

Fish Population Responses to Chronic and Acute Pollution: The Influence of Life History Strategies

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ABSTRACT: We have developed a simulation model to estimate pollution effects on economically important estuarine-dependent fish populations. Traditionally, pollution studies have focused upon impacts on individual organisms; however, wise management of marine resources depends upon an understanding of dynamics at the population level. As a required first step toward conducting relevant pollution studies, we have compiled available life history data on eight species (14 spatial-temporal stocks), concentrating on age-specific rates of growth, survival, and fecundity. Leslie matrix models of species population dynamics were used to predict pollutant impacts—mediate through changes in 1st-year survival. On average, and without compensation, these modelled stocks respond to a one-time-50% reduction in first-year survival by taking ten years to equilibrate at 88% of their preimpact abundance. Our synthesis of the data included a search for derived (standardized) population parameters to evaluate differences in susceptibility among and within fish populations to pollutant stresses. We demonstrated that knowledge of a species' age-specific fecundity pattern provides additional predictive power of its response to pollution perturbation.

Introduction

There is an urgent need to develop a methodology to assess the impact of human activities on marine fish populations and ecosystems. Anthropogenic impacts on the coastal zone are accelerating, and many economically important fish species have already been stressed from heavy exploitation and other causes. It has been demonstrated that pollution kills fish, at least in experimental tanks at high enough concentrations. It is also readily apparent that fish abundance in some natural systems, usually freshwater and small, although some as large as Lake Erie (Smith 1968), has been drastically altered by human activities in addition to fishing. It is not so evident that we have yet begun to affect the abundance of marine fish stocks by polluting and by physically altering the environment.

Lack of evidence for pollution effects on marine fish abundance is no cause for optimism. We may already be severely impacting some stocks and are simply unable to detect it (Vaughan and Van Winkle 1982). Unfortunately, detection of the impact may depend upon a catastrophic decline in abundance, with a consequent demise of a fishery. The principal reasons for the difficulty of assessing pollution effects in the marine environment are size

and variability. The geographic range of most marine species is quite large relative to any point-source pollution impact, and no convenient boundaries are recognized by the migrating fish. So, it is usually difficult to relate local causes to dispersed effects. The fecundity of most marine fishes is extremely high relative to that required for replacement at prevailing adult mortality rates. Therefore, most of the mortality of a cohort occurs during its first year of life, and small variations in the first-year survival rate (S_0) can have very large effects on subsequent year class size. The myriad of factors influencing S_0 are all subject to unknown, sometimes large variations. These are usually considered density-independent, or environmental variations. Many attempts have been made to correlate population size with some key variables in the environment (Carruthers 1938; Walford 1938; Radovich 1962; Cushing 1969; Nelson et al. 1977). In general these attempts seem to have limited success, depending on which environmental variable seems to be the dominant one operating during the time series investigated. Species with fairly simple life histories, like shrimp, have been more amenable to this approach (Hettler and Chester 1982).

The long-term effect of a variation in S_0 on fu-

ture recruitment, and hence population size, can be greatly influenced by the life history strategy of a fish stock. Life history strategy may be conveniently summarized by the age distribution of the expected egg production (V_x), which is the product of survival probability to age x (l_x) and average fecundity per individual at age x (f_x). The vector, V_x , determines how soon and how much a variation in S_0 is dampened. Both S_0 and V_x may be dependent on population density. Consequently, an independent perturbation of S_0 away from equilibrium might result in density-dependent feedback on future recruitment, and greatly complicate prediction.

Much of the previous work on pollution-induced changes in fish abundance has been concerned with the effects of power plants, because of extensive litigation. Emphasis has been on gathering data and estimating parameters for single species case histories. Direct impact assessment has usually been attempted with deterministic models of single species (Van Winkle 1977). Recent studies have incorporated stochastic variability in these single species models (O'Neill et al. 1981; Goodyear 1985). Most of the studies relating stock structure to population dynamics and subsequent response to perturbation have been theoretical developments. One of the few comparative studies of species susceptibility to pollution stress using data from marine fishes (and deterministic, density-independent models) was by Horst (1977), whose work influenced the strategy employed herein. Our goal in this study is to develop a technique for assessing the population effect of acute and chronic pollution, and for comparing relative vulnerability to pollution among several marine fish stocks. A version of the Leslie matrix model (Leslie 1945) was used to simulate population changes through time. Deterministic, stochastic, density-independent and -dependent versions of the simulations were accomplished by appropriate modifications of one element of the matrix, S_0 . We relate the various population responses among the stocks to V_x . We demonstrate that knowledge of the age-specific egg production of a stock enables one to predict that species' response to pollution perturbation. The confounding influence of degree of exploitation is also examined for some stocks.

