

Influences of Anadromous Spawning Behavior and Optimal Environmental Conditions Upon Striped Bass (*Morone saxatilis*) Year-Class Success¹

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An analysis of the spatial and temporal abundance patterns of developing striped bass (*Morone saxatilis*) ichthyoplankton stages in the Potomac Estuary, including a Markovian description of transport, indicates that annual differences in the distribution of spawning fish are not likely to account wholly for the wide fluctuations in year-class success. Year-class success can be decomposed into the product of two factors — one extrinsic, acting upon the eggs and larvae, and the other, a behavioral property of the adult stock. The effect of extrinsic environmental conditions upon year-class success can be measured relative to the maximum computed survival of eggs to post-finfold larvae among all locations and times during a given year. Apparently, the behavior of the spawning adult fish is not well matched with the environmental conditions favorable to ichthyoplankton survival, and therefore, the actual spawning distribution yields only a fraction (the spawning fitness) of the maximum production possible during that year. Spawning fitnesses were estimated to be small (<0.02 out of 1.0) and varied by less than a factor of two over the three seasons observed. In contrast, the year-class success as measured by post-finfold production differed 35-fold over the same 3 yr. It appears most likely that the large range in success is due primarily to the extrinsic, density-independent environmental factors which determine the optimum survivals in combination with spawning behavior. However, no strong case can be made for behavioral compensation by spawning fish to offset changes in the annual optimum survival conditions for ichthyoplankton.

Key words: anadromous, ichthyoplankton development, Markovian transition probabilities, optimal survival, spawning behavior, spawning fitness, striped bass, transport model, year-class success

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Une analyse des modalités de l'abondance spatiale et temporelle de stades ichtyoplanctoniques de bars d'Amérique en voie de développement dans l'estuaire du Potomac, y compris une description markovienne du transport, indique que les différences annuelles de distribution des reproducteurs ne peuvent probablement pas expliquer complètement les grandes fluctuations d'abondance d'une classe annuelle à l'autre. Le succès d'une classe annuelle peut être décomposé comme résultant de deux facteurs — un facteur extrinsèque agissant sur les oeufs et les larves, et l'autre, une propriété de comportement du stock adulte. L'effet de conditions ambiantes extrinsèques sur le succès d'une classe annuelle peut être mesuré en relation avec la survie maximale calculée depuis l'oeuf jusqu'à la larve avec repli cutané des nageoires, à tout endroit et temps d'une année donnée. Le comportement des reproducteurs, semble-t-il, ne s'accorde pas très bien avec les conditions ambiantes favorables à la survie de l'ichtyoplancton. Comme conséquence, la distribution effective de la fraie ne produit qu'une fraction (aptitude reproductrice) de la production maximale possible cette année-là. On estime que l'aptitude reproductrice est faible ($<0,02$ sur 1,0) et varia de moins de un ou deux facteurs durant les trois saisons d'observation. Par contraste, le succès d'une classe annuelle mesurée par production de larves au stade postrepli varia de 35 fois durant les mêmes 3 années. Il semble très probable que la gamme étendue de succès est surtout due à des facteurs ambiants extrinsèques, indépendants de la densité, qui déterminent la survie optimale, auxquels s'ajoute le comportement reproducteur. On ne peut toutefois pas prouver que les reproducteurs ont un comportement compensatoire pour contrebalancer les changements de conditions optimales annuelles de survie de l'ichtyoplancton.

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THE most significant mortalities for many fish populations occur during the early planktonic or juvenile life stages. In most fish populations, year-class strength is determined by the end of larval development, and all age-groups remain roughly proportional to the annual abundance of the fingerling cohort (Chadwick et al. 1977). If the developmental process is biologically controlled through density-dependent mechanisms such as competition, predation, or cannibalism, adult population levels reach long-term equilibrium values and age structure stabilizes. However, when annual survival during early development is significantly affected by extrinsic, density-independent environmental conditions, adult population levels display large annual fluctuations, and the age structure becomes highly time-dependent. Striped bass populations seem to display the latter behavior, as indicated by dominant year-classes controlling catches in the fishery (Koo 1970). Catch records show population levels to be unstable, lacking a definable, long-term equilibrium point (Van Winkle et al. 1979). Knowledge of environmental conditions in the spawning-nursery area during years with very large or very low survivals is, therefore, of utmost importance to anyone seeking to understand and manage such a fishery. This is especially true in instances when the management objective is the protection of early life stage habitats instead of the traditional maximization of yield.

For species with spawning and nursery areas very small in geographical extent, the problem of larval habitat protection can be resolved into monitoring conditions at the spawning and nursery site over a series of seasonal spawning events, and then quantitatively

correlating these spawning stock conditions and environmental factors with the subsequent production figures of young adults. A more likely situation, however, is that temporally prolonged spawning and early development occur over a diffuse area having significant environmental gradients. Further complications arise when one realizes that a given individual spawned at a certain site in the area may be transported through differentially favorable environments within the region before either succumbing or being recruited into the population as a young adult. An investigator with data on spatial and temporal abundances of various egg, larval, and juvenile stages is, thus, faced with the task of deconvoluting the effect of passive transport upon the observed abundance patterns, in order to estimate the most likely times and places where greater or lesser mortalities (or, inversely, lesser or greater survivals) have occurred.

Having assessed the successive survival patterns through various stages, the nontrivial next step is to answer the question, "What are the key sites and times within the general nursery area for which survival of the various early stages contributes most to recruitment into the population?" If the ultimate goal of the manager is the maintenance of the reproductive capability of the species through the conservation of spawning-nursery habitats, it is evident that the crucial times and places must be protected from excessive perturbation by man.

A closely related, but separate question, a manager might pose is, "At what time, place, and life stage do larvae and juveniles have the greatest probability of contributing to the adult stock?" The answer to this

query could be the foundation of an attempt to artificially increase the production of the fishery. Such considerations can dictate how long to raise larvae and juveniles under artificial conditions before releasing them at some optimal time and location to supplement natural reproduction. Of more theoretical interest is the corollary question, "How efficient was a given spawning season; or, what is the spawning fitness of the population?" By comparing the actual spatial and temporal distribution of production with the hypothetical production of the same number of eggs released at optimal locations and times, one can obtain a quantitative measure of the fitness of the observed spawning distribution. The changes in fitness from year-to-year might shed some light on the adaptive significance of specific spawning distribution and behavior in the adult population.

The techniques for approaching answers to these questions form the subject matter of this article. The methods presented here were developed to analyze the results of an extensive striped bass (*Morone saxatilis*) population study in the Potomac estuary during the spawning seasons 1974–76. Ichthyoplankton, juvenile, and spawning stock surveys comprised the biological elements in this study. Full details on the study area, sampling procedures and abundance estimates can be found elsewhere (Polgar et al. 1976; Polgar 1977; Boynton et al. 1977; Mihursky et al. 1976; Setzler et al. 1978) and will be described only briefly below. Full explanations of the uniform age-class model and of the spatial transition probabilities are in preparation (T. T. Polgar and P. A. Souza unpublished data). Only the points necessary for comprehension of the spawning fitness analysis are repeated here.

