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clutch size & reproduction

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# 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-

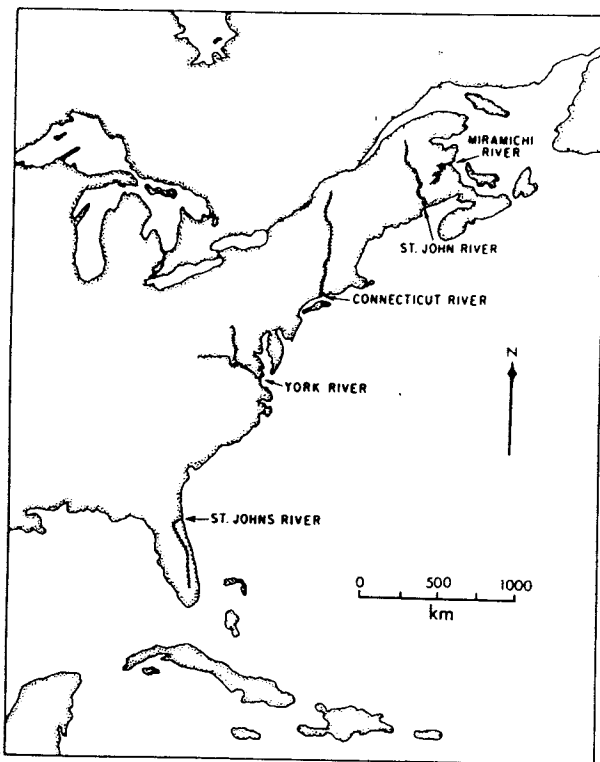


FIG. 1. Location of natal rivers of shad populations investigated.

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  $46 \pm 14.5$  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.

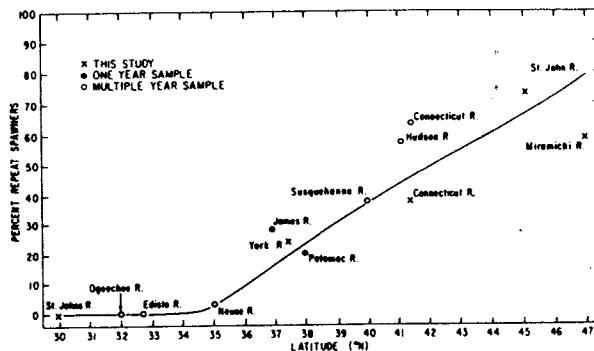


FIG. 2. Percent repeat spawners in American shad populations spawning in Atlantic coast rivers located at various latitudes. Data other than that developed in this study from: Ogeechee, Sykes 1956; Edisto, Walburg 1956; Neuse and Susquehanna, Lapointe 1957; James and Potomac, Walburg and Sykes 1957;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

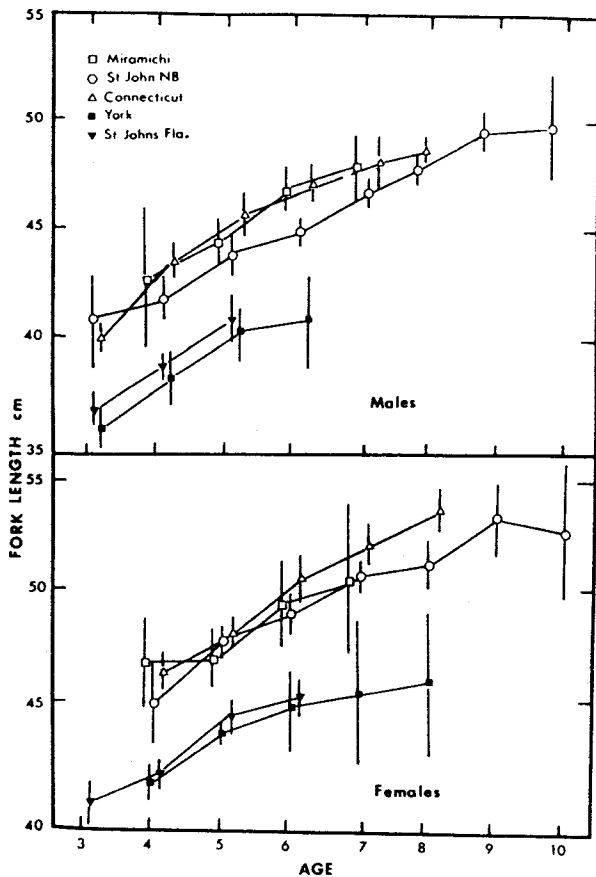


FIG. 3. Observed growth of male and female American shad in populations spawning in five Atlantic coast rivers. Vertical bars represent 99% confidence intervals for means.