Data

Two types of life history data were used, age-specific fecundity and average annual age-specific survival rates (Table 1). These data were obtained directly from prior studies or estimated from related information. In several instances, indicated in Table 1, the fecundity vector was calculated from separate studies showing the length at age and the

relationship between fecundity and length. A few of the survival rates, also indicated in Table 1, were estimated from age distributions of the catch using Robson and Chapman's (1961) technique. In subsequent text and figures we refer to species by the code shown in column two of Table 1.

All species included in the analysis are important components of recreational and commercial fishery landings from the marsh-estuarine-nearshore ecosystem that borders the eastern United States. Additional members of the community were not included because the necessary life history information was unavailable. When the data on a species indicated that disparate life history strategies existed, separate stocks were analyzed. These different stocks illustrate the adaptability of the species even though it is usually uncertain whether the differences are temporally or spatially induced.

Models

Life history information summarized in the appendix was expressed in matrix form, usually called a Leslie matrix (Leslie 1945), for the purpose of calculating population responses to various perturbations. This matrix (M) is of the following form:

$$M = \begin{bmatrix} f_1 & f_2 & f_3 & \cdots & f_j & \cdots & f_k \\ S_0 & 0 & 0 & \cdots & 0 & \cdots & 0 \\ 0 & S_1 & 0 & \cdots & 0 & \cdots & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & S_i & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & \cdot & \cdot & \cdot & \cdot & S_{(k-1)} & 0 \end{bmatrix}$$

where, for k age classes, the first row of the matrix (f_j) represents age-specific fecundity. Age-specific survival rates (S_i) are shown on the principal sub-diagonal. If $N(t)$ represents a vector of numbers-at-age at time t , then

$$N(t+1) = MN(t).$$

The Leslie matrix provides a simple tool for tracking future numbers-at-age. Simulated perturbations are expressed as changes in certain elements of the matrix, notably S_0 .

All elements in the matrix for each species were obtained directly from the life tables in the Appendix, except for S_0 . This element, the survival rate during the first year of life, is rarely known for marine fish stocks. For this reason, and because we wanted a common base for comparing the responses of the stocks, we computed an equilibrium S_0 as

$$S_{0c} = 1 / \sum_{i=1}^k l_i f_i = 1/V$$

where

TABLE 1. Sources of life history information.

Species and Stock	Key for Figures	Survival	Fecundity
<i>Brevoortia tyrannus</i> (menhaden)			
Atlantic coast 1955	m1	Vaughan and Smith ^a	Higham and Nicholson 1964
1965	m2	Vaughan and Smith ^a	Dietrich 1979
1975	m3	Vaughan and Smith ^a	Lewis ^b
<i>Cynoscion nebulosus</i> (spotted seatrout)			
Southern Florida and Gulf of Mexico	t1	Rutherford et al. 1982	Sundararaj and Suttkus 1962
Northern Florida	t2	Tabb 1961 (age distribution)	Tabb 1961
<i>C. regalis</i> (weakfish)	w	Merriner 1973	Merriner 1976
<i>Micropogonias undulatus</i> (croaker)	c	Ross ^c	Morse ^d (by length) Ross ^c (length at age)
<i>Morone saxatilis</i> (striped bass)			
Hudson River	b1	Saila and Lorda 1977	Saila and Lorda 1977
Chesapeake Bay	b2	Goodyear 1985	Goodyear 1985
<i>Paralichthys dentatus</i> (flounder)			
Delaware Bay	f1	Smith and Daiber 1977 (age distribution)	Morse 1981 (by length) Smith and Daiber 1977 (length at age)
New York	f2	Poole 1961 (age distribution)	Morse 1981 (by length) Poole 1961 (length at age)
<i>Pomatomus saltatrix</i> (bluefish)			
Atlantic coast	b1	FMP 1982 ^e	Morse ^d (by length) Wilk 1977 (length at age)
New York	b2	Lund and Maltezos 1970 and FMP 1982 ^e	Morse ^d
<i>Scomberomorus cavalla</i> (king mackerel)	mk	Ivo 1974	Ivo 1974 Ivo 1972

^a Vaughan, D.S., and J.W. Smith. unpublished manuscript. A stock assessment of the Atlantic menhaden, *Brevoortia tyrannus*, fishery. National Marine Fisheries Service, NOAA, Southeast Fisheries Center, Beaufort Laboratory, Beaufort, North Carolina 28516.