Study Area and Sampling Procedures

The spawning-nursery ground under study is the upper Potomac Estuary, from 69 km above the mouth, in the oligohaline region, to 151 km, well into the freshwater region and above the major area of spawning activity. The sampling design description is specific to the 1974 survey and no significant alterations in design were made in subsequent years. Twelve transects were established along the study area and spaced so as to divide the estuarine reach into equal volume ($2 \times 10^8 \text{ m}^3$) segments, each having a length greater than a single tidal excursion (see Fig. 1). A single boat sampled all transects weekly throughout the 17-wk duration of the spawning and developmental periods. Several tows were taken perpendicular to each cross-stream transect at 38 separate locations (total for all 12 transects) as shown on Fig. 1.

All ichthyoplankton were identified to species (where possible) and were counted for each tow. Striped bass ichthyoplankton were further classified into four life stages: eggs, yolk-sac larvae, finfold larvae, and post-finfold larvae. Similar ichthyoplankton surveys were carried out during the 1975 and 1976 spawning seasons.

During the beginning of the 1974 spawning season, 13 current meter stations were established along the Maryland Point, Douglas Point, Possum Point, and Indian Head transects (Fig. 1). Divided among the 13 stations were 21

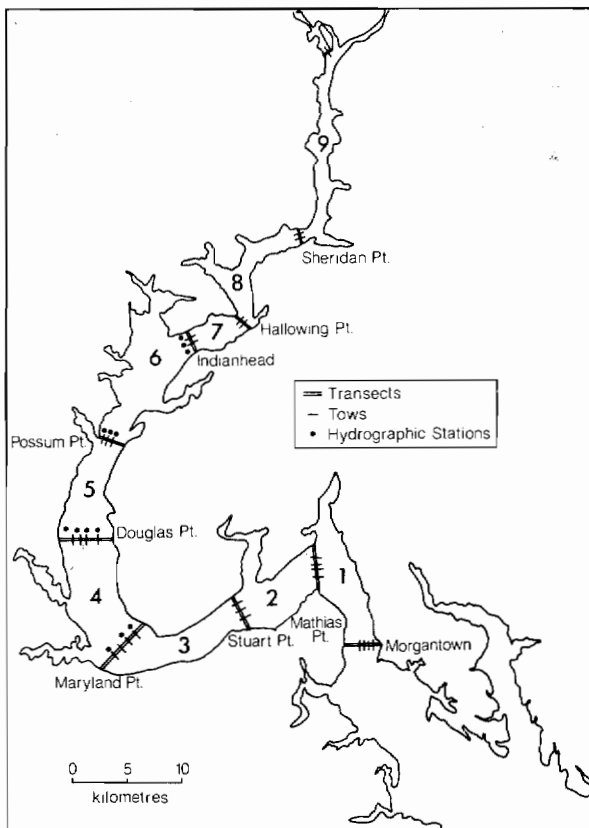


FIG. 1. Study area, showing estuarine segment designations used in the analysis.

Braincon Histogram recording current meters. Current speed and direction were automatically recorded at 10-min intervals over a 15-d period from April 23 through May 8. These hydrodynamic data were intended for use in a vertically averaged, two-dimensional model of ichthyoplankton dispersion, but also were employed in estimating the one-dimensional longitudinal dispersion and advection characteristics necessary to calculate the spatial transition probabilities required in this analysis.

Abundance and Survival Patterns

ESTIMATION OF ABUNDANCES

Data from the field collections and the laboratory sorting provided information on the catches in each tow. Each tow was associated with a transect and a week of the season, and was characterized by the volume of water strained in cubic metres and the numbers of each life stage of striped bass caught. It was necessary to transform these numbers into estimates of abundance of each life stage within each of the estuarine segments.

Pyne (1979) demonstrated that the minimum variance, unbiased estimator of the average density for a series of tows from the same distribution of organisms

collected in varying tow volumes was simply the sum of all the numbers of a given age-class from all tows divided by the sum of the respective volumes sampled. A given segment was bounded by two transects and the density estimator for the segment was obtained by extending the sums of number and volume over all tows made on the two boundary transects. The abundance of life stage k during week j in segment i was calculated by multiplying the corresponding average density by the river volume of segment i (Polgar 1977). The derived abundance is designated by the symbol A^k_{ji} .

SPATIAL TRANSITION PROBABILITIES

It was clear from the outset that because the spawning and nursery area is distributed in space, information was necessary on how the ichthyoplankton are transported throughout the study area. Transport, even in the fresher portions of the estuary, like most large-scale fluid flows, is known to contain a stochastic element, termed dispersion, which is the net result of small scale random motions viewed on a larger scale. Advection, or net displacement, is also part of the transport process, but is deterministic, given river geometry and freshwater inflow. Hence, it is impossible to say with certainty where an organism originating in segment i will be found at the end of a week. Rather, it is necessary to speak of the probability, P_{il} , that a given animal in segment i during one time interval will appear in cell l during the next time interval, assuming that the organism does not suffer mortality nor develop into the next stage during the interim. That is, P_{il} is the transition probability applicable to an organism transported from location i to location l due to weekly spatial movement in the absence of mortality.

In what follows, P_{il} will refer to transitions between segments of a linear chain during fixed time intervals, but the reader should bear in mind that this in no way restricts the application of the subsequent methodology to one-dimensional situations. Stationary but spatially dependent transport within any two- or three-dimensional spatial network can be characterized by a Markovian matrix of P_{il} 's so long as the cells are denumerable.

Eggs and larvae of the age-classes under consideration are assumed to have no appreciable ability to overcome the water movements. They are assumed to ride passively with the currents, being considered planktonic in these life stages. The assumption of passive transport during the first 8 wk is consistent with approximations made in some other striped bass models (Wallace 1975). Graham et al. (1972) suggest how herring larvae might maintain their position by vertical migration to take advantage of two-layer estuarine net flows, but during the striped bass spawning seasons the region described herein is almost completely upstream of the estuarine segment in which two-layer flow is normally observed. Hence, an appropriate hydrodynamic model for the dispersion of a chemical species

may be employed to calculate the transition probabilities. Polgar et al. (1975) described how Hunter's (1975) one-dimensional mass, momentum, and species balances are calibrated against the current meter data recorded during this study.

