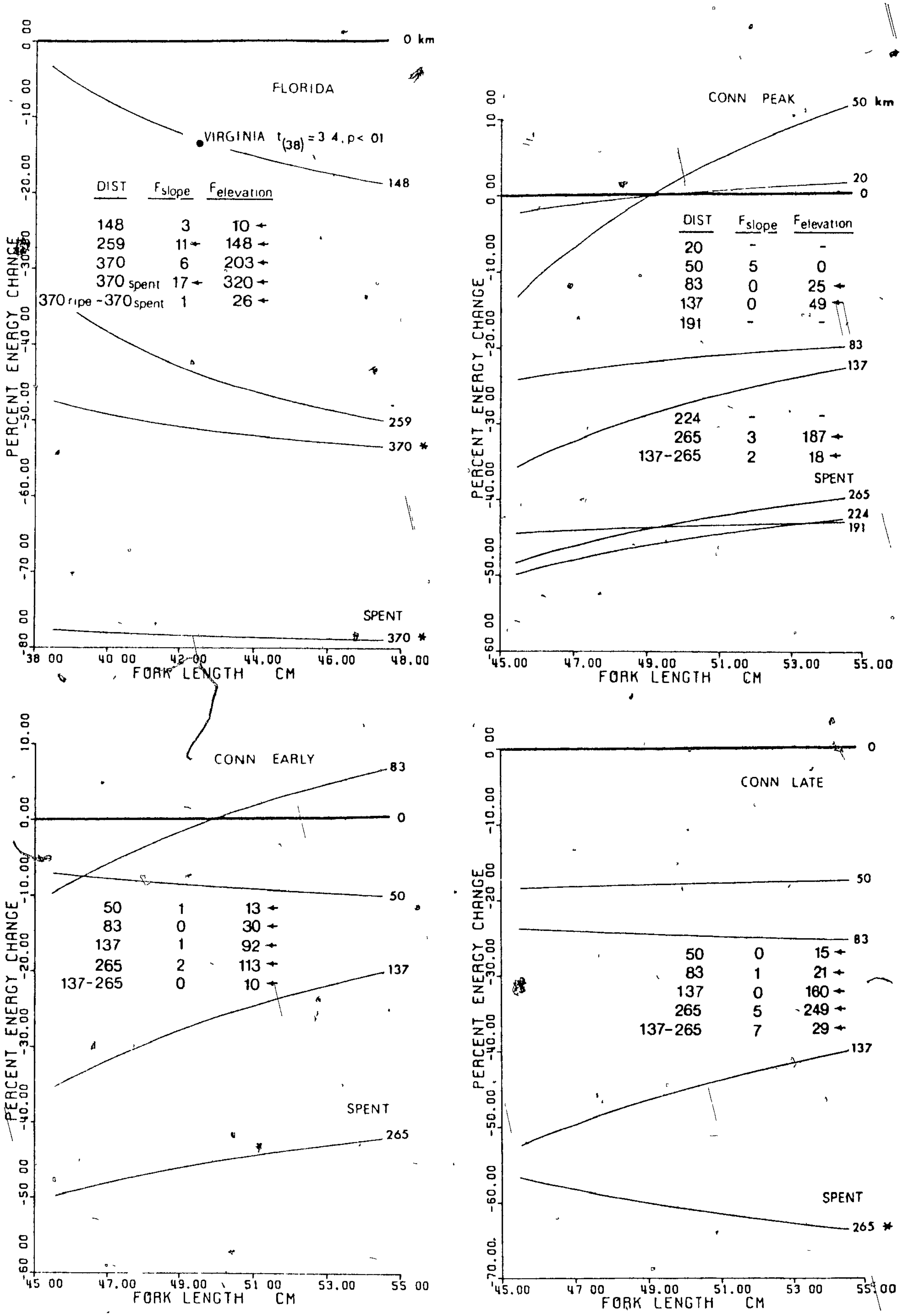
females (2879 kcal) was intermediate to calculated reserves of Florida females (3024 kcal) and Connecticut females (mean = 2628 kcal) of equivalent lengths. Subsequent energy losses associated with upriver migration were greatest among Florida females (up to 50%). Losses by Connecticut and Virginia shad approximated 30 and 13% respectively (Fig. 17). Maximal within river depletions during total river residence were 63% (late Connecticut River migrants) and 78% (Florida).

Within the Connecticut River, peak run females entered with significantly greater somatic energy reserves than "early" and "late" conspecifics whose energy reserves were approximately equal (Table 6). These differences were maintained at the spawning areas. However after spawning, late migrants were significantly more depleted than earlier migrants. Proportionate losses indicated late run females utilized approximately 10% more energy (Fig. 17) than early or peak run shad.

Comparisons of somatic energy content between the river mouth and upriver stations in Connecticut revealed a significant depletion both preceding and following spawning for all shad (Figs. 16, 17). Since viscera energy was significantly reduced only during the prespawning period, the 15-30% decrease in somatic reserves following spawning represented the total cost of seaward migration.

Changes in the slopes of the body length/somatic energy relationships during the freshwater migration indicated disproportionate energy expenditure according to body size. The slopes for "peak" and "early" Connecticut male migrants and for all Florida shad decreased with distance (Figs. 16, 17) indicating a greater energy expenditure by larger

Figure 17. Proportional changes in female somatic energy content during the freshwater migration. Changes associated with specific distances (km) are relative to initial somatic energy content. See Fig. 4 for an explanation of symbols and terminology.

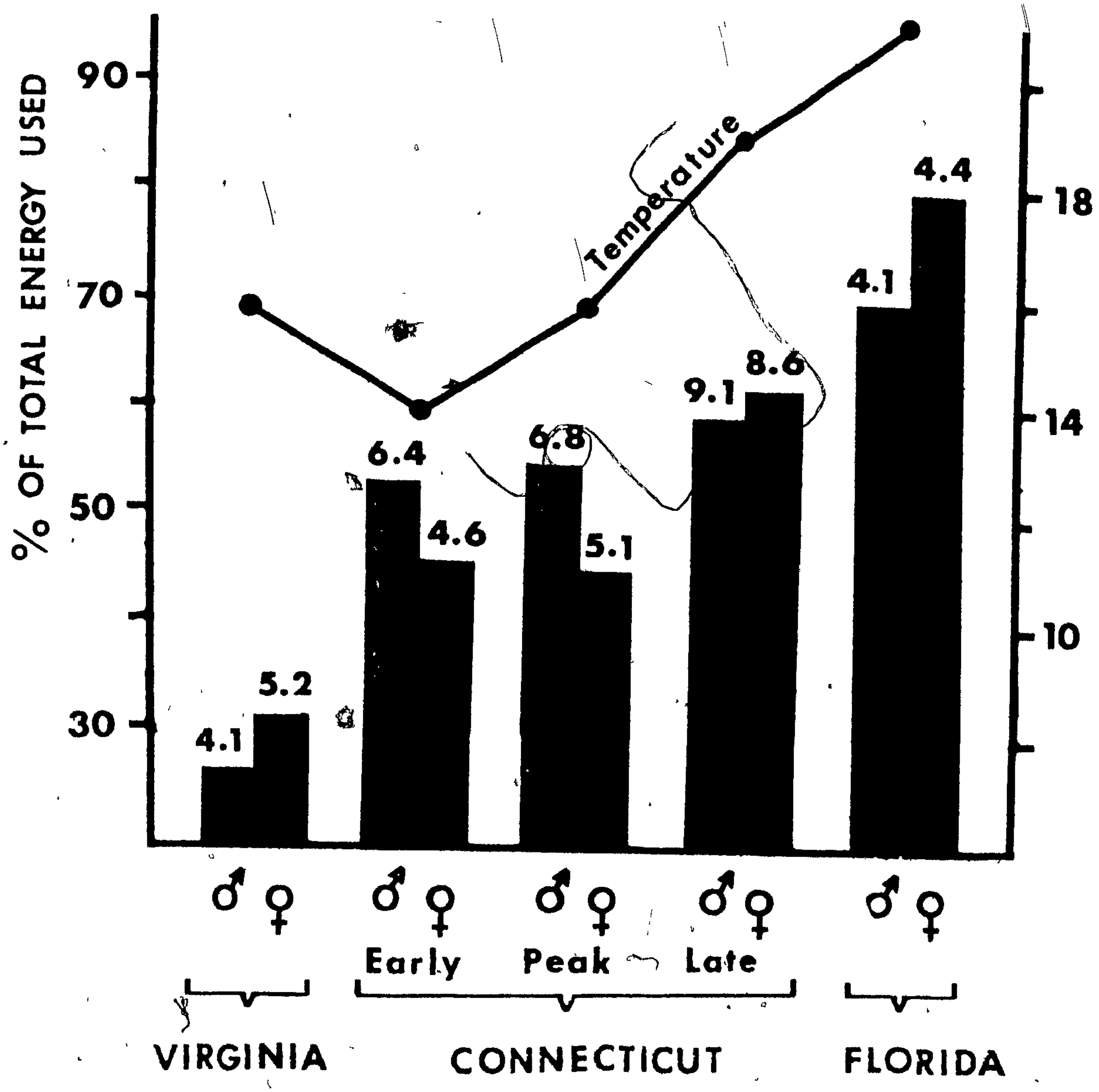

FLORIDA
0 km
VIRGINIA $t_{(38)}=3.4, p<.01$
148
DIST | $F_{slope}$ | $F_{elevation}$
148 | 3 | 10
259 | 11 | 148
370 | 6 | 203
370 spent | 17 | 320
370 ripe - 370 spent | 1 | 26
259
370 *
SPENT
370 *
PERCENT ENERGY CHANGE
FORK LENGTH CM
CONN PEAK
50 km
20
0
DIST | $F_{slope}$ | $F_{elevation}$
20 | - | -
50 | 5 | 0
83 | 0 | 25
137 | 0 | 49
191 | - | -
224 | - | -
265 | 3 | 187
137-265 | 2 | 18
83
137
SPENT
265
224
191
PERCENT ENERGY CHANGE
FORK LENGTH CM
CONN EARLY
83
0
50
50 | 1 | 13
83 | 0 | 30
137 | 1 | 92
265 | 2 | 113
137-265 | 0 | 10
137
SPENT
265
PERCENT ENERGY CHANGE
FORK LENGTH CM
CONN LATE
0
50
83
50 | 0 | 15
83 | 1 | 21
137 | 0 | 160
265 | 5 | 249
137-265 | 7 | 29
137
SPENT
265 *
PERCENT ENERGY CHANGE
FORK LENGTH CM

individuals. Consequently, proportional energy losses tended to be greater for these fish. Where the slope did not vary significantly with distance, disproportionate expenditures with body size did not exist.

Comparative energy expenditures The comparative costs of migration for the average shad (determined by summing viscera and somatic expenditures; viscera expenditures of "early" and "late" Connecticut migrants were assumed to equal those of "peak" migrants) indicated the cost per kilogram of wet body weight per kilometer of upriver displacement varied both between rivers and temporally in Connecticut (Fig. 18). Florida shad, migrating at the highest water temperatures, expended the least energy per kilometer; the cost varying from 4.1 to 4.4 kcal/km. The comparative costs for Virginia shad were similar for males (4.1 kcal/km) and slightly higher for females (5.2 kcal/km). The energy expenditures of Connecticut shad, ranging from 4.6 to 9.1 kcal/km, tended to be the highest among all shad. Within the Connecticut River, the energy cost of migration increased as the spawning migration progressed. Late migrants, which experienced the highest water temperatures, utilized between 8.6 and 9.1 kcal/km. Between sex differences were also apparent. Connecticut males expended more energy per km than females. This pattern was reversed in Florida and Virginia.

The proportion of total viscera and somatic energy utilized to complete the migration was greatest in Florida (70–75%; Fig. 18). Losses experienced by Virginia migrants (26–32%), estimated by doubling the proportional losses associated with upstream migration, were considerably less than those of both Florida and Connecticut shad. The assumption

Figure 18. Caloric expenditure per kg wet body weight (somatic tissue and viscera only) per km of upriver displacement (no. above histogram) and percentage of total energy (viscera and somatic combined) utilized to complete the migration. Values given are for the average shad (by sex) in each population (Connecticut males and females of 45 and 50 cm respectively; Florida males and females of 40 and 42 cm respectively; Virginia males and females of 37 and 42 cm respectively). Average water temperatures encountered by migrants are shown.


% OF TOTAL ENERGY USED
90
70
50
30
Temperature
TEMPERATURE (°C)
18
14
10
4.1
5.2
6.4
4.6
6.8
5.1
9.1
8.6
4.1
4.4
♂ ♀
♂ ♀
♂ ♀
♂ ♀
♂ ♀
Early
Peak
Late
VIRGINIA
CONNECTICUT
FLORIDA

that downstream costs equalled those associated with the upriver migration in Virginia prevented an underestimate of total energy expenditures required to complete the migration (maximal energy expenditure after spawning did not exceed 60% of upstream losses in Florida and Connecticut). Total proportional energy expenditures varied between sexes. The magnitude of this variance reflected differences in sex specific costs per km of upstream displacement.