^b Lewis, R.M. unpublished manuscript. Spawning and sexual maturity of Atlantic menhaden. National Marine Fisheries Service, NOAA, Southeast Fisheries Center, Beaufort Laboratory, Beaufort, North Carolina 28516.

^c Ross, S.W. unpublished manuscript. Age, growth and mortality of the Atlantic croaker, in North Carolina with comments on population dynamics. North Carolina Marine Fisheries, P.O. Box 769, Morehead City, North Carolina 28557.

^d Morse, W.W. personal communication. Northeast Fisheries Center, Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, New Jersey 07732.

^e Mid-Atlantic Fishery Management Council. 1982. Bluefish Fishery Management Plan. Mid-Atlantic Management Council in cooperation with the National Marine Fisheries Service, New England Fishery Council and South Atlantic Management Council, Dover, Delaware 109 p.

$$I_x = \prod_{i=1}^x S_i$$

and V is the expected life-time egg production of a one-year-old recruit. If the survival and fecundity rates do not change, then setting S_0 equal to S_{0e} ensures that the population will not change through time (i.e., is in equilibrium), provided the population vector N has a stable distribution. The stable N vector is one that is a single multiple of the I_x vector (i.e., $N_x = cI_x$ for all x). If N is not stable initially, it will eventually become so, provided M

does not change. This stability property is usually, but not always, true for fish populations. It does hold for all the stocks modelled here. Pathologic cases may exist where an N , deflected from equilibrium, never returns, but exhibits undamped oscillations (Demetrius 1971).

This is the basic model from which we began, and against which we compared all pollution simulation scenarios. We held all elements of M constant except S_0 . The type of pollution perturbation and degree of population compensation was reflected in how we perturbed S_0 away from S_{0e} .

The first case we considered was acute pollution (e.g., an oil well blow out). To simulate this, we decreased S_{oe} by 50% only in the first year and then followed the population through time until it stabilized, considering how long it takes the population to stabilize and at what level. With a density-independent M (all elements constant, or simple functions of time), the population will stabilize at a level different from the original equilibrium.

We modelled chronic pollution (e.g., permanent habitat loss), also without compensation, by decrementing S_{oe} by 0.5% per year every year. The dynamics of these simulated populations are obviously not very complicated, but the level to which they fall after x years is of interest. This level cannot be predicted *a priori* (from the decrement rate alone) and is greatly influenced by life history strategy (V_x).

For both of these pollution scenarios, we can consider how the population fluctuations are modified by compensation (increased survival with decreased population). To accomplish this, S_o is made a function of population size. Only for the Atlantic menhaden stocks (three different time periods), did we have sufficient information to actually estimate the parameters of such a function. We used a Ricker model:

$$S_o = \exp(a - bE)$$

where E is the spawning stock, measured by its potential egg complement (Ricker 1975).

All of the results from these deterministic models must ultimately be evaluated against the natural variability inherent in such systems. This is a very complicated problem, which we have just begun to address, by constructing a hypothetical model for the error around S_o . We ran some simulations of the equilibrium model (unperturbed S_{oe}) with a random error term included. If we assume that S_o/S_{oe} has a log-normal distribution with mean = μ and variance = σ^2 , then

$$S_o = (S_{oe})\exp(Z_\sigma + \mu)$$

where Z is a standard normal deviate, and generating Z 's generates random S_o 's. We have arbitrarily set $\sigma^2 = 1$ and $\mu = -0.5$, so that the expected value of the ratio S_o/S_{oe} will equal 1, and looked at the frequency distribution of repeated simulations with these random S_o 's against the equilibrium population line.