Briefly, Hunter's model is one-dimensional and nonlinear, including both the dynamic and kinematic equations taken from Harleman and Lee (1969), Harleman (1971), and Thatcher and Harleman (1972). The geometric parameters describing the river were taken from statistics compiled by Cronin and Pritchard (1975) and Cronin (1971). The model was driven at the landward end by freshwater and tidal flows. Freshwater flow was taken to be the average input (over the study period) as measured at the Chain Bridge gauging station in Washington, D.C. The amplitudes of the tidal flows were taken to be transect averages of the values of curve-fitted current meter records at Indian Head. The seaward boundary was driven by predicted tidal heights initially, and thereafter the phases and amplitudes were tuned until the net velocities, tidal velocity amplitudes, and tidally averaged exchange coefficients reasonably approximated estimated values from measurements in 1974.

Transition probabilities were estimated from the calibrated model by placing a known initial concentration only in segment i and running the model over 14 tidal cycles (approximately 1 wk). The ratios of the final concentrations in the segments to the initial amount in segment i determined the elements of P_{il} . This procedure was repeated with each segment as the origin of organisms. Transition probabilities for 200 and 500 m^3/s riverine inputs are shown in Table 1. The rows do not sum to unity in all cases because of the finite probability of transport out of the region. The lower flow characterized the 1974 and 1976 seasons, whereas 500 m^3/s prevailed in 1975. In the following analysis, the transition probabilities will be assumed stationary over the 17 or so weeks of each of the three study periods. Constancy of transition probabilities is a mathematical convenience permitting the analytical solution which follows. Variations in the flow regime are being investigated.

SURVIVAL ESTIMATES

Thus far a model has been described to account for conservative spatial-temporal transitions; it remains for the uniform age-class model to represent how an organism enters the succeeding life stage or dies in the process. It is possible to project an expected abundance pattern forward in time as though mortality did not occur. These projections should be greater than the observed abundances for the following week, and the survival can be estimated from comparison of observed and projected abundances, given some hypotheses about the rates of development.

In reality, transport and development occur continuously. The fact that populations can only be sampled

TABLE 1. Spatial transition probabilities for weekly periods.

	1	2	3	4	5	6	7	8	9
<i>A) Probabilities at 200 m³/s riverine input</i>									
1	0.195	0.146	0.045	0.010	0.001	0.000	0.000	0.000	0.000
2	0.250	0.200	0.145	0.047	0.010	0.001	0.000	0.000	0.000
3	0.156	0.239	0.196	0.146	0.046	0.009	0.001	0.000	0.000
4	0.088	0.165	0.216	0.254	0.148	0.049	0.009	0.001	0.000
5	0.034	0.080	0.158	0.279	0.261	0.125	0.031	0.005	0.000
6	0.006	0.018	0.062	0.184	0.319	0.262	0.112	0.029	0.002
7	0.000	0.002	0.013	0.065	0.207	0.306	0.264	0.123	0.015
8	0.000	0.001	0.004	0.029	0.130	0.268	0.336	0.199	0.030
9	0.000	0.000	0.002	0.013	0.078	0.210	0.362	0.271	0.057
<i>B) Probabilities at 500 m³/s riverine input</i>									
1	0.125	0.075	0.015	0.001	0.000	0.000	0.000	0.000	0.000
2	0.200	0.130	0.070	0.012	0.001	0.000	0.000	0.000	0.000
3	0.153	0.204	0.120	0.061	0.011	0.001	0.000	0.000	0.000
4	0.143	0.228	0.205	0.159	0.051	0.009	0.001	0.000	0.000
5	0.087	0.168	0.223	0.256	0.135	0.036	0.004	0.000	0.000
6	0.027	0.070	0.155	0.293	0.283	0.124	0.020	0.002	0.000
7	0.005	0.019	0.068	0.204	0.344	0.259	0.080	0.012	0.000
8	0.002	0.008	0.036	0.139	0.322	0.326	0.138	0.025	0.000
9	0.001	0.004	0.022	0.100	0.289	0.357	0.186	0.037	0.000

at discrete time intervals, however, makes information on the detail of this continuous change inaccessible. Therefore, the following three assumptions will introduce errors which we feel are commensurate with, but not greater than, the error due to the discrete sampling rate:

- 1) The members within an age-class are uniform in age between any given pair of sampling intervals.
- 2) Death can occur only at the time of development into the next age-class and after transport has been calculated.
- 3) Developmental rate is uniform and proportional to the number of generations occurring between sampling periods.

Optimally, of course, one wishes to minimize the sampling interval with respect to life stage durations, but economic constraints forced the choice of the weekly sampling rates.

If no maturation or death occurred from one sampling time to the next, the observed abundance of age-class $k + 1$ in segment l at the next sampling time would be equal to the product:

$$(1) \quad A_{j+1,l}^{k+1} = \sum_{i=1}^{nseg} A_{ji}^{k+1} P_{il}$$

where $nseg$ is the number of river segments.

If organisms are allowed to mature from one age-class to the next, the estimate in equation (1) would change in two ways. First, there would be a gain of organisms from age-class k entering into $k + 1$. If t^k represents the average time an individual spends in class k , then after the sampling interval, t^* , the fraction t^*/t^k of those organisms with age k arriving at segment l would develop into class $k + 1$ organisms, i.e. the gain

would be:

$$\frac{t^*}{t^k} \sum_{i=1}^{nseg} A_{ji}^k P_{il}$$

Similarly, the amount lost to age-class $k + 2$ due to development would be:

$$\frac{t^*}{t^{k+1}} \sum_{i=1}^{nseg} A_{ji}^{k+1} P_{il}$$

Making these two corrections, the expected abundances without mortality become:

$$(2a) \quad A_{j+1,l}^{k+1} = \sum_{i=1}^{nseg} A_{ji}^{k+1} P_{il} + \frac{t^*}{t^k} \sum_{i=1}^{nseg} A_{ji}^k P_{il} - \frac{t^*}{t^{k+1}} \sum_{i=1}^{nseg} A_{ji}^{k+1} P_{il}$$

or,

$$(2b) \quad A_{j+1,l}^{k+1} = \frac{t^*}{t^k} \sum_{i=1}^{nseg} A_{ji}^k P_{il} + \frac{t^{k+1} - t^*}{t^{k+1}} \sum_{i=1}^{nseg} A_{ji}^{k+1} P_{il}$$

Mortality is inevitable, and only the fraction $S_{j+1,l}^k$ of those organisms developing into class $k + 1$ survive the transition from class k . Whence,

$$(3) \quad A_{j+1,l}^{k+1} = S_{j+1,l}^k \frac{t^*}{t^k} \sum_{i=1}^{nseg} A_{ji}^k P_{il} + \frac{t^{k+1} - t^*}{t^{k+1}} \sum_{i=1}^{nseg} A_{ji}^{k+1} P_{il}$$

become the elements of the time-space matrix of forecasted abundances of stage $k + 1$ organisms during interval $j + 1$. This forecast includes both the develop-

mental and mortality processes. Equation (3) is the fundamental iterative relation upon which the remainder of this paper will be built.