## Discussion

Adult shad do not feed in freshwater (Atkinson, 1951). There is, therefore, a rapid decline in energy reserves, accumulated at sea, during the freshwater phase of the spawning migration. This rapid and extensive use of energy reserves is reflected in the extreme weight loss suffered by shad during the migration (Chittenden, 1969; Leggett, 1972; this study). The use of tissue weight change as a morphophysiological index for the evaluation of the energy dynamics of fish populations has been criticized in the past (Shulman, 1974; Gerking, 1952). However we found that, for shad, changes in tissue mass closely parallel changes in tissue energy content and for this reason tissue weight change is considered to be a reliable index of the extent of energy utilization.

The important variables influencing the rate and extent of energy utilization by shad are body size, sex, water temperature and current velocity at the time of migration, stage of gonad development prior to entry into freshwater and distance to spawning areas. The large number of contributing factors resulted in high variability in measures of tissue weight change and energy depletion both within and between the Connecticut, York, and St. Johns River populations. There were, however, important differences in the patterns of tissue weight dynamics and energy use in the three populations which appear to be important in determining individual survival and, ultimately, the life history characteristics of the populations.

GONAD DEVELOPMENT

There was a clear latitudinal trend in the state of development of the gonads at the time of entry into the rivers. Gonads of the St. Johns River shad were the least developed, those of the Connecticut River the most fully developed, while gonads of the Virginia population were intermediate in condition. In the St. Johns River population gonad weight and energy content increased 40 to 70% in females and 20 to 30% in males during upriver migration to the spawning grounds. This energy was drawn from somatic and viscera reserves. The transfer of energy to the gonads of York River shad during the migration was smaller, averaging approximately 5% for both males and females. In the Connecticut River, those shad which entered freshwater at the peak of the migration exhibited virtually no change in gonad weight or gonad energy content during the migration to the spawning grounds. In this group gonad development was completed at sea. There was, however, a temporal variation in the state of maturity of the gonads of Connecticut River shad. In contrast to those shad migrating at the peak of the run, the gonads of early and late migrant shad were less mature at time of entry and small but significant increases in gonad weight occurred during the freshwater migration.

The positive relationship between gonad development at the time of river entry and latitude of the home river leads us to hypothesize that gonad development commences at approximately the same time in all Atlantic coast stocks. Shad from all Atlantic coast populations migrate together, north and south, along the Atlantic coast between Florida and New Brunswick in response to seasonal changes in the location of preferred water temperatures (Leggett and Whitney, 1972). Consequently, shad from all Atlantic coast populations experience virtually identical environmental conditions while at sea and are near the southern extreme of their geographic range in December (Leggett and Whitney, 1972; Leggett and Carscadden, 1977). Assuming synchronous initiation of gonad development, possibly in response to increasing day length (Baggerman, 1957), Florida shad would arrive at their home river with their gonads in an early stage of development relative to gonad development in shad of more northern populations which enter their home rivers to spawn later in the spring. The orderly south-north sequence of river entry (Walburg and Nichols, 1967; Leggett and Whitney, 1972) would produce the latitudinal trend observed.

The temporal variation in gonad maturity in the Connecticut River population is believed to result, in part, for the same reason. Assume the initiation of gonad maturation is synchronous in all stocks. Early migrant Connecticut River shad would have 2-4 weeks less time to develop their gonads than shad migrating at the peak of the run. This time difference is similar to the difference in the timing of the peaks of migratory activity between the York and Connecticut Rivers (Leggett and Whitney, 1972). The gonad development of early run Connecticut River and peak run York River shad is also similar. The retarded gonad development of late migrant Connecticut River shad does not fit this hypothesis. It is important to note however, that late run shad in this population also enter the river with somatic fat and protein reserves that are significantly lower than the early and peak run migrants. The late run component may thus represent a portion of the stock having inferior overall growth during the marine life phase. Delayed river entry may facilitate the development of additional energy reserves in this group in preparation for migration and spawning.

A considerable portion of the energy utilized for the development of the gonads while at sea is drawn from somatic and viscera reserves. This conclusion is based on our finding that the somatic and viscera reserves of female Virginia and Connecticut River shad were proportionally lower at the time of river entry than those of female Florida shad, in spite of their longer ocean residence. Thus the transfer of energy to the gonads is apparently faster than the rate of acquisition of energy from the environment. Similar patterns of energy transfer have been reported for herring (Clupea harengus; Blaxter and Holliday, 1963; Channon and Saby, 1932) and Sardinia (Clupeidae; Hickling, 1945).

In shad, the total energy content of the testes is much less than that of the ovaries (128 kcal versus 385 kcal for the standard length male (45 cm) and female (50 cm) gonad respectively) and the relative energetic cost of gonad development appears to be reflected in the somatic stores of the two sexes. Males, which require less energy for the maturation of the gonads, have higher somatic and viscera energy reserves than females at the time of entry into freshwater. The testes of male York and Connecticut River shad are virtually mature at the time of river entry, while those of St. Johns River males require a relatively small transfer of energy (10 kcal for the average (40 cm) shad in the population) during the migration. This explains the absence of a latitudinal trend in somatic and viscera energy reserves in males sampled at the mouths of their respective rivers.

Transfer of energy to the gonads prior to, and during the freshwater migration significantly influenced the total energy available to meet the requirements of the freshwater migration.

MIGRATION ENERGETICS

The energetic cost of migration to the spawning grounds differed both within and between populations and was dependent on body size, water temperature and current velocity at the time of migration, and distance to spawning areas. In the Connecticut River, male shad migrating at the beginning and at the peak of the migration expended more energy (7 kcal/kg/km of upstream displacement) than did females (5 kcal/kg/km of upstream displacement). This appears to result primarily from the difference in average size of males and females since conditions experienced during the migration and the average rates of upriver migration were similar for the two groups. Size related differences in metabolic rates are common in fish and appear to result from both physiological and hydrodynamic factors (Winberg, 1956; Fry, 1971; Brett and Glass, 1973; Webb, 1975). The higher energy cost in smaller shad is consistent with the results of these laboratory studies. Late migrant male and female Connecticut River shad experience approximately equivalent energy expenditures (9 kcal/kg/km of upstream displacement) during the migration. The increased rate of energy expenditure in females, relative to the smaller, less efficient males, reflects the transfer of energy to the ovaries in late migrating females and does not imply a reduction in locomotory efficiency in females as the season progresses.

In the St. Johns River population, somatic and viscera energy losses were higher in females than in males (4.4 and 4.1 kcal/kg/km of upstream displacement respectively) and are higher for large females than for small females. Similarly, Virginia females exhibited greater energy losses (5.2 kcal/kg/km) than did males (4.1 kcal/kg/km) but no comparable data is available on differences in energy expenditure with variation in female body size. These disparities in the typical body size, migration efficiency relationship appear to result from differences in the rate of transfer of energy to the gonads within and between populations. Females of the St. Johns and York River populations enter the river at earlier stages of gonad development and large females are considerably less mature than smaller fish in the St. Johns population. The resulting transfer of energy reserves from somatic to gonad tissue during the freshwater migration produces a greater rate of energy loss in females than males and, in Florida, a higher loss among large females relative to smaller individuals of the same sex. The somatic energy loss for gonad development thus overrides the metabolic advantage of size in these populations. Idler and Clemens (1959) reported similar trends in energy utilization by sockeye salmon. Female sockeye expended 20% more energy per kilometer than males. They attributed this disparity to the greater demands of gonad maturation in females.

The higher energy utilization of large males compared with small fish of the same sex, in both the Florida and Connecticut populations, is inconsistent with the general pattern of increasing locomotory efficiency with increasing size. Since males do not transfer significant quantities of energy to the testes during migration, large individuals should have a metabolic advantage but do not. The burden of spawning for large males may be greater than that indicated solely by changes in gonad energy content. Hickling (1930) reported the cost of spawning in male Merluccius merluccius doubles for every 10 cm increase in body length. The reasons for this disparity are, however, unknown.

The average cost of the migration for the Florida and Virginia population was 4.2 and 4.6 kcal/kg/km of upriver displacement. This was significantly less than that recorded for peak and late run segments of the Connecticut population which migrated at temperatures approximately equivalent to those experienced by St. Johns and York River shad. Reduced current velocities in the St. Johns and York Rivers, indicated by diminished angular displacement to the spawning areas (approximately 5 m deg compared to 20 m deg in the Connecticut River) are believed to account, in part, for this difference. It is also possible that the lower migration costs per unit distance in southern rivers results from differences in migratory behaviour. Leggett (1976) reported that considerable meandering and downriver movement occurs during the spawning run of shad.

in the Connecticut River. Perhaps the migration is more direct in southern rivers. Unfortunately no information is available to test this possibility.

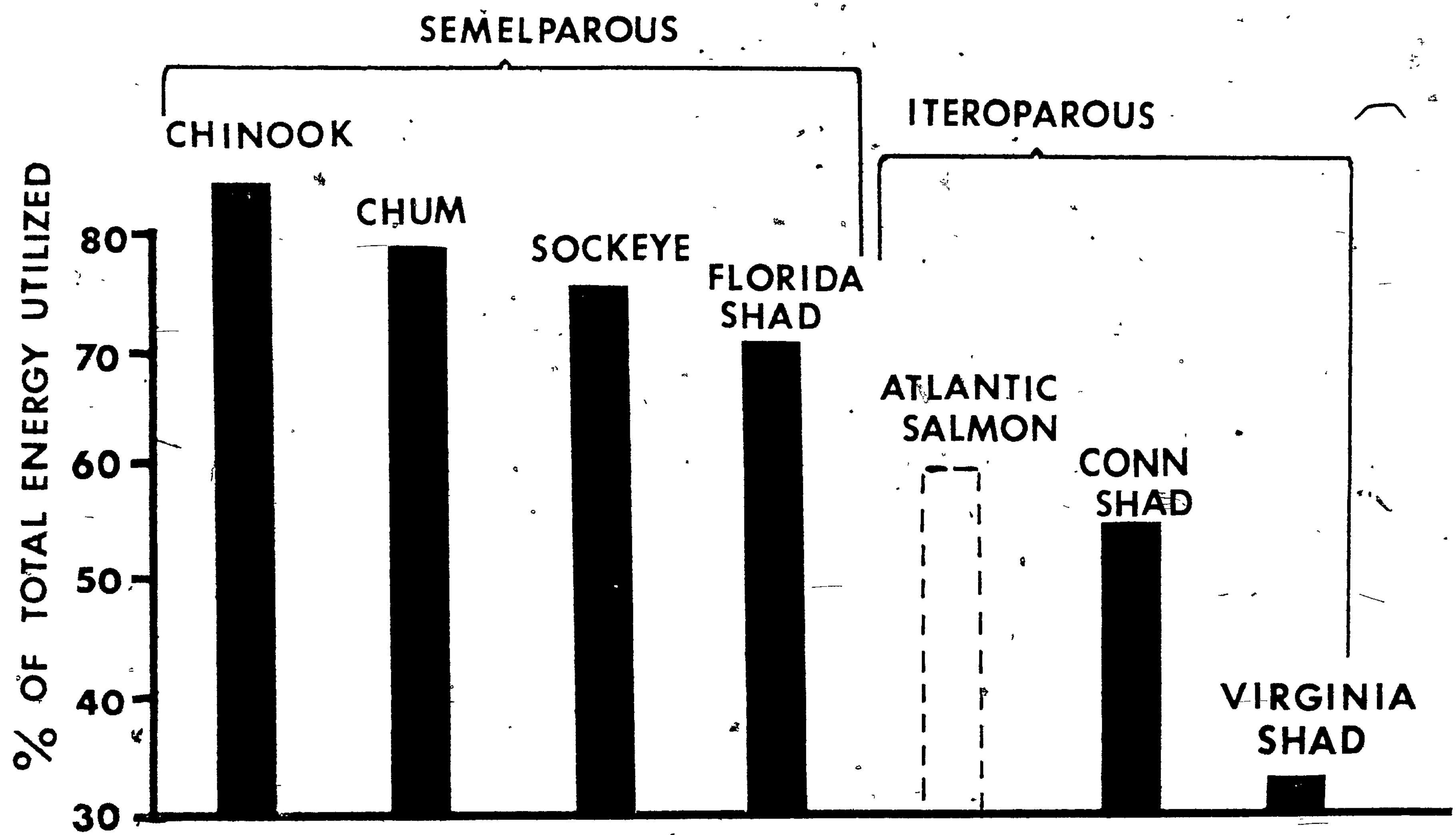
In the Connecticut River the significant increase in energy expended per kilometer of upriver migration by both late migrant males and females, relative to fish migrating earlier in the season, reflects the effects of higher average water temperatures on migration energetics. Late migrant males and females expend 2.7 and 4.0 kcal more energy/kg/km of upstream displacement than equivalent size early migrant males and females respectively. This corresponds well with expected metabolic responses to temperature (Prosser, 1973), the related increases for the 5°C increase in average migration temperature experienced by late migrants, as predicted by the $Q_{10}$ law, being approximately 3 kcal/kg/km.