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-

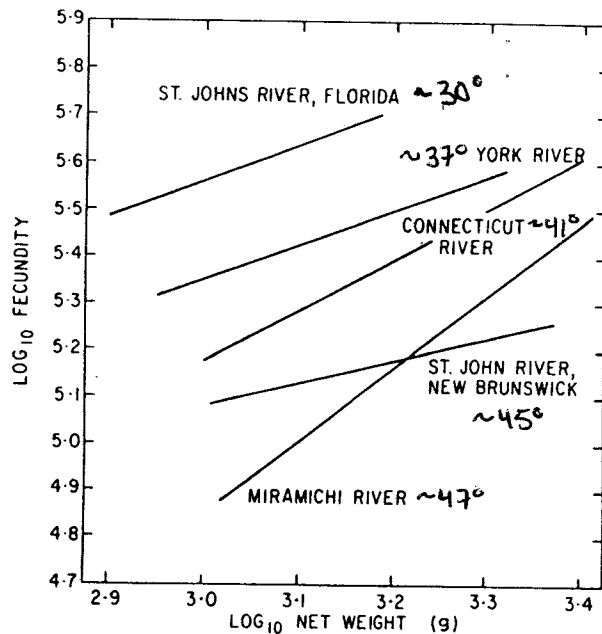


FIG. 4. Relative fecundity of five Atlantic coast populations of American shad.

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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TABLE 1. Summary of intercepts, regression coefficients, correlation coefficients, and analyses of variance for multiple regressions of log fecundity on log length, log net weight, and age. Order of addition of variables in the stepwise regression is shown. \*\**P* < 0.01.

	Coefficients			Intercept	Multiple <i>r</i>	100 <i>r</i> <sup>2</sup> (%)	<i>F</i> -value
	log length	log net weight	age				
St. Johns R.	1.55093	0.27331	0.01499	2.18965	0.6082**	36.99	9.200**
Order	1	2	3				
York R.	-0.66635	1.00491	-0.02258	3.52096	0.6516**	42.46	11.313**
Order	3	1	2				
Connecticut R.	1.70313	-2.94763	n.s.	4.91354	0.7311**	53.45	26.988**
Order	2	1					
St. John R.	-1.71382	1.04082	-0.01132	4.79754	0.3719**	13.83	13.914**
Order	2	1	3				
Miramichi R.	1.56528	1.17387	-0.00662	-1.18556	0.8609**	74.11	49.608**
Order	2	1	3				

weight, and mean age of virgin and repeat spawning fish into the respective multiple regression equation. There is a high degree of intracorrelation among the independent variables in the multiple regression equations. Our aim, however, was to account for the maximum variance possible, not to determine partial correlation coefficients.

All regressions were significant at the *P* < 0.01 level. In the St. Johns (Fla.), York, Connecticut and Miramichi rivers, they accounted for 37-74% of the total variation in fecundity. In the St. John River (N.B.) only 14% of the variance in fecundity was accounted for by the regression (Table 1). The elevations of these regressions differed significantly (*F*[4, 463 df] = 178.45, *P* < 0.01), as did the slopes (*F*[4, 451 df] = 3.77) BMD 09V, Dixon 1975). The difference in slopes was attributed to the St. John River for which we combined fecundity values for fish sampled from subpopulations native to three tributaries each having different fecundity relationships (Carscadden and Leggett 1975a) to produce an average value for this river. This may also account for the higher level of unexplained variance in fecundity for that population (Table 1).

As with relative fecundity, mean virgin and lifetime fecundities declined with increasing latitude of the home river (Table 2).

The trend to higher fecundity in southern rivers was

TABLE 2. Mean virgin and lifetime fecundities of five Atlantic coast shad populations.

Population	Mean virgin fecundity	Mean lifetime fecundity
St. Johns R. (Fla.)	406 000	406 000
York R.	259 000	327 000
Connecticut R.	256 000	384 000
St. John R. (N.B.)	135 000	273 000
Miramichi R.	129 000	258 000

not due to the annual fecundity variations noted for other species by Bagenal (1957, 1965); Hodder (1963, 1965); and Nikolskii (1962). We compared fecundity and total weight relationships calculated for 19 shad collected from the St. Johns River in 1958 (Walburg 1960), 18 from the York River in 1959 (Nichols and Massman 1963), and 22 from the Hudson River in 1950 (Lehman 1953) with those determined in this study (Fig. 5). These, too, reveal a decrease in fecundity to the north. Davis (1957) reported a similar pattern. In addition, fecundity was constant from year to year within subpopulations native to three tributaries of the St. John River (N.B.) and in the Miramichi River (Carscadden and Leggett 1975b).

