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clutch size & reproduction

Geoffrey B. Plankton

Latitudinal Variation in Reproductive Characteristics of American Shad (*Alosa sapidissima*): Evidence for Population Specific Life History Strategies in Fish

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The reproductive characteristics of five populations of American shad (*Alosa sapidissima*) on the Atlantic coast were studied. The proportion of repeat spawners increased with the latitude of the home river. Relative and absolute fecundities decreased as the proportion of repeat spawners increased. These reciprocal trends in reproductive characteristics are independent of growth parameters. The principal factor influencing reproductive strategies in shad appears to be variability in the thermal regime of the home river which influences egg and larval survival. Northern populations, spawning in environments that are thermally harsh and variable, allocate a greater proportion of their energy reserves to migration thereby ensuring higher postspawning survival. This is accomplished by reducing the energy allocated to gonads. The pattern of reproductive responses of shad to the thermal environment of the natal river is consistent with existing ecological theory concerning the evolution of reproductive strategies in response to differing environmental conditions. Available literature for several other fishes suggests that fine tuning of reproductive strategies to local environmental conditions may be widespread among fish and may be the ultimate basis for the evolution of homing.

Key words: American shad, *Alosa sapidissima*, reproductive strategies, fecundity, frequency of reproduction, energy allocation, latitudinal variation, theoretical ecology

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Les auteurs ont étudié les caractéristiques de la reproduction de cinq populations d'aloses savoureuses (*Alosa sapidissima*) sur la côte de l'Atlantique. La proportions des poissons qui frayent à nouveau augmente avec la latitude de la rivière natale. La fécondité relative et absolue diminue à mesure qu'augmente la proportion des poissons qui frayent à nouveau. Ces tendances réciproques dans les caractéristiques de la reproduction sont indépendantes des paramètres de croissance. Le principal facteur qui influe sur le comportement reproducteur des aloses semble être la variabilité du régime thermique de la rivière natale, qui affecte la survie des oeufs et des larves. Les populations septentrionales, frayant dans des environnements hostiles et variables sous le rapport de la température, affectent une plus grande proportion de leurs réserves énergétiques à la migration, assurant ainsi une meilleure survie après la fraie. Elles accomplissent ceci en diminuant l'énergie affectée aux gonades. Les modalités des réponses reproductrices de l'alose à l'environnement thermique de la rivière natale sont conformes à la théorie écologique actuelle concernant l'évolution des stratégies reproductrices en réponse à diverses conditions ambiantes. La littérature disponible sur plusieurs espèces de poissons suggère qu'un accord précis des stratégies reproductrices aux conditions ambiantes locales peut être répandu chez les poissons et peut être le fondement ultime de l'évolution du retour à la rivière natale.

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FISHER (1930) and Severtsov (1941) were apparently the first to argue that the life history characteristics of populations reflect their adaptations to the environ-

ment. However, the adaptive significance of different life history strategies was not clearly demonstrated until Cole's (1954) classic study. Cole's conclusion that "the reproductive potentials of existing species are related to their requirements for survival; that any life history features affecting reproductive potential are subject to natural selection; and that such features observed in existing species should be considered adaptations just as purely morphological or behavioral patterns are

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commonly so considered" is now generally accepted and its implications have been extensively studied by theoretical ecologists (reviewed in Stearns 1976, 1977). Empirical support for this theory is less abundant, however, and has come mainly from studies of plants, terrestrial vertebrates, and invertebrates (Stearns 1976, 1977).

Geographical variations in life history have been observed in many fish species and frequently occur in latitudinal clines (see Carscadden and Leggett 1975b). To date, only a few studies on fish have directly addressed the adaptive significance of life history characteristics and attempted to relate their findings to existing ecological theory (see Murphy 1968a, b; Carscadden and Leggett 1975b; Schaffer and Elson 1975). In this paper we further evaluate the hypothesis that intraspecific variation in reproductive characteristics represents a fine tuning of life history to long-term features of the environment by natural selection.