In spite of the lower energy expenditure/unit distance travelled, shad from the St. Johns River population experienced significantly greater total reductions in body weight and energy reserves than did Connecticut and York River shad. These fish experienced somatic weight losses of 20 to 50% and utilized 70-80% of their combined somatic and viscera energy to reach the spawning grounds and complete the spawning act. In contrast, Connecticut River shad experienced body weight losses of 25-35% and utilized 40-60% of their combined somatic and viscera energy reserves during the complete freshwater migration from the sea to the spawning grounds and back to the sea. Extrapolation of the energy utilized by York River shad to reach the spawning area indicates these fish utilize approximately 32% of their total energy reserves to complete the freshwater migration. The higher total energy expenditure in Florida results from the combination of greater energy transfer to the gonads during the freshwater migration and the longer freshwater migration required to reach the spawning areas in the St. Johns River.

LIFE HISTORY CONSEQUENCES

The high body weight loss and energy expenditure experienced by the St. Johns River shad during the freshwater migration to the spawning area precludes a successful return migration to sea. Energy expenditures of similar magnitude have been reported for Pacific salmon (Fig. 19; Greene, 1926; Pentegov _et. al._, 1927; Idler and Clemens, 1959) which, like St. Johns River shad (Leggett, 1969; Leggett and Carscadden, 1977) suffer complete postspawning mortality (semelparous reproduction). At the proximate level, therefore, the combined energetic costs of gonad development and the freshwater migration are the reason for the semelparous reproductive character of the Florida shad population. Even by delaying maturity and thereby increasing the average body size (and energy reserves) of fish in the population to that of the Connecticut stock, Florida shad would experience lethal energy expenditures preventing a successful return migration to the sea. The lack of repeat spawners in other southern rivers (Ogeechee R., Edisto R.; Leggett, 1969), where shorter migration distances (160-200 km; Walburg and Nichols, 1967) should permit a return migration to sea, indicates that factors other than migration energetics regulate the life history characteristics of these populations. Leggett (1969) and Leggett and Carscadden (1977) have

Figure 19. Percentage of total available body energy reserves utilized by five species of anadromous fish to successfully spawn. Repeat spawning (iteroparous) and single spawning (semelparous) populations are indicated. The expenditure by Atlantic salmon is estimated from reported weight losses (Greene, 1926). Pacific salmon data are from: Greene, 1926 (chinook); Pentegov et. al., 1927 (chum); Idler and Clemens, 1959 (sockeye).



SEMELPAROUS
ITEROPAROUS
CHINOOK
CHUM
SOCKEYE
FLORIDA SHAD
ATLANTIC SALMON
CONN SHAD
VIRGINIA SHAD
% OF TOTAL ENERGY UTILIZED
80
70
60
50
40
30

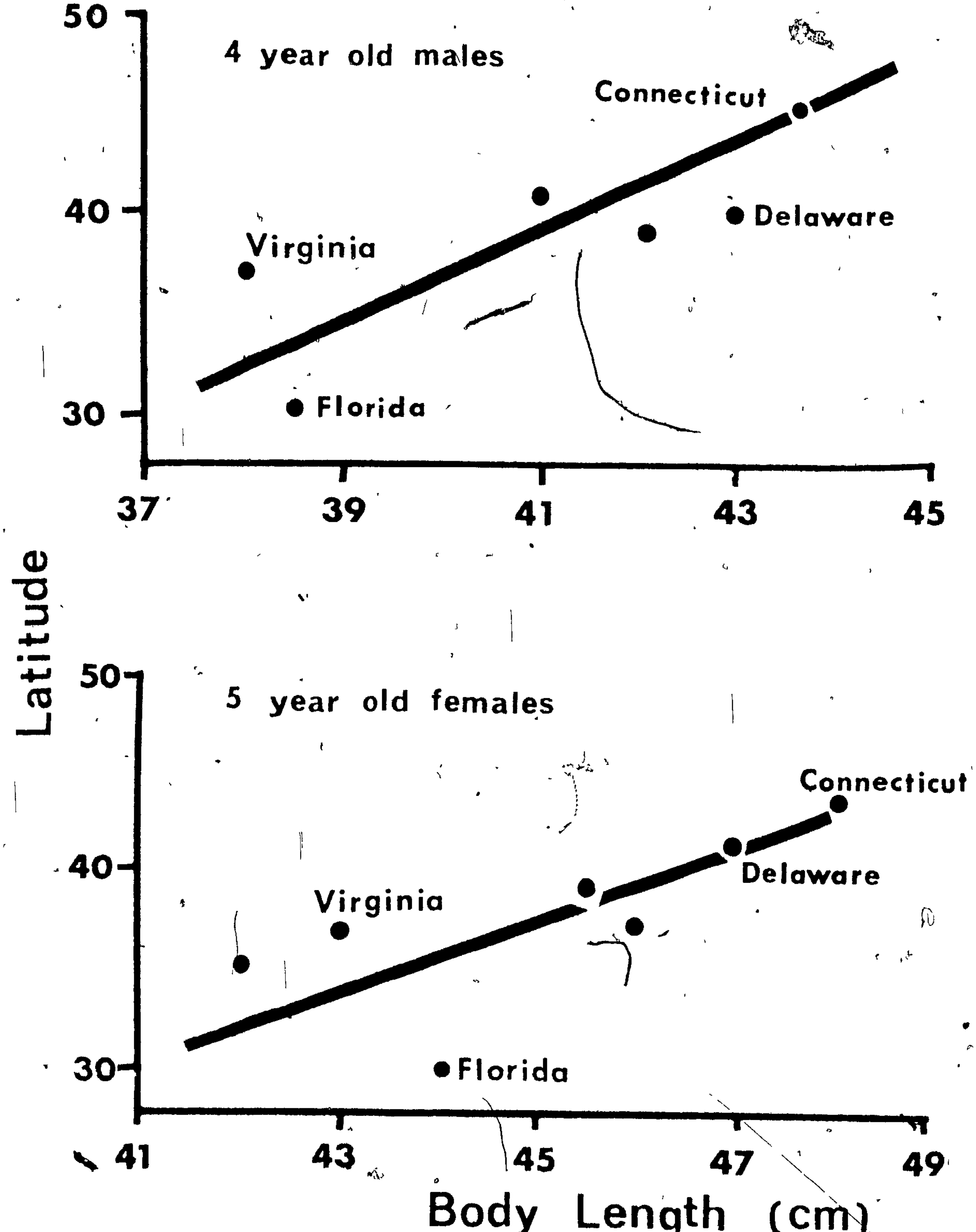
suggested that the freshwater environment is more predictable in the southern portion of the range of shad. This appears to be true for temperature and flow conditions during the spawning period (E. Shoubridge, McGill Univ., pers. comm.). Since temperature and flow conditions at this time significantly influence spawning success, year class strength and recruitment (Marcy, 1976; Leggett, 1977) density independent variations in year class strength should be significantly smaller in the south. Such increased reproductive predictability reduces the selective advantage of repeat reproduction (Ricker, 1954; Beverton and Holt, 1957; Murphy, 1968) and may be the ultimate regulator of the life history characteristics in those southern shad populations where energy constraints are not limiting postspawning survival.

St. Johns River shad have compensated for the loss of reproductive potential resulting from complete postspawning mortality by an approximate doubling of the average number of eggs spawned per female relative to those of northern populations (Leggett, 1969; Leggett and Carscadden, 1977). This adaptation is in accord with predictions based on theoretical analysis of life history strategies (Cole, 1954; Cody, 1966; ~~Holgate, 1967~~; Charnov and Krebs, 1973; Mountford, 1973). This increase in egg number has been achieved by a significant reduction in the average energy content of the egg (0.4 cal/ovum vs. 1.3 cal/ovum for the York and Connecticut populations. This reduced energy content may be made possible by higher average survival (due to increased environmental stability) and by shorter development times caused by the higher average water temperatures in the south (Ryder, 1887; Leim, 1924; Leach, 1925; Fig. 18).

In the York River and Connecticut Rivers, where migration distances are shorter than in the St. Johns River and the resulting utilization of stored energy less severe, a significant portion of the population spawns more than once (York 23%; Connecticut 38%; Leggett and Carscadden, 1977). Estimated energy consumption of Atlantic salmon, an iteroparous species, during the freshwater migration is similar to that of Connecticut River shad and significantly less than that of semelparous Pacific salmon and St. Johns River shad (Fig. 19). This suggests a relationship between relative energy expenditure during the freshwater migration and post-spawning survival in anadromous fish species. The larger body size at any given age (Fig. 20), and the later mean age at maturity in northern populations (Leggett, 1969) may represent adaptations to increase energy reserves and hence increase the probability of repeat spawning thereby compensating for reduced population stability resulting from low environmental predictability during the spawning period. Such adaptations are known to exist in Atlantic salmon (Kalturin, 1957; Schaffer and Elson, 1975).

Intrapopulation differences in total energy expenditures experienced by individual fish, as a result of differences in hydrologic conditions, migration distances, size related migration efficiencies, and the condition of the gonads prior to the commencement of the freshwater migration, may also influence the repeat spawning characteristics of different portions of the stocks. The higher postspawning mortality experienced by late migrating shad in the Connecticut River (Leggett, 1969) is positively related to the higher tissue weight losses and energy utilization in that

Fig. 20. The relationship between shad body size (fork length) and the latitude of the home river. Data are from Carlander (1969), Chittenden (1969) and this study. Line fitted to the points by eye.



4 year old males
Connecticut
Delaware
Virginia
Florida
50
40
30
37
39
41
43
45
Latitude
5 year old females
Connecticut
Delaware
Virginia
Florida
50
40
30
41
43
45
47
49
Body Length (cm)

group. Similarly, the higher migration energy requirements of large relative to small males may explain the tendency for males to mature earlier and at a smaller average size than females.

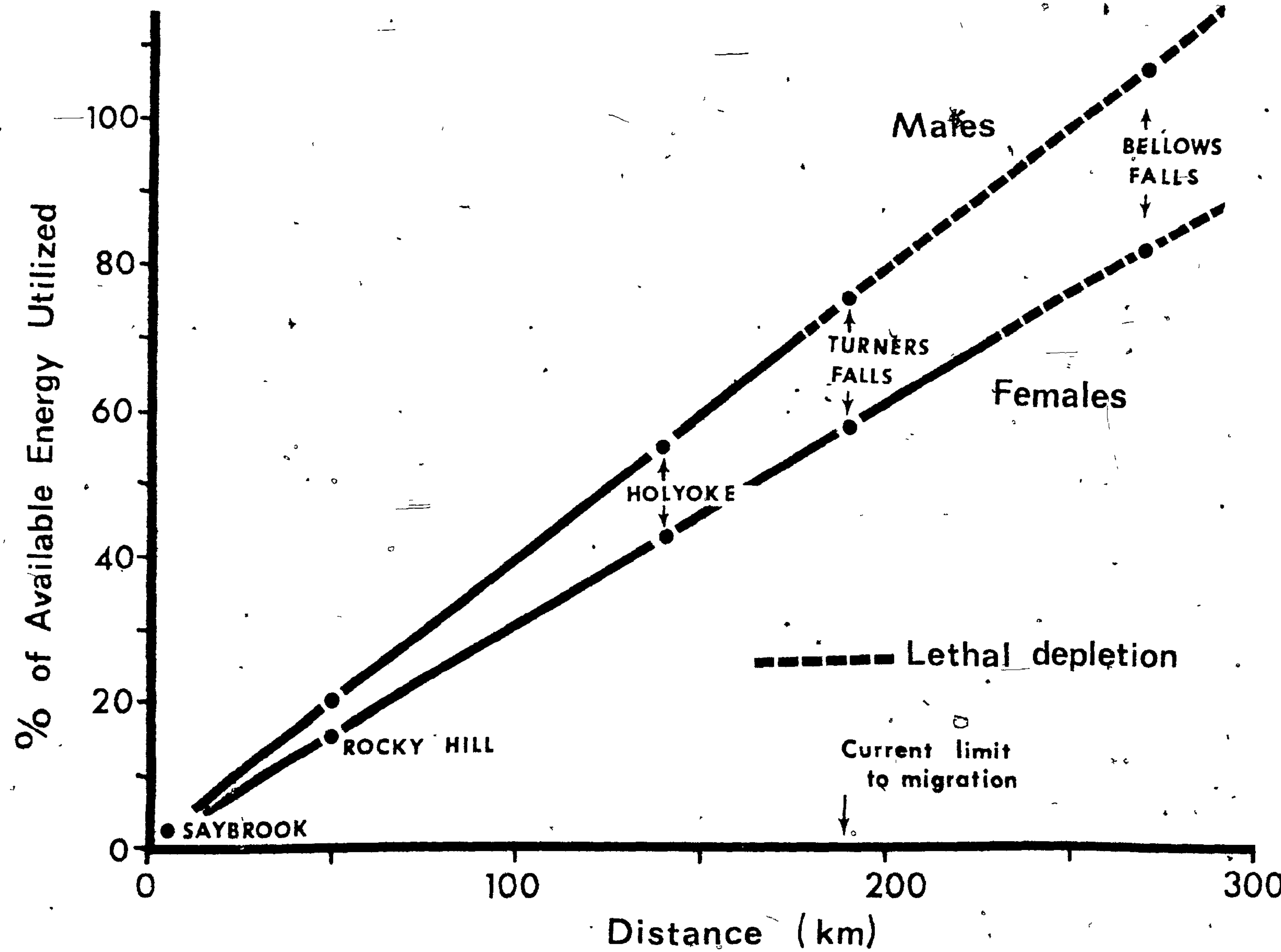
The upriver migration of shad in the Connecticut River is currently blocked by a power dam at Turners Falls (km 184), although historically shad migrated to Bellows Falls (km 270). Extrapolation of observed rates of energy consumption for the Connecticut River population (Fig. 21), and assuming lethal energy expenditures to be equivalent to the total expenditures observed in the semelparous St. Johns River population, leads us to predict that the frequency of repeat spawning among shad spawning between Turners Falls and Bellows Falls following completion of fish lift facilities at Turners in 1981 will be significantly below that reported for the lower river. The reduced frequency of repeat spawning among shad spawning above Holyoke (R. Reed, Univ. of Mass., pers. comm.) supports this prediction.