If the abundances are available from field data, and the transition probabilities are known from Table 1, equation (3) may be solved to give an estimate of the stage survivals:

$$(4) \quad S_{j+1,l}^k = \left(A_{j+1,l}^{k+1} - \frac{t^{k+1} - t^*}{t^{k+1}} A_{j,l}^{k+1} P_{jl} \right) / \left(\frac{t^*}{t^k} \sum_{i=1}^{nseg} A_{j,i}^k P_{ji} \right)$$

A full description and analysis of the abundance and survival patterns for striped bass in the Potomac Estuary is in preparation (T. T. Polgar and P. A. Souza unpublished data).

Spawning and Nursery Production Analysis

In managing the nursery area, it is quite useful to know the abundance and survival patterns. In the absence of further analysis, one may guess that regions and times with high abundances and survivals are critical to the yield of the fishery and should be protected. But such guesses are apt to be imprecise. For example, it is altogether possible that a large abundance of eggs with a high survival into the yolk-sac stage is observed, and the conclusion is drawn that that particular time in the breeding season and reach of the river should be given top priority for protection. It may turn out, however, that these yolk-sac larvae suffer heavy mortality in the next transition and actually make less of a contribution to the next life stage than a more moderate spawn at a different place and time. The point here is that the manager is not in the business of protecting the young *per se*, but of maximizing the contribution of the spawning-nursery area to the adult stock.

In the particular survey under discussion, no systematic data exist on juvenile stages between the post-finfold and the adult fish, hence an analysis of the ultimate contribution of the observed abundances to the fisheries stocks cannot easily be made. The post-finfold juveniles, however, have attained some mobility, and it is probably reasonable to assume that subsequent mortality rates, while not negligible, do not approach the magnitude of that which has already transpired. For our purposes, it is reasonable to assume that year-class strength is defined by post-finfold stage abundances, and that compensatory mechanisms affect only earlier stages. As a consequence, the relative size of any particular year-class can likely be judged by its total production of post-finfold larvae.

Under the assumptions culminating in equation (3), it is possible to write an expression for the total production of post-finfold juveniles.

Numbering the eggs, yolk-sac, finfold, and post-finfold age-classes one through four, respectively, the total post-finfold production, T , becomes:

$$(5) \quad T = \frac{t^*}{t^3} \sum_{i,l=1}^{nseg} \sum_{j=2}^{nwks} S_{jl}^3 P_{jl} A_{j-1,i}^3$$

where $nwks$ refers to the number of weekly samples in the time series. Equation (4) describes the total production of post-finfold fish in terms of the abundances of the finfold individuals. It is also desired to express T in terms of egg and yolk-sac abundances. With some patience it is possible to substitute successively the iterative equation (3) into the finfold abundance terms in equation (5) and express the total production in terms of the yolk-sac abundances:

$$(6) \quad T = \frac{t^*}{t^3} \frac{t^*}{t^2} \sum_{p,i,q=1}^{nseg} \sum_{v=1}^{nwks-2} \sum_{j=v+2}^{nwks} \times \left\{ \left(\frac{t^2 - t^*}{t^2} \right)^{v-1} S_{jl}^3 S_{j-v,p}^2 (P_{pl})^v P_{qp} A_{j-v-1,q}^2 \right\}.$$

Repeating this substitution process, one derives an expression in terms of egg abundances:

$$(7) \quad T = \frac{t^*}{t^3} \frac{t^*}{t^2} \frac{t^*}{t^1} \sum_{p,m,l,q=1}^{nseg} \sum_{v=1}^{nwks-3} \sum_{w=1}^v \sum_{j=v+w}^{nwks} \times \left\{ \left(\frac{t^2 - t^*}{t^2} \right)^{w-1} \left(\frac{t^1 - t^*}{t^1} \right)^{v-w} \times S_{jl}^3 S_{j-w,m}^2 S_{j-v-1,p}^1 (P_{ml})^w (P_{pm})^{v-w+1} P_{qp} A_{j-v-2,q}^1 \right\}.$$

The subscripts m , p , q , v , and w are dummy indices defined solely to prevent ambiguities from arising during multiple summations. Superscripts after a right parenthesis indicate an algebraic power.

The derivation of equations (5), (6), and (7) has not been an idle algebraic exercise, since the variation of T with any particular survival event or abundance is contained explicitly in these equations. In particular, it is useful to ask what the variation in a given survival event, say S_{tr}^k , might mean. One expects the survivals will depend primarily on extrinsic quantities such as water quality or food availability. Anthropogenic point-source perturbations, such as power plant cooling system effects or sewage discharges are likely to impact the survivals. It is desirable, therefore, to calculate the sensitivity coefficients of T with respect to a survival event through each of the developmental stages into the post-finfold stage as

$$(8) \quad \frac{\partial T}{\partial S_{tr}^3} = \frac{t^*}{t^3} \sum_{i=1}^{nseg} P_{tr,i} A_{i-1,i}^3$$

$$(9) \quad \frac{\partial T}{\partial S_{tr}^2} = \frac{t^*}{t^3} \frac{t^*}{t^2} \sum_{i,q=1}^{nseg} \sum_{v=1}^{nwks-i} \left\{ \left(\frac{t^2 - t^*}{t^2} \right)^{v-1} \times S_{tr,v,i}^3 (P_{tr})^v P_{qr} A_{i-v-1,q}^2 \right\},$$

$$(10) \quad \frac{\partial T}{\partial S_{tr}^1} = \frac{t^*}{t^3} \frac{t^*}{t^2} \frac{t^*}{t^1} \sum_{m,l,q=1}^{nseg} \sum_{v=1}^{nwkS-t-1} \sum_{w=1}^v \times \left\{ \left(\frac{t^2 - t^*}{t^2} \right)^{w-1} \left(\frac{t^1 - t^*}{t^1} \right)^{v-w} \times S_{t+v+1,l}^2 S_{t+v+1-w,m}^2 (P_{ml})^w (P_{rp})^{v-w+1} P_{qr} A_{t-1,q}^1 \right\}.$$

Comparison of equations (8), (9), and (10) with (5), (6), and (7), respectively, reveals that the sensitivity of coefficients may be interpreted as the sequential contributions to the total production of post-finfold animals that would come from all organisms participating in each corresponding stage-to-stage survival event S_{tr}^k , if they all had survived that particular transition. Since only the fraction S_{tr}^k actually survive from each previous stage to the post-finfold stage, the contribution of time t and location r to the post-finfold production,

$$(11) \quad V_{tr}^k = S_{tr}^k \frac{\partial T}{\partial S_{tr}^k}$$

is a proper measure of the significance the conditions that time t and river segment r have upon the total production. Conversely, it is also a measure of the vulnerability of the production to any disturbance at the given location and time. A useful check upon one's calculations is the relation

$$(12) \quad T = \sum_{t=1}^{nwkS} \sum_{r=1}^{nseg} V_{tr}^k \quad \text{for } k = 1, 2, 3.$$

Relation (12) highlights the fact that the V_{tr}^k also trace the histories of organisms which eventually survived as post-finfold larvae. One may, for example, use V_{tr}^1 to map out the pattern of eggs which developed into post-finfold larvae.