The species studied was the anadromous American shad (*Alosa sapidissima*). It ranges on the Atlantic coast of North America from the St. Johns River, Florida, to the St. Lawrence River, Canada (Bigelow and Schroeder 1953). Shad migrate extensively during the ocean phase of their life and home to their natal rivers and specific tributaries (Hammer 1942; Fischler 1959; Hill 1959; Carscadden and Leggett 1975a, b) to spawn. The populations are thus reproductively isolated. Subadult and adult shad from all Atlantic rivers follow a similar migratory path at sea (Talbot and Sykes 1958; Gabriel et al. 1976) in response to seasonal changes in ocean temperatures (Leggett and Whitney 1972). As a result, shad from Atlantic populations experience similar environmental conditions except during early life when the juveniles are in rivers, and during the freshwater phase of spawning migration.

Materials and Methods

The reproductive characteristics of shad populations native to five rivers spanning most of the range of shad on the Atlantic coast were investigated: St. Johns River, Fla.; York River, Va.; Connecticut River, Conn.; St. John River, N.B., and Miramichi River, N.B. (Fig. 1). These rivers were chosen because they are distributed over the species' range, and because the three southern populations had previously been studied and some supplementary data were available for them. These data have been incorporated into our analysis wherever possible. St. Johns River (Fla.) fish were obtained in 1967 from commercial haul seines (wing 11.4 cm; body 7.6 cm; bag 5.1-cm stretched mesh) operated approximately 144 km upriver. York River specimens were collected in 1967 and 1968 from pound nets (head 5.1 cm; lead 12.7-cm stretched mesh) located in the estuary of that river. Connecticut River shad were collected in the years 1965-73 from a commercial drift gill net (13.9-cm stretched mesh) fished at the river mouth and also from a sport fishery centered approximately 80 km from the sea and well upstream from the commercial fishery. St. John River (N.B.) samples used for age and spawning history analyses were obtained in 1972 and 1973 using an experi-

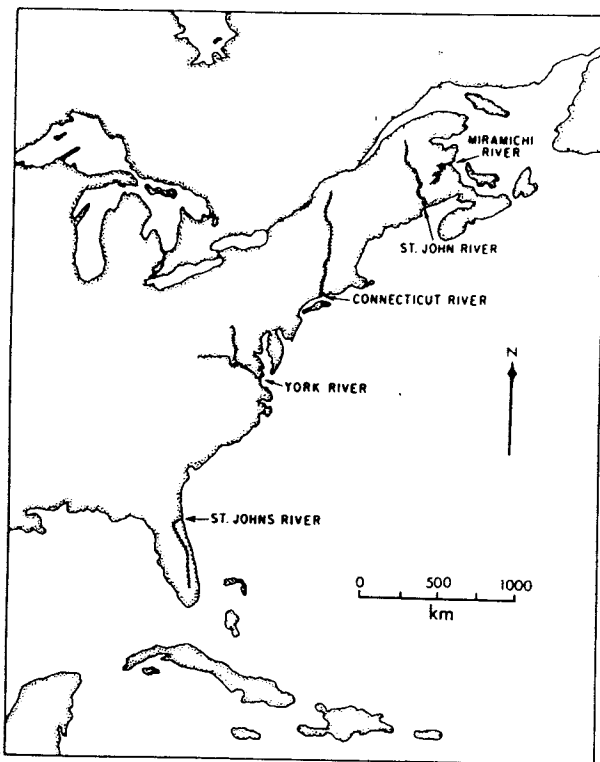


FIG. 1. Location of natal rivers of shad populations investigated.

mental drift gill net (9.5-14.0-cm stretched mesh). These were collected at the river mouth. Specimens for fecundity analyses came from subpopulations spawning in three tributaries of the St. John system (see Carscadden and Leggett 1975b for full details). We combined these samples in our analyses. Miramichi River samples were collected during the years 1971-73 from a salmon trap net (leader and bay 12.7 cm; trap 5.1-cm stretched mesh) located in the upper estuary at Millbank. We consider the seine, trap, and pound nets to have been nonselective for adult shad. Carscadden and Leggett (1975b) have shown that the nets used in the St. John River (N.B.) were nonselective for that population. The commercial gill nets employed in the Connecticut River are selective for larger repeat spawning fish. This bias was corrected by grouping gill net and sport fishery samples giving equal weight to each (Leggett 1976).