A correlation analysis of the relationship between fecundity and repeat spawning revealed a significant negative correlation (*r* = 0.91, *P* < 0.05) between these two variables: as the proportion of repeat spawners declines with decreasing latitude, the relative fecundity increases in linear fashion. This inverse relationship results in a greater uniformity of lifetime fecundity (maximum difference between populations 1.6 times) as compared with relative fecundity of individuals of equivalent sizes between populations (3.5-5 times).

AGE AT MATURITY

Mean age at maturity varied between populations. St. Johns River (Fla.) shad mature at a significantly younger age than in any of the other rivers. There are no significant differences in age at maturity for males in other rivers. Female shad of "northern rivers," as represented by the St. John (N.B.) and Miramichi rivers, mature at a significantly younger age than those in mid-Atlantic rivers (Table 3). There was no latitudinal gradient in age at maturity.

Discussion

Shad native to rivers south of latitude 32°N (see

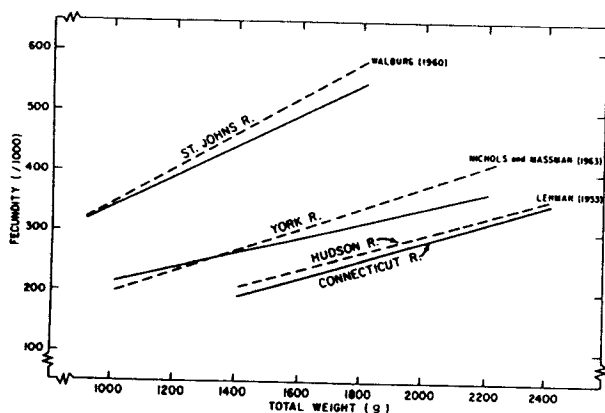


FIG. 5. Relative fecundity of American shad as determined in this study (solid line) and by earlier investigators (dashed line).

Fig. 2) are semelparous (all fish die following spawning). The proportion of repeat spawners in populations north of 32°N increases with the latitude of the home river and populations from northern rivers such as the St. John (N.B.) and Miramichi exhibit a high degree of iteroparity (60–80% repeat spawners). Differences in relative fecundity with latitude are also dramatic; southern populations produce 3–5 times more eggs per kilogram body weight than northern populations. The reciprocal trends in relative fecundity and frequency reproduction tend to reduce the differences in mean lifetime egg production between populations.

Geographical variations in life history have been observed in several other fishes (see Carscadden and Leggett 1975b); although, in general, only one character (usually fecundity or age at maturity) has been investigated at a time. One factor known to influence fecundity and age at maturity is the quantity and quality of food available (see Bagenal 1963, 1966, 1969; Nikolskii 1962, 1969; Scott 1962). In shad it is unlikely that differences in food availability and/or quality during the pre-reproductive period influence the reproductive characters studied, because the migrations of juvenile and adult shad from all Atlantic populations are highly regulated by ocean temperatures causing them to have similar migration routes at sea (Talbot

and Sykes 1958; Leggett and Whitney 1972). They should experience similar environmental conditions during most of their marine life. The smaller mean size at age of "southern" shad may result mainly from differences in the duration of their marine residence rather than from differences in food availability. Juveniles spawned in "southern" rivers spend 3–5 mo longer in freshwater than their northern counterparts (Walburg and Nichols 1967) and have less time to exploit the more abundant marine food supply. The observed pattern in shad (highest fecundity in slow growing populations) also contrasts with the generally observed relationship between growth and fecundity (Bagenal 1966, 1969; Scott 1962). These observations, coupled with similar findings by Carscadden and Leggett (1975b) that shad homing to three separate tributaries within the St. John River, N.B., exhibited differences in reproductive characteristics, suggest that these differences represent genetically based adaptations to the reproductive environment. McGregor (1923) working with king salmon, Wolfert (1969) with walleyes, and Moore (1975) with anadromous arctic char have reported similar geographical differences in reproductive characteristics that appear to have a genetic base.

Another possible hypothesis explaining the combination of reproductive characteristics observed in shad over both macro- (this study) and microgeographical (Carscadden and Leggett 1975b) ranges is that changes in fecundity and frequency of reproduction are adaptations to geographical differences in juvenile survival rates. Marcy (1976) has shown that in the Connecticut River temperature variation during spawning is strongly correlated with variation in abundance of juveniles which, in turn, determines recruitment to the adult population (Leggett 1977a). The relationship between the thermal regime and year-class strength apparently results from the narrow temperature optima for egg and larval survival (Bradford et al. 1968; Leggett 1977a). Shoubridge (1977) analyzed the thermal regimes in several Atlantic coast rivers from the St. Johns (Fla.) to the St. John (N.B.) and found that the duration of the thermal optima for egg and larval development decreased, and the variability of the thermal regime increased from south to north. This suggests that variation in egg and larval survival, year-class strength, and recruitment also increases with latitude.