Survival Probabilities Computed Through to the Early Juvenile Stage

The previous section dealt with changes in extrinsic factors affecting survival. It is possible to repeat the analysis to examine the effects of directly interfering with the abundances at various locations and times during any stage of development. Such a situation would be encountered, for instance, if larvae or juveniles from a hatchery operation were being introduced into a natural nursery area. The optimal release strategy will depend upon balancing the cost of raising animals to a given age, then transporting them to a given location at a specified time, against the highest probability that an organism of stage k released at time t in location r will survive to contribute to the adult stock.

To address the latter issue in this optimization, one must compute how T varies with a change in abundance, i.e. $\partial T / \partial A_{tr}^k$ must be calculated from equations (5), (6), and (7) to get:

$$(13) \quad \frac{\partial T}{\partial A_{tr}^k} = \frac{t^*}{t^3} \sum_{l=1}^{nseg} S_{t+1,l}^3 P_{rl}$$

$$(14) \quad \frac{\partial T}{\partial A_{tr}^2} = \frac{t^*}{t^3} \frac{t^*}{t^2} \sum_{p,l=1}^{nseg} \sum_{v=1}^{nwkS-t-1} \left\{ \left(\frac{t^2 - t^*}{t^2} \right)^{v-1} \times S_{t+v+1,l}^2 S_{t+1,p}^2 (P_{pl})^v P_{rp} \right\}, \quad \text{and}$$

$$(15) \quad \frac{\partial T}{\partial A_{tr}^1} = \frac{t^*}{t^3} \frac{t^*}{t^2} \frac{t^*}{t^1} \sum_{m,l,p=1}^{nseg} \sum_{v=1}^{nwkS-t-2} \sum_{w=1}^v \times \left\{ \left(\frac{t^2 - t^*}{t^2} \right)^{w-1} \left(\frac{t^1 - t^*}{t^1} \right)^{v-w} \times S_{t+v+2,l}^2 S_{t+v+2-w,l}^2 S_{t+1,p}^2 (P_{ml})^w (P_{pm})^{v-w+1} P_{rp} \right\}.$$

In words, the derivatives described in equations (13)–(15) compute the addition to the total post-finfold or early juvenile production, T , which arises from a unit increase in abundance of organisms of stage k at time t and location r . Any of these derivatives may be recognized as the probability of a single organism in any stage surviving into the post-finfold stage. One may use equations (13)–(15) to map out times and locations of varying survival probabilities for each life stage.

The Fitness of Natural Spawning

With the ultimate survival probabilities now at hand it is interesting to focus upon the fate of the eggs originally spawned. While eggs are distributed over space and time, there will usually be particular spawning times and locations from which the eggs would have the greatest chances for ultimate survival. If the spawning stock were well adapted to conditions controlling the survival of the young, they would tend to have spawned all their eggs under optimal circumstances, and the total production under such conditions could be estimated by multiplying the total number of eggs spawned over the entire season by the optimal survival probability for that spawning season. The ratio of the actual production of post-finfold larvae to this hypothetical maximum production provides a measure of how fit the spawning population was in its behavior to produce viable offspring under the environmental conditions which prevailed.

There is no reason to expect a priori that this spawning fitness measure will be extremely high. Spawning fish would have evolved, at most, only weak responses to specific environmental conditions, such as water quality or food plankton productivity that would ensure survival of the early stages. More likely, they are adapted to spawn according to environmental cues which result in juvenile distributions most likely to succeed during the average conditions of the past several hundred or so spawning seasons. A key question might be how the spawning fitness varies with spawning potential, or population fecundity, to discern whether or not a density-dependent compensatory mechanism is at work to stabilize long-term population levels. As we shall see from the subsequent analysis, the answer to this question appears to be negative.

Analysis of Spawning Seasons

The three spawning seasons surveyed differed significantly in terms of overall survival of eggs into post-finfold larvae. Using the computational method explained in Polgar (1977), the overall survival was poorest in 1974 (5.92×10^{-5}), greatest in 1975 (2.07×10^{-3}), and intermediate in 1976 (6.97×10^{-4}).

With survivorships differing by 35-fold, the question immediately arises whether any significant change in the spawning pattern could account for these differences. To address this issue, we performed the calculations specified by equations (4), (8), (9), (10), (13), (14), and (15) upon the egg and larval abundance patterns for the 3 yr. The 200 m³/s transition matrix was used in the 1974 and 1976 calculations (Table 1A), whereas the 500 m³/s probabilities were used to represent the 1975 flow regime (Table 1B). Development times t^1 , t^2 , t^3 , t^4 of 2, 12, 11, and 30 d, respectively, were used for the four stages and a sampling interval, t^* , of 7 d was the actual approximate period between surveys. Survivals should vary between zero and unity. When calculated from the raw data, however, a fraction of the survivals exceeded these bounds due to random and systematic sampling errors. The survivals were artificially constrained within their natural bounds by setting negative survival values equal to zero, and those over one are reduced to unity. The error this convention engenders in the absolute values of the results can be assessed by evaluating how the check according to equation (12) is violated. Using such a check on balances, the total productions from each life stage seem to be in error by about 25%, but we do not believe that the qualitative character of survivorship distributions has been excessively warped in space or time. The results presented in the following figures were normalized with respect to their totals to yield percentage distribution patterns.

The significant computational results are displayed in Fig. 2, 3, and 4. On each graph, time is displayed in weeks along the abscissa beginning with the first week in April, while spatial position is arranged on the ordinate according to river segment number. Upstream is toward the top of each graph. Since a strong correlation exists between time, temperature and photoperiod throughout the estuary, some may find it more convenient to regard the abscissa time variable as an aggregate indicator of conditions controlling the spawning distribution.