Specimens used for fecundity studies were collected in the latter half of the spawning runs to obtain fish that were approaching readiness to spawn but were not yet running ripe or partially spent. In the St. Johns (Fla.) and York rivers, additional specimens used for growth and spawning history studies were collected at the same time as the fish used for fecundity studies. In the three northern rivers these additional samples were obtained at regular (normally weekly) intervals throughout the spawning runs. All shad were sexed, weighed to the nearest 25 g, and measured to the nearest 0.25-cm fork length. Scales were taken from each fish and three independent determinations of age and spawning history were made following Cating (1953) and Judy (1961). The most common reading of three was accepted.

Fecundity was estimated by subsampling following Carscadden and Leggett (1975b).

Results

FREQUENCY OF REPRODUCTION

Walburg (1960) found no evidence of previous spawning in 4087 St. Johns River (Fla.) shad collected between 1950 and 1958. Our analysis of scales from 449 fish collected in 1967 and of a subsequent sample of 268 collected in 1974 confirm this. All shad die after spawning in the St. Johns River.

In the York River the 5-yr (1957-59, Nichols and Massman 1963; 1967-68 this study) mean proportion of repeat spawners (males and females combined) in the population was $23 \pm 8.0\%$. The proportion of repeat spawning in males was consistently higher than in females, the mean values for the two sexes being $31 \pm 9.5\%$ and $19 \pm 4.3\%$, respectively.

The proportion of repeat spawners (sexes combined) in the Connecticut River population averaged $38 \pm 10.2\%$ over the 12 yr for which data were available. In the Connecticut River the proportion of repeat spawning in males was higher than in females in 10 of the 12 yr. The 12-yr means for males and females were 46 ± 14.5 and $32 \pm 10.4\%$, respectively. Considerable year to year variation in the proportion of repeat spawning males and females occurred due to fluctuations in year-class strength. For example, the pronounced changes (males 44-73%; females 23-51%) observed during 1965-68 (Leggett 1976, table 129) resulted from the influence of a very strong year-class spawned in 1960 which recruited significant numbers of males and females to the spawning population for the first time in 1964 and 1965, respectively (Leggett 1976, table 126). The effect of this dominant year-class was first to depress the percent repeat spawners as the year-class recruited to the adult stock (1964 males; 1965 females) and subsequently to elevate the percent repeat spawners as the survivors returned to spawn a second and third time (1965, 1966 males; 1966, 1967 females). Similar changes in year-class strength presumably contribute to observed annual differences in the proportion of repeat spawners in all populations studied.

The frequency of repeat reproduction in the St. John River (N.B.) was higher than in any other river investigated. The 2-yr mean (sexes combined) for the population was 73% (range 70-77). The frequency of repeat spawning in males (81%; range 78-85) was higher than in females (65%; range 64-67), as in the York and Connecticut rivers.

In the Miramichi River, the 3-yr mean (sexes combined) in the proportion of repeat spawners was 57% (range 55-69). In two of the three years the frequency of repeat spawners was greater in males than in females. The 3-yr means for males and females were 59 (range 42-82) and 54% (range 51-58), respectively.