These findings support the hypothesis of Carscadden and Leggett (1975) that differences in the frequency of repeat reproduction in shad populations native to three tributaries of the St. John River, N.B. result from differences in the length of the freshwater migration to the spawning grounds. In these populations, as with that of the St. Johns River, Florida, increased fecundity and earlier maturity were associated with reduced frequencies of repeat reproduction.

SWIMMING EFFICIENCY

Extrapolation of Brett's (1965a,b) metabolic rate/body weight relationships for salmon swimming at various speeds, and the resulting derivations

Figure 21. Total energy expenditures by shad to reach various upriver locations in the Connecticut River and return to sea.



% of Available Energy Utilized
0
20
40
60
80
100
0
100
200
300
Distance (km)
Males
Females
Lethal depletion
SAYBROOK
ROCKY HILL
HOLYOKE
TURNERS FALLS
BELLOWS FALLS
Current limit to migration

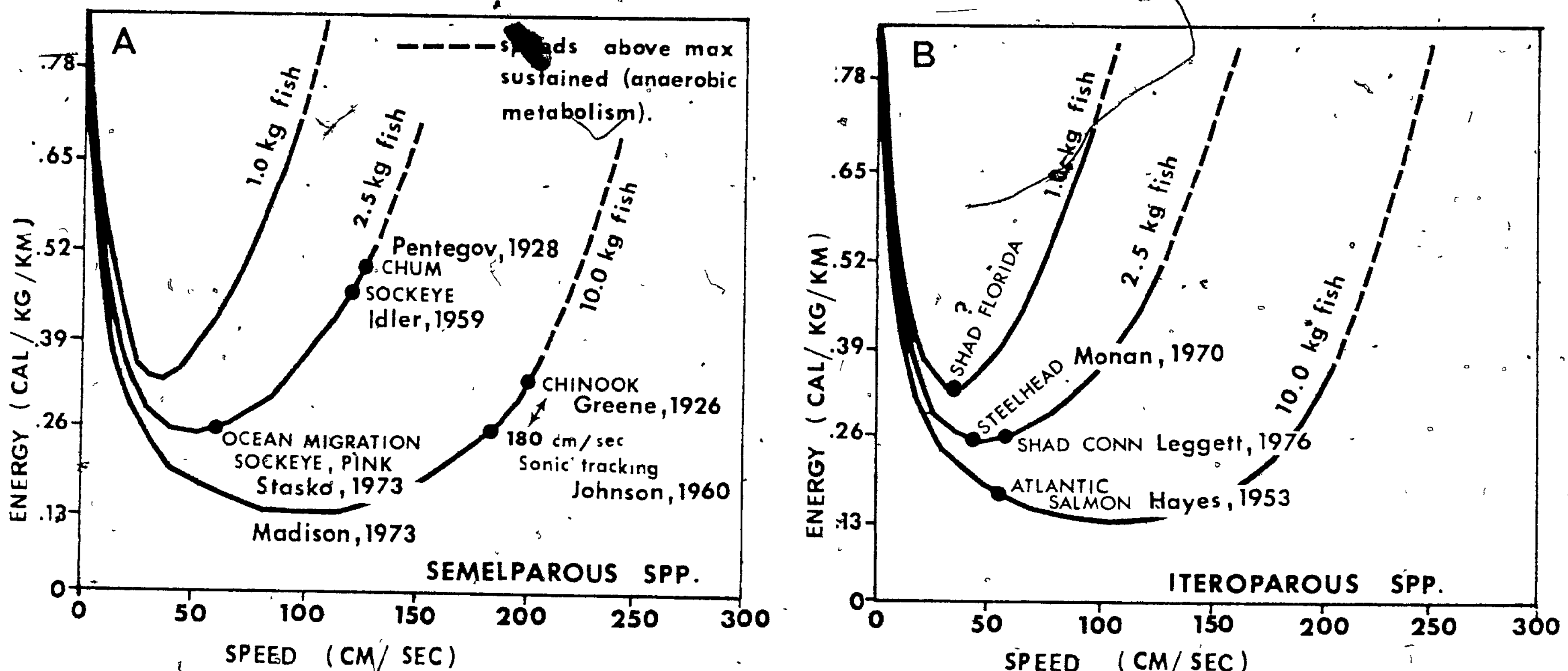
of the relationship between energy efficiency (calories expended per kilometer swum), body size and swimming speed (Fig. 22 A,B) indicate that freshwater migration rates in American shad are near the speed of maximum efficiency. Similar migration efficiencies are reported for two other iteroparous species, steelhead trout (S. gairdnerii) and Atlantic salmon (S. salar) (Fig. 22 B). In sharp contrast semelparous species such as chum (O. keta), sockeye (O. nerka) and chinook (O. tshawytscha) salmon migrate at higher, less efficient speeds (Fig. 22 A). In the case of shad, maximum efficiency is required in order to accomplish the spawning migration. For Florida shad the increase in energy consumption/km at speeds below or above the optimum are great. Since these fish use virtually all their expendable energy to reach the spawning grounds, any significant reduction in swimming efficiency would result directly in reduced fitness. For Connecticut River shad, which are larger, the change in migration efficiency is less abrupt. However, maximum swimming efficiency is required to ensure that energy reserves are adequate to permit a successful return to the sea following spawning, and to ensure a high frequency of repeat reproduction.

## Summary

1. This study has provided the first detailed information on the tissue weight changes and energy costs associated with the spawning migration of American shad.

2. Tissue weight change is a reliable index of the physiological state of shad. Inferences concerning energy expenditures associated with

Figure 22. Speed efficiency curves for sockeye salmon of various sizes. Reported freshwater swimming speeds of semelparous (A) and iteroparous (B) anadromous species are shown on the appropriate curves.


A
spurts above max sustained (anaerobic metabolism).
1.0 kg fish
2.5 kg fish
10.0 kg fish
Pentegov, 1928
CHUM
SOCKEYE
Idler, 1959
CHINOOK
Greene, 1926
OCEAN MIGRATION
SOCKEYE, PINK
Stasko, 1973
180 cm/sec
Sonic tracking
Johnson, 1960
Madison, 1973
SEMELPAROUS SPP.
ENERGY (CAL/KG/KM)
SPEED (CM/SEC)
B
SHAD FLORIDA
STEELHEAD
Monan, 1970
SHAD CONN
Leggett, 1976
ATLANTIC SALMON
Hayes, 1953
ITEROPAROUS SPP.
0
.13
.26
.39
.52
.65
.78
0
50
100
150
200
250
300

the freshwater migration in other rivers can be made from measures of gross weight change.

3. Extensive gonad development of Connecticut and Virginia shad during active oceanic feeding reduces energy demands for this purpose during the freshwater fast. This may enhance the survival of individuals in this population and permit repeat spawning. Conversely, significant transfer of somatic and viscera energy reserves to the gonads by members of the St. Johns River population clearly taxes the available reserves of these migrants and contributes to the complete postspawning mortality.

4. Distance to the spawning grounds is the most important determinant of total energy demand associated with the freshwater migration. Florida shad, despite encountering higher water temperatures during the freshwater migration, are more energetically efficient than Connecticut migrants in terms of calories expended per kilometer of upriver displacement. However, the long migration to the spawning grounds in the St. Johns River results in extensive utilization of energy reserves and complete postspawning mortality. Reduced depletion of energy reserves and postspawning survival is associated with the shorter freshwater migrations in Connecticut and Virginia.

5. Water temperature, through its influence on metabolic rate, influences the rate and magnitude of energy utilization during the spawning migration and appears to influence survival as a result. Significantly higher total energy utilization and higher mortalities are indicated for shad migrating late in the shad run. These fish experienced average water temperatures 5$^{o}$C higher than those migrating

at the peak of the run. Further increases in average river temperatures can thus be expected to directly influence the migration energetics of shad in the Connecticut or other rivers.

6. Reduced angular displacements to spawning areas in the York and St. Johns Rivers indicate migrants in these rivers encounter reduced current velocities relative to those encountered by Connecticut River migrants. This may be a factor in the reduced caloric expenditure per unit distance of upstream movement in the southern study rivers.

7. Larger body size and later mean age at maturity of Connecticut River shad may be an adaptation to increase energy reserves and thereby enhance postspawning survival necessary for population stability in a fluctuating environment. Energetic advantages for small Florida migrants may ensure a higher spawning success and hence a selective advantage for these individuals. Florida shad have adapted to small body size and complete postspawning mortality by greatly increasing relative fecundity thereby maintaining a high reproductive potential (Leggett 1969). This implies that shad are highly adapted both energetically and reproductively to their specific home rivers and that changes in the characteristics of these rivers could lead to significant alterations in population structure and reproductive success.

8. Extension of the Connecticut River migration to the historical range of the species in the river will greatly increase the average energy expenditure of the Connecticut population and shad spawning in areas above the existing sites will experience significantly higher energy costs and proportionately higher postspawning mortality. It is unlikely

that shad migrating to the extreme upriver areas (Bellows Falls) will have sufficient reserves to complete the freshwater migration to the sea. Thus an increasing proportion of virgin fish in the Connecticut population is predicted as the restoration program proceeds. The extent of changes in age structure and repeat spawning characteristics will depend on the relative contribution of these new areas to the total shad production of the Connecticut River. However, in view of the importance of repeat spawning shad for year to year population stability (Leggett 1976, Marcy 1976) these parameters should be carefully monitored as the restoration program continues. Some alteration of exploitation strategies may be required to maintain a proper balance between virgin and repeat spawning shad if significant changes result.

9. Freshwater migration rates of shad are near the speeds of maximum metabolic efficiency. Therefore migration rate may be an adaptation to maximize spawning success and postspawning survival by reducing the energetic cost of swimming.

BIBLIOGRAPHY

ATKINSON, C.E. 1951. Feeding habits of adult shad (Alosa sapidissima) in fresh water. Ecology 32: 556-557.

BAGGERMAN, B. 1957. The role of external factors and hormones in migration of sticklebacks and juvenile salmon, p. 24-37. In A. Gorbman (ed.) Symposium on comparative endocrinology. John Wiley and Sons Ltd. New York.

BELDING, D. L. 1934. The cause of high mortality in the Atlantic salmon after spawning. Trans. Amer. Fish. Soc. 64: 219-224.

BEVERTON, R.J.H., and S.J. HOLT. 1957. On the dynamics of exploited fish populations. Fishery Invest., Lond. Ser. II 19: 1-533.

BLAXTER, J.H.S., and F.G.T. HOLLIDAY. 1963. The behaviour and physiology of herring and other clupeids. Adv. Mar. Biol. 1: 261-293.

BRETT, J.R. 1965a. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Canada 22: 1491-1501.

BRETT, J.R. 1965b. The swimming energetics of salmon. Sci. Amer. 213: 80-85.

BRETT, J.R., and N.R. GLASS. 1973. Metabolic rates and critical swimming speeds of sockeye salmon, Oncorhynchus nerka, in relation to size and temperature. J. Fish. Res. Bd. Canada 30: 379-387.

CARLANDER, K.D. 1969. Handbook of freshwater fishery biology. Vol. 1. Iowa State Univ. Press. 752 p.

CARSCADDEN, J.E., and W.C. LEGGETT. 1975. Life history variations in populations of American shad, Alosa sapidissima (Wilson), spawning in tributaries of the St. John River, New Brunswick. J. Fish. Biol. 7: 595-609.

CATING, J.P. 1953. Determining the age of Atlantic shad from their scales. U.S. Fish. Wildl. Serv., Fish Bull. 54: 187-199.