Results

Most of the stocks examined in the present study, when impacted by an acute perturbation, exhibited a time trajectory qualitatively similar to that shown by the broken line in Fig. 1 for the Atlantic menhaden stock, 1955–1960 (m1). A new equilibrium

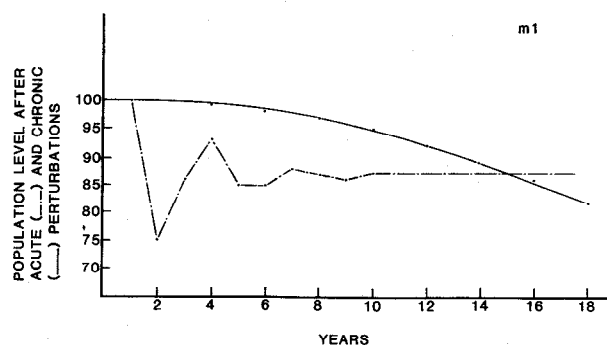


Fig. 1. Simulated response of m1 (an equilibrium stock of Atlantic menhaden, parameters estimated from data of 1955 to 1960) to two kinds of pollution perturbation. The solid line represents a response to a chronic pollution event that decreases first-year survival rate (S_o) by 0.5% per year (e.g., permanent habitat loss); the broken line, a response to a one-time (acute) reduction in S_o of 50% (e.g., an oil well blowout). Population level in this and all subsequent figures is expressed as a percentage of the initial equilibrium value.

of 0.87 was reached by m1 in about eight years. The solid curve in Fig. 1 shows the relative level reached by m1 after x years of a chronic impact on S_o . In this case, the population was reduced to a level equivalent to the acute perturbation (0.87) in about 15 yr. The pertinent features of this figure for the current study can be summarized by

- 1) the new relative equilibrium level (EL) reached after an acute perturbation,
- 2) the time (Y) to reach this equilibrium, and
- 3) the relative level (RL_x) reached after x years of chronic pollution.

The time trajectories for all the other stocks, except m2 (Atlantic menhaden, 1965–1970) and m3, (Atlantic menhaden, 1975–1979) were similar enough to m1 that graphical presentation was unwarranted. All other species did stabilize and differed mainly in the three summary measures EL, Y , and RL_x . Before summarizing the stress re-

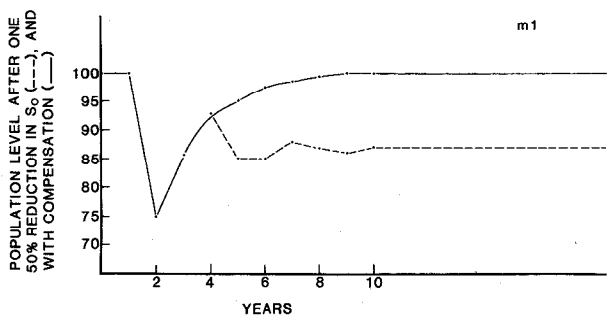


Fig. 2. Simulated responses of m1 to an acute pollution event, without compensation (dashed line) and with Ricker-type compensation (solid line). Curves are identical until four years, when impacted age-class enters spawning stock.

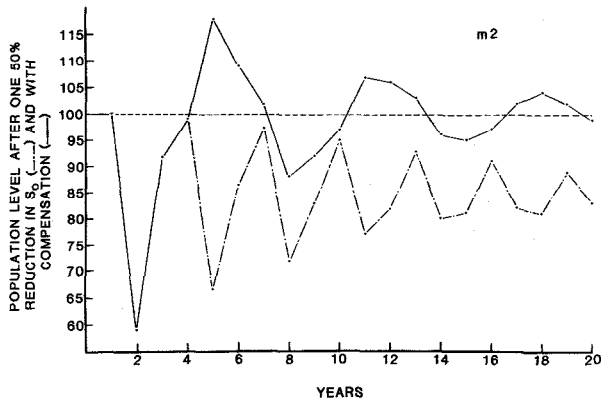


Fig. 3. Simulated response of m2 (an equilibrium stock of Atlantic menhaden estimated from data of 1965–1970) to an acute pollution perturbation. Broken line represents the population response without compensation; solid line, with Ricker-type compensation. Straight dashed line represents unimpacted, equilibrium population for comparison.

sponse of these stocks, however, we have shown in Figs. 2, 3, and 4 the effect of compensation in the three temporal menhaden stocks, the only ones for which we have estimated Ricker spawner-recruit curves.