Figures 2a, b, c display the egg distribution patterns observed during the three seasons. Contrasting the best and the worst seasons, the 1975 spawn is seen to be the most tightly clumped spatially and temporally. In 1974 spawning occurred earlier and was more in evidence further downstream. Nonetheless, the major portion of both spawns was contained in the quadrant defined by weeks 4 and 5 and segments 5 and 6. Spawning during 1976 was the most dispersed of all 3 yr, but even then, the aforementioned quadrant was an active locus of egg release. To summarize, the centroid of

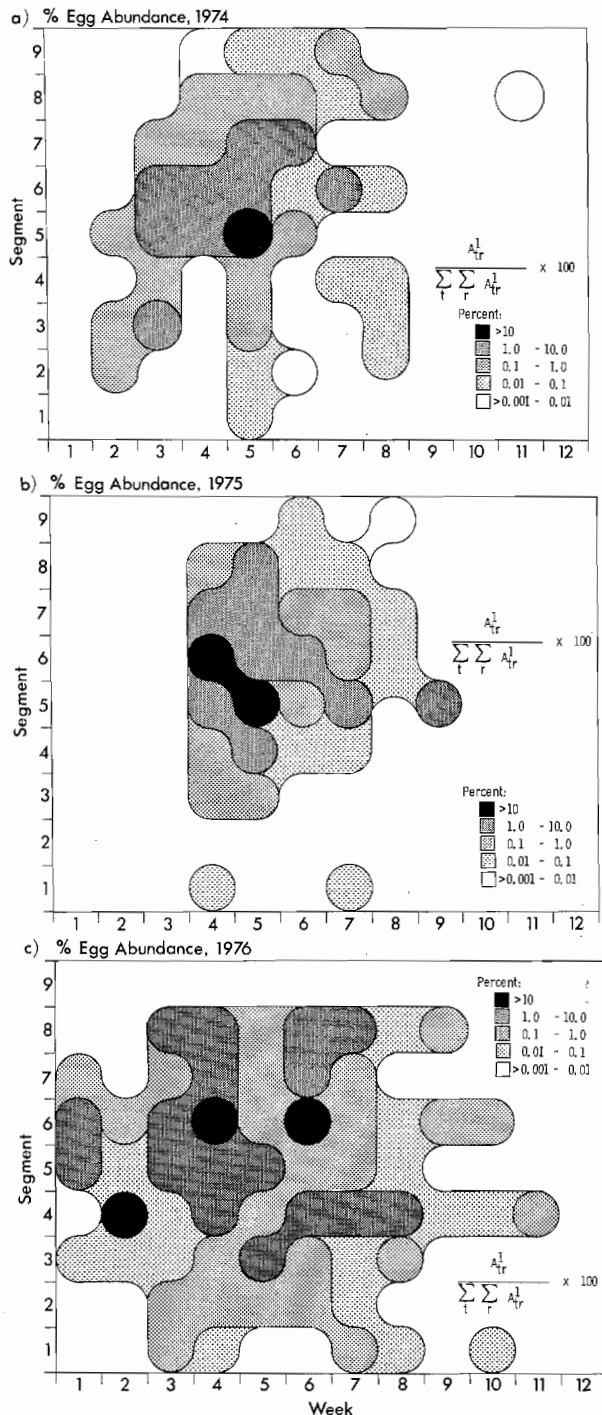


FIG. 2. Relative distributional pattern of eggs during the a) 1974 spawning season, b) 1975 spawning season, and c) 1976 spawning season.

spawning appears to be roughly the same in all seasons, whereas the egg pattern dispersion does differ from season to season.

By employing equations (11) and (12) it becomes possible to map out where and when the surviving post-finfold larvae probably originated as eggs, i.e. one may sketch the pattern of "successful" eggs. These percentile distributions are depicted in Fig. 3a, b, and c. Comparing these patterns with their counterparts in Fig. 2 provides only minor contrasts. In 1974 the most successful spawning took place upstream and subsequent to the major egg pulse at Douglas Point. In 1975 there was no apparent spatial shift between the major spawn and the successful eggs, but survivors did appear in greater numbers from the eggs spawned later in the season. The tendency for surviving eggs to come from later spawn is repeated again in 1976. Despite obvious differences in the patterns of success, there remains good overlap in survivorship among the three seasons during weeks 5 and 6 in segments 5 and 6.

Perhaps the most interesting distributions are provided by the computed survivals depicted on Fig. 4a, b, and c. Graphed are the results of applying equation (15) — the cumulative probability that an egg spawned at a given time and location will survive into the post-finfold stage. That these patterns appear to vary more continuously than those in Fig. 2 and 3 is merely a reflection of the fact that survivorship is mathematically independent of the actual number of eggs spawned at a point in space and time.

It is noteworthy that processes in 1974 and 1975, with their great contrast in success, should yield highly similar patterns for observed survival. Maximal survival in both instances lies well upstream and later in the season from the centroid of spawning. It clearly appears that the spawning stock during these two seasons "underutilized" the propitious domain (weeks 6 and 7 in segments 8 and 9) for successful spawning and development. This discrepancy does not seem as apparent in 1976, when better overlap between successful eggs and high-survival regions occurred.

While these qualitative observations are interesting and informative to fisheries managers, they do not allow a direct approach to answering the fundamental question of the relative importance of environmental conditions favoring successful spawning and development versus adult spawning behavior in determining year-class success. To begin such an analysis it may be assumed that year-class success can be partitioned into a factor characterizing the environment for a given year times a factor which gauges the fitness of the spawning strategy for the same year, i.e.

$$(16) \quad Y = U \times F$$

where Y is the year-class success, U embodies the environmental conditions, and F is a measure of the fitness of the spawning behavior. U and F can be given more precise definition if we further define E as the number of eggs produced and Q as the number of post-finfold survivors produced during the year. Then, by definition