CHANNON, H.J., and M.K. EL SABY. 1932. Fat metabolism of the herring. A preliminary survey. Biochem. J. 26: 2021-2026.

CHARNOV, E.L. and J.R. KREBS. 1973. On clutch size and fitness. Ibis 116: 217-219.

CHITTENDEN, M.E., Jr. 1969. Life history and ecology of the American shad, Alosa sapidissima, in the Delaware River. Ph.D. Thesis. Rutgers Univ., New Brunswick, N.J. xi - 458 p. Univ. Microfilms, Ann Arbor, Mich.

CODY, M.L. 1966. A general theory of clutch size. Evol. 20: 174-184.

COLE, L.C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29: 103-137.

DOWGIALLO, A. 1975. Chemical composition of an animal's body and of its food, p. 160-199. In W. Grodzinski, R.Z. Klekowski and A. Duncan (ed.), Methods for ecological bioenergetics. IBP Handbook No. 24. Blackwell Sci. Publ., Oxford and Edinburgh.

FRY, F.E.J. 1971. The effect of environmental factors on the physiology of fish, p. 1-98. In W.S. Hoar and D.J. Randall (ed.) Fish physiology. Academic Press, New York.

GERKING, S.D. 1952. The protein metabolism of sunfish of different ages. Physiol. Zool. 25: 358-372.

GREENE, C.W. 1926. The physiology of the spawning migration. Physiol. Rev. 6: 201-241.

HAYES, F.R. 1953. Artificial freshets and other factors controlling the ascent and population of Atlantic salmon in La Have River, Nova Scotia. Biol. Bd. Canada Bull. 99. 47 p.

HICKLING, C.F. 1930. The natural history of the hake. Fishery Invest., Lond. Ser. 2, 12. 78 p.

HICKLING, C.F. 1945. The seasonal cycle in the Cornish pilchard. J. mar. biol. Ass. U.K. 26: 115-138.

HOLGATE, P. 1967. Population survival and life history phenomena. J. Theor. Biol. 14: 1-10.

HORWITZ, W. 1965. Ash - official final action, p. 487. In Official methods of analysis of the association of official agricultural chemists. Assoc. Off. Agr. Chemists, Washington.

IDLER, D.R. and W.A. CLEMENS. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stewart Lakes. Int. Pac. Salmon Fish. Comm. Progr. Rep. No. 6. 80 p.

JOHNSON, J.H. 1960. Sonic tracking of adult salmon at Bonneville Dam, 1957. U.S. Fish. Wildl. Serv. Fish. Bull. 60: 471-485.

JUDY, M.H. 1961. Validity of age determinations from scales of marked American shad. U.S. Fish. Wildl. Serv. Fish Bull. 61: 161-170.

KHALTURIN, D.K. 1967. Magnitude of the angular displacement as a characteristic of anadromous migration of salmon of the genus Salmo. Doklady Akademii Nauk SSSR 177: 1462-1464 (Transl. from Russian by Consultants Bureau, Plenum Publ., New York).

KLEIBER, M. 1975. The fire of life: an introduction to animal energetics. Krieger Publishing, New York. 453 p.

KORN, S., and D. MACEDO. 1973. Determination of fat content in fish with a nontoxic, noninflammable solvent. J. Fish. Res. Bd. Canada 30: 1880-1881.

LEACH, G.C. 1925. Artificial propagation of shad. Bureau of Fisheries Document 981. Dept. of the U.S. Fish. Comm. for 1924. Appendix viii: 459-486.

LEGGETT, W.C. 1969. Studies on the reproductive biology of the American shad (Alosa sapidissima, Wilson). A comparison of populations from four rivers of the Atlantic seaboard. Ph.D. Thesis. McGill Univ., Montreal, Quebec. xi - 125 p.

LEGGETT, W.C. 1972. Weight loss in American shad (Alosa sapidissima) during the freshwater migration. Trans. Amer. Fish. Soc. 101: 549-551.

LEGGETT, W.C. 1976. The American shad (Alosa sapidissima), with special reference to its migration and population dynamics in the Connecticut River, p. 169-225. In D. Merriman and L.M. Thorpe (ed.) The Connecticut River Ecological Study. Monograph No. 1. Amer. Fish. Soc., Wash. D.C.

LEGGETT, W.C., and R.R. WHITNEY. 1972. Water temperature and the migrations of American shad. U.S. Fish Wildl. Serv. Fish. Bull. 70: 659-670.

LEGGETT, W.C., and J.E. CARSCADDEN. MS 1977. Latitudinal variation in reproductive characteristics of American shad (Alosa sapidissima): evidence for population specific life history strategies in fish. M.S. Report. 71 p.

LEIM, A.H. 1924. The life history of shad (Alosa sapidissima, Wilson) with special reference to the factors limiting its abundance Contr. Can. Biol. Fish. 2: 163-284.

MADISON, D.M., R.M. HORRALL, A.B. STASKO, and A.D. HASLER. 1972. Migratory movement of adult sockeye salmon (Oncorhynchus nerka) in coastal British Columbia as revealed by ultrasonic tracking. J. Fish. Res. Bd. Canada 29: 1025-1033.

MANSUETI, R., and H. KOLB. 1953. A historical review of the shad fisheries of North America. Chesapeake Biological Laboratory, Solomons, Maryland. Publ. No. 97. 293 p.

MARCY, B.C., Jr. 1972. Spawning of the American shad, Alosa sapidissima, in the lower Connecticut River. Chesapeake Sci. 13: 116-119.

MARCY, B.C., Jr. 1976. Early life history studies of American shad in the lower Connecticut River and the effects of the Connecticut Yankee Plant, p. 141-168. In D. Merriman and L.M. Thorpe (ed.) The Connecticut River Ecological Study. Monograph No. 1. Amer. Fish. Soc., Wash. D.C.

MASSMANN, W.H. 1952. Characteristics of spawning areas of shad (Alosa sapidissima, Wilson) in some Virginia streams. Trans. Amer. Fish. Soc. 81: 78-93.

McCAY, C.M. 1931. Phosphorus distribution, sugar and hemoglobin in the blood of fish, eels and turtles. J. Biol. Chem. 90: 497-505.

MIDDLETON, K.R. 1960. New Nessler reagent and its use in the direct nesslerization of Kjeldahl digests. J. Appl. Chem. 10: 281-286.

MONAN, G.E., K.L. LISCOM, and J.R. Smith. 1970. Sonic tracking of adult steelhead in Ice Harbour Reservoir, 1969. Bureau Comm. Fish. Biol. Lab. Final Report, Seattle, Wash. 13 p.

MOSS, D.D. 1946. Preliminary studies of the shad (Alosa sapidissima) catch in the lower Connecticut River, 1944. Trans. N. Amer. Wildl. Conf. 11: 230-239.

MOUNTFORD, M.D. 1973. The significance of clutch size, p. 315-325. In M.S. Bartlett and R.W. Hiorns (ed.) Mathematical theory of the dynamics of biological populations. Academic Press, New York.

MURPHY, G.I. 1968. Patterns in life history and the environment. Am. Nat. 102: 391-403.

PENTEGOV, B.P., YU. N. MENTOV and E.F. KURNAEV. 1928. Physico-chemical characteristics of the breeding migration fast of Keta. Bull. Pacific Sci. Fish. Res. Station (Vladivostok) 2: Pt. 1.

PROSSER, C.L. 1973. Oxygen: respiration and metabolism, p. 165-211. In C.L. Prosser (ed.) Comparative animal physiology. Saunders, Philadelphia.

RICKER, W.E. 1954. Stock and recruitment. J. Fish. Res. Bd. Canada 11: 559-621.

ROBERTSON, O.H., M.A. KRUPP, S.F. THOMAS, C.B. FAVOUR, S. HANE, and B.C. WEXLER. 1961. Hyper-adrenocorticism in spawning migratory and non-migratory rainbow trout (Salmo gairnerii); comparison with Pacific salmon (genus Oncorhynchus). Gen. Comp. Endocrinol. 1: 473-484.

RYDER, J.A. 1887. On the development of osseous fishes, including marine and fresh water forms. Rept. U.S. Fish. Comm., 1885, 13: 489-604.

SCHAFFER, W.M. and P.F. ELSON. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. Ecology 56: 577-590.

SHULMAN, G.E. 1974. Life cycles of fish, physiology and biochemistry. Halsted Press, New York. 258 p. (Transl. from Russian of Fiziologo-Biokhim-icheskie Osobennosti Godovykh Tsiklov Ryb, Izdatel'stvo "Pishchevaya Promyshlennost", Moscow, 1972).

SNEDECOR, G.W. and W.G. COCHRAN. 1967. Statistical methods. Iowa State Univ. Press, Iowa. 593 p.

STASKO, A.B., R.M. HORRALL, A.D. HASLER, and D. STASKO. 1973. Coastal movements of mature Fraser River pink salmon (Oncorhynchus gorbuscha) as revealed by ultrasonic tracking. J. Fish. Res. Bd. Canada 30: 1309-1316.

STRICKLAND, J.D.H. and T.R. PARSONS. 1972. A practical handbook of seawater analysis. Fish. Res. Bd. Canada Bull. 167. 310 p.

VLADYKOV, V. 1956. Fecundity of wild speckled trout (Salvelinus fontinalis) in Quebec lakes. J. Fish. Res. Bd. Canada 13: 799-841.

WALBURG, C.H. and P.R. NICHOLS. 1967. Biology and management of the American shad and status of the fisheries, Atlantic coast of the United States, 1960. U.S. Fish. Wildl. Serv. Special Sci. Rept. Fish. 550: 1-105.

WEBB, P.W. 1975. Hydrodynamics and energetics of fish propulsion. Fish. Res. Bd. Canada Bull. 190. 158 p.

WILLIAMS, R.O. and G.E. BRUGER. 1972. Investigations on American shad in the St. Johns River. Florida Dept. Nat. Resources Mar. Res. Lab. Tech. Series No. 66. 49 p.

WINBERG, G.G. 1956. Rate of metabolism and food requirements of fishes. Nauchn. Tr. Belorunk. Gos. Univ. Im. Vopr. Issled. Lenina, Minsk. 253 p. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 194, 1960).

WITHLER, I.L. 1966. Variability in life history characteristics of steelhead trout (Salmo gairdnerii) along the Pacific coast of North America. J. Fish. Res. Bd. Canada 23: 365-393.

Appendix A. The distance from location of tagging to upstream recovery locations and the average time free before recapture for the years 1967 to 1973. N represents the number of fish included in the average time free for each recovery station.

| Year | Distance (km) | Males Av. days free | N | Females Av. days free | N |
|---|---|---|---|---|---|
| 1967 | 0 | 9.9 | 117 | 7.9 | 75 |
| | 5.6 | 11.4 | 15 | --- | --- |
| | 9.3 | 13 2 | 17 | 13.4 | 23 |
| | 14.8 | 15.6 | 93 | 14.2 | 89 |
| | 24.0 | 16.5 | 49 | 14.7 | 37 |
| | 29.6 | 15.3 | 13 | 13.1 | 19 |
| | 38.9 | 25.6 | 6 | ---- | -- |
| | 50.0 | 17 0 | 43 | 15.0 | 37 |
| | 88.8 | 23.3 | 9 | ---- | -- |
| | 96.2 | 25.2 | 11 | 25.6 | 13 |
| 1968 | 0 | 9.7 | 61 | 6.6 | 95 |
| | 5.6 | 9.4 | 12 | 5.7 | 10 |
| | 9.3 | 8.8 | 43 | 8.3 | 73 |
| | 14.8 | 10.9 | 65 | 12.3 | 91 |
| | 24.0 | 17.3 | 9 | 24.9 | 10 |
| | 38.9 | 16.5 | 29 | 11.5 | 50 |
| | 50.0 | 12.9 | 52 | 12.5 | 103 |
| | 96.2 | 18.3 | 16 | 19.2 | 22 |
| | 136.9 | 31.0 | 16 | 30.0 | 15 |
| 1969 | 0 | 9.6 | 70 | 8.1 | 87 |
| | 5.6 | 9.5 | 8 | 8.8 | 9 |
| | 9.3 | 12.5 | 25 | 8.6 | 40 |
| | 14.8 | 12.4 | 36 | 12.8 | 63 |
| | 24.0 | 12.9 | 20 | 12.0 | 57 |
| | 29.6 | 11.7 | 11 | 11.4 | 34 |
| | 38.9 | 15.6 | 9 | 10.0 | 26 |
| | 50.0 | 19.3 | 62 | 15.1 | 105 |
| | 96.2 | 28.0 | 8 | 18.8 | 22 |
| | 136.9 | 29.2 | 13 | 27.5 | 23 |
| 1970 | 0 | 10.2 | 78 | 7.6 | 51 |
| | 9.3 | 11.6 | 17 | 9.1 | 19 |
| | 14.8 | 14.7 | 41 | 11 2 | 64 |
| | 20.4 | 10.6 | 14 | 11.9 | 21 |
| | 24.0 | 15.5 | 17 | 14.2 | 16 |
| | 29.6 | 14.3 | 38 | 12.3 | 36 |
| | 44.4 | 18.2 | 6 | 17.9 | 16 |
| | 50.0 | 17.7 | 37 | 15.8 | 65 |
| | 96.2 | 19.9 | 21 | 15.9 | 25 |
| | 136.9 | 34.0 | 43 | 24.3 | 51 |
| 1971 | 0 | 11.3 | 77 | 9.9 | 59 |
| | 5.6 | 13.0 | 14 | 13.7 | 7 |
| | 9.3 | 15.5 | 20 | 13.8 | 26 |
| | 14.8 | 16.4 | 57 | 13.8 | 49 |
| | 20.4 | 14.6 | 22 | 9.7 | 23 |
| | 24.0 | 16.2 | 13 | 11.3 | 17 |
| | 29.6 | 16 5 | 22 | 16.6 | 26 |
| | 44.4 | 14.7 | 14 | 14.8 | 25 |
| | 50.0 | 20.9 | 27 | 17.3 | 50 |
| | 88.8 | ---- | -- | 16.5 | 6 |
| | 96.2 | 25.7 | 22 | 19.3 | 37 |
| | 136.9 | 31.5 | 44 | 26.5 | 32 |