Although menhaden were heavily exploited during the 1950's, the m1 stock exhibits much more compensatory resiliency than the stocks during the 1960's and 1970's. With seven spawning age-classes and survival rates three to five times higher than m2 and m3, V for this stock equals 36,000 versus 14,000 for m2 and 18,000 for m3. A Ricker model (1954) of the following form:

$$S_0 = \exp(a - bE)$$

where E equals the population of eggs, was used to explore the three stock responses to acute perturbation when S_0 is allowed to vary with stock abundance (E). Data were available to estimate S_0 and E annually from cohort analysis and, subsequently, to estimate a and b from log-linear regression. While two of the three fits were statistically significant, none (being based on only six points) may be considered accurate estimates of true compensatory capacity. They are used only to illustrate the range of potential effects on population recovery of observed changes in V_x and S_0 , which appear to be related to density. For m1 the replacement point (a/b) equals 93 and is to the left of the point of maximum recruitment ($1/b = 100$) on the Ricker stock-recruit curve. The near equality of these points implies that the stock was fished down to about the maximum sustainable level during this period. Obviously the slope of the Ricker curve at a/b , since it is to the left of the maximum, is positive. Acute displacements from equilibrium (the

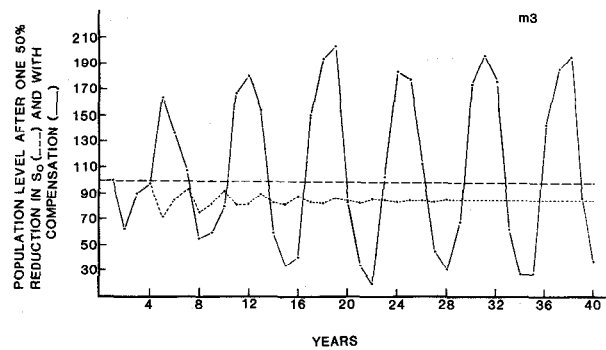


Fig. 4. Simulated response of m3 (Atlantic menhaden 1975–1979) to acute perturbation, with (solid line) and without (broken line) compensation compared to the straight (dashed) line representing unimpacted equilibrium.

replacement point) will be followed by a gradual, smooth return to the original equilibrium. This is precisely the observed behavior of the simulated m1 stock, shown in Fig. 2.

For m2 we estimated the following model:

$$S_0 = \exp(1.79 - 0.15E)$$

and the slope of the Ricker stock-recruit curve at replacement (12) is -0.79 . For slopes between 0 and -1 , displacements from equilibrium result in damped oscillations that will return the population eventually to equilibrium (Ricker 1954). Stock m2 has nearly achieved this in twenty years as shown in Fig. 3, though the uncompensated stock has yet to approach equilibrium.

By the mid-1970's, m3 appeared to be rebounding from the heavily stressed stock of the 1960's. The expected life-time egg production of a one-year-old recruit, V , has increased nearly 30% and the equilibrium (replacement) population has more than doubled to 29. However, from the fitted Ricker model

$$S_0 = \exp(2.65 - 0.092E)$$

we observed that the slope at equilibrium (equal to $1-a$) was less than -1 . Hence, the simulated population with compensation, shown in Fig. 4, exhibited repeating cycles of oscillations of increasing amplitude, while the uncompensated stock leveled out in about 25 years. The inherent compensatory capacity of this stock would preclude detection of any pollution perturbation.

A detectability problem of equal severity may arise from random, density-independent variability in S_0 . We have only begun to investigate this difficult problem. Along the vertical line at year 10 in Fig. 5 we have indicated by horizontal bars the observed frequency distribution of fifty simulated population values for m1 generated from the

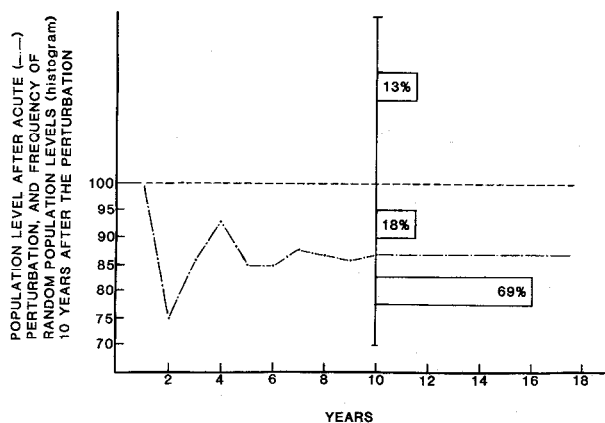


Fig. 5. The distribution of randomly generated population levels (histogram), at year ten, around the simulated response of m1 to acute perturbation.