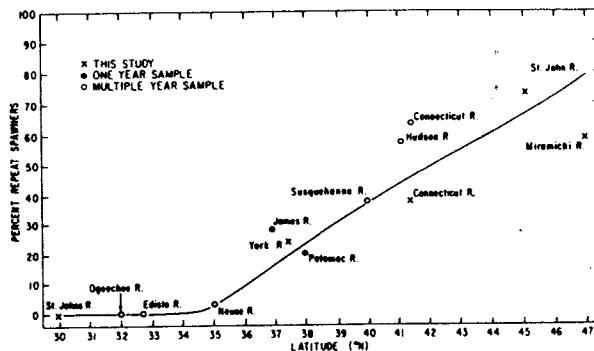


FIG. 2. Percent repeat spawners in American shad populations spawning in Atlantic coast rivers located at various latitudes. Data other than that developed in this study from: Ogeechee, Sykes 1956; Edisto, Walburg 1956; Neuse and Susquehanna, Lapointe 1957; James and Potomac, Walburg and Sykes 1957; Hudson, Talbot 1954.

A strong positive relationship exists between the proportion of repeat spawners and latitude of the home river, especially north of 35°N. The percentages of repeat spawners in the five populations investigated in the present study (Fig. 2) were significantly different (males $\chi^2 = 1390$, $df = 4$, $P < 0.001$; females $\chi^2 = 1579$, $df = 4$, $P < 0.001$). Published frequencies of repeat spawning in other Atlantic coast populations show similar latitudinal trends (Fig. 2).

Small deviations from this trend occur, notably in the James and Potomac rivers (Walburg and Sykes 1957). However, these estimates were based on samples collected in only 1 yr; and annual variation in the proportion of repeat spawners in individual populations are sufficient to account for this. High values recorded for the Hudson and Connecticut rivers (Talbot 1954; Fredin 1954) may be due to bias introduced by sampling with large mesh gill nets. The value observed in the Miramichi River is low relative to the overall trend. It may be a real change, but the proportion of repeat spawners in that shad population may have been negatively affected by heavy metal and pulpmill pollution. Adult salmon returns and parr densities were so affected in that river system (Elson et al. 1973).

GROWTH

Growth in shad appears to be quite uniform from year to year within populations. We examined the growth of shad from all populations studied. Bartlett's test for homogeneity of variance (Sokal and Rohlf 1969) of lengths at age within populations revealed significant heteroscedasticity in only one sample (York River females $\chi^2 = 17.4$, $df = 4$, $P > 0.05$). No intrapopulation heteroscedasticity occurred in variances of lengths of fish at age when tested between populations. No significant intrapopulation differences in annual mean lengths at age were found using Student's *t*- and/

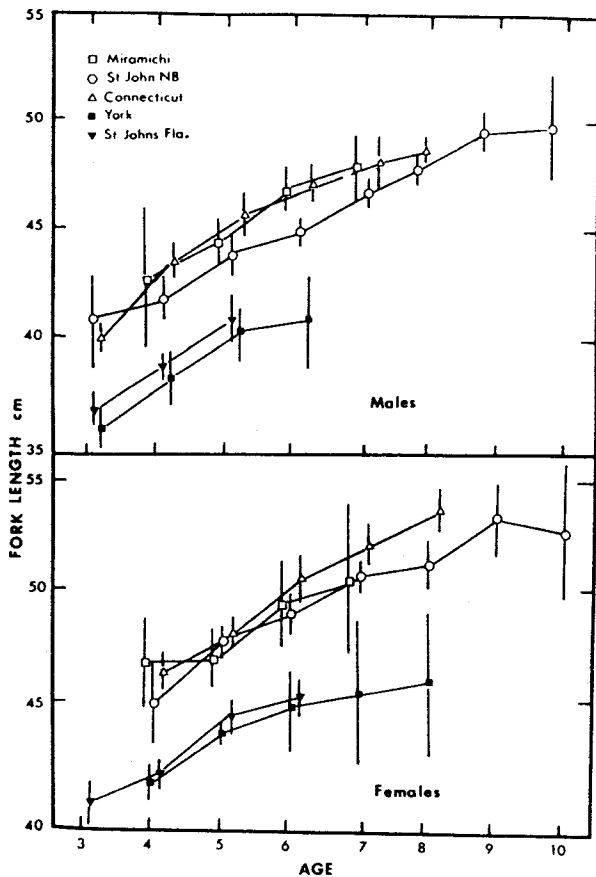


FIG. 3. Observed growth of male and female American shad in populations spawning in five Atlantic coast rivers. Vertical bars represent 99% confidence intervals for means.

or Student-Neuman-Keuls test (Sokal and Rohlf 1969).