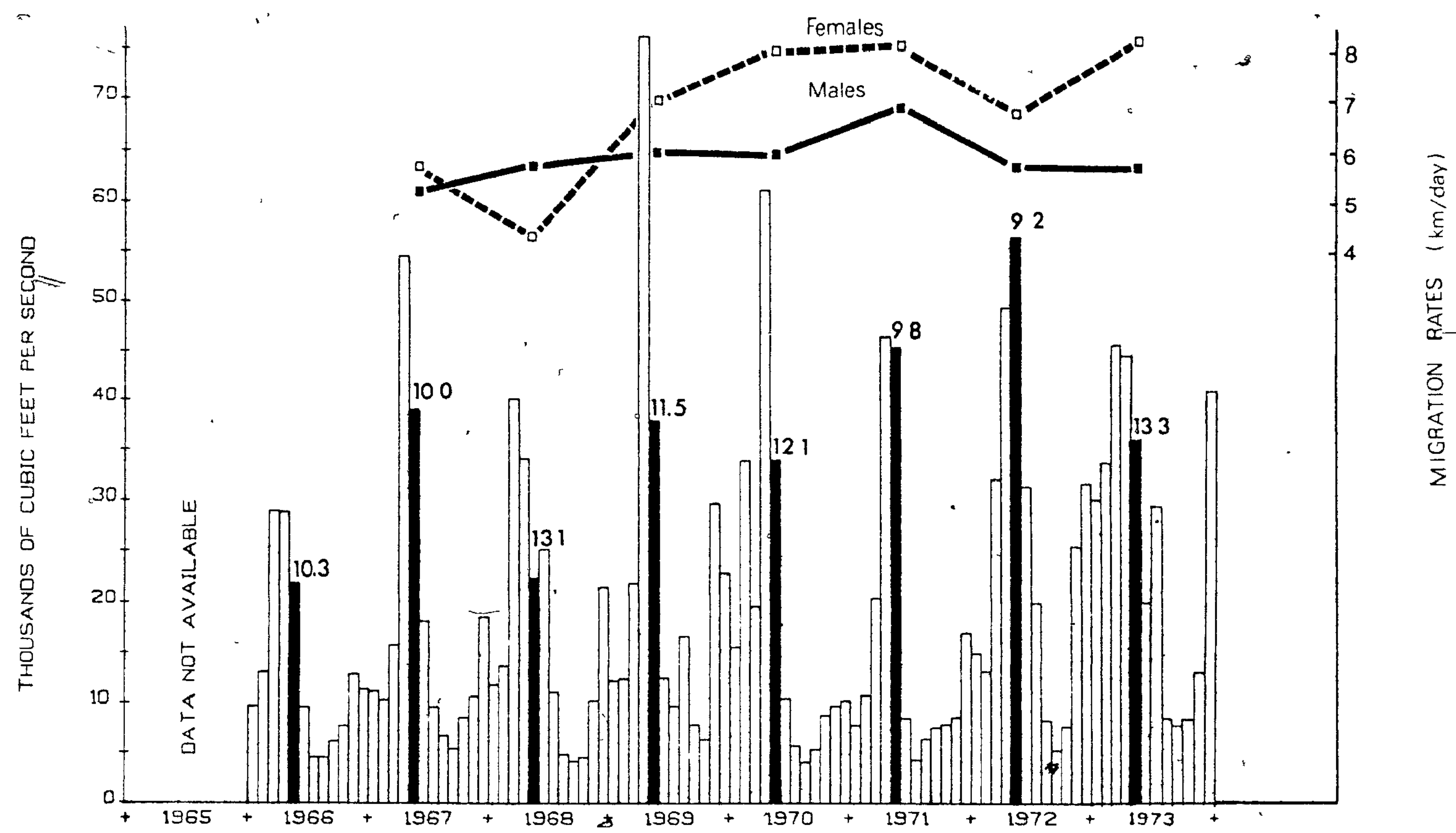
continued....

| Year | Distance (km) | Males Av. days free | N | Females Av. days free | N |
|---|---|---|---|---|---|
| 1972 | 0 | 10.9 | 76 | 9.5 | 64 |
| | 9.3 | 17.0 | 8 | 15.0 | 18 |
| | 14.8 | 14.0 | 42 | 12.5 | 51 |
| | 20.4 | 16.1 | 14 | 13.3 | 20 |
| | 24.0 | 12.8 | 20 | 11.7 | 25 |
| | 25.9 | ---- | -- | 12.0 | 8 |
| | 29.6 | 15.2 | 42 | 11.9 | 40 |
| | 44.4 | 15.1 | 15 | 11.0 | 13 |
| | 50.0 | 19.5 | 20 | 16.4 | 62 |
| | 96.2 | 25.7 | 15 | 18.6 | 15 |
| | 136.9 | 35.2 | 40 | 29.0 | 55 |
| 1973 | 0 | 8.8 | 54 | 8.0 | 56 |
| | 9.3 | 12.0 | 10 | 8.3 | 13 |
| | 14.8 | 9.8 | 46 | 11.2 | 53 |
| | 20.4 | 11.4 | 10 | 12.6 | 19 |
| | 24.0 | 10.9 | 14 | 10.6 | 26 |
| | 29.6 | 13.2 | 21 | 12.1 | 32 |
| | 44.4 | ---- | -- | 12.7 | 7 |
| | 50.0 | 13.5 | 28 | 13.5 | 52 |
| | 88.8 | 22.1 | 12 | ---- | -- |
| | 96.2 | 25.6 | 9 | 19.4 | 5 |

Appendix B. F values for analysis of covariance comparisons of yearly male and female shad migration rates (regressions slopes) and delay before resumption of upriver movement (adjusted means) in the Connecticut River. Significant differences ($P < .05$) are indicated by (+) or (-). The sign indicates whether the slopes and adjusted means for females are greater (+) or less (-) than those for males. Asterisks (*) indicate the residual variance (RV) is heterogeneous ($P < .05$). All joint regression F values are significant at the .01 probability level.

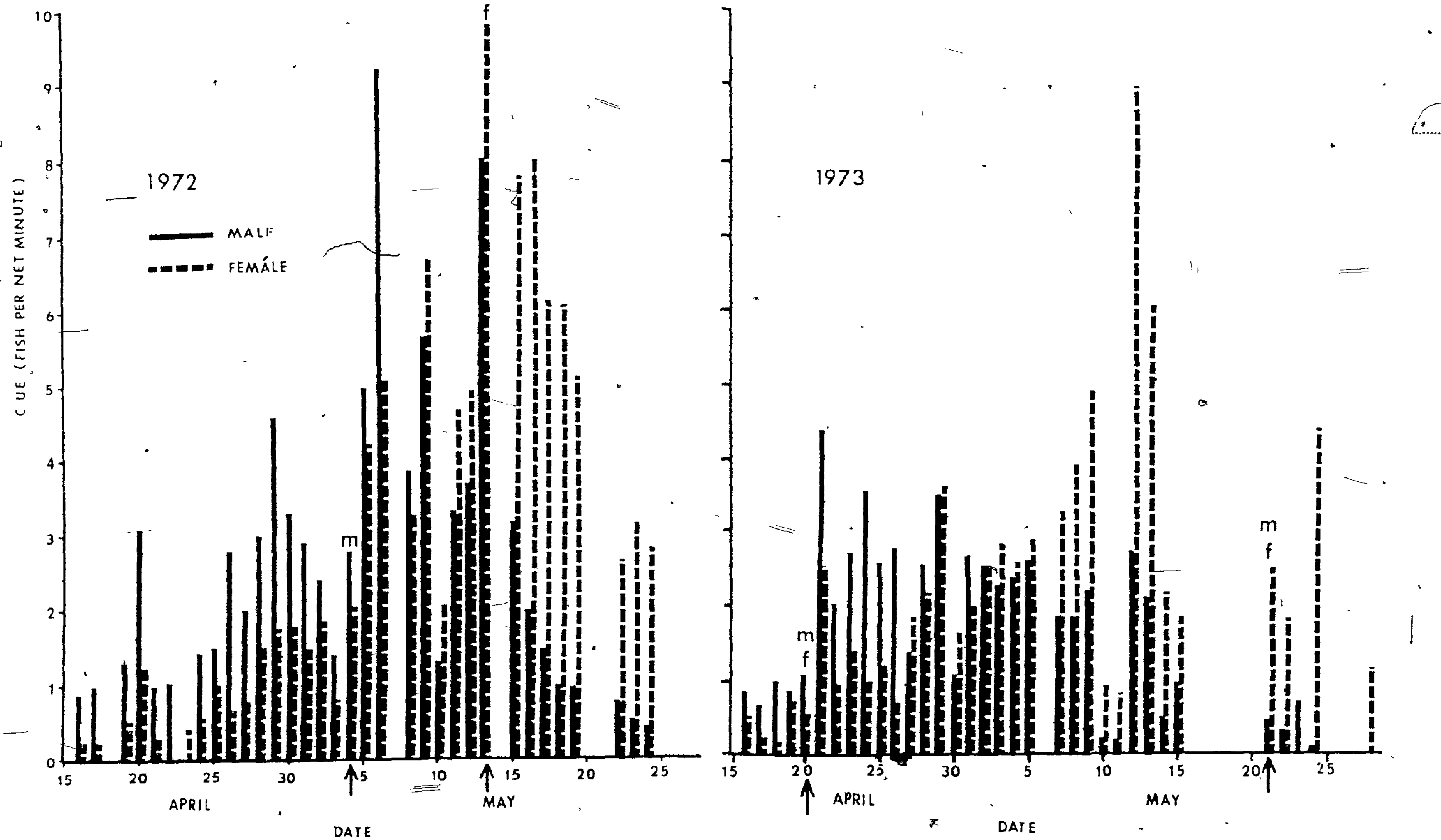
| year | RV | Slope | Adjusted mean | Joint F |
|---|---|---|---|---|
| 67 | | 0.1 | 1.1 | 43.3 |
| 68 | | 0.3 | 0.0 | 48.7 |
| 69 | | 1.5 | 10.8 (+) | 222.7 |
| 70 | | 2.2 | 4.7 (+) | 87.6 |
| 71 | * | 0.8 | 15.1 (+) | 68.7 |
| 72 | | 0.9 | 6.7 (+) | 104.6 |
| 73 | | 4.6 (+) | 3.3 (+) | 164.3 |

Appendix C. Monthly mean Connecticut River discharge into Long Island Sound (Water Resources Data for Connecticut, 1966-1973. U.S. Dept. Interior, Geological Survey, Hartford Conn.) and average water temperature (at Saybrook Bridge; Connecticut River Study data) for the month (solid bar) when upstream movement of peak numbers of shad occurred. Migration rates (slopes of days free after tagging/upstream distance travelled regressions (Appendix A)) are indicated.




MONTHLY MEAN CONNECTICUT RIVER DISCHARGE

Appendix D. Daily catch per unit effort (C/UE) of male and female shad at the Connecticut River mouth for the years 1972 and 1973. Arrows indicate dates of sampling initiation for males (m) and for females (f) in these years.