error model specified above in the Model section. If a real population exhibited this kind of "noise" in S_0 , then by chance alone, 13% of the time the impacted population will be above the unperturbed equilibrium value, and we might conclude that the environment for that stock is improving. Conversely, most of the time (69%) we might rightly conclude that pollution has adversely impacted the stock, but we will overestimate its effect. The remaining 18% of the time we probably will not know what to say, but theoretically we might again correctly deduce a pollution impact, but underestimate its impact. These kinds of probability statements depend entirely on the error model specified and the parameters (μ , σ^2) assumed or estimated.

Returning now to a consideration of the three summary measures (EL, Y, RL_x) of pollution impact for all stocks, there are some remarkably consistent patterns among their responses to both acute and chronic pollution stresses. In Fig. 6 we have

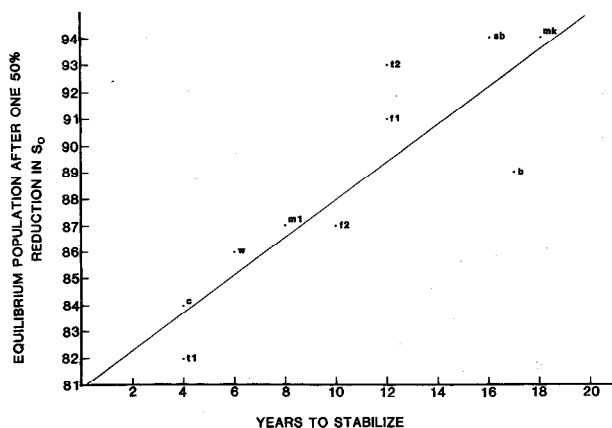


Fig. 6. Linear relationship between equilibrium population level after acute perturbation and the years required to reach the new level. Species codes are given in Table 1.

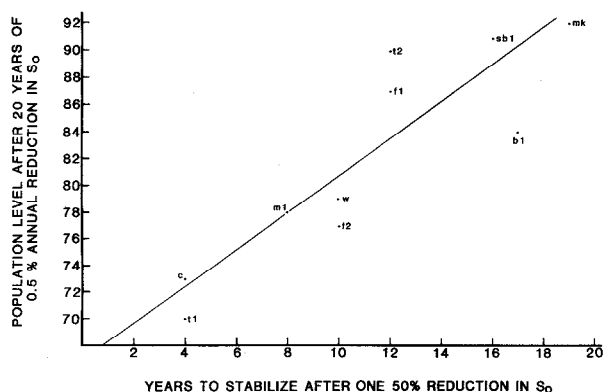


Fig. 7. Linear relationship between population level reached after twenty years of chronic perturbation and years required to equilibrate after one acute perturbation. (Abscissa same as Fig. 6.)

plotted, for ten stocks, the EL after acute stress against Y. Those stocks (e.g., croaker and "southern" trout) that stabilize most rapidly also are impacted the most (i.e., have a lower EL). Mackerel, by contrast, are only reduced by 6%, but take 18 years to achieve this new equilibrium. We used an arbitrary working definition of stability—no more than 1% change in the relative population for at least three years running. The regression line fit to these data was significant:

$$EL = 0.81 + 0.007Y, r^2 = 0.74$$

The significant regression for responses to chronic perturbation

$$RL_{20} = 0.67 + 0.014Y, r^2 = 0.78$$

is shown in Fig. 7, which also shows the ten stocks to be ranked nearly identically to the acute case in their relative response. Since the slope of the