TABLE 3. Mean (SD) age at maturity of shad from five Atlantic coast populations. Populations having similar mean ages at maturity are indicated by the same letter in the significance column (Duncan Multiple Range; Student-Neuman-Keuls  $P < 0.05$ ).

Males			Females		
Mean age at maturity	Significance	River system	Mean age at maturity	Significance	River system
3.8	a	St. Johns (Fla.)	4.2	a	St. Johns (Fla.)
4.1	b	Connecticut	4.5	b	St. John (N.B.)
4.2	b	York	4.6	b	Miramichi
4.2	b	St. John (N.B.)	4.7	c	York
4.2	b	Miramichi	4.8	c	Connecticut

Several authors (Ricker 1954, 1958; Beverton and Holt 1957; Holgate 1966; Murphy 1966, 1968a, b; Murdoch 1966; Charnov and Schaffer 1973; Schaffer 1974) have examined, both empirically and theoretically, the relationship between reproductive success and frequency of reproduction. They have concluded that when reproductive success is unpredictable, iteroparity (as exhibited by shad populations north of 32°N) significantly increases population stability, lowers the probability of extinction, and will be selected for.

The latitudinal changes in repeat spawning and relative fecundity suggest a negative functional relationship between these variables. There may be a trade-off in energy allocation between spawner survival and gonad production. Cody (1966), Holgate (1967), Gadgil and Bossert (1970), Charnov and Krebs (1973), and Mountford (1973) have variously hypothesized that the total amount of time and energy available to an individual in its lifetime is fixed, and that optimum life history strategy allocates resources to growth, maintenance, and reproduction in a way that maximizes the individual's contribution to future genotypes. Comparisons of the energy allocation to gonad production vs. spawner survival is not possible except in the St. Johns (Fla.), York, and Connecticut rivers where Glebe and Leggett (1976) have studied the energetics of the freshwater migration of American shad. Evaluation of energy allocation in these rivers is complicated by differences in the timing of gonad development: Connecticut River shad enter freshwater with fully developed gonads while St. Johns River (Fla.) shad transfer much energy from somatic tissue to the gonads during the upriver migration, and York River shad are intermediate. In the York and Connecticut rivers, the average energy content/ovum of unspawned fish on the spawning grounds is 5.4 J, and the total energy allocated to the gonad by the average female is about 1425–1466 kJ. In contrast, the average energy content/ovum for shad near the spawning grounds in the St. Johns (Fla.) River is 1.7 J. We can only approximate the total energy allocated to the gonad by the average St. Johns (Fla.) River female. The Florida shad expended about 50% of their total somatic energy reserves to migrate 370 km to the spawning grounds, and spent shad sampled later at the same site had expended a further 20–30% of their initial somatic reserves. This compares with an approximate 40% expenditure of initial somatic reserves by Connecticut River shad to reach the spawning grounds (137 km) and an additional 15% of initial reserves to complete the postspawning migration back to the sea. As Shoubridge (1977) noted, it is improbable that the rapid and extensive decline in somatic reserves experienced by St. Johns River (Fla.) shad on the spawning grounds could result from maintenance metabolism requirements alone, because it represents about half of the total energy expenditure required to reach the spawning grounds. Because St. Johns River shad also transfer energy to the gonads during the

prespawning migration, it appears that much of the reduction in somatic reserves during the spawning period results from final transfer of energy to the gonad just before spawning. If we conservatively assume that as little as 10–15% of the energy reserves depleted on the spawning grounds are transferred to the gonad, the average energy content of the ovum in the Florida population would be 5.0–6.3 J and the total energy allocation to the ovary approximately 2053–2589 kJ. This is 1.4–1.8 times the absolute energy allocated to the gonad by Connecticut and York River females each year. A much greater relative allocation of energy is made to gonad production in St. Johns River shad since the somatic reserves of these fish are about 30–40% less than those of Connecticut and York River shad at the time of river entry (Glebe and Leggett 1976). This is so even if energy content/ovum equals or is slightly less than that of the Connecticut and York River populations. We therefore conclude that selection for iteroparity in "northern" populations has resulted in greater allocation of total energy to the somatic resources required to complete the freshwater spawning migration and return to the marine feeding areas. This has been achieved by reducing the energy allocated to gamete production with a corresponding reduction in relative fecundity. The benefit achieved by this adaptation is greater population stability to balance the greater environmental variation faced by iteroparous populations in accordance with Ricker 1954, 1958; Beverton and Holt 1957; Holgate 1966; Murphy 1966, 1968a, b; Murdoch 1966; Charnov and Schaffer 1973; and Schaffer 1974. In the St. Johns River (Fla.) population, and presumably in other southern populations, the predictable spawning environment has selected for semelparous reproduction in which a much greater proportion of the total energy reserve is allocated to gamete production. The energy allocated to somatic reserves is reduced to that required to complete a suicidal freshwater migration to the spawning grounds. St. Johns River (Fla.) shad, and presumably other southern populations, expend about 80% of their initial energy reserves to reach the spawning grounds and spawn and are energetically incapable of surviving a return migration to the sea (Glebe and Leggett 1976).