$$(17) \quad Y = \frac{Q}{E}$$

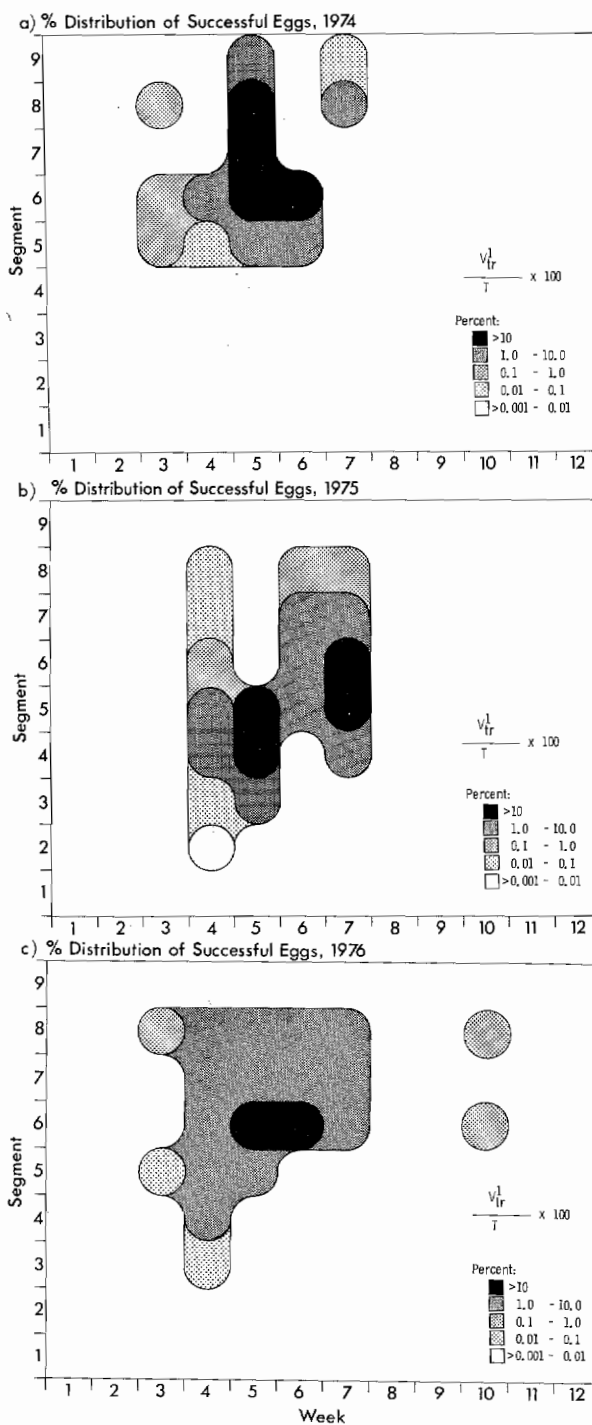


FIG. 3. Computed relative distribution of successfully developed eggs (or post-finfold larvae) during a) 1974, b) 1975, and c) 1976, according to equations (11) and (12).

Supposing that H is the hypothetical production of post-finfolds if the year-class survival had been uniformly at the greatest value observed during that par-

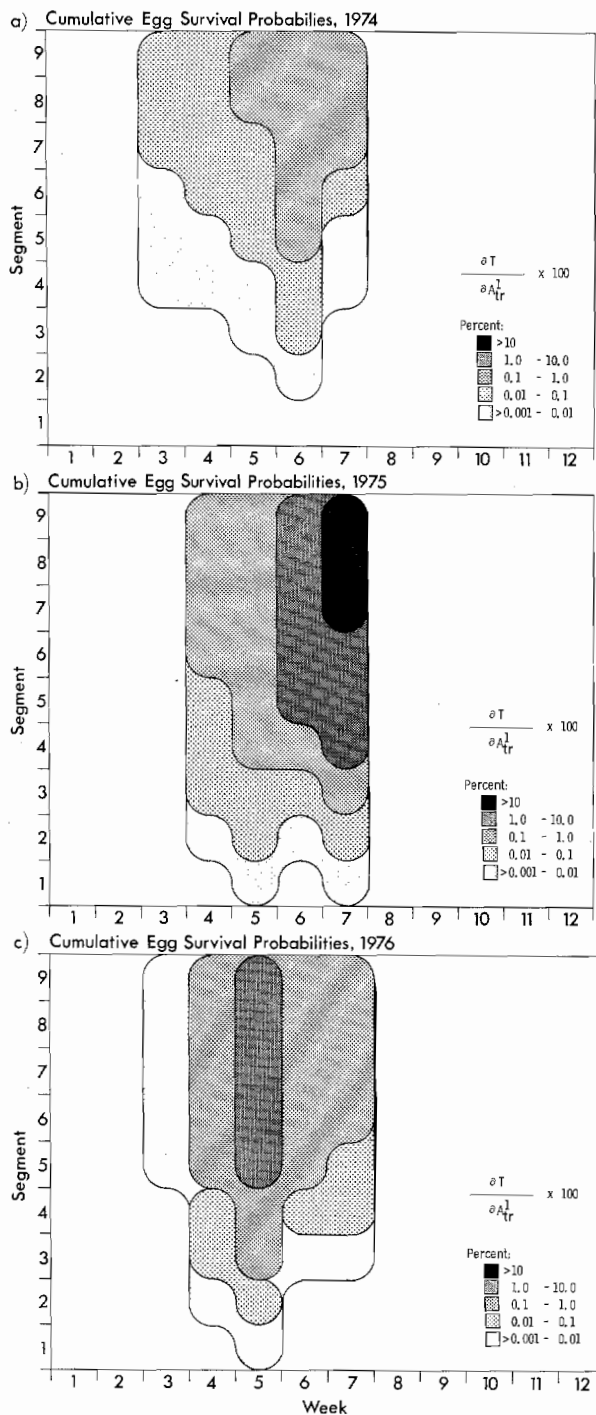


FIG. 4. Computed relative cumulative survival patterns of eggs through to the post-finfold stage during a) 1974, b) 1975, and c) 1976, according to equation (15).

ticular year, then we may write

$$(18) \quad Y = \frac{H}{E} \times \frac{Q}{H}$$

TABLE 2. Results of success and fitness analysis.

	Year-class success Y	Maximal survival U	Spawning fitness F
1974	5.9×10^{-5}	0.0039	0.015
1975	2.1×10^{-3}	0.2100	0.010
1976	7.0×10^{-4}	0.0360	0.019

Arbitrarily choosing $U = H/E$ and $F = Q/H$ attaches straightforward meanings to these two factors. U is seen to be the ultimate year-class success possible during the year if all the eggs had been subject to the optimal conditions seen during that year. The fitness, F , becomes a measure of how well the spawning population distributed its eggs to take advantage of the best conditions available to foster egg and larval development.

The hypothetical optimal production, H , is calculated by multiplying the egg production for the year by the maximum observed survival for any time and place as calculated from equation (15).

Year-class success and its two components are displayed in Table 2. The calculated values for the fitness are interesting on two counts. First, they are quite small (<0.02). One might expect that the adult stock would have acquired migratory strategies consistent with environmental cues which would allow them better to exploit conditions favorable to ichthyoplankton survival. Secondly, the spawning fitness varies relatively little in 3 yr (2-fold), in comparison to the variation in overall year-class success (35-fold). The major element of variation in overall success is apparently determined by the independent and random environmental factors affecting optimal survival.

There are possibly two other trends seen in Table 2 which cannot be confirmed on the basis of only three seasons' data. It appears, for instance, that the calculated fitnesses are directly related to the dispersion of eggs in time and space as displayed on Fig. 2a, b, and c. Secondly, the variations in maximal survival and fitness (53-fold and 2-fold, respectively) mitigate one another slightly (success varies by 35-fold). This mitigation could easily be due to chance, to random errors in sampling, or it might be ascribed to a compensation mechanism in the spawning behavior. The type of behavioral compensation referred to here is not to be confused with the classical, density-dependent compensation in stock-recruitment relationships (Ricker 1968; Cushing 1968). Catch records and adult sex ratios show spawning stock declining over the 3 yr studied. Should behavioral compensation exist, however, it is evidently not strong enough to appreciably dampen the radical effects of environmental conditions upon larval survival.

It remains likely that maximal survival and spawning fitness are keyed by two independent variables. Apparently, year-class success and optimum-survival conditions vary radically on an annual basis due to

density-independent environmental factors. Although the spatial-temporal origin of the most successful offspring remains relatively constant from year-to-year, the strength of overall success undergoes great variation. This phenomenon seems to result from an annually constant mismatch, or "misfit," between spawning stock behavior (distributing eggs over the spawning grounds) and the larval survival patterns. There is no reason to believe that either of these phenomena is governed by factors related to each other or to conditions dependent on adult or larval population sizes.