1972
MALE
FEMALE
CUE (FISH PER NET MINUTE)
APRIL
MAY
DATE
1973
APRIL
MAY
DATE

Appendix E. F values for analysis of covariance of within river comparisons of shad gonad weight/length regressions at the river mouth (0 km) with subsequent upriver sampling stations. Stations are indicated by channel distances travelled after entry to freshwater. Significant differences ($p < .01$) are indicated by (+) or (-). The sign indicates whether the slopes and elevations at upriver stations are greater (+) or less (-) than the slopes and elevations at 0 km. * indicates the residual variance (RV) of compared regressions is heterogeneous at the .01 probability level.

| | CONNECTICUT | | | | | | | | | FLORIDA | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stations compared | Peak 1972 | | | Early 1973 | | | Late 1973 | | | Stations compared | 1974 | | |
| | RV | slope | elevation | RV | slope | elevation | RV | slope | elevation | | RV | slope | elevation |
| **Male** | | | | | | | | | | | | | |
| 0 x 50 | | 0.4 | 0.2 | | 0.0 | 1.6 | | 0.5 | 32.9(-) | 0 x 148 | | 0.0 | 6.9 |
| 83 | | 0.9 | 1.6 | | 0.2 | 1.0 | | 1.6 | 39.3(-) | 259 | | 0.0 | 28.6(+) |
| 137 | | 2.8 | 20.9(-) | | 5.7 | 2.7 | | 0.1 | 33.6(-) | 370 | | 0.0 | 2.8 |
| 265 | * | 24.5(-) | 512.1(-) | | 15.1(-) | 382.4(-) | * | 3.4 | 180.2(-) | 370(spent) | | 0.9 | 1.5 |
| **Female** | | | | | | | | | | | | | |
| 0 x 50 | | 2.2 | 2.8 | | 0.0 | 0.9 | * | 3.0 | 17.7(+) | 0 x 148 | | 4.4 | 38.7(+) |
| 83 | * | 0.1 | 0.1 | | 0.6 | 12.4(+) | * | 0.0 | 0.6 | 259 | * | 1.3 | 93.6(+) |
| 137 | | 3.5 | 3.4 | | 0.3 | 1.9 | * | 1.2 | 4.0 | 370 | * | 21.9(+) | 51.0(+) |
| 265 | * | 37.8(-) | 606.8(-) | * | 10.8(-) | 270.4(-) | | 16.8(-) | 319.1(-) | 370(spent) | | 0.1 | 10.1(-) |

Appendix F. F values for analysis of covariance of within river comparisons between shad viscera weight / length regressions at the river mouth (0 km ) and regressions at subsequent upriver sampling stations and for comparisons between the viscera weight / length regressions for ripe shad at the spawning areas (137 km. in Connecticut; 370 km in Florida) and regressions for spent shad (265 km. in Connecticut; 370 km. in Florida). Stations are indicated by channel distances travelled after entry to freshwater. Significant differences are indicated by (+) or (-). The sign indicates whether the slopes and elevations at upriver stations are greater (+) or less (-) than the slopes and elevations at 0 km and whether the slopes and elevations for spent shad are greater (+) or less (-) than those of ripe shad at the spawning areas. * indicates the residual variance (RV) of compared regressions is heterogeneous at the .01 probability level.

| Connecticut | | | | | | | | | | Florida | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stations compared | Peak 1972 | | | Early 1973 | | | Late 1973 | | | Stations compared | 1974 | | |
| | RV | slope | elevation | RV | slope | elevation | RV | slope | elevation | | RV | slope | elevation |
| **Male** | | | | | | | | | | | | | |
| 0 x 50 | * | 0.0 | 7.5(-) | | 0.1 | 22.6(-) | * | 1.9 | 56.1(-) | 0 x 148 | | 0.2 | 1 2 |
| 83 | | 2.0 | 41.3(-) | | 0.0 | 20.6(-) | | 0.8 | 50.1(-) | " 259 | | 7.3(-) | 122.9(-) |
| 137 | | 4.7 | 146.6(-) | | 0.6 | 191.9(-) | * | 0.6 | 64.8(-) | " 370 | | 7.3(-) | 224.6(-) |
| 265 | | 0.7 | 178.0(-) | | 0.1 | 206.4(-) | * | 0.9 | 70.1(-) | " 370(spent) | * | 4.4 | 114.7(-) |
| 137x 265 | | 2.5 | 0.5 | | 0.2 | 0.1 | | 0.0 | 0.0(-) | 370(ripe x 370(spent) | | 0.1 | 6.2 |
| **Female** | | | | | | | | | | | | | |
| 0 x 50 | | 2.5 | 12.9(-) | | 0.8 | 18.5(-) | | 0.0 | 46.1(-) | 0 x 148 | | 3.8 | 1.8 |
| 83 | | 0.0 | 51.0(-) | | 5.6 | 0.3 | | 0.0 | 39.1(-) | 259 | | 3.7 | 29.1(-) |
| 137 | | 0.2 | 186.8(-) | | 1.4 | 101.5(-) | * | 0.0 | 161.0(-) | 370 | | 1.8 | 83 3(-) |
| 265 | | 0.1 | 201.3(-) | | 1.8 | 112.5(-) | * | 0.4 | 152.6(-) | 370(spent) | | 2.6 | 61.9(-) |
| 137 x265 | | 0.0 | 0.2 | | 0.1 | 2.3 | | 2.3 | 0.7(-) | 370(ripe) x 370(spent) | | 0.0 | 4.8 |

Appendix G. F values for analysis of covariance of within river comparisons between shad body weight / length regressions at the river mouth (0 km) and regressions at subsequent upriver sampling stations and for comparisons between the body weight / length regressions for ripe shad at the spawning areas (137 km in Connecticut, 370 km. in Florida) and regressions for spent shad (265 km. in Connecticut, 370 km. in Florida) Stations are indicated by channel distances travelled after entry to freshwater. Significant differences are indicated (+) or (-) The sign indicates whether the slopes and elevations at upriver stations are greater (+) or less (-) than the slopes and elevations at 0 km. and whether the slopes and elevations for spent shad are greater (+) or less (-) than those of ripe shad at the spawning areas. * indicates the residual variance (RV) of compared regressions is heterogeneous at the .01 probability level.

| | Connecticut | | | | | | | | | Florida | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stations | | Peak 1972 | | | Early 1973 | | | Late 1973 | | Stations | | 1974 | |
| compared | RV | slope | elevation | RV | slope | elevation | RV | slope | elevation | compared | RV | slope | elevation |
| **Male** | | | | | | | | | | | | | |
| 0 x 50 | | 0.1 | 0.7 | | 0.7 | 0.1 | | 3.3 | 21.9(-) | 0 x 148 | | 0.0 | 10.3(-) |
| " 83 | | 2.0 | 1.9 | | 0.3 | 5.6 | | 2.1 | 36.6(-) | " 259 | | 4.8 | 62.2(-) |
| " 137 | * | 10.8(-) | 38.5(-) | | 3.8 | 58.1(-) | | 1.7 | 59.7(-) | " 370 | | 3.6 | 146.7(-) |
| " 265 | | 15.8(-) | 387.7(-) | | 18.5(-) | 297.9(-) | | 6.3 | 131.1(-) | " 370(spent) | | 6.2 | 128.1(-) |
| 137 x 265 | | 0.2 | 37.5(-) | | 6.2 | 98.4(-) | | 1.5 | 22.9(-) | 370(ripe)x370(spent) | | 1.0 | 12.3(-) |
| **Female** | | | | | | | | | | | | | |
| 0 x 50 | | 1.6 | 0.2 | | 0.0 | 2.3 | | 4.5 | 34.5(-) | 0 x 148 | | 1.1 | 0.9 |
| " 83 | | 0.1 | 22.3(-) | | 2.1 | 0.1 | | 1.4 | 36.2(-) | " 259 | | 9.8(-) | 79.0(-) |
| " 137 | | 0.4 | 38.1(-) | | 0.0 | 30.3~~(-)~~ | | 1.7 | 131.3(-) | " 370 | | 3.1 | 172.3(-) |
| " 265 | | 7.1 | 222.3(-) | | 1.3 | 161.6(-) | | 6.4 | 273.1(-) | " 370(spent) | | 24.1(-) | 303.2(-) |
| 137 x 265 | | 3.0 | 52.1(-) | | 1.7 | 35.0(-) | | 2.2 | 41.7(-) | 370(ripe)x370(spent) | | 2.2 | 19.[illegible](-) |

Appendix H. Linear regression coefficients for gonad energy content/ body length regressions of Connecticut and St. Johns River shad. Predictive equations take the form Y = C + bX where Y is the predicted gonad energy content and X is fork length. Station is indicated by distance along the migratory route. Those regressions not significant at the 5% probability level are indicated by an asterisk (*).

Connecticut River

| SEX | Reprod. stage | Station | Peak C | 1972 b |
|---|---|---|---|---|
| Male | Maturing | 0 | -242.48 | 7.97 |
| | " | 20 | -202.79 | 6.96 |
| | " | 50 | -227.51 | 7.54 |
| | " | 83 | -121.00 | 4.98 |
| | " | 137 | -150.91 | 5.47 |
| | Spent | 191 | - 71.88 | 2.57 |
| | " | 224 | - 70.76 | 2.35 * |
| | " | 265 | - 67.72 | 2.19 |
| Female | Maturing | 0 | -1174.74 | 31.12 |
| | " | 20 | -1255.07 | 32.68 |
| | " | 50 | - 771.64 | 22.35 |
| | " | 83 | - 622.17 | 18.33 |
| | " | 137 | - 94.88 | 8.35 * |
| | Spent | 191 | - 474.62 | 11.10 * |
| | " | 224 | - 85.92 | 2.72 * |
| | " | 265 | - 20.20 | 1.43 * |

St. Johns River

| SEX | Reprod. stage | Station | C | b |
|---|---|---|---|---|
| Male | Maturing | 0 | -62.86 | 2.47 * |
| | " | 148 | -81.84 | 3.13 |
| | " | 259 | -12.13 | 1.41 * |
| | " | 370 | -61.37 | 2.33 |
| | Spent | 370 | -61.53 | 2.16 * |
| Female | Maturing | 0 | - 54.07 | 3.55 * |
| | " | 148 | -328.96 | 11.11 |
| | " | 259 | -152.77 | 7.20 * |
| | " | 370 | -559.62 | 16.02 |
| | Spent | 370 | -118.35 | 3.98 * |

Appendix I. Linear regression coefficients for viscera energy content/body length regressions of Connecticut and St. Johns River shad. Predictive equations take the form Y = C +bX where Y is the predicted viscera energy content and X is fork length. Station is indicated by distance along the migratory route. Those regressions not significant at the 5% probability level are indicated by an asterisk (*).

**Connecticut River**

| SEX | Reprod. stage | Station | Peak 1972 C | b | |
|---|---|---|---|---|---|
| Male | Maturing | 0 | -351.06 | 12.82 | |
| | " | 20 | -485.71 | 15.45 | |
| | " | 50 | -443.12 | 13.45 | |
| | " | 83 | -177.96 | 7.17 | * |
| | " | 137 | -102.02 | 3.93 | |
| | Spent | 191 | -200.03 | 6.14 | |
| | " | 224 | -366.82 | 9.65 | |
| | " | 265 | -132.72 | 4.46 | |
| Female | Maturing | 0 | -116.38 | 5.24 | * |
| | " | 20 | - 10.19 | 3.11 | * |
| | " | 50 | -379.86 | 10.49 | |
| | " | 83 | -216.43 | 6.13 | * |
| | " | 137 | -141.96 | 4.20 | * |
| | Spent | 191 | - 74.22 | 2.75 | * |
| | " | 224 | -156.98 | 4.38 | |
| | " | 265 | -137.92 | 3.92 | |

**St. Johns River**

| SEX | Reprod. stage | Station | 1974 C | b | |
|---|---|---|---|---|---|
| Male | Maturing | 0 | -361.54 | 13.18 | |
| | " | 148 | -183.78 | 7.43 | |
| | " | 259 | 86.12 | - 0.50 | * |
| | " | 370 | 41.36 | 0.34 | * |
| | Spent | 370 | - 58.51 | 1.97 | * |
| female | Maturing | 0 | -503.93 | 15.26 | |
| | " | 148 | 18.62 | 1.87 | * |
| | " | 259 | 40.88 | 0.07 | * |
| | " | 370 | -108.06 | 3.47 | |
| | Spent | 370 | - 51.66 | 1.74 | |

Appendix J. Linear regression coefficients for somatic energy content / body length regressions of Connecticut and St. Johns River shad Predictive equations take the form Y = C + bX where Y is the predicted energy content of the body and X is fork length. Station is indicated by distance along the migratory route. Those regressions not significant at the 5% probability level are indicated by an asterisk (*)