The earlier maturity of iteroparous southern shad populations may, in combination with high relative fecundity, help to compensate for the potential reduction in lifetime egg production resulting from the absence of repeat spawning. This effect is likely to be small, however, because as Cole's (1954) figure 3 clearly demonstrates, if compensation were to be achieved through earlier maturity alone the St. Johns River (Fla.) population would be required to mature in <1 yr which is, no doubt, biologically unattainable. The existence of earlier maturity in the south does suggest, however, that it may convey a selective advantage to the population. The selection for an earlier age at maturity in the south may occur because a further increase in the energy allocated to egg production is

impossible without a related increase in prespawning mortality.

Latitudinal trends in life history strategies in shad are consistent with ecological theory reviewed by Stearns (1976, 1977). We consider this agreement between observed reproductive strategies in American shad and the predictions of current life history theory to be supportive of our hypothesis (Carscadden and Leggett 1975b) that differences in the reproductive strategies of local populations of American shad are adaptive. It should be possible to identify similar trends in other species because numerous authors (Slobodkin 1961; Margalef 1963; Cody 1966) have concluded that middle and high latitude environments are less stable and less predictable than those of the subtropics and tropics. Therefore, in general, there should be selection for increasing frequency of reproduction and decreasing relative fecundity with increasing latitude. Nikolskii (1970) reported this to be the dominant trend in life history characteristics of fishes.

This general pattern need not apply in all cases, however. For example, Rounsefell (1957) reported that in four of five *Oncorhynchus* species, southern populations produced more eggs and matured earlier. These four Pacific salmon are semelparous, so that selection of reproductive characteristics in the group must be influenced mainly by reduced reproductive success in the south. In support of this, Neave (1948) found that Pacific salmon that inhabited more hazardous environments in freshwater as juveniles had higher fecundities and that these differences were not related to growth. The *Oncorhynchus* species have longer spawning migrations than the iteroparous Pacific steelhead (*Salmo gairdneri*), and this increased migratory "effort" may be the cause of their semelparity (G. Bell, McGill University, unpublished data). Pacific salmon occupy more restricted ranges than steelhead (Bulkley 1967). The trend towards increased fecundity and earlier maturity in southern populations of both steelhead (Bulkley 1967) and the *Oncorhynchus* species suggests that they may encounter similar selective pressures, and that repeat spawning may be significant in the southward extension of the steelhead range.

In Atlantic salmon (Schaffer and Elson 1975), age at maturity is governed not by environmental changes related to latitude, but by the distance to their spawning grounds. However, variability in age at maturity changes in response to latitudinal differences in the predictability of egg to adult survival in a manner consistent with theoretical predictions (Schaffer 1974).

Based on the foregoing we conclude that reproduction characteristics exhibited by shad and other species represent population adaptations to their environment. Fecundity, frequency of reproduction, and age at maturity may exhibit varying degrees of plasticity in response to short-term environmental changes (Bagenal 1957); however, the combination of characteristics, not one alone, defines the nature of adaptation and ensures population survival. Leggett (1977b) hypothesized that

homing to the natal spawning area, common in freshwater and anadromous species, provides the mechanism for developing these adaptations through reproductive isolation and for ensuring that populations continue to occupy habitats compatible with their life history.

The concept of population specific reproductive strategies is important to fishery management. Alterations of the reproductive characteristics of a population through differential exploitation, changes in environmental quality, or fish culture practices may reduce population fitness. This has been demonstrated for the Pacific sardine (Murphy 1966), for herring (Beverton 1963), and for whitefish (Bell et al. 1977). Marked changes in habitat characteristics without change in reproductive characteristics may yield similar results. Greater understanding of the relation between reproductive strategy and habitat characteristics is needed to evaluate exploitation strategies and permissible habitat changes.

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