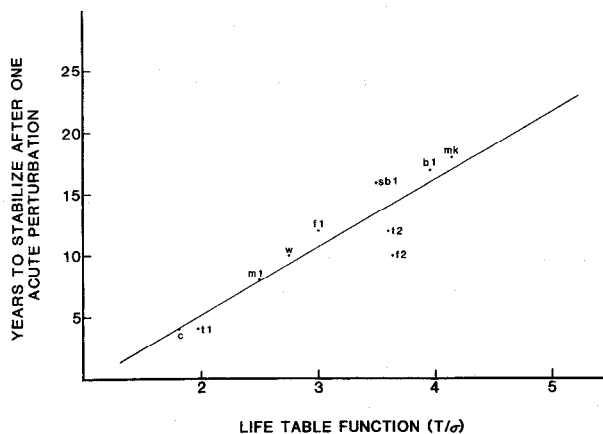


Fig. 8. Linear relationship between years to equilibrate after acute perturbation and an index of reproductive value derived from life tables (Appendix I); see text for computation. In denominator, σ is replaced by sample standard deviation (s).

chronic regression is greater than the acute slope, stocks most susceptible to acute stress are, relatively, even more susceptible to chronic stress for at least up to twenty years, for the stocks considered here. Four data sets from Appendix I were not used in these regressions (sb2, m2, m3, b2). The data set for b2 was judged incomplete and probably representative of only a migratory sub-stock. The other three will be discussed below.

An ability to estimate Y would permit the estimation of either EL or RL_x and, hence, assessment of population pollution effects, at least on a comparative basis. It is reasonable to expect Y to be some function of the life history table. Since Leslie (1945), the literature on population projection matrices has proposed several functions of the eigenvalues (λ_i) of M , with the most popular function being the ratio of $|\lambda_2|/|\lambda_1|$ (Lefkovich 1969). In Fig. 8 we show a significant ($r^2 = 0.85$) regression of Y on an empirically determined life table index that is heuristically more appealing to us, because of its simplicity, and it requires no computer use. This index is simply the mean (T) divided by the standard deviation (s) of the age distribution of V_x ($=l_x f_x$). So, from the life history data in the appendix, we can estimate EL and RL_x . This procedure allows a relative assessment of a species' susceptibility to acute and chronic pollution stress.

Discussion

We believe that we have demonstrated a coherent approach toward the problem of assessing the effects of pollution on fish populations. The traditional toxicological methodology may not be translated directly from experimental individuals to population effects. Likewise, a somewhat traditional approach to the simulation of single species population dynamics has some potentially severe detectability problems associated with either density-dependent or density-independent variation in S_0 . Nevertheless, a simulation model of this type, which provides likely bounds on the magnitude and time horizon for the impacts, should provide a useful tool for planning impact studies and in certain management deliberations. We recommend that more effort be devoted to specifying appropriate error models and estimating their parameters. This approach, of course, requires estimation of S_0 , without which no meaningful impact analyses can be conducted at all. Also, the nature of the compensation factor is crucial to predicting the time trajectory of a stock after impact. As statistically messy as this problem is, we must try to get estimates of parameters for stock-recruit curves for more species. Our quite scanty evidence seems to indicate that these parameters might change fairly significantly over rather surprisingly short time pe-

riods (maybe only three generations for menhaden).

The aspect of the present study that we consider potentially most useful, however, was the generality that emerged from comparisons among stocks. Being able to predict the stabilization time (Y), and hence either the EL or RL_x from the life table alone (T/s), of a species seems inherently useful. The consistent pattern among the stocks is perhaps even more useful from a systems monitoring point of view. This observation suggests which stocks are likely to be more vulnerable to pollution and should be monitored more closely; it suggests that we monitor temporal (and spatial) changes in the life table directly; and it may provide useful clues to the amount of exploitation or other stress on stocks that have partially exhausted their compensatory reserves.

The ten stocks used in the regression analyses have adult survival rates (S) that do not deviate much from their mean of 0.38. Survival rates differing markedly from these, for a given fecundity vector, may indicate differences in the intensity of exploitation, to which the stock has not yet adjusted (i.e., S and T should be highly correlated and are, $r = 0.9$, for these ten stocks). Stocks that are lightly exploited would be expected to lie above the line in Fig. 6. The Chesapeake Bay striped bass stock (sb2) has a survival rate 37% greater than the next highest one (mk) in the data set, coupled with a V that is 75 times that for sb1. The projected sb2 population stabilized at 0.96 in 11 years, a point considerably above the regression line. In fact this point is so aberrant we suspect that the survival rates and fecundity rates may not be representative of the same spatial-temporal stock. We expect heavily exploited stocks to be represented by points below the line. The two unequivocal cases of increased, and heavy, exploitation are m2 and m3. The survival rate for menhaden dropped from 0.26 in the 1950's to 0.10 in the 1960's. The simulated m2 stock had not stabilized after 40 years and could not have been plotted in Fig. 6. By the 1970's, m3 had rebounded slightly to an $S = 0.13$. This stock stabilized at 2% below m1, but required three times as long to do so. In this sense, the heavily exploited menhaden population is more susceptible to additional pollution stress.