Connecticut River

| Sex | Reprod. stage | Station | Peak 1972 C | Peak 1972 b | Early 1973 C | Early 1973 b | Late 1973 C | Late 1973 b |
|---|---|---|---|---|---|---|---|---|
| Male | Maturing | 0 | -7816.65 | 254.24 | -6397.56 | 213.26 | -3603.68 | 144.88 |
| | " | 20 | -7156.63 | 240.75 | ---- | ---- | ---- | ---- |
| | " | 50 | -6697.79 | 224.08 | -4764.99 | 174.29 | -1948.15 | 95.12 |
| | " | 83 | -5239.62 | 191.55 | -6454.70 | 213.06 | -4505.31 | 145.39 |
| | " | 137 | -3091.25 | 123.41 | -1861.89 | 90.62 | -2888.06 | 98.33 |
| | Spent | 191 | -3814.52 | 127.66 | ---- | ---- | ---- | ---- |
| | " | 224 | -5747.89 | 167.13 | ---- | ---- | ---- | ---- |
| | " | 265 | -3154.33 | 107.17 | - 777.35 | 51.67 | -2066.79 | 73.03 |
| Female | Maturing | 0 | -8656.16 | 265.33 | -5576.07 | 194.18 | -4972.74 | 180.90 |
| | " | 20 | -9689.01 | 286.38 | ---- | ---- | ---- | ---- |
| | " | 50 | -14891.78 | 392.46 | -4480.90 | 165.02 | -4295.96 | 152.83 |
| | " | 83 | -7869.18 | 229.92 | -9196.55 | 266.82 | -3408.18 | 129.53 |
| | " | 137 | -9421.24 | 255.36 | -7509.46 | 211.25 | -5470.66 | 154.21 |
| | Spent | 191 | -5273.33 | 157.64 | ---- | ---- | ---- | ---- |
| | " | 224 | -6521.73 | 180.97 | ---- | ---- | ---- | ---- |
| | " | 265 | -7000.86 | 192.70 | -4767.21 | 140.68 | - 440.94 | 40.75 * |

St. Johns River

| Sex | Reprod. stage | Station | 1974 C | 1974 b |
|---|---|---|---|---|
| Male | Maturing | 0 | -5106.39 | 191.90 |
| | " | 148 | -4182.63 | 155.19 |
| | " | 259 | -1489.83 | 76 48 |
| | " | 370 | -1142.08 | 61.83 * |
| | Spent | 370 | -2845.89 | 92.04 * |
| Female | Maturing | 0 | -7597 52 | 251.10 |
| | " | 148 | -4531 48 | 169 55 |
| | " | 259 | -2024.84 | 88.27 |
| | " | 370 | -2908.65 | 103 79 * |
| | Spent | 370 | -1466.26 | 50.09 * |

Appendix K. F values for analysis of covariance of within river comparisons between shad gonad and viscera energy content / length regressions at the river mouth (0 km) and regressions at subsequent upriver sampling stations and between regressions for ripe shad at the spawning areas (137 km in Connecticut, 370 km. nn Florida) and regressions for spent shad (265 km in Connecticut; 370 km in Florida). Stations are indicated by channel distances travelled after entry to freshwater. Significant differences are indicated by (+) or (-), the sign indicating whether the slopes and elevations at upriver stations are greater (+) or less (-) than the slopes and elevations at0 km and whether the slopes and elevations for spent shad are greater (+) or less (-) than those of ripe shad at the spawning areas. Asterisks (*) indicate heterogeneous residual variance in compared regressions at the .01 probability level.

| Male | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Connecticut 1972 | | | | | | | Florida | | | | | | |
| | | Gonad | | | Viscera | | | | Gonad | | | Viscera | |
| Stations compared | RV | Slope | elevation | RV | slope | elevation | Stations compared | RV | slope | elevation | RV | slope | elevation |
| 0 x 50 | | 0.0 | 0.4 | | 0.0 | 8.4(-) | 0 x 148 | | 0.0 | 3.2 | | 1.5 | 26.9(-) |
| " 83 | | 3.5 | 4.4 | | 1.1 | 16.5(-) | 259 | | 0.0 | 6.4 | | 7.7(-) | 100 5(-) |
| " 137 | | 2.0 | 8.0(-) | | 4.8 | 84.5(-) | 370 | | 0.1 | 1.9 | | 6 2 | 163 2(-) |
| " 265 | * | 21.8(-) | 368.9(-) | | 4.1 | 112.3(-) | 370(spent) | * | 0.2 | 6.0 | * | 2.7 | 128 3(-) |
| 137 x 265 | * | 6.6 | 139.8(-) | | 0.0 | 0.4 | 370(ripe)x370(spent) | | 0.0 | 6.8 | * | 0.1 | 23 6(-) |
| Female | | | | | | | | | | | | | |
| 0 x 50 | | 1.6 | 2.3 | | 1.8 | 0.1 | 0 x 148 | | 3.9 | 24.7(+) | | 7.1(-) | 10 3(-) |
| " 83 | | 2.3 | 13.9(-) | | 0.0 | 24.7(-) | 259 | | 0.8 | 42.2(+) | * | 10.3(-) | 87.8(-) |
| " 137 | | 6.8 | 3.0 | | 0.1 | 57.2(-) | 370 | | 7.9(+) | 7.1(+) | * | 4.6 | 114.2(-) |
| " 265 | * | 42.2(-) | 488.3(-) | * | 0.3 | 104.3(-) | 370(spent) | | 0.0 | 25.6(-) | * | 5.8 | 56.6(-) |
| 137 x 265 | * | 1.2 | 191.0(-) | | 0.0 | 2.2 | 370(ripe)x370(spent) | | 5.7 | 28.2(-) | * | 1.0 | 16.6(-) |

Appendix L. F values for analysis of covariance of within river comparisons between shad eviscerated body energy content - length regressions at the river mouth (0 km.) and regressions at subsequent upriver sampling stations and between regressions for ripe shad at the spawning areas (137 km in Connecticut; 370 km in Florida) and regressions for spent shad (265 km in Connecticut; 370 km in Florida). Stations are indicated by channel distances travelled after entry to freshwater. Significant differences are indicated by (+) or (-), the sign indicating whether the slopes and elevations at upriver stations are greater (+) or less (-) than the slopes and elevations at 0 km. and whether the slopes and elevations for spent shad are greater (+) or less (-) than those of ripe shad at the spawning areas. Asterisks (*) indicate hetergeneous residual variance in compared regressions at the .01 probability level.

| | Connecticut | | | | | | | | | Florida | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stations compared | RV | Peak slope | 1972 elevation | RV | Early slope | 1973 elevation | RV | Late slope | 1973 elevation | Stations compared | RV | 1974 slope | 1974 elevation |
| **Male** | | | | | | | | | | | | | |
| 0 x 50 | | 0.6 | 4.3 | | 0.3 | 0.7 | | 0.3 | 5.3 | 0 x 148 | | 1.1 | 56.3(-) |
| " 83 | | 6.3 | 6.2 | | 0.0 | 0.1 | | 1.8 | 0.3 | " 259 | | 6.9 | 135 6(-) |
| " 137 | | 14.0(-) | 63.3(-) | | 4.7 | 56.2(-) | | 0.1 | 50.3(-) | " 370 | | 7 5(-) | 245.1(-) |
| " 265 | | 25.1(-) | 346.2(-) | * | 11.2(-) | 197.2(-) | | 1.5 | 224.5(-) | " 370(spent) | | 3.1 | 285.0(-) |
| 137 x 265 | | 0.2 | 30.4(-) | | 0.9 | 36.3(-) | | 2.2 | 19.2(-) | 370(ripe)x 370(spent) | | 0.2 | 29.4(-) |
| **Female** | | | | | | | | | | | | | |
| 0 x 50 | | 4.7 | 0.1 | | 0.6 | 12.9(-) | | 0.2 | 15.0(-) | 0 x 148 | | 2.8 | 10 2(-) |
| " 83 | | 0.2 | 24.5(-) | | 0.0 | 29.6(-) | | 0.5 | 20.8(-) | " 259 | | 10.5(-) | 147 7(-) |
| " 137 | | 0.0 | 49.1(-) | * | 0.6 | 91.8(-) | * | 0.2 | 159.5(-) | " 370 | | 5.6 | 203.0(-) |
| " 265 | | 2.7 | 187.4(-) | | 1.5 | 113.0(-) | * | 5.3 | 248.7(-) | " 370(spent) | * | 17.1(-) | 320.1(-) |
| 137 x 265 | | 1.5 | 18.1(-) | | 0.4 | 0.5(-) | | 6.5 | 28.6(-) | 370(ripe)x 370(spent) | * | 0.6 | 25.6(-) |

Appendix M. Mean length by age and sex of Connecticut R. (1972 and 1973 samples combined) and St. Johns R. shad (1974). Standard deviations (SD) and Students - t test results for between river comparisons (where possible) are given.

| SEX | AGE CLASS | Connecticut R. N | Connecticut R. Mean Length | Connecticut R. SD | St. Johns R. N | St. Johns R. Mean Length | St. Johns R. SD | t - value |
|---|---|---|---|---|---|---|---|---|
| Male | 3 | 9 | 37.8 | 1.7 | 4 | 35.5 | 1.4 | 2.2 NS |
| | 4 | 85 | 42.4 | 2.5 | 113 | 38.8 | 1.9 | 36.3 * |
| | 5 | 95 | 44.8 | 2.4 | 17 | 40.0 | 1.5 | 13.4 * |
| | 6 | 83 | 46.7 | 1.9 | -- | ---- | --- | ----- |
| | 7 | 49 | 47.8 | 2.0 | -- | ---- | --- | ----- |
| | 8 | 24 | 48.5 | 1.6 | -- | ---- | --- | ----- |
| | 9 | 8 | 49.4 | 1.5 | -- | ---- | --- | ----- |
| Female | 4 | 62 | 46.3 | 1.8 | 75 | 40.5 | 1.5 | 20.2 * |
| | 5 | 149 | 48.1 | 2.4 | 58 | 43.1 | 1.6 | 43.2 * |
| | 6 | 97 | 50.5 | 1.8 | -- | ---- | --- | ------ |
| | 7 | 35 | 51.8 | 2.2 | -- | ---- | --- | ------ |
| | 8 | 10 | 53.4 | 2.1 | -- | ---- | --- | ------ |
| | 9 | 8 | 53.4 | 1.4 | -- | ---- | --- | ------ |

* indicates significant comparisons ( p < .01); NS indicates non-significant comparisons

Appendix N. Mean age at maturity for the Connecticut and St.Johns River shad populations. Students t value is given for between sex comparisons.

| Population | Year | N | Males Age at Maturity (years) | Standard Deviation | N | Females Age at Maturity (years) | Standard Deviation | t value |
|---|---|---|---|---|---|---|---|---|
| Connecticut R. | 1972 | 173 | 4.2 | 0.7 | 172 | 4.9 | 0.7 | 9.3* |
| | 1973 | 180 | 4.2 | 0.5 | 189 | 4.7 | 0.6 | 11.8* |
| | Combined | 365 | 4.2 | 0.6 | 349 | 4.8 | 0.6 | 13.7* |
| St. Johns R. | 1974 | 134 | 4.1 | 0.4 | 133 | 4.4 | 0.5 | 6.2* |

* indicates comparison is significant ( p <.01).

Appendix O. Student $t$ test comparisons of mean age of maturity (by sex) between rivers and between sampling years (Connecticut only).

| | Connecticut R. Males 1972 | Connecticut R. Females 1972 | St. Johns R. Males 1974 | St. Johns R. Females 1974 |
|---|---|---|---|---|
| Conn. R. males 1972 | | | 1.1 | |
| females 1972 | | | | 7.0* |
| males 1973 | 1.0 | | 0.9 | |
| females 1973 | | 3.6* | | 5.9* |
| Combined males (Conn. R.) | | | 1.5 | |
| females | | | | 6.4* |

* indicates $t$ values are significant ($p < .01$).

Appendix P. Spawning histories of Connecticut and St. Johns River shad populations. Numbers in parentheses indicate sample sizes.

| Populations | Year | Percent repeat spawners: Male | Female | Sexes combined |
|---|---|---|---|---|
| Connecticut R. | 1972 | 68 (173) | 44 (172) | 56 (345) |
| | 1973 | 56 (180) | 36 (189) | 44 (369) |
| | 72 and 73 combined | 59 (365) | 41 (349) | 50 (714) |
| St. Johns R. | 1974 | 0 (134) | 0 (133) | 0 (267) |

Appendix Q. Non-protein nitrogen (NPN) content of the eviscerated body tissue ( expressed as a percentage of the total nitrogen) of early and late Connecticut River migrants. Percentage NPN is compared between river mouth (o km.) and upriver stations at 137 km., and 265 km., using Student's $t$ test. Number of values (n) included in the mean, standard deviation (SD), and $t$ values are given. Significant differences at the .01 probability level are indicated by asterisks (*).

| Sex | | n | 0 km % NPN | SD | n | 137 km. %NPN | SD | $t$ | n | 265 km. % NPN | SD | $t$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Male | early | 20 | 11.65 | 1.37 | 21 | 11.63 | 0.78 | 0.06 | 18 | 11.78 | 2.20 | 0.20 |
| | late | 15 | 11.76 | 0.82 | 16 | 10.61 | 0.56 | 4.54* | 18 | 11.21 | 0.96 | 1.74 |
| Female | early | 18 | 11.12 | 1.06 | 21 | 11.64 | 0.53 | 1.98 | 16 | 12.40 | 1.31 | 2.91 |
| | late | 18 | 11.70 | 0.69 | 20 | 10.92 | 1.26 | 2.34 | 20 | 11.95 | 0.76 | 1.04 |