The enigma of the very low, but relatively constant, values of the spawning fitness could be the result of a more universal ecological principle manifesting itself in the adaptation of the stock to prevailing environmental conditions. Ecological systems do not always run at maximum efficiency, and may, at times, tend only to maximize the rate of energetic storage, or production (Odum and Pinkerton 1955). It is unclear here, however, what rate process is being maximized (if any).

There are any number of other hypotheses which may explain the observed low spawning fitness. The spawning stock might be the victim of a changing environment and may not have had sufficient time to adapt behaviorally to new optimal conditions. The population may be adapted for persistence, rather than maximal production. By spawning in this inefficient manner, large pulses of production, which might cause the population to outstrip the carrying capacity of its environment, are avoided. Some spawn in the optimal regions, however, assures a residual population in bad years, thereby allowing the population to persist.

The list of speculations could go on, but would not be warranted by the present data base. A longer series of breeding seasons needs to be observed in solid quantitative fashion. Likewise, extrinsic conditions need to be closely examined to identify the factors driving the large fluctuations in year-class success.

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BOYNTON, W. R., E. M. SETZLER, K. V. WOOD, H. H. ZION, M. HOMER, AND J. A. MIHURSKY. 1977. Final report on Potomac River fisheries study: Ichthyoplankton and juvenile investigations. Univ. of Maryland, CEES Ref. No. 77-169-CBL. Chesapeake Biological Laboratory, Solomons, Md., 328 p.

CHADWICK, H. K., D. E. STEVENS, AND L. W. MILLER. 1977. Some factors regulating the striped bass population in the Sacramento-San Joaquin Estuary, California, p. 18-35. In W. Van Winkle [ed.], *Proceedings of the Conference*

Assessing the Effects of Power Plant Induced Mortality on Fish Populations. Gatlinburg, Tenn., May 3-6, 1977. Pergamon Press, New York, N.Y.

- CRONIN, W. B. 1971. Volumetric, aerial and tidal statistics of the Chesapeake Bay and its tributaries. Special Report 20, The Chesapeake Bay Institute, Johns Hopkins University, Baltimore, Md. 135 p.
- CRONIN, W. B., AND D. W. PRITCHARD. 1975. Additional statistics on the dimensions of the Chesapeake Bay and its tributaries. Report 42, The Chesapeake Bay Institute, Johns Hopkins University, Baltimore, Md. 478 p.
- CUSHING, D. 1968. Fisheries biology: a study in population dynamics. University of Wisconsin Press, Madison, Wisc. 200 p.
- GRAHAM, J. J., S. B. CHENOWETH, AND C. W. DAVIS. 1972. Abundance, distribution, movements and lengths of larval herring along the western coast of the Gulf of Maine. *Fish. Bull.* 20: 307-321.
- HARLEMAN, D. R. F. 1971. One dimensional models. Estuarine modelling: an assessment. Tracor, Inc., Austin, Texas. 497 p.
- HARLEMAN, D. R. F., AND C. H. LEE. 1969. The computation of tides and currents in estuaries and canals. Committee on Tidal Hydraulics, Corps of Engineers, U.S. Army, Tech. Bull. 16: 143 p.
- HUNTER, J. F. 1975. A one-dimensional dynamic and kinematic numerical model suitable for canals and estuaries. Special Report 47, The Chesapeake Bay Institute, Johns Hopkins University, Baltimore, Md. 49 p.
- KOO, T. S. Y. 1970. The striped bass fishery in the U.S. *Chesapeake Sci.* 11: 73-93.
- MIHURSKY, J. A., W. R. BOYNTON, E. M. SETZLER, K. V. WOOD, H. H. ZION, E. W. GORDON, L. TUCKER, P. PULLES, AND J. LEO. 1976. Final report on Potomac Estuary fisheries study: Ichthyoplankton and juvenile investigations. Univ. of Maryland, CEES Ref. No. 76-12-CBL. Chesapeake Biological Laboratory, Solomons, Md. 241 p.
- ODUM, H. T., AND R. C. PINKERTON. 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. *Am. Sci.* 43: 331-343.
- POLGAR, T. T. 1977. Striped bass ichthyoplankton abundance, mortality, and production estimation for the Potomac River population. In W. Van Winkle [ed.], *Proceedings of the Conference on Assessing the Effects of Power Plant Induced Mortality on Fish Populations*. Gatlinburg, Tenn., May 3-6, 1977. Pergamon Press, New York, N.Y.
- POLGAR, T. T., R. E. ULANOWICZ, D. A. PYNE, AND G. M. KRAINAK. 1975. Investigations of the role of physical transport processes in determining ichthyoplankton distributions in the Potomac River. Interim Report for 1974 Spawning Season Data, Maryland Power Plant Siting Program, Ref. No. PPRP 11/PPMP 14: 133 p.
- POLGAR, T. T., J. A. MIHURSKY, R. E. ULANOWICZ, R. P. MORGAN, II, AND J. S. WILSON. 1976. An analysis of 1974 striped bass spawning success in the Potomac Estuary, p. 151-165. In *Estuarine processes*, Vol. 1, Uses, stresses, and adaptations to the estuary. Academic Press, New York, N.Y.
- PYNE, D. A. 1979. Single variable Poisson regression: a goodness-of-fit test and the comparison of regression coefficients. *J. Am. Stat. Assoc.* 74: 489-493.
- RICKER, W. C. 1968. Methods for assessment of fish production in freshwaters, Blackwell Scientific, Oxford. 313 p.
- SETZLER, E. M., W. R. BOYNTON, T. T. POLGAR, J. A. MIHURSKY, AND K. V. WOOD. 1978. Spatial and temporal distribution patterns of striped bass ichthyoplankton and juveniles in the Potomac Estuary. In J. Cooper [ed.]

- Proceedings of a symposium on advances in striped bass life history and population dynamics. Am. Fish. Soc. 108th Ann. Meeting, Univ. of Rhode Island, Kingston, R.I., Aug. 23, 1978.
- THATCHER, M. L., AND D. R. F. HARLEMAN. 1972. A mathematical model for the prediction of unsteady salinity intrusion in estuaries. Massachusetts Institute of Technology, School of Engineering, Ralph M. Parsons Laboratory, Rep. 144: 234 p.
- VAN WINKLE, W., B. L. KIRK, AND B. W. RUST. 1979. Periodicities in Atlantic Coast striped bass (*Morone saxatilis*) commercial fisheries data. J. Fish. Res. Board Can. 36: 54-62.
- WALLACE, D. N. 1975. A critical comparison of the biological assumptions of Hudson River striped bass models and field survey data. Trans. Am. Fish. Soc. 4: 710-717.