Interpopulation comparisons of the mean sizes at age were less consistent (Fig. 3). Shad from the three northern rivers were significantly larger in every age-class than their counterparts from the York and St. Johns (Fla.) populations. Walburg and Nichols (1967) and Glebe and Leggett (1976) reported a similar pattern of differences in mean length at age between northern and southern populations. These findings differ from those of Lapointe (1957) who reported no difference between growth of shad collected in three rivers (St. Johns, Fla; Neuse, N.C.; and Susquehanna, Md.) and in Scotsmans Bay, Nova Scotia (Leim 1924). Lapointe's comparison of growth of shad in the three rivers with growth of shad in Leim's sample may be questionable, because these two workers differed in their ageing techniques and these differences are difficult to correct for. In addition, Lapointe did not evaluate the possible influence of gear selection on growth estimates. A portion of his fish from each river came from 12.7-15.2-cm stretched mesh gill nets. This gear would under-

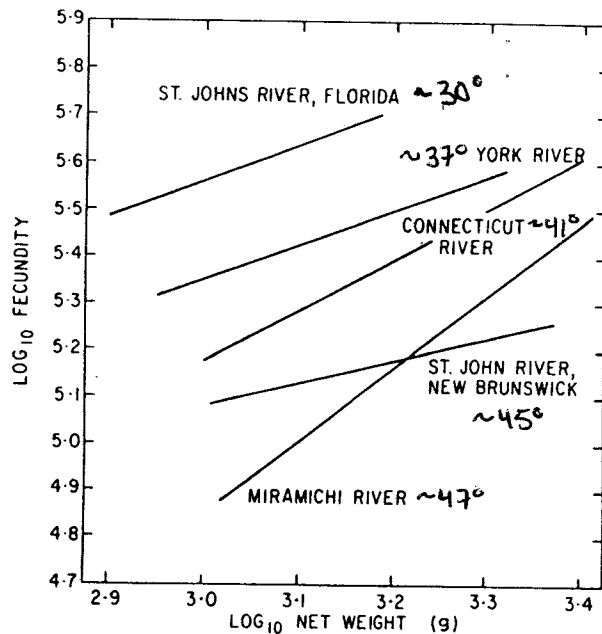


FIG. 4. Relative fecundity of five Atlantic coast populations of American shad.

sample the smaller fish from these populations (Carscadden and Leggett 1975b) thereby creating a positive bias in mean lengths at age.

FECUNDITY

For shad of a given size or age, relative fecundity (number of eggs per kilogram body weight) was highest ($P < 0.01$) in the populations at the south of the range and decreased to the north (Fig. 4). We also determined mean virgin fecundity (fecundity of the average virgin female in the population) and mean lifetime fecundity (number of eggs produced during the expected reproductive life of a female) for each population. Mean virgin fecundity was derived by first performing a series of stepwise multiple linear regression analyses (BMD 02R, Dixon 1975) of the relationship between log fecundity and log length, log net (total weight-gonad weight) weight and age (Table 1) and then substituting mean length, mean net weight, and mean age of virgin females in each population into the appropriate equations. Mean lifetime fecundity was calculated as

$$F(j) = Y(j) + \sum_{i=1}^n (Y(i,j) \times P(i,j))$$

where $F(j)$ = mean lifetime fecundity, population j ; $Y(j)$ = mean virgin fecundity, population j ; $Y(i,j)$ = mean fecundity of females in population j spawning for the i th time; $P(i,j)$ = proportion of females in population j which spawn i times. $Y(j)$ and $Y(i,j)$ were calculated by substitution of mean length, mean net

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