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APPENDIX I. Age specific survival and fecundity rates (S = annual survival of population; Sf = survival of females; $f \times 10^3$ = eggs per female, i.e., corrected for percent mature where available). Figure symbols for each stock are shown in parentheses.

<i>C. nebulosus</i> Southern Florida (t1)			<i>C. nebulosus</i> Northern Florida (t2)		<i>C. regalis</i> (w) Total Coast	
Age	Sf	f	S	f	S	f
0						
1	0.25	140	0.53		0.32	
2	0.25	354	0.53		0.32	160
3	0.25	661	0.53	15	0.32	250
4	0.25	1,144	0.53	82	0.32	557
5			0.53	150	0.32	1,726
6			0.53	400		
7			0.53	633		
8			0.53	867		
9			0.53	1,100		
<i>M. undulatus</i> (c) Total Coast			<i>P. dentatus</i> Delaware Bay (f1)		<i>P. dentatus</i> New York (f2)	
Age	Sf	f	S	f	S	f
0						
1	0.27	118	0.58		0.24	
2	0.27	385	0.58		0.24	469
3	0.27	682	0.58	477	0.24	948
4	0.27	1,111	0.58	867	0.24	1,489
5	0.27	1,841	0.58	1,306		
6	0.27	2,483	0.58	1,838		
7	0.27	3,267	0.58	2,494		
8			0.58	3,136		
<i>M. saxatilis</i> Hudson River (sb1)			<i>M. saxatilis</i> Chesapeake Bay (sb2)		<i>S. cavalla</i> (mk) Total Coast	
Age	Sf	f	S	f	S	f
0						
1	0.4		0.82		0.6	
2	0.6		0.82		0.6	
3	0.49		0.82		0.6	
4	0.49	24	0.82	66	0.6	7
5	0.49	172	0.82	340	0.6	74
6	0.49	462	0.82	700	0.6	544
7	0.49	855	0.82	1,060	0.6	839
8	0.49	1,350	0.82	1,360	0.6	1,092
9	0.49	1,500	0.82	1,800	0.6	1,310
10	0.49	1,800	0.82	1,000	0.6	1,528
11	0.49	2,200	0.82	2,400	0.6	1,746
12	0.49	2,200	0.82	3,000	0.6	1,964
13	0.49	2,200	0.82	3,200		
14	0.49	2,200	0.82	3,600		
15	0.49	2,600	0.82	3,800		
16	0.49	2,700	0.82	4,200		
17	0.49	2,800	0.82	4,400		
18	0.49	2,900	0.82	4,800		
19	0.49	3,000	0.82	5,000		
20	0.49	3,000	0.82	5,200		
21				5,400		
22				5,600		
23				5,800		
24				6,000		
25				6,200		

APPENDIX I. Continued.

<i>P. saltatrix</i> Atlantic Coast (b1)			<i>P. saltatrix</i> New York (b2)	
Age	Sf	f	S	f
0				
1	0.2		0.31	
2	0.2		0.31	1,885
3	0.2	327	0.31	2,612
4	0.28	1,381	0.31	3,044
5	0.28	2,201	0.31	3,623
6	0.28	2,904		
7	0.28	3,373		
8	0.28	3,842		
9	0.28	4,076		
10	0.28	4,310		
11	0.28	4,545		
12	0.28	4,721		
13	0.28	4,896		
14	0.28	5,014		

<i>B. tyrannus</i> 1955-1960 (m1)			<i>B. tyrannus</i> 1965-1970 (m2)		<i>B. tyrannus</i> 1975-1979 (m3)	
Age	Sf	f	S	f	S	f
0						
1	0.14		0.09		0.10	
2	0.30	125	0.13	128	0.19	143
3	0.37	242	0.08	199	0.16	199
4	0.31	320	0.06	256	0.14	248
5	0.20	378	0.10	296	0.08	291
6	0.30	405	0.10	322	0.08	331
7	0.30	451	0.10	338		
8	0.